UNIVERSITY OF SOUTHAMPTON

FACULTY OF ENGINEERING, SCIENCE AND MATHEMATICS

School of Ocean And Earth Science

THE NEMATODE ECOLOGY OF A UK COASTAL SALINE LAGOON SYSTEM

By

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ABSTRACT

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Nematode assemblage dynamics were studied with regard to variable environmental parameters, and in comparison to the lagoonal specialist macrofauna assemblage, between lagoons in a UK Special Area of Conservation. It is shown the nematode assemblages are more sensitive to environmental change than tne lagoonal community, but that this may reflect a greater diversity and abundance of nematodes. Nematodes share essentially the same adaptive traits as lagoonal macrofauna and possibly, as a result of this, no specialist nematode species were identified

Most nematode species were known from estuarine and marine environments, although some smaller morphological differences were found which could indicate the existence of eco-morphotypes. Further study of these nematodes would be necessary to establish differences at the species level.

Nematodes and macrofauna have similar distributions at the species level. It is suggested that nematode assemblages will be a useful tool for monitoring the small lagoonal resource in the UK. Sampling effort, and therefore destructive sediment and faunal remove, will be reduced if the nematode fauna rather than the macrofauna are monitored.

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1 Introduction

1.1 Natural Coastal Lagoons

Coastal saline lagoons are semi-isolated shallow bodies of marine or brackish water, separated from an adjacent marine area by a low-lying barrier of sand, shingle or rock (Brown *et al.*, 1997). They are dynamic, geologically temporary habitats, thought to persist for periods of less than 1000 years, although age may be positively correlated with size (Barnes, 1980). Barriers may be formed by the enclosure of a section of coastline by the shoreward movement of sediment, or lagoons may be created due to subsidence, the inundation of low-lying areas, or during river evolution (Barnes, 1980). Water exchange between the two water bodies may occur through channels in the barrier and/or by percolation (Barnes, 1980), however, the barrier retains the majority of water in a lagoon during a tidal cycle (Barnes, 1989) and, consequently, an intertidal zone may be absent (Bamber *et al.*, 1992).

The physical environment within a lagoon depends on its location and formation as well as external environmental parameters: The position of a lagoon relative to the coastline and wind direction may influence the frequency of physical disturbance to lagoon waters and sediment (O'Brien, 1969). Location and type of lagoon formation may also influence the type of sediment forming a lagoonal bed. Lagoon barriers are usually sand, whilst often bed sediments are composed of a fine flocculent surface layer of mud and organic matter covering sand (Barnes, 1980). The surface flocculent material arrives via riverine input, coastal/sedimentary erosion and internal recycling (Johnson, 1974; Nichols and Boon, 1994). Seasonality of freshwater outflow, drying, sediment deposition/erosion and currents and wave strength may also influence the size and position of barrier inlets and, therefore, the impact of the external tidal range and may cause seasonality of internal lagoonal hydrodynamics (Bird, 1994).

Most lagoons are shallow (< 10 m) as a result of the net accumulation of sedimentary material and the height of the outlet as well as topography (Barnes, 1994). Sediment sinks may be irregularly distributed throughout a lagoon and change seasonally (Barnes, 1980), their location dependent on a variety of factors including tidal range,

turbidity, circulatory patterns, lagoon shape, floral coverage (creating local sediment traps) and sediment type (Nichols and Boon, 1994). Net sedimentation may result in reduction in lagoon area and eventual evolution of a lagoon area into swamp, marsh and eventually dry land both by sedimentation and successional plant colonisation (Barnes, 1980). Alternatively, isolated lagoons with continued fluvial water input may evolve into freshwater lakes, whilst destruction of a sea barrier may create an open coastal habitat or a lagoon may be engulfed by the continued landward migration of the seaward barrier (Sklar and Browder, 1998).

Those habitats defined as lagoons may vary widely both between each other and temporally, on a diurnal and seasonal basis. Lagoons may rapidly reflect ambient air temperature owing to their shallowness and consequently diurnal variation in water temperature (up to five times that of ambient sea-water temperature) and pH are common (Bamber *et al.*, 1992). Salinity, temperature (including ice formation), pH, organic content and nutrient levels may also vary seasonally and stratification of the water column may develop (Guelorget and Perthuisot, 1992; Bamber *et al.*, 1992). However, wind generated mixing is frequent, re-suspending silty and muddy surface sediments and redistributing nutrients and oxygen (Barnes, 1980; Souchu, *et al.*, 1998). Nevertheless, extended or permanent stratification has been recorded in deeper, sheltered lagoons (Bamber *et al.*, 2001a). Temperature and salinity are particularly important in the geomorphological evolution of coastal lagoons owing to their influence on floral colonisation, which in turn influences rates of sedimentation, erosion and organic deposition (Bird, 1994). Unlike temperature, salinity is generally stable on a diurnal basis, however, it may vary with temperature (owing to evaporation or freezing), as well as type, volume and frequency of fresh and marine water input (Guelorget and Perthuisot, 1992).

1.1.1 Classification of Lagoons

Salinity is often used to define lagoonal habitat types (Barnes, 1980). They are usually divided in to four salinity zones, the hyperhaline (> 40 ppt), seawater-dominated (30 – 40 ppt), brackish (5 – 20 ppt) and freshwater-dominated (< 5 ppt) zones. Salinity may vary between lagoons from 1 - 260+ ppt; however, within a lagoon it is usual to find only two salinity areas graded together, exceptionally three

in large or very elongate lagoons (Barnes, 1980). The majority of lagoons are seawater dominated (Barnes, 1994), but salinity is most marine adjacent to the entrance channel where tidal fluctuations are greatest (Barnes, 1980). Freshwater point sources will determine the location of a freshwater-dominated zone, which usually has the highest level of turbidity and is most likely to freeze over during winter. A brackish zone is the area of marine and freshwater mixing and consequently represents the widest range of salinities, but current movements and tidal ranges are minimal and an intertidal zone is absent. A hyperhaline zone may form where there is no direct fresh or marine water source and evaporation concentrates any retained solutes. If isolated over hundreds of years, hyperhaline lagoons may eventually evolve into hyperhaline lakes with an ionic composition and biota related to inland salt lakes.

This definition of lagoon type essentially follows the "Venice System" for the classification of marine waters (International Association of Limnology, 1959). The Venice system defines salinity conditions as one of mixohaline, 0.5 - 30 (~ 40) ppt; oligohaline, 0.5 - 5 ppt; mesohaline, 5 – 18 ppt (α-mesohaline, 10 – 18 ppt; β-mesohaline, 5 – 10 ppt); polyhaline, 18 – 30 ppt; euhaline or marine, 30 – 40 ppt; and hyperhaline, > 40 ppt. However, Dahl (1956) earlier devised a system for classifying brackish water to incorporate differences between open and enclosed water bodies, including overlapping salinity ranges (Fig. 1.1).

To summarise, the physical/environmental characteristics used to define lagoons include (Barnes, 1980; Bamber, *et al.*, 1992):

1. High degree of shelter from tidal and current action;
2. Relatively stable longitudinal salinity profiles;
3. Soft mud and/or sand substrata;
4. Shallowness;
5. Unstratified water column;
6. Organically rich benthos;
7. Dynamic and temporary nature; and
8. Pronounced seasonality of salinity and/or water level, where rainfall and freshwater input are seasonal.

1.1.2 Species Distribution by salinity

Fringing macroflora communities are similar to those in estuaries, being either salt marsh, mangrove or reed-swamp (Barnes, 1994). Salt marshes and mangroves dominate the sea water influenced zone and may extend into the brackish and hyperhaline zones, if there is a relatively regular tidal regime (Barnes, 1980). In areas closest to sea water influence *Zostera* and *Ruppia* species tend to dominate, with *Potamogeton* and Characeae becoming more dominant towards freshwater dominated zone, where cyanobacteria tend to dominate (Guelorget and Perthuisot, 1992). In tropical climates or where freshwater input is absent, microbial mats become dominant in the hyperhaline zone.

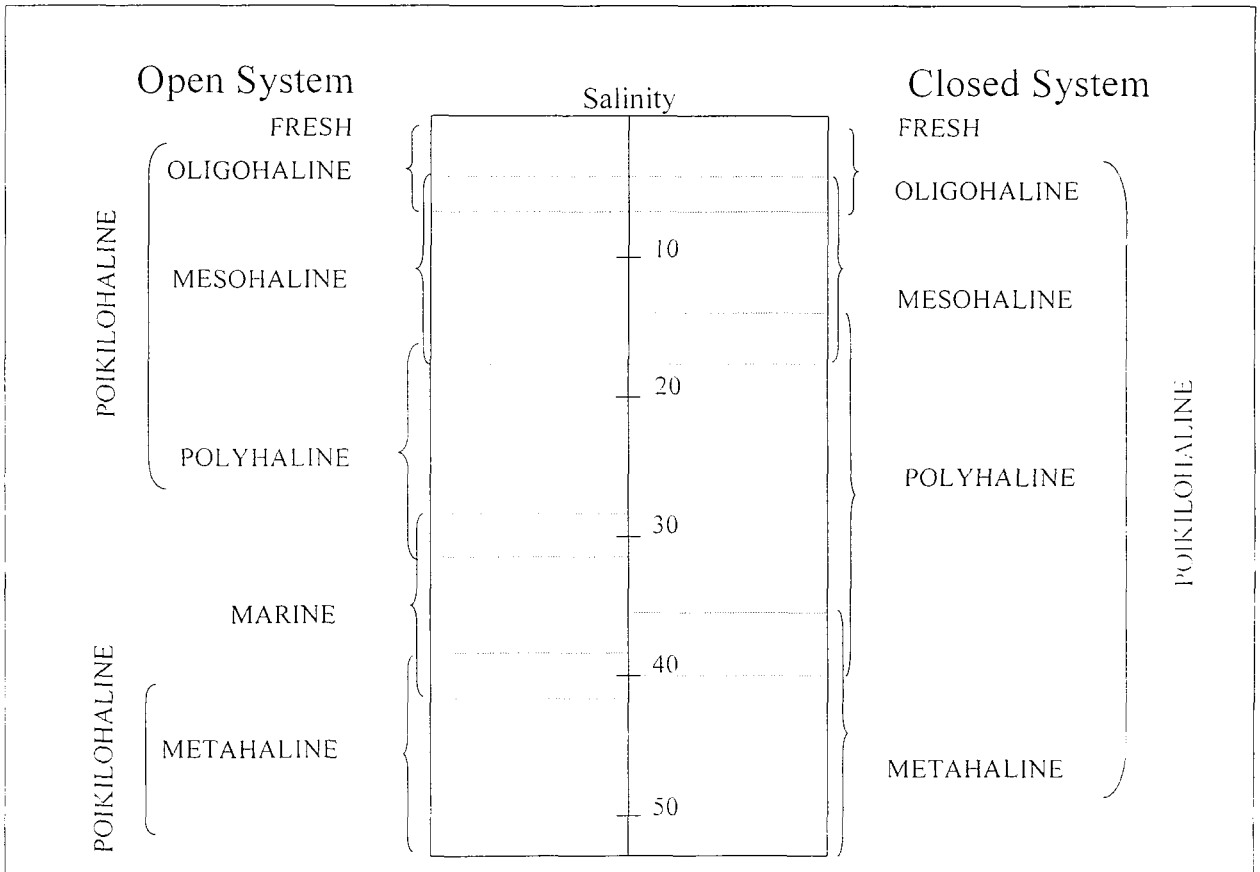


Fig.1.1. A classification of brackish water in open and closed systems. Redrawn from Dahl, 1956.

Marine and lagoonal specialist faunas are prevalent in salinity between 20 and 40 ppt. In the benthos they are dominated by annelids, crustaceans (isopods, amphipods and decapods) and molluscs (gastropods and bivalves) (Barnes, 1980), whilst echinoderms are restricted to a narrow salinity range around ambient marine salinity (Guelorget and Perthuisot, 1992). Characteristic brackish water species are

poikilohaline and species assemblages may be more influenced by sediment type and degree of shelter than salinity regime (Barnes, 1994). Marine species can usually only withstand reduced salinity for approximately one week and may take more than a year to recover biomass levels (Bamber *et al.*, 2001a). Freshwater macrofauna usually dominate in salinities up to 10 ppt (exceptionally 15 ppt) and are primarily insects, including diptera larvae, beetles, dragonfly larvae and caddis flies, and, where salinity is stable, pulmonate snails, flatworms and leeches (Barnes, 1980). Chironomid larvae and corixid bugs dominate in salinity around 6 - 10 ppt (Bamber *et al.*, 2001a). A minimum number of species has been estimated to occur between 3 – 7 ppt in brackish water (Remane, 1934).

The floral and faunal assemblages in lagoons are also influenced by environmental fluctuations such as temperature, rainfall, evaporation/precipitation ratios, gales and lagoon geography (Barnes, 1987). Migration between lagoons, either actively or passively, will be important in order to maintain diversity and abundance of the communities and the genetic diversity of species (Bamber *et al.*, 1992). Rates of water exchange with the sea will influence the recruitment and colonisation potential of both larvae and adults, whilst success of such colonisation is thought to be increased by rafting (eg. tanaids, amphipods and bivalves; Highsmith, 1985). Rafting has been recorded on algae disturbed during storms (Verhoeven, 1980; Fava and Volkman, 1975), and incidental transport of infauna associated with filamentous algae by birds has also been noted in meiofauna (Gerlach, 1977b). However, a study in the UK found that lagoons used by waders and wildfowl did not have similar macrofaunal assemblages (Barnes, 1988a).

1.1.3 Food webs and productivity

Lagoons account for approximately 13 % of the world's coastline (Cromwell, 1971) and are economically important owing to their high levels of biological productivity. Food webs in lagoons are very similar to those in estuaries, but macroalgae and sea-grasses are the dominant primary producers (Dhargalkar and Shaikh, 2000; Welsh *et al.*, 2000), whilst phytoplankton (Vaulot and Frisoni, 1986) and submerged macrophytes are the dominant food resources to secondary consumers (Alvarez-Borrego, 1994). Most lagoonal invertebrates are deposit feeders and/or browsers.

although some may suspension feed (Barnes, 1980). The majority of lagoonal vertebrates (birds and fish) are dominated by opportunistic omnivores and carnivores, feeding on benthic algae, detritus, benthic infauna, epifauna and fish (Barnes, 1980).

Estimates of lagoonal productivity are complicated by high inputs of fluvial and terrestrial organic matter, variable and sporadic output to the marine coastal zone, and seasonally variable herbivory (Sfiso and Marcomini, 1997), however, lagoonal net production is estimated to be comparable with other highly productive systems (Barnes, 1980). For example, net productivity in sea-grass meadows is estimated to average 1012 g dw m^{-2} yr^{-1} (Duarte and Chiscano, 1999) [sub-tropical sea-grass beds - 953 +/- 136 g dw m^{-2} yr^{-1} (Kaldy and Dunton, 2000); Mediterranean lagoon sea-grasses - 2470 g dw m^{-2} yr^{-1} (Agostini *et al.*, 2003)]. Directly comparable data is lacking due to the use of different measures of productivity between authors, however, it has been noted that productivity between lagoons may vary owing to differences in seasonality of nutrient use and recycling by key plant species. In the Venice Lagoon, for example, areas dominated by macroalgae (e.g. *Ulva* spp.) have been found to have gross primary productivity 2 – 3 times higher than rhizophyte-dominated (e.g. *Zostera* spp.) areas (Sfiso and Marcomini, 1997).

1.1.4 Lagoons in Europe

Lagoons are rare in Europe, and relatively uncommon in the UK owing to a macro-tidal range (> 4 m range of spring tide) which reduces the likelihood of shingle barrier formation; intertidal salt marshes are more common (Barnes, 1980, 1988b, 1994b). Lagoons occur around the microtidal Mediterranean Sea and the Baltic Sea is a large microtidal lagoon habitat, whilst in macrotidal regions most lagoons are smaller and enclosed by shingle-barriers. Much of the coastline in macrotidal regions is enclosed by sea walls built to prevent coastal erosion and to reclaim low-lying land, and, where land is not fully reclaimed, lagoonal pools may form by percolation into the protected low-lying areas created (Barnes, 1994).

Although world-wide most lagoons are fully marine, they tend to be brackish in north west Europe (Barnes, 1994). Remane (1971), for example, lists seven natural

brackish water habitats – inland seas, estuaries, fjords, rock pools, salt pans, coastal groundwater and lagoons. They tend to have a restricted salinity range on a spatial or diurnal basis due to reduced water exchange with the marine system, but differ in terms of seasonal salinity fluctuation. (Barnes, 1988b). Two examples are the Baltic Sea and the Etang du Prevost. The Baltic Sea in the largest brackish water habitat in north-west Europe, it is a reduced salinity system due to a large number of freshwater point sources and limited exchange with the North Sea. Salinity declines eastwards from the North Sea, but at any one site the salinity regime is relatively stable throughout the year. Conversely in the Etang du Prevost lagoons salinity has a polyhaline distribution both spatially and seasonally (Guelorget and Michel, 1976).

In the UK, lagoons are concentrated along the coastlines of Hampshire, Sussex, East Anglia and the Scottish Isles. However, the definition of lagoons in the UK varies between authors, dependant on whether they are defined by their characteristic species or the presence of a shingle barrier and other physical parameters (Barnes, 1994). Some authors consider only those lagoons of 'natural' origin (Barnes, 1980), others add man-made salt pans and ditches (Sheader and Sheader, 1989; Bamber *et al.*, 2001a), whilst in Scotland, the large fjordal lochs which have relatively low salinities, are considered to be lagoonal (Thorpe *et al.*, 1998). Most lagoons in the England are managed, either for environmental, leisure or coastal defence purposes, those in East Anglia, for example, are a maximum of 160 years old and most persist due to management activities (Barnes, 1980; Barnes, 1988b). Sea wall construction has inevitably altered lagoon hydrodynamics and may ultimately influence salinity regimes (either in terms of range or distribution within an area), and sedimentation and could considerably alter niche availability (Sklar and Browder, 1998), but consequently such protected lagoons are most likely to escape inundation during predicted sea level rise over the next century (Barnes, 1992).

UK lagoons are much smaller than lagoons internationally, and range in size from < 0.1 ha to several hundred hectares (The Fleet, Dorset, 450 ha) with a mean size in England of 10 ha (Bamber *et al.*, 1992), although the Scottish lochs are much larger (e.g. Loch of Stenness, Orkney 860 ha). Also, salinity range in UK lagoons is reduced in comparison to larger systems, particularly those in dry, tropical systems; however, salinity may range from fresh to hyperhaline (80‰), although it is

generally between 20 and 35 ppt (Bamber *et al.*, 1992). Habitat conditions and the macrofaunal community are used to classify lagoons and an identification system has been devised for English (Bamber, 1997), British (Connor *et al.*, 1997) and Scottish (Covey *et al.*, 1998) brackish water systems. As such brackish water ditches are grouped with lagoons due to similar or identical habitat conditions and fauna, including lagoonal specialist fauna (Bamber *et al.*, 2001a).

UK lagoons typically have a reduced macrofaunal assemblage, dominated by short-lived opportunists and include species almost or entirely restricted to lagoons (Sheader, 1995; Bamber, *et al.*, 1992). Macrofaunal lagoonal specialists generally have a short life span (approx. 1.5 years), reach sexual maturity early and produce few, advanced young (Barnes, 1980). They are thought to have survived due to a lack of competition with less tolerant marine/estuarine species (Bamber *et al.*, 1992); short-term and seasonal occurrence of sub-optimal conditions result in high levels of mortality (McArthur, 1998; Bamber *et al.*, 2001a). Predation of lagoonal macro-infauna by shorebirds and epibenthic and epifaunal predators (e.g. fish and invertebrates) is also thought to influence population dynamics, and parasitism may be increased in lagoonal populations relative to adjacent intertidal marine populations, thought its impacts are unknown (Barnes, 1990).

1.2 Meiofauna

The term meiofauna was first use to describe metazoa (and foraminifera - unicellular) that pass through a 1 mm mesh sieve but are retained on a 0.1 mm mesh by Mare (1942) - *meion* meaning lesser (Greek). It is now used to define organisms that fall between the macrofauna and microfauna categories, 42 – 500 or 1000 μm (Giere, 1993). Meiofauna are represented in 22 of the 33 metazoan phyla (Somerfield and Warwick, 1996; Table 1), although not all are permanent meiofauna, some phyla are represented only by 'temporary' juvenile or larval life stages (McIntyre, 1969).

However, meiofauna may also be described in terms of life history traits, and larger nematodes (> 1000 μm) are also grouped with the meiofauna. This is due to a constancy of feeding and dispersal strategies. Nevertheless, habitat preferences differ

between the meiofaunal taxa, Gastrotricha and Tardigrada, for example are usually found interstitially in coarse sediments, whilst kinorhyncha are usually burrowers in muddy sediments (Somerfield and Warwick, 1996). Also, meiofaunal taxa may be epibenthic as well as infaunal and whilst some are hemi-sessile, rates of dispersal (as frequency of resuspension in the water column) vary as a result. Harpacticoids, ostracods and turbellarians, for example, are found in the water column far more frequently than nematodes and oligochaetes (Giere, 1993).

Table 1. Phyla with permanent meiobenthic species.

* Exclusively meiofaunal taxa (Somerfiled and Warwick, 1996); †Aplanktonic larvae only (Pechenick, 1999)

Gastrotricha*†	Entoprocta
Gnathostomulida*†	Mollusca
Kinorhyncha*†	Brachiopoda
Loricifera*	Echinodermata
Tardigrada*†	Tunicata
Rotifera	Priapulida
Nematoda†	Sipuncula
Annelida	Copepoda (Arthropoda)
Platyhelminthes	Ostracoda (Arthropoda)
Hydrozoa	Mystacocarida (Arthropoda)
Nemertina	Acari (Arthropoda)

Permanent meiofaunal species tend to have a conservative reproductive strategy (low gamete production, brood protection and absence of pelagic larvae), and consequently stable, spatially heterogeneous populations (Platt, 1981). Small centimetre-scale patchiness may result from their limited motility, generating a mosaic of independently distributed species populations (Hogue, 1982), each patch reflecting local environmental parameters (Li *et al.*, 1997; Walter and Hengeveld, 2000). Species patchiness combined with short generation times and high diversity may enable rapid responses of the meiofaunal assemblage to variable food supply. Dispersal between patches and to new patches is dependent on rates of horizontal migration by adults and random abiotic displacement by bedload movement and wind or wave induced sediment resuspension (Sherman and Coull, 1980; Chandler and Fleeger, 1983; Highsmith, 1985).

It is thought that meiobenthos may have a biomass equivalent to one tenth to one fifth that of macrobenthos, but, due to their small size, may have a higher metabolic activity and productivity per unit biomass (Platt, 1981). Estimated average production/ biomass (P/B) ratios for meiofauna of 10 (range from 9 to 37 P/B in nematodes (Gerlach, 1971; Vranken *et al.*, 1986) and 2 in macrofauna, suggests that meiofaunal production may be at least half that of the macrobenthos (Platt, 1981). Meiofauna are therefore thought to provide an important nutritional source for predatory macrofauna and other meiofauna. For example, laboratory experiments have shown that adult shrimp can survive on a diet consisting solely of nematodes, whilst examination of gut contents from grey mullet has identified the ingestion of meiofauna, diatoms and sediment, but no macrofauna (Platt, 1981).

Although meiofauna may be an important food source it is unlikely that predation will control its abundance owing to high turnover rates and high abundance (Coull, 1999). However, meiofauna species are thought to have a significant impact on their sedimentary environment. Their activity reworks sediment, extending the depth of the oxic zone in surface sediments, and stimulates solute fluxes and reaction rates, particularly aerobic decomposition and nitrification (Cullen, 1973; Chandler and Fleeger, 1984; Nehring, *et al.*, 1990; Aller and Aller, 1992). Bioturbation may similarly stimulate bacterial production and improve the quality of detritus available to macro-consumers (Coull, 1999), whilst mucus excretion may stabilise sediments (Fager, 1964; Eckman *et al.*, 1981) and provide a source of food (Warwick, 1981).

Environmental parameters structuring meiobenthic assemblages include sediment type, salinity and temperature. Meiofauna abundance and biomass tend to be highest in organically enriched mud, whilst diversity is usually higher in fine sands (Coull, 1999; Vitello, 1974, 1976). Meiofaunal diversity also tends to decrease with decreasing salinity and increasing rates of seawater exchange (Arlt *et al.*, 1982; Soetaert *et al.*, 1995; Attrill, 2002), however they do not show as large a decline in species richness at the brackish/freshwater transition area (Gerlach, 1971) as described for macrofauna (Remane, 1934). Equally, meiofauna are generally less effected than macrofauna by hypoxia, although taxonomic diversity may be reduced (Josefson and Widbom, 1988; Vopel *et al.*, 1996; Moodley *et al.*, 1998).

Hypoxic and sulphidic sediments tend to be dominated by the Plathelminthes (Turbellaria and Gnathostomulida) and Aschelminthes (Nematoda, Gastrotricha and Rotatoria), although nematodes and gnathostomulids penetrate deepest (Boaden, 1975). Dominance tends to increase in hypoxic sediments, however, abundance and biomass can be high, and nematodes are the most abundant taxon (Jensen, 1987a; Lorenzen *et al.*, 1987; Alongi, 1987; Ott *et al.*, 1991). In oxygen-deficient environments where specialist macrofaunal communities exist, such as hydrothermal vents, specialist meiofauna species are also recorded, although specialist genera have not been found (Vanreusel *et al.*, 1997).

1.2.1 Nematoda

Nematodes may represent between 50 - 99 % of individuals in meiofaunal assemblages (Soetaert *et al.*, 1995) and are probably the most abundant metazoans in the biosphere (Heip *et al.*, 1985), accounting for around 60 – 90% of all metazoa (Giere, 1993; Coull, 1999). There are currently approximately 20,000 nominal nematode species known, of which around 4000 species are free living marine forms. The class is divided into two subclasses (Chitwood and Chitwood, 1950; De Coninck, 1965; Lorenzen, 1994) – the Secernentea, predominantly freshwater and terrestrial species and including most plant and animal parasites and the Adenophorea, primarily marine free-living species and some parasites. The parasitic forms are important human, animal and agricultural pests, whilst the free-living forms are primarily benthic. There are no truly planktonic species because they lack buoyancy devices (Nicholas, 1984) and they also lack a pelagic larval phase (Gerlach 1977b; Josefson and Widbon, 1988), but a few benthic species may swim (Jensen, 1981).

a *Morphological characteristics*

Nematodes are small multicellular (typically 1000 non-gonadial cells) vermiform organisms that reach an average adult body length of 1 – 2 mm. They have bilaterally symmetrical bodies and a triradiate anterior region, which includes cephalic sensilla, mouth, lips and the anterior region of the alimentary canal (Nicholas, 1984). They are essentially formed of two tubes, the body wall comprising an external cuticle lay and internal longitudinal muscles and the gut which extends terminally from the anterior to a

sub-terminal anus (Platt and Warwick, 1983). The cuticle may be smooth or exhibit external structure such as striations or punctations (which may appear raised depending on the light source), whilst some species may be heavily ornamented. It provides a hydrostatic skeleton by maintaining a high internal turgor that allows bending but not expansion (Platt and Warwick, 1983) and is consequently shed up to 4 times through the juvenile life stages, a new cuticle forming beneath the first before the latter is shed (Bonner *et al.*, 1970). The cuticle is formed by the epidermis, a single cell layer which also contains dendrites and axons of the nervous system and unicellular glands associated with the cephalic sense organs (Nicholas, 1984). Beneath the epidermis obliquely striated muscles are divided into dorsal and ventral blocks, which contract alternately for undulatory propulsion (Platt and Warwick, 1983; Nicholas, 1984).

The internal gut is divided into a buccal cavity, oesophagus (pharynx), an intestine and rectum. The buccal cavity is an important taxonomic aid due to a great diversity of form, which probably reflects food sources. It varies in size between species, from small or even absent to enlarged with cuticular plates, teeth or mandibles (Wieser, 1953). The Oesophagus (pharynx) is a muscular tube that pumps food from the buccal cavity into the intestine. It may also have small cardia or a muscular bulb terminally, which act as an oesophago/intestinal valve (Platt and Warwick, 1983). In contrast the intestine is usually a made up of relatively few cells, without musculature or specialised glands, although there may be functional differentiation along the length of the intestine (Nicholas, 1984). The rectum is a short cuticle-lined tube with associated muscles.

The anterior region usually tapers to a central terminal mouth without a sharply defined head. The mouth is usually surrounded by 3 or 6 lips, which may be off-set and have varying degrees of ornamentation. Surrounding the mouth are three concentric rings of sensilla, typically 6 inner labial papillae, 6 outer labial setae and 4 cephalic setae, although the outer labial and cephalic rings may be combined. Two associated specialised sensory structures, amphids, are located bilaterally in the anterior cervical (neck) region. These are pocket-like structures containing a gelatinous substance, which are thought to perform as a chemical receptor. On the cuticle surface they may appear round, cup-shaped, extended and looped or spiralled. Paired pigment spots or ocelli may also be found on or in the anterior part of the oesophageal region (Platt and Warwick, 1983)

Nematodes reproduce sexually and some representatives are viviparous (Nicholas, 1984). Males usually have a single gonad opening into a single terminal gonoduct and two hollow spicules for internal fertilisation. Some species also have pre- cloacal supplements and/or gubernacula associated with spicules which aid copulation. The male reproductive structures are complex and species specific and are thought to aid speciation by maintaining reproductive barriers. Females are usually didelphic and have a mid-ventral vulva, although in monodelphic species the vulva is usually posterior. Spermatozoa are non-flagellate and lack an acrosome, whilst the female gonads are non-muscular and eggs are released by body movement.

Finally, tail shapes can grouped in to four generalised morphological types (Bussau, 1993; Thistle *et al.*, 1995). Round, short tails less than 2 anal body diameters (abd) with a blunt end; conico-cylindrical tails with an extension at the tip (clavate); conical tails, less than 5 abd with a pointed tip and; long, conico-cylindrical tails greater than 5 abd with an extended cylindrical portion. Long tails tend to be found in animals anchored to the substrate for long periods (Riemann, 1974; Fegley, 1987). Most species also have a terminal spinneret on the tail and associated unicellular caudal glands (most often three) which produce a mucus secretion (Platt and Warwick, 1983). The mucus has adhesive properties and is thought to aid a sedentary life, but has been also suggested to aid the 'gardening' of bacteria (Warwick, 1981).

b *Ecology*

Nematode species distribute independently in random centimetre scale patches, with juveniles and adults of the same species occurring together (Hogue, 1982). Patchiness may result from low dispersal ability and the requirement for contact during sexual reproduction, whilst the expenditure of energy to actively maintain a uniform distribution (when resources are not limiting) would be disadvantageous (Heip, 1975). Both small scale patchiness within an otherwise homogenous habitat area and larger scale habitat patchiness may increase species diversity by acting as a network of habitats each with complimentary populations (Grassle, 1989; Hanski, 1998).

Nematodes reproduce by direct benthic development with no planktonic phase and have a limited capacity for active dispersal. However, they are known to passively disperse by rafting on algae and other flotsam (Platonova and Gal'tsova, 1985), and may be suspended in the water column by storms and wave action (Gerlach, 1977b; Palmer, 1984). One study found that, whilst nematodes represented 95.8 % of meiofaunal individuals in the benthos, they represented only 38.9 % of animals found in suspension above the sediment bed (Commito and Tita, 2002). In contrast copepods represented only 1.5 % of the benthos, but 56.7 % of suspended individuals. These authors also noted a division of suspension rates within the nematoda - epigrowth-feeders were most frequently dispersed although non-selective deposit-feeders (infaunal) were the most abundant, further indicating the importance of passive bedload movement. In calmer conditions nematodes may be also entrained in the surface water film (Platonova and Gal'tsova, 1985) and some have been observed to swim under laboratory conditions (Jensen, 1981). Their recolonisation abilities are relatively unknown, however, recorded rates being anything from hours (Sherman and Coull, 1980) to years (Chandler and Fleeger, 1983). The success of passive dispersal does not guarantee settlement success. Platonova and Gal'tsova (1985), for example, notes that species abundant at 25 m depth were also recorded as singletons in association with algae, and conversely species recorded in abundance with algae intertidally also occurred as singletons at 53 m depth.

Sediment particle size, temperature and salinity are the three primary physical factors controlling spatial patchiness of meiofaunal abundance and species composition. Biological factors such as food availability and predation are not thought to be limiting to abundance (Gee *et al.*, 1985; Glassom and Branch, 1997; Coull, 1999), however, food specificity (with buccal morphology) is likely to influence nematode species distributions (Jensen, 1981, 1987b; Olafsson and Elmgren, 1997). Nematode species feed both selectively and non-selectively on bacteria, algae, detritus, other animals (including other nematodes and juvenile macrofauna) and dissolved organic matter (Wieser, 1953; Heip *et al.*, 1985; Riemann and Helmke, 2002). Consequently, food specificity has been used to explain the co-occurrence of generic sibling species (Castillo-Fernandez and Lambshead, 1990; Rice and Lambshead, 1994). However, where generic sibling species can only be distinguished by their male reproductive characters (and therefore do not differ in buccal structure) feeding group definitions do

not provide an adequate reason for species diversification. Also, there may be a partitioning of food preference and lifestyle between juveniles and adults as body shape changes with life stages (Warwick, 1984). If food sources are abundant it may suggest that high species diversity is due to a lack of competition (Nilsson *et al.*, 1991).

Nematode assemblage dynamics tend to reflect the ambient sedimentary environment. Species diversity (and endemism) is generally found to be highest in sandy sites, whilst abundance and dominance are usually highest in mud and fine sands (Tietjen, 1977; Heip *et al.*, 1985; Boucher, 1990; Kennedy, 1994). As grain size increases further to gravel, nematode abundance and diversity tend to be reduced as habitat availability is reduced (Heip *et al.*, 1985). The increased space between larger sediment grains may reduce the available substrate against which individuals can move. It is thought that this results from a division of species by their mode of locomotion and feeding (Wieser, 1959; Coull, 1988; Tita *et al.*, 1999). It is generally considered that in muddy sediment with a median grain size < 120 μm, nematodes will tend to a burrowing life strategy with a mean body width of 32.0 – 45.5 μm and will be predominantly ciliate- and deposit-feeders. In contrast, nematode assemblages in sandy sediment with a median grain size > 120 μm, tend to be dominated by interstitial species with a mean body width of 19.3 – 22.6 μm that feed on epigrowth or are predators. However, nematode assemblage dynamics can be sensitive to slight changes in sediment type (Herman *et al.*, 1982) and species assemblages may change without an associated change in species diversity (Vanaverbeke *et al.*, 2000).

Ambient sediment type may also influence the response of meiobenthic communities to other environmental parameters (Hockin, 1983). Schratzberger and Warwick (1998), for example, found that increasing frequency and quantity of organic enrichment produced a greater reduction in nematode diversity and evenness in samples from a sandy rather than muddy estuarine site, and that the latter were not affected by low level chronic additions. It is probable that the nematode assemblage occurring at each of these sites differed, as discussed above, the muddy site having a larger percentage of deposit-feeding species with a greater tolerance to high levels of organic matter. Such differences might also be expected with seasonality of organic addition (ie. plant decay), with a greater seasonal change in nematode assemblages in sandy sediments.

Salinity is also an important environmental parameter influencing nematode assemblage dynamics and a brackish water species minimum has been recorded in the Nematoda as for the macrofauna (Riemann, 1966; Gerlach, 1971). This is due to varying physiological tolerance to salinity fluctuations between species (Riemann, 1966); marine species found at different heights on a shore may have different salinity tolerances and levels of osmoregulation, for example (Forster, 1998). However, nematodes do not have osmo-regulatory organs and it has been suggested that the alimentary canal, hypodermis and the excretory system play a role in salinity tolerance (Nicholas, 1984).

Tolerance to fluctuations in temperature (particularly freezing) is thought to be related to tolerance of salinity variability owing to the similarity of osmotic stress during these two processes (Farke *et al.*, 1984), although combined salinity and freezing stress may reduce survival rates (Wharton, 1996). It is also probable that those species successfully reproducing (or at least surviving) in extreme environmental conditions, particularly those occurring over short time scales, are predisposed to a greater tolerance to other environmental stresses.

Most marine species recorded in brackish water are euryhaline and classification based on salinity tolerance has been attempted (Gerlach, 1953; Warwick, 1971). However, absolute tolerance is likely to relate to salinity range (Attrill, 2002), rates of change and length of exposure to non-ambient salinity (Forster, 1998). Also, many species have been recorded in salinity ranging from 2 – 30 ppt (Brenning, 1973; Warwick and Gee, 1984; Soetaert *et al.*, 1995) and it is possible that tolerance varies between populations of the same species in relation to other environmental parameters, including sediment type (Heip *et al.*, 1985). It is possible that within a given physiological tolerance range in salinity other variables will have a greater influence on brackish water nematode assemblages (Vernberg and Vernberg, 1972; Newell, 1979; Little, 1986). For example, an increasing number of species has be recorded with decreasing salinity owing to increasing sediment grain size along the same gradient (Warwick, 1971).

Vertical zonation patterns are also exhibited by nematode assemblages, similarly dependant on environmental parameters such as oxygen availability (Sikora and Sikora, 1982; Hiep *et al.*, 1975), salinity (Heip *et al.*, 1985), and food availability (Platt, 1977).

Most shallow water organisms live epibenthically or in the top 10 cm of sediment (Reise, 1985; Heip *et al.*, 1985), although in sandy sediments nematodes are recorded at 50 + cm depth (Giere, 1993). In brackish waters and intertidal regions, for example, organisms that can burrow to 2 – 3 cm depth or below are more likely to survive due to a dampening of salinity change or drying during low tide (Boaden, 1968; Peterson, 1991; Coull, 1999). Where salinity fluctuates diurnally, for example, nematodes are found to inhabit deeper sediments than where salinity is more stable (Heip *et al.*, 1985).

Nematode assemblages may also differ along a vertical gradient of oxygen availability (Hendelberg and Jensen, 1993). Nematode species inhabiting the hypoxic sediments may differ from oxic assemblages (Vanreusel *et al.*, 1997; Lorenzen, *et al.*, 1987). They may exhibit adaptations such as low body volume to body surface area ratio, which may indicate transepidermal uptake of oxygen (Jensen, 1986; 1987a), and epidermal- or gut-associated bacteria (Ott, 1996). Bacterial associations may provide (almost) all of an individuals food requirements, in fact some nematode species lack a mouth or true gut and are entirely dependent on the bacteria derived food (Ott *et al.*, 1982; Giere *et al.*, 1995). However, some studies have shown no change in meiofaunal density or vertical zonation with eutrophication, which effectively reduces oxygen content and raises the height of the RPD layer (Le Guellec and Bodin, 1992).

As well as spatial zonation, species assemblages may have seasonal, predicable patterns in response to changes in salinity, temperature, food availability/type and sediment deposition (Heip *et al.*, 1985; Villano and Warwick, 1995; Coull, 1999; Olafsson, *et al.*, 2000). Seasonality of feeding types is particularly noted in association with plants. Epiphytic nematodes may over-winter in sediment and emerge to colonise new macrophyte stands in the spring (Jenson, 1984), whilst deposit-feeders may peak at the onset of vegetal degradation (Hopper, 1970; Hopper *et al.*, 1973; Villano and Warwick, 1995) and omnivorous predator densities match that of their prey (Myers, 1997). Also, whilst nematode assemblages may not respond to short-term salinity changes, longer-term seasonal salinity changes may influence species diversity and abundance (Olafsson, 2000).

Whilst large-scale environmental parameters (and physical disturbance) may act to structure a habitat, nematodes also interact with the physical environment creating local

patchiness. Nematodes may extend the lag phase of bacterial growth by consuming them or by providing a food source in the form of metabolites in mucus secretions, which may also stabilise the sediment by acting as a binding agent (Warwick, 1981). Studies of nematode cultures has suggested they may 'garden' food species – for example, mono-specific non-motile chlorophytes were found only in the presence of *Praeacanthonchus punctatus* and only in their mucus trails (Warwick, 1981). However, Riemann and Helmke (2002) did not observe nematodes feeding on bacteria in similar conditions and the bacterial communities outlived the nematodes. Associations are also noted between nematodes and bacteria, which may grow on the body wall, within the gut or in the cuticular ornamentation of nematodes (Heip *et al.*, 1985: Ott *et al.*, 1982, 1991; Giere *et al.*, 1995; Ott, 1996).

c *Nematodes in UK Lagoons*

Lagoon systems in the UK differ from others found internationally in that they tend to have muddy sediments and a high organic matter content. Thus, in an international contexts they provide a habitat more comparable to estuaries or mangrove systems. Nematodes are usually the dominant taxon in muddy sediments with a high organic matter component (Van Damme *et al.*, 1980; Josefson and Widbom, 1988; Lorenzen *et al.*, 1987; Hendelberg and Jensen, 1993). Their dominance in estuarine sediments, for example, has been attributed to variety in burrowing capacity, tolerance to environmental stress and diversity of feeding types (Bouwman, 1983). Consequently the observation that nematodes are reduced in abundance in UK lagoons relative to lagoonal macrofauna and marine intertidal meiofauna (Bamber *et al.*, 1992) is contrary to expectations.

Where macrofaunal diversity becomes more variable due to stress, meiofaunal communities usually remain more stable (Warwick *et al.*, 1990) and nematodes are known to be abundant and diverse in habitats where macrofauna are limited due to either natural, physical or anthropogenic stress (Lorenzen *et al.*, 1987; Hendelberg and Jensen, 1993). Nematodes are usually present even when macrofaunal communities are absent such as in hypoxic sediments (Josefson and Widbom, 1988; Hendelberg and Jensen, 1993). Nematodes also have the capacity to recover quickly following disturbance events owing to their short life cycles (Josefson and Widbom, 1988).

Lagoonal systems, however, are small, geographically isolated habitats that are subject to whole habitat disturbance, providing little or no refugia, particularly for species with limited motility.

Only eighteen nematode species are thought to be restricted to brackish water, whilst 155 species are either predominantly recorded in brackish-water or invade brackish-water from marine areas (Heip *et al.*, 1985). In muddy, brackish water sites between 30 and 98 species have been recorded, and likelihood of finding lagoonal specialist species is perhaps limited. However, it is possible that brackish water species recorded from mainland Europe, particularly the Baltic Sea, may be added to the UK nematode species list during the course of this survey.

1.3 Project Rationale

The EU "Habitats Directive" (EEC 1992) states that coastal lagoons are a habitat type whose conservation requires the designation of Special Areas of Conservation (SAC) and are a "priority" habitat (considered in danger of disappearance and for the conservation of which the European Community has particular responsibility). In the UK, saline lagoons and specialist lagoonal macrofauna and flora are recognised as a "priority" under the Biodiversity Action Plan (BAP), requiring conservation efforts through actions for the habitat. However, there is still disagreement concerning the classification of British lagoons; whilst maintaining broadly similar environments and communities, they may have widely diverse macrofaunal communities.

Nematoda are the dominant meiofaunal organisms and are tolerant (as a taxon) to a wide variety of environmental stressors. As a general rule they are more abundant than macrofaunal species and maintain a high level of diversity even when conditions become limiting for macrofauna. The initial aim, therefore, has been to determine nematode community dynamics within a saline lagoon system and the tolerance of the nematode assemblage and individual species to environmental variability. The possibility of nematode lagoon specialists will also be discussed.

The study focuses on one lagoon system and will therefore highlight differences between the individual lagoons, in terms of their unique habitat characteristics, and will

not give definite answers with regard to nematode assemblage dynamics along a salinity gradient within a single lagoon or in UK lagoons as a whole. Nevertheless, by employing multivariate techniques to compare nematode and macrofaunal assemblages and environmental parameters, a generalised nematode assemblage for UK lagoons may be inferred. The macrofaunal assemblages in the lagoon system studied is restricted by the 'stressful' lagoonal environment, which comprises reduced fine mud sediments with a high percentage of organic matter and a range of salinity regimes (Bamber *et al.*, 2001a). It is thought that the range and combination of environmental parameters recorded throughout the system provide a good representation of UK lagoons.

The lagoon system studied was chosen owing to the variability of environmental variables between lagoons. Abundance and diversity of macrofaunal species is known and the intention has been to determine whether nematode assemblages are distributed independently of the macrofauna or whether they are influenced by similar environmental parameters. Whether seasonality of the nematode assemblage occurs, and whether there is a specialist nematode lagoonal fauna was studied. The application of nematode functional groups in association with the distribution of nematodes in the system are discussed in terms of these assemblages.

2 Materials and Methods

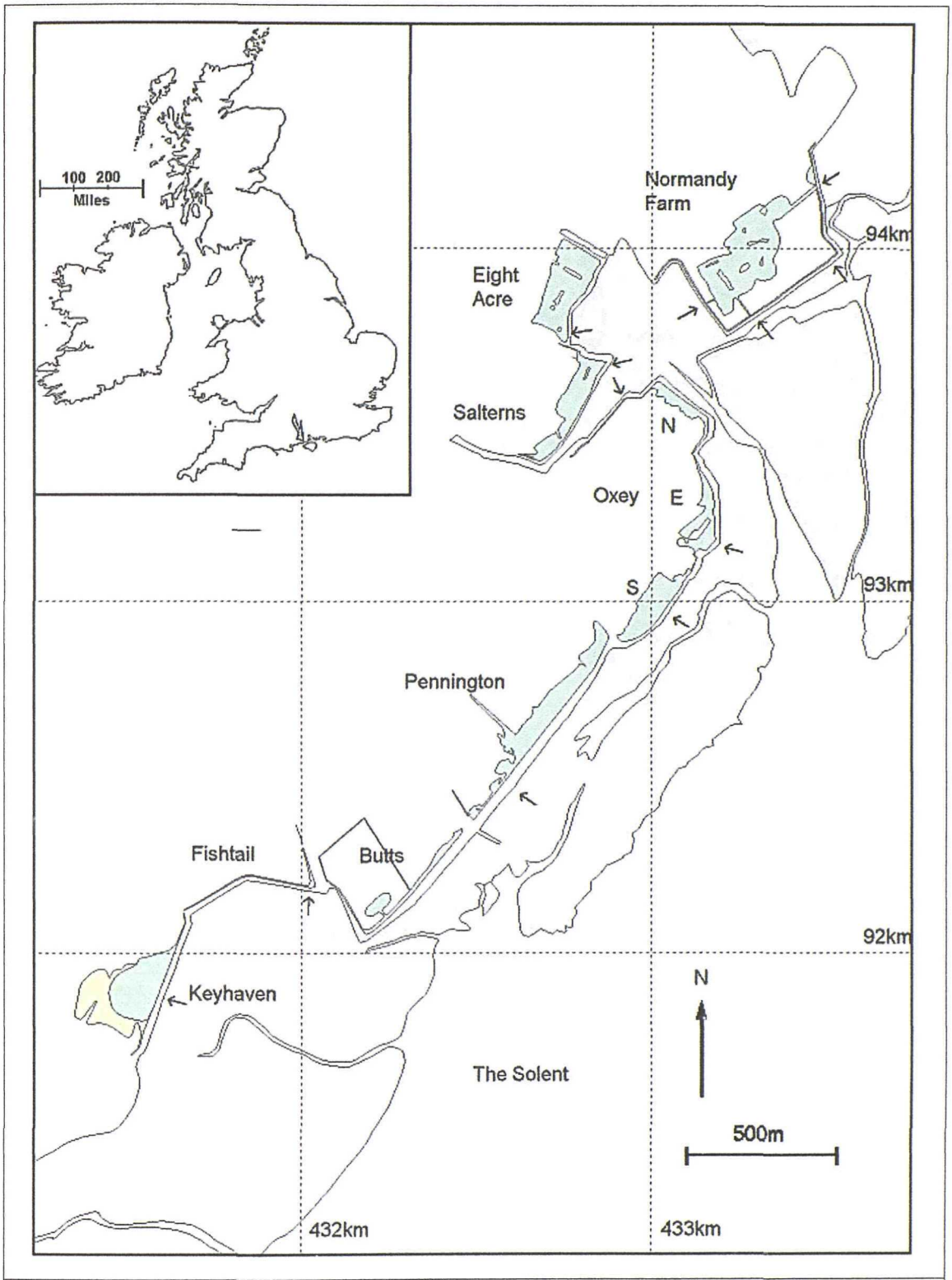
2.1 Site Selection

Of the UK lagoons discussed by Bamber *et al.* (1992), the Keyhaven-Lymington lagoon system, Hampshire, within the Solent Lagoons Special Area of Conservation (SAC), was chosen for study (Map 2.1). The lagoons surveyed were Normandy Farm, Eight-Acre Pond, Salterns, Oxey South, Pennington and Butts. An additional site in a drainage ditch surrounding Normandy Farm was also sampled – this might be expected to be intermediate between Normandy Farm Lagoon and the adjacent coast and therefore to support a mixed fauna of marine and lagoonal species. The sites are described individually below.

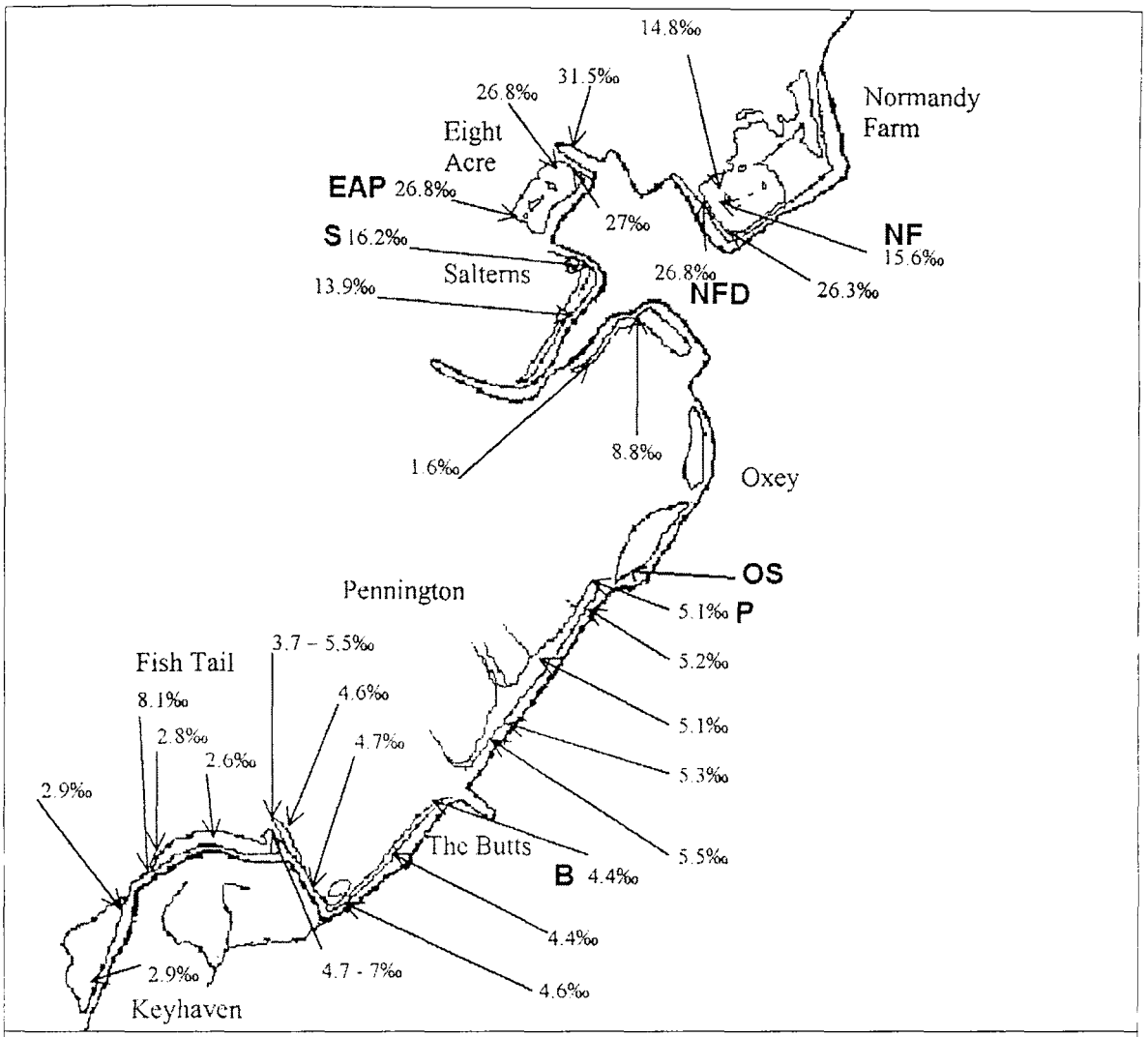
Sampling sites were chosen following a survey of salinity along the whole lagoonal series on 24 January 2000 (Map 2.2). In addition to salinity range, macrofaunal distribution and sediment type were considered in order to represent fully the diverse habitats within the system. Also, the close proximity of the lagoons (kilometre scale) should remove latitudinal bias: macrofaunal species diversity in UK lagoons has been negatively correlated with latitude (Bamber *et al.*, 1992). To the west of Pennington Sewer, only Butts Lagoon was sampled owing to the degradation of benthic communities by disturbance from groundwater extraction and mine-water disposal. This impact is severe in all the lagoons west of Pennington Sewer and no additional information would be expected from further sampling (Bamber *et al.*, 2001a; Bamber and Evans, 2003).

The seven study sites were surveyed during 2000. A dual survey of meiofauna and macrofauna abundance and diversity was undertaken. Core samples were collected over a full year at three monthly intervals beginning at the end of January and subsequently in April, July and October 2000. This sampling strategy was chosen in order to detect any influence of large-scale seasonal changes on faunal communities. Seasonal changes might include plant growth and decay, and salinity and water level fluctuations associated with precipitation, land run-off, drainage and ambient temperature. Meiofauna, macrofauna, granulometry, organic matter content, and chlorophyll a samples were taken concurrently with surface temperature and salinity measures. Core sizes were chosen to account for the size of the target fauna or

environmental parameter to be measured (Table 2.1).



Map 2.1. Sampling sites in the Keyhaven-Lymington lagoon system.
Map courtesy of Bamber *et al.*, (2001b).
Inset: Location of the Lymington-Keyhaven Lagoon System in the UK (indicated by arrow).



Map 2.2. Preliminary salinity survey of the Keyhaven-Pennington lagoon system.
Recorded 24 January 2000.

	Diameter/cm	Depth/cm	Volume/ml	Replicates
Meiofauna	2.65	9	50	4
Macrofauna	5.5	20	475	4
Sediment*	5.5	20	475	4
Bacteria	2.65	1	5.5	4
Chlorophyll	2.65	1	5.5	4

Table 2.1. Core sizes and replicates.
* Mixed and divided for granulometric and organic matter analysis.

2.1.1 Site Locations

a *Normandy Farm*

The sampling site for this study is on the western side of the lagoon (Grid Reference: *SZ 3312 9393)*, within the 'mid-section' assigned by Sheader (1991), opposite to sluice 2 ('NF' on Map 2.2). An additional set of samples was collected from the

drainage ditch immediately to the south of sluice 2 ('NFD' on Map 2.2).

b *Eight-Acre Pond*

Samples were taken from the north-western corner of the lagoon (Grid Reference: SZ 3269 9386; 'EA' on Map 2.2), where initial inspection suggested some fine material remained in the shallow sub-littoral.

c *Salterns*

Samples were taken from the north-eastern shore (Grid Reference: SZ 3285 9368), adjacent to *Ruppia* beds ('S' on Map 2.2).

d *Oxey South*

Samples were taken in the southern part of the lagoon (Grid Reference: SZ 32939 92890; 'OS' on Map 2.2), just beyond dense *Ruppia* beds in deep, organically rich anoxic mud. The site was also relatively near an underground ditch connecting Oxey to Pennington lagoon and well south of the sluice.

e *Pennington Lagoon*

Samples were collected from the northern part of the lagoon (Grid Reference: SZ 32874 92886), parallel to the path between Pennington and Oxey South lagoons ('P' on Map 2.2). The sediment here was shingle in mud. The site was quite exposed and during high wind, waves were noted to wash on to the path.

f *Butts Lagoon*

Samples were taken from the eastern-most section of the lagoon (Grid Reference: SZ 32455 92325; 'B' on Map 2.2) in fine mud, also adjacent to *Ruppia* beds.

2.2 Experimental Procedure

2.2.1 Field Sampling

a *Meiofauna*

Meiofauna cores samples were taken with modified disposable 50ml plastic syringes (2.65 mm internal diameter). The end of each syringe was sawn off and the edges gently bevelled. The plungers were also modified so that they had a flat surface in order to limit disruption of the sediment surface when in use. When taking a core the plunger was set level with the cutting edge of the corer, and the corer then gently placed on to the sediment surface. The plunger was held at the sediment surface

whilst the coring tube was pushed into the sediment to a depth of 9 cm (50 ml). This technique created a vacuum that helped to prevent sediment compression. The corer was then slowly and carefully removed whilst maintaining the position of the plunger relative to the syringe tube, which helped to remove the core intact. The outside of the syringe was wiped clean and the collected sediment levelled to the base of the corer using a flat blade. Each sediment core was placed into a 120 ml leak-proof screw-top Sterilin plastic pot and fixed with 10 % formalin. The sample pot was shaken to ensure thorough mixing of the formalin and sediment, both immediately after collection and before storage.

Meiofaunal core size was designed to account for possible non-random distribution of animals. For example, whilst nematodes species often distribute independently, juveniles and adults of the same species may aggregate forming heterogeneous patches at the centimetre scale (Hogue, 1982). Therefore, the 2.65 cm diameter core used should be large enough not to sample isolated patches at this scale. Also, the sample depth (9 cm) was chosen since most shallow water organisms live within the top few centimetres of sediment (Sherman *et al.*, 1983; Hendelberg and Jensen, 1993; Barmawidjaja *et al.*, 1992). Also, lagoons generally have an RDP layer within 1cm of the sediment surface (Barnes, 1980; Bamber *et al.*, 2001c). In such reduced oxygen environments nematode distribution have been shown to follow the RDP layer (Hendelberg and Jensen, 1993), the majority of animals aggregating in the top 1cm of sediment (Fenchel and Jansson, 1966; Platt, 1977; Jensen, 1987a), or even at the sediment surface in highly organically polluted sites (Lorenzen *et al.*, 1987).

Since the diversity and abundance of the meiofauna in this lagoon system were not known, five samples were taken from each site at each season. Each core was treated as a whole in order to evaluate the meiofaunal communities in terms of total abundance and diversity values with respect to environmental parameters (Schwinghamer, 1981; Heip *et al.*, 1988; Guidi-Guilvard and Buscail, 1995).

b *Macrofauna*

Benthic macrofauna samples were collected using a hand corer (5.5 cm internal diameter) to a depth of 15 cm where possible. Four replicate cores were taken per

site. These were sieved over a 500 μm mesh and all retained material was stored in 10% formalin with rose bengal.

c *Photosynthetic Pigments*

Pigment core samples were taken with a modified disposable 50 ml plastic syringe as described for meiofauna, but only the top one centimetre of sediment was collected. This was to ensure a representative measure of pigment mass (de Jonge and Colijn, 1994). Four replicate samples were taken at each site. Samples were stored in 60 ml sterilin pots and frozen at –70 °C on return to the laboratory to ensure preservation of pigments (Lucas and Holligan, 1999).

d *Environmental Variables*

For estimates of granulometry and organic matter content, 15 cm depth sediment cores were taken using a 5.5 cm internal diameter hand corer, as for the macrofauna. Four replicate samples were taken at each site. Samples were bagged and frozen at –20 °C until required. Salinity at each site was measured to the nearest 0.1 ‰ using a salinometer (a WTW Profi Lab LF597 on all occasions except July, when a WTW Multi-line P4 was used. A Tetracon 325 probe tip was used with both meters). The salinity of both surface and bottom water was measured.

e *Baseline Data*

The April samples were used as a baseline of the lagoonal populations: Nematode densities have been shown to peak in late spring and either autumn (Vincx, 1989; Guidi-Guilvard and Buscail, 1995) or summer (Tietjen, 1969) in shallow subtidal sites. Also, meiofaunal populations in salt marshes, similarly highly organically enriched and productive environments (Barnes, 1980), have been shown to peak in abundance during spring and winter, with a summer minimum (Armonies, 1997). Normandy Farm lagoon samples were used to study seasonal dynamics, since flooding throughout October and November 2000 prevented effective sampling by cores at other sites.

Every effort was made during field work to minimise the impact on the lagoon

habitat, with respect to Section 16(3) (a) of the Wildlife and Countryside Act 1981 (amended by the Environmental Protection Act 1990). All fieldwork was carried out on behalf of Dr Roger Bamber under Licence Number 20000908.

2.2.2 Laboratory Methods

a *Meiofauna*

i Washing

Each sample was prepared for extraction by washing out fine organic and sediment particles. Filtered (45 μm mesh) tap water was used throughout sample processing. This was to remove the risk of contamination by freshwater fauna from tap water, since freshwater species might be present in lagoonal samples, particularly those from the lower salinity sites. Firstly, a sample was gently washed into a 2 litre measuring-cylinder which was then filled with water. The cylinder was stoppered and fully inverted 5 times, suspending all the sediment in the water column. The stopper was removed and any sediment remaining on it and on the sides of the cylinder washed back into the water column. The sample was then left for between 5 and 20 minutes, until all large particles had settled out of the water column and there was no further downward movement of the remaining suspended matter. The supernatant was slowly poured off through a 45 μm mesh aperture sieve, taking care not to disturb any material settled at the bottom of the cylinder. This prevented clogging of the fine mesh.

The washing procedure was repeated for each sample at least five times or until clay and other aggregates were broken down. The main purpose of this treatment was to clean and unbind aggregated sediment and, therefore, to make the meiofauna more available in the next stage of extraction rather than to extract the meiofauna. The whole sample was eventually washed onto the mesh. After this thorough washing, any large stones were washed and removed from each sample to prevent damage to the fine mesh of the sieves. Sediment retained on the mesh after washing was immediately rinsed into a 120 ml round-bottomed polypropylene centrifuge tube with 10% formalin, sealed with propylene snap-on lids, and stored until required.

The next stage of meiofaunal sample processing, particularly for free-living marine nematodes, usually involves a flotation technique using the colloidal silica, Ludox-TM, specific gravity 1.15, which liberates meiofauna into the supernatant (de Jonge and Bouwman, 1977). However, this technique removed large quantities of detritus (5mm depth in an 8.8cm internal diameter petri dish) from the lagoonal samples, owing to the highly flocculent nature of these sediments and the large quantity of plant material they contain. Picking and mounting worms was therefore very difficult and time consuming. To improve extraction efficiency, meiofauna were recovered by centrifugation (Fig. 2.1) with ludox-TM (De Jonge and Bouwman, 1977; Hooper, 1988; Platt and Warwick, 1988).

ii Centrifugation

Samples of an approximately similar wet weight of sediment were centrifuged in batches of four. To each polypropylene centrifuge tube approximately 1 g (2 heaped spatulas) of kaolin powder was added. Each was filled with water to approximately 100 ml (+/- 10 ml) and the content vigorously stirred to thoroughly mix the sediment and kaolin. The stirrer was rinsed into the tube and further water was added to ensure that the weight of each sample was equal to within 0.05 grams. This provided a balanced rotor during centrifugation. The tubes were re-sealed with the poly-propylene snap-on lids and spun at 2500 rpm for 10 minutes. During centrifugation the Kaolin formed a plug that 'held down' any debris, particularly phytal detritus, allowing the supernatant to be poured off. Any material in the supernatant was retained on a 45 μm mesh sieve (separate sieves were maintained for each sample in a batch), washed and rinsed back into its original 250 ml sterilin pot and 10% formalin solution added.

The first spin acted as a blank to remove all water and indicated whether enough kaolin had been added or removed excess kaolin. The same procedure was repeated for subsequent spins, but with the water replaced by ludox-TM. On addition of ludox-TM, and before each spin, the samples were vigorously stirred to thoroughly resuspend the sediment and kaolin. After each spin, the ludox-TM was retained (separately for each sample), as the supernatant was poured off though the mesh, and

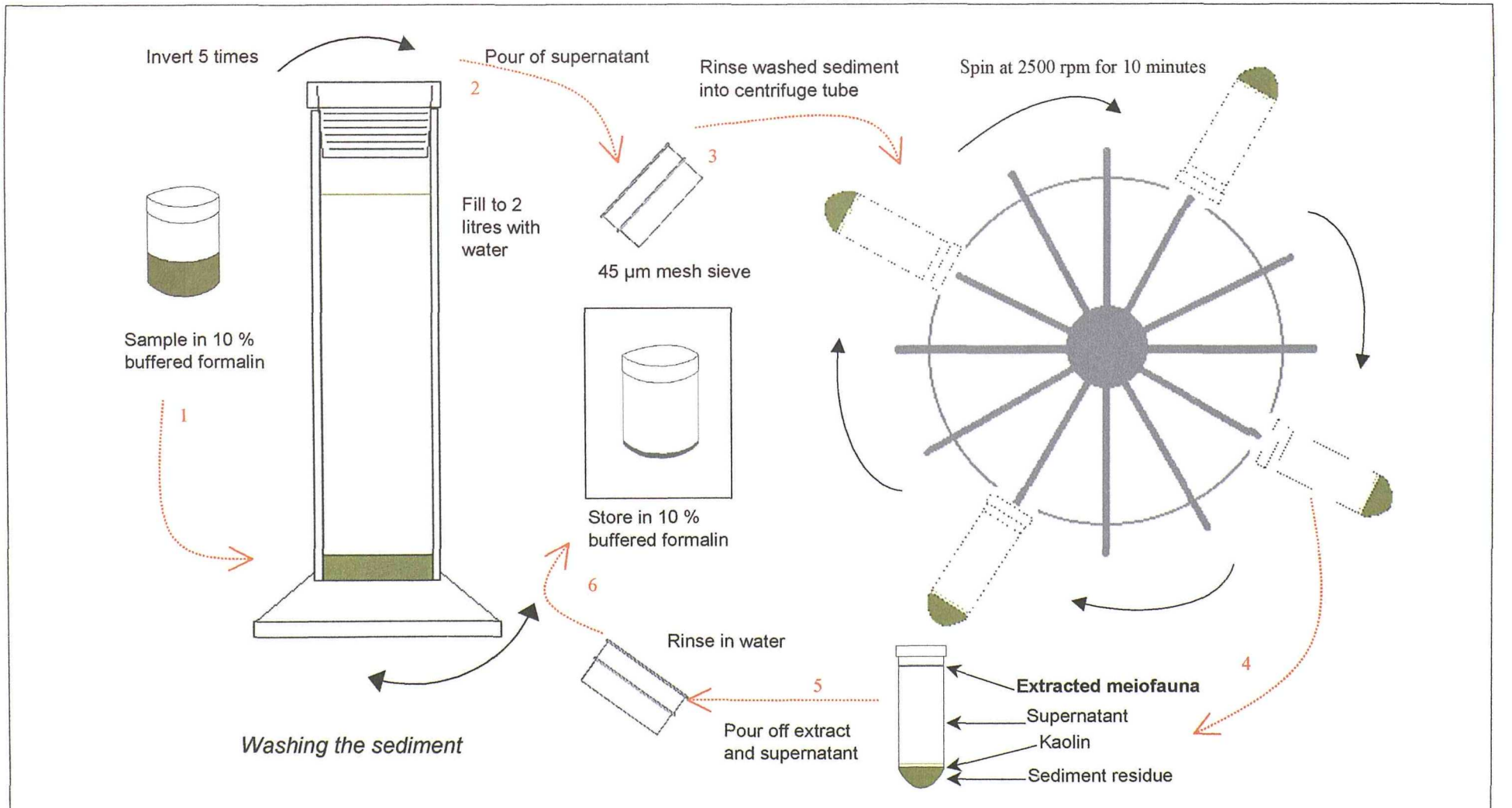


Fig. 2.1. Decanting and centifugation technique. Not to scale.

re-used. The Ludox- TM was changed after every fourth spin, or when it began to look 'dirty', which ever occurred first.

To determine the efficiency of extraction the method was tested with practice samples. After each spin, the retained material was washed and then rinsed directly into a prepared petri dish (see below) and the number of Nematoda counted. Extraction was considered complete when 3 consecutive nil results were obtained. The proportion of the sample extracted by each spin (as a cumulative percent) was then calculated. During practice runs, an extraction efficiency of 95 % was obtained after 6 spins and 99 % efficiency after 12 spins (including the initial blank). However, twenty spins were carried out to process the spatial data, because three consecutive nil results were not obtained until the 20th spin for one of practice samples. It is likely that this reflected the high proportion of fines at some sites, which is known to reduce ludox efficiency (Mitchell, pers. com.). For the seasonal data from Normandy Farm, 15 centrifuge spins were performed since the sediment at this site was predominantly clay and coarse material. This type of material was washed out at the preparatory stage and the remaining sediment did not 'clog' the ludox.

iii Sample Splitting and Picking

Practice centrifuge runs removed up to 1300 nematodes from one 50 ml core and (though reduced in comparison to the flotation method) large quantities of detritus. Consequently, samples were split to reduce the amount of detritus in each petri dish and therefore increase sorting efficiency. Each sample was split into 8 equal parts using a sample splitter as described by Elmgrem (1973, Fig. 2.2). The splitter was constructed from a closed Plexiglas cylinder, the base of which was divided into 8 equal chambers. These chambers and the main part of the cylinder each had a tap for drainage that was stoppered with a rubber bung during use.

The splitter was thoroughly washed before each use. A sample was gently rinsed into the splitter and then mixed by a high-power stream of water. The splitter was filled to approximately one inch below the lid, suspending all material in to the water column. A small drop of detergent was added to the water to reduce its surface tension and therefore encourage any floating material to sink. One hour after settling

the sample in the splitter, it was tapped firmly on the side with a ruler, whilst holding the lid in place. This dislodged any material still held by the surface tension. Each sample was then allowed to settle overnight. In the morning, the splitter was tapped again to dislodge any material settled onto the dividing walls between segments. It was then allowed to settle for at least a further hour.

Material from each segment was treated as a discrete sub-sample. The main bulk of water was first drained from the splitter ('Drainage Bung' in Fig.2.2) through the 45 μm aperture mesh sieve. Any material retained on the mesh was washed into a prepared petri dish. Petri dishes were pre-scored on the underside at approximately half centimetre intervals as a guide for picking, to ensure that no animals were missed. Material was then gently washed out of each segment in turn. To remove a sub-sample from the splitter, the 45 μm mesh was placed under each segment in turn and the appropriate bung removed. Once the segment was drained, it and the surrounding walls to that segment were carefully rinsed with a directed jet of water from a 1 litre wash bottle. Care was taken to ensure that the other segments were not disturbed. The material from each segment was washed in to separate pre-scored petri dishes.

To estimate abundance, all meiofauna from at least three segments were enumerated under a stereoscopic dissecting microscope. The first 250 nematodes encountered were picked. If less than 250 nematodes were counted in three petri dishes, nematodes were picked from further segments until this minimum was reach. All petri dishes were counted in full. Other meiofauna encountered was also counted and those found whilst picking the first 250 nematodes also picked. It should be noted that the extraction technique targets the Nematoda and that no single extraction method has been found to efficiently remove all meiofaunal taxa (Armonies, 1997). The possibility of under-estimating the abundance of other meiofauna will be considered. Residues and material from unused segments were returned to the original sample pots and stored in 10 % formalin for reference, if necessary.

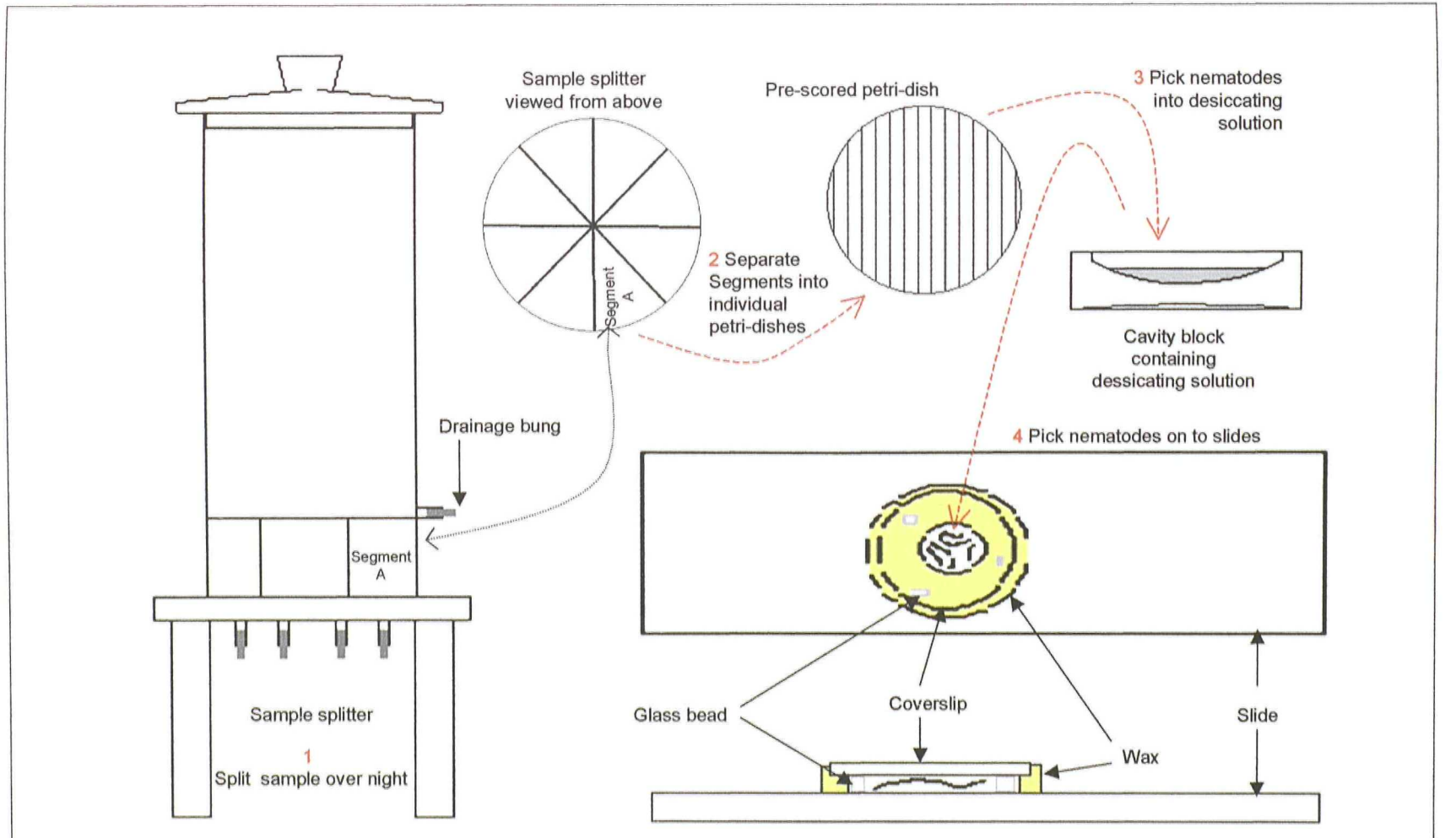


Fig. 2.2. Sample splitting and mounting. Not to scale.

Opposite segments were chosen to limit bias that might have been generated by the distribution of material in the splitter. The meiofauna were picked using either an eyelash fixed into a glass pipette by wax, an entomological pin secured into a metal holder, or a glass pipette, whichever was most appropriate. Picked nematodes were placed directly into a cavity block (Fig. 2.2) three-quarters-filled with a dehydrating solution of 5 % anhydrous glycerol, 5 % IMS alcohol and 90 % distilled water with phenol crystals to prevent fungal growth. The cavity block was covered to prevent contamination of the sample. Other meiofaunal animals were picked into 10 % formalin in small glass pots with snap on lids and stored for reference if necessary.

The dehydrating solution prepared the nematodes for mounting on to slides in a glycerol mountant, so that they did not collapse (Seinhorst, 1959). It also allowed for the removal of any remaining detritus that could have interfered with identifications. The cavity block was placed in a dessicator with its glass cover slightly open and left over night or until the desiccating solution had evaporated to 100% anhydrous glycerol.

iv Slide Mounting

Slides were made following a standard wax-ring method (Hooper, 1988) with 76 mm x 26 mm glass slides and 19mm diameter round coverslips. These were stored in 100 % IMS and cleaned and dried using soft tissue as required. Once a slide was cleaned, a paraffin wax ring was made in its centre using a short length of 15 mm diameter copper tubing with a wooden handle. The wax was melted, and the copper tubing heated to the same temperature, in a flat-bottomed crystallising dish placed on a heater plate (Fig. 2.2). Once at the correct temperature (approximately 45 °C) and when all the wax had melted, the copper tubing was shaken to remove excess wax and then placed steadily and uniformly on to a glass slide (Fig. 2.2). The tube was gently rotated to ensure an even, circular application of wax. This was done quickly, before the wax solidified. The copper tubing was returned to the crystallising dish between applications and left for approximately 2 minutes after every fourth or fifth application to prevent it from cooling.

A small quantity of clean 100 % anhydrous glycerol was placed in the centre of the resulting wax ring. Under a stereoscopic dissecting microscope, nematodes were picked from the cavity block into this glycerol. Approximately 10 nematodes, dependant to some extent on the size of individuals, were mounted per slide. To prevent bias, nematodes were always picked from the top right-hand corner of the cavity block, working right to left and top to bottom (Fig.2.2). The slide was then place under the stereoscopic microscope and the nematodes arranged equidistantly in the glycerol. Glass beads with a diameter > 45 μm and < 90 μm were placed between the glycerol and wax ring, near the wax and a cover slip placed centrally on top. The wax was re-melted on the hotplate to fix the cover slip in place. Beads help to ensure an even slide depth and prevented crushing of the nematodes by the coverslip during high-power microscopy. The coverslips were sealed with a slide sealant such as Glyceel. Slides were clearly labelled in pencil on self-adhesive white label. Enough slides were made to mount 200 animals from each sample.

v Identification

For each sample 150 nematode individuals were identified (i.e. the first 150 specimens encountered, if an animal was lying on a slide such that it's head was obscured it was excluded from the total). Animals were identified on an Olympus BH-2 microscope at high power (1000 x magnification) under an oil immersion lens with Nomarski Differential Interference-Contrast illumination (NDIC). Where identification proved problematic, such as an animal lying in a bad position, or with very juvenile animals, identification was finalised on a Leica DMR. Identification to species was made where possible. The Linnean Society Synopses 28, 38 and 53 (Platt and Warwick, 1983 and 1988; Warwick, Platt, and Somerfield, 1998, respectively) were used for identification, using the key to world genera and the reference guides for the British marine nematode fauna. The Bremerhaven Checklists of Aquatic Nematodes (Gerlach and Riemann, 1973 and 1974) were used to reference other relevant taxonomic papers. Documents published after the last edition of the Bremerhaven Checklist were consulted where possible. Dr Tim Ferrero has provided taxonomic training at the Natural History Museum, London.

vi Nematode Functional Groups

Functional group analysis is based on observed and predicted usage and/or adaptation of morphological features (Wieser, 1953 and Thistle *et al.*, 1995). All identified nematode species were assigned to one of four feeding groups (Wieser, 1953) and one of four tail shape functional groups (Thistle *et al.*, 1995). This was standardised within species and no account was taken of juvenile development patterns. It is recognised that early juveniles may have different feeding strategies to adults, particularly in carnivorous species, where teeth develop with molt stages.

Feeding type functional groups are based on buccal cavity structure (Table 2.2 and Fig. 2.3; Wieser, 1953). Feeding type 1 classifies species with an unarmed buccal cavity: Type 1A have a small or absent buccal cavity and Type 1B a medium-sized buccal cavity. Feeding type 2 classifies species with a buccal cavity with teeth or mandibles present: Type 2A species have a mid-sized buccal cavity with small teeth and Type 2B a large buccal cavity with teeth and or mandibles.

Group	Feeding Type	Buccal Cavity	Teeth	Mandibles
1A	Selective deposit	Small / Absent	Absent	Absent
1B	Non-selective deposit	Medium	Absent	Absent
2A	Epistrate	Medium	Small	Absent
2B	Predator / Omnivore	Large	Large	Present

Table 2.2. Feeding groups as defined by Wieser (1953).

Tail shapes are grouped in to morphological types thought to indicate similar functional uses (Fig. 2.4; Thistle *et al.*, 1995). These are;

i. Round, short tails less than 2 anal body diameters (abd) with a blunt end;
ii. Clavate conico-cylindrical tails with an extension at the tip;
iii. Conical tails, less than 5 abd with a pointed tip and;
iv. Long, conico-cylindrical tails with an extended cylindrical portion, greater than 5 abd as a whole.

Tail length was measured as described below for morphometrics.

vii Morphometrics

Nematode morphometric analysis employed detailed measurement of the morphological features of mature individuals. Measurements of body length

(anterior to anus), tail length (anus to tail tip), maximum body diameter and anus body diameter were taken. Measurements were made from every third individual encountered during identification to remove the possibility of introducing bias when selecting nematodes for measurement. Body length and tail length were taken at the mid-line of an animal. Measurements were transcribed onto paper using a camera lucida at the highest possible magnification and measured using a map measurer (Forster, 1998) - Kasper and Richter 'onLine 5' - pre-programmed with the appropriate conversion factors.

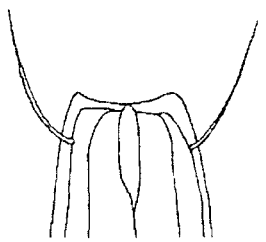
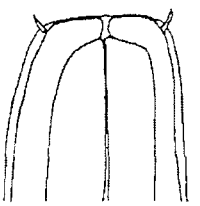
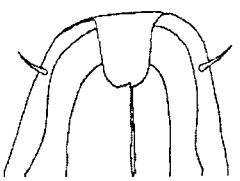
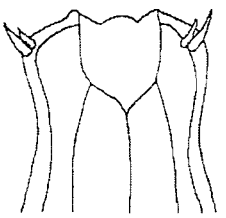
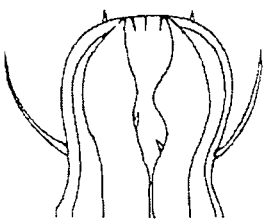
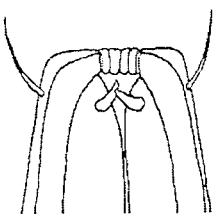
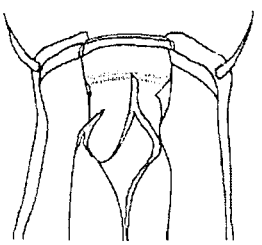
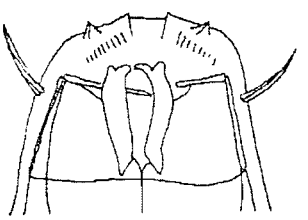
 Parachromagasteriella  Terschellingia	Type 1A Small or absent buccal cavity. Unarmed.
 Sabatieria  Paramonhystera	Type 1B Medium sized buccal cavity. Teeth absent.
 Microlaimus  Chromadora	Type 2A Medium sized buccal cavity. Small teeth present.
 Eurystomatina  Enoplus	Type 2B Large buccal cavity. Teeth or mandible present.

Fig. 2.3. Feeding type functional groups, redrawn from Wieser (1953).

Fig. 2.4. Tail shape functional groups. Adapted from Thistle *et al.*, 1995.
i. Round, short tails less than 2 anal body diameters (abd) with a blunt end;
ii. Clavate conico-cylindrical tails with an extension to the tip;
iii. Conical tails less than 5 abd with a pinted tip and;
iv. Long conico-cylindrical tails with an extended cylindrical portion, totally > 5 abd.

	Measurement	Formula	Reference
a	Length/width ratio	Body length (anterior to anus) / greatest body width	De Man, 1880
b	Oesophageal length	Body length / distance from anterior to intestino-oesphageal junction	De Man, 1880
c'	Tail length	Tail length / body width at anus or cloaca	De Man, 1880
V	Vulva postion	Distance of vulva from anterior end / body length x 100	De Man, 1880
V'		Distance from anterior to vulva / distance from anterior to anus x 100	Geraert, 1968
	Spinneret length	Length of spinneret / tail length x 100	

Table 2.3. Morphometric measurements and their calculation.

Variation of mean specific morphometric parameters both between sites and within species was estimated (Forster, 1998; Tita *et al.*, 1999). From each sample twenty randomly selected adults of each of the most abundant species (as both abundance per sample and total system abundance) were measured for comparison. Measurements were taken to compare the length/width ratio, tail length, oesophageal length, vulva position, and spinneret length of individuals. These are fully described

in Table 2.3.

Vulva position (as percent body length) and spinneret length (as percent tail length) were of particular interest due to observations made during identification. For example, in all *Daptonema procerum* females observed during this study, vulva position was recorded minimally at 60 % of the total body length from the anterior, yet in 'type' material it is recorded at 45 – 50 % of total body length from the anterior (Warwick, *et al.*, 1998). Also, spinneret length in *Spilophorella* sp. *D* was noted to vary considerably (between 15 and 45 % of tail length). Equally, spinneret length is expected to be an important identification feature between species of *Thalassomonhystera*.

The same measurements were used to assess seasonal variation of morphological characters within species in Normandy Farm Lagoon. As before, all measurements were drawn at the highest possible magnification using a camera lucida and measured with a pre-programmed map-measurer.

b *Macrofauna Picking and Identification*

Stored macrofaunal samples were washed with tap water over a 500 μm mesh sieve. A sample was washed into a white-bottomed metal tray and covered by a little water. Macrofaunal animals were picked from the retained material under direct illumination and low power magnification. They were divided into phyla and stored in glass vials before identification to species, where possible, under a binocular microscope. All species or species groups were counted. Abundance was expressed per 1 m^2 and per 10 cm^2, the former for comparison with other macrofaunal data collected at the sampling sites and the latter to allow comparison with the meiofaunal data collected in this study.

c *Photosynthetic Pigments*

Pigment analysis followed the methods described by Lucas *et al.* (2000). Core samples were freeze-dried for 24 – 72 hours, to improve pigment extraction (Buffan-Dubau and Carman, 2000). A dried sample was homogenised and a sub-sample of approximately 0.5 g transferred to a conical plastic micro-centrifuge tube with a

snap-on lid. Chloroplastic pigments were extracted from the sediment in 10 ml 90 % acetone by ultra-sonification for 30 seconds and incubation of the supernatant overnight in a refrigerator in the dark. After incubation samples were centrifuged at 3000 rpm (2000 x g) for 15 minutes. The supernatant was then assayed for chlorophyll-a and phaeopigments.

Fluorescence of the supernatant was measured before and after acidification (by addition of 2 drops of 10 % HCl) using an Aminco fluorometer. Acetone was used as a blank. The supernatant was transferred to a 1 cm cuvette and its absorbence and that of a chlorophyll a standard were measured spectrophotometrically at 664 nm with a turbidity correction made at 750 nm using a Cecil 1010 spectrophotometer. Total chlorophyll a and phaeopigment concentrations were calculated (Eq.'s. 2.1 & 2.2; Lorenzen, 1967) and expressed as mg of pigment per square meter, for the top centimetre of sediment.

Eq. 2.1. $$\text{Chl a (mg/m3)} = [A.K.v\ (665o - 665a)] / Vf.l$$

Eq. 2.2. $$\text{Pheo (mg/m3)} = [A.K.v\ (R\ \{665a\} - 665o)] / Vf.l$$

A = absorption coefficient of chlorophyll a, 11.0
K = factor to equate reduction in absorbency to initial chlorophyll concentration, 1.7 : 0.7
v = volume of acetone used for extraction (ml)
665o = absorbance before acidification
665a = absorbance after acidification
Vf = litres of water filtered
l = path length of cuvette (cm)
R = maximum ratio of 665o: 665a in the absence of phaeopigments, 1.7

d *Environmental Variables*

Sediment samples were defrosted and mixed by stirring. A sub-sample was taken from each and dried in an oven at 55 °C leaving approximately 110 g of dried sediment. The dried sediment was stirred and a small quantity (approximately 10g) taken for organic matter analysis. This material was transferred to a small ceramic crucible of a known weight, weighed (as dry weight) and then heated at 550 °C for 6 hours (to constant weight). The crucible and content were re-weighed and the difference in sediment weight expressed as percentage loss on ignition (LOI). Of the sediment remaining after oven drying, approximately 100 g was used for granulometric analysis. Sediment granulometry was estimated as phi (Φ) fractions

by stacked sieving on an electric shaker. Each fraction was weighed to the nearest 0.01 g and expressed as a percentage of the total weight.

The high level of organic matter and fines in the sediment rendered the basic drying technique at the start of the analysis unsuitable. The resultant granulometric data is therefore unreliable. A parallel survey by and on behalf of Hampshire County Council produced equivalent information (Bamber *et al.*, 2001a) and permission has been given to use this data in subsequent analyses rather than replicating their technique. Bamber (1997) suggests that large within-site variability of lagoonal granulometry limits the usefulness of precise analysis. Data are therefore analysed both as half-phi fractions and relative mud/ sand/ gravel/ shingle.

2.3 Data Analysis

2.3.1 Univariate statistics

The data were analysed unsing univariate and multivariate techniques to determine any correlation between the biological assemblages and the environmental parameters throughout the system. All analyses were performed in PRIMER-E (PRIMER 5.1.2 for Windows).

a *Diversity Measures*

The absolute values of the faunal data were reduced to single-value diversity coefficients, which were used to indicate generalised trends within and between communities. A variety of univariate diversity indices have been developed, those used were the Shannon-Weiner, Margalef's and Pielou's diversity indices, Caswell's Neutral Model. Each index weighs the two components of diversity - species number and the distribution of individuals between species - differently (Table 2.7). Differences between the values of individual indices between sites were tested by ANOVA at a 95% confidence level.

i Species Richness

The Shannon-Weiner diversity index of diversity, H', is calculated as the joint probability of selecting all individuals of a species from a population (Eq. 2.3). So, if p_i is the proportion of individuals found in the ith species, $H' = \sum p_i \log p_i$.

However, as is usually the case, the entire population was not quantified. Therefore, p_i was estimated as $(n_i / N)^{n_i}$, the probability of selecting n_i individuals of species i from a sample population of N individuals. The probability of selecting all individuals for all species was calculated and the summation, the joint probability, expressed as the Shannon-Weiner diversity index.

The joint probability, $P = \left(\frac{n_1}{N}\right)^{n_1} x \left(\frac{n_2}{N}\right)^{n_2} ... x \left(\frac{n_i}{N}\right)^{n_i} ... x \left(\frac{n_s}{N}\right)^{n_s}$

Or, $$P = n_1.\log n_1 - n_1.\log N + n_2.\log n_2 - n_2.\log N... + n_i.\log n_i - n_i.\log N... + n_s.\log n_s - n_s.\log N$$

So, $$\log P = \sum_1^s n.\log n - \sum_1^s n.\log N$$

$$\text{Log } P = \sum_1^s n.\log n - N.\log N$$

And $$\text{-log } P = N.\log N - \sum_1^s n.\log n$$

So, $$\text{-log } P = H'$$ Eq. 2.3.

The Shannon-Weiner index calculates the evenness of species abundance (Peet, 1974) and is weighted towards species richness (Lambshead *et al.*, 1983). The lowest possible value of H' is 0, where there is only one species, but it has no absolute upper limit owing to its dependence on n_s. H' increases with increasing number of species, and the number of species may increase with an increasing sample size, N. H' is therefore sample size dependent (Shannon and Weaver, 1963; Pielou, 1966, 1969; Clifford and Stephenson, 1975; Lambshead *et al.*, 1983).

Margalef's species richness index, d, Eq. 2.4, was also used to calculate species richness by total abundance of individuals (Margalef, 1957). In fact, Magurran (1988), suggests that it is a more reliable, if less widely used diversity measure than the Shannon-Weiner index, particularly owing to its simplicity.

Eq. 2.4. $$d = (S-1)/\log N$$

Where, S = total number of species

ii Evenness

The Shannon-Weiner index can be used to calculate species, rather than sample, evenness as the ratio of the observed diversity to the theoretical maximum, given the number of species (Magurran, 1988). This is termed Pielou's equitability-weighted index, J' (Eq. 2.5; Pielou, 1969). The theoretical maximum assumes that each individual represents a different species, so N = S,

When $$J' = H'/H_{\max}$$

And, $$H_{\max} = -\sum_{1}^{S} 1/S.\log 1/S$$

$$H_{\max} = \log S$$

So, $$J' = H'/\log S \qquad \text{Eq. 2.5}$$

This ratio constrains J' between 0 and 1, and facilitates the comparison of disparate sampling stations. As with H', it assumes that all species are sampled (ie. all species in the population are represented in the sample). However, since H' is sample size dependent, Pielou's index is also dependent on sample size. It is also very sensitive to the occurrence of rare species (Heip *et al.*, 1985).

iii Caswell's Neutral Model

Caswell's neutral model (Eq. 2.6.) was used to estimate the level of diversity of a sample with respect to a sample of the same size taken from a standard 'neutral' system. The model assumes no interaction between species and that all species react equally to abiotic factors (Caswell, 1976), that is, biological neutrality is assumed. It is [reasonably] independent of sample size, due to inclusion of N and S. It predicts sample diversity under neutrality and compares the prediction to the observed diversity, H'. Deviation from neutrality is measured by comparing the evenness of the [distribution of] relative species abundances to the model prediction. Deviation from the model by the observed community is expressed as a diversity index, the V statistic.

Eq. 2.6. $$V = \left[H' - E(H')\right]/S.D.(H')$$

H' =observed diversity

$(E(H'))$ = predicted of the neutral model

If,

V = 0; Neutrality

V > 0; Greater diversity than expected, increased biological interaction
V < 0; Lower diversity than expected, reduced biological interaction
-2 > V > +2; Significant departure from neutrality
Evenness or richness may have changed

iv K-dominance Curves

K-dominance curves were used to pictorially examine differences in diversity and dominance between samples and sites. Percentage cumulative abundance was plotted against log species rank in decreasing order of abundance (Lambshead *et al.*, 1983; Platt *et al.*, 1984). The sample with the most elevated curve had the lowest diversity. It was expected that when the curves did not intersect, the order of samples was the same in all other measures of intrinsic diversity (e.g. Shannon-Weiner).

The intersection of sample k-dominance curves indicated that the different diversity indices calculated above would rank samples differently, since a relative shift in the position of a k-dominance curve describes a shift in species dominance relative to richness (Magurran, 1996).

b *Nematode Functional Groups and Morphometrics*

Functional group data were analysed by ANOVA and multivariate methods, described below, and by proportionate rank similarity. For each sample, abundance of individuals by tail shape group was ranked for each buccal-morphology group and vice versa (Thistle *et al.*, 1995). The number of ranking mismatches, per site, was counted and the probability of that number of mismatches occurring by chance estimated by G-test. This is a log-likelihood ratio test for the goodness-of-fit of the data as divided proportionately into the classes. The null hypothesis is that the observed frequencies between classes are proportionate. For example, in fine grained sediments with a high organic content, nematodes might be selective deposit feeders (Type 1A buccal cavity) with a conico-cylindrical tail. It was expected that the number of mismatches would not be significant if the distribution of functional groups was due to species dominance (rather than gross environmental parameters).

c *Statistical analysis between sites*

Analysis of Variance (ANOVA) was used to describe in more detail the significance of difference between sites (H_0: There was no difference between sites and there was no difference between seasons). It was carried out on the univariate indices and the various size-class data. The ANOVA test was not used per species, since the probability of making a false inference would cumulatively increase with number of species. Non-parametric ANOVA was used to test the significance of difference between univariate means accounting for within sample variability. ANOVA assumes normality of the data with constant variance about site means across sites (Clarke and Warwick, 1994). Gross departures from the normality (such as magnitudinal changes in SD) were, therefore removed by transformation of the data, as necessary: normality is rare in biotic data owing to the prevalence of zero values and other extreme values. Normality and the level of transformation required were estimated from gradient of the slope, β, produced by plotting log (SD) against log (mean). If $\beta = 0$ no transformation was required, if $\beta = 0.5$ square root, and if $\beta = 1$ log transformation (Clarke and Warwick, 1994). ANOVA was carried out using Graph Pad Prism, version 3.02.

ANOVA is a multiple pairwise comparison of all samples and expresses actual variation of the group averages in terms of expected variation. A single F-ratio was produced for the whole data set, where *F*=(measured variation of the group averages)/(expected variation of the group averages), at significance level, p. The F-ratio is based on expected variation, $\sigma/\sqrt{N}$, where σ is the standard deviation and N is the number of values. If $F \cong 1$, H_0 is accepted; there is no significant difference between sites. If F is large and significant, H_0 is rejected and a significant difference between samples is assumed.

ANOVA was complimented by Tukey's multiple comparison. This was used to estimate the significance of difference for each pair of samples. All samples were compared, producing an individual index of variation of each pair in terms of expected variation. The Tukey's test is a modified t-test, which accounts for the multiple comparison tests and the interrelationship between each pairwise comparison. It highlights the source of any difference between samples, without

compounding testing error, as discussed above for ANOVA.

2.3.2 Multivariate statistics

Univariate analyses were used to determine broad community/sample differences (similarities, or randomness) within and between sites. They are very simple tools, however, that reduce the information contained within community data. They do not identify the basis, at species or community level, of any observed difference. Multivariate statistics were therefore used to analyse data between sites and seasons, accounting for species composition (including diversity and abundance) and environmental variables. The combination of biotic and environmental data in community analyses allowed the discussion of biotic variation in relation to possible abiotic influences.

a *Similarity*

Multivariate analysis of data followed the methods set out by Clarke and Warwick (1994). Firstly, triangular similarity matrices were constructed from pairwise comparisons of species abundance data between sites and between seasons. Both non-transformed and fourth-root-transformed abundance data were analysed. Non-transformed data are naturally weighted towards the most common species, whilst transforming the data reduced the importance of dominant species, giving greater emphasis to the less abundant and rare species in subsequent analysis. All multivariate analyses of data were carried out using PRIMER-E (PRIMER 5.1.2 for Windows; Clarke and Warwick, 1994).

A triangular similarity matrix (Clarke and Warwick, 1994) was produced by pair-wise comparison between all samples using the Bray-Curtis similarity coefficient (Bray and Curtis, 1957). The Bray-Curtis coefficient was used because it is not affected by joint absences (Field and McFarlane, 1968), and is weighted to abundant species (Field *et al.*, 1982). Similarity between the *j*th and *k*th samples was measured as the sum of the difference (the absolute value of difference) in abundance of the *i*th species between the *j*th and *k*th samples divided by the sum of the abundance of the *i*th species in both sites. The total similarity between the *j*th and *k*th samples for all species, S_{jk} is the Bray-Curtis coefficient (Eq. 2.7). By calculating the Bray-Curtis

coefficient for all possible pairs of samples, a similarity matrix was produced.

Eq. 2.7. $$S_{jk} = 100\left\{1 - \frac{\sum_{i=1}^{p}\left|y_{ij} - y_{ik}\right|}{\sum_{i=1}^{p}\left(y_{ij} + y_{ik}\right)}\right\}$$

The information held in the resulting values of similarity were described graphically (using the values as proximity data; Davison, 1983) by two methods. Unrooted hierarchical agglomerative cluster diagrams (dendrograms) were plotted by group average similarity (Clifford and Stephenson, 1975; Hodda, 1986). Ordinations of similarity were plotted by rank order of similarity, calculated by non-metric Multi-Dimensional Scaling, nMDS (Shepard, 1962a and b; Kruskal, 1964a and b; Field *et al.*, 1982).

i Cluster Analysis

Cluster analysis is a continuation and graphical simplification of similarity/dissimilarity analysis. It was used to 'group' samples together, in terms of similarity, thus aiding the interpretation of the similarity data. An unrooted tree of similarity between samples is produced, with no x-axis scale, but with a y-axis of similarity ranging from 0 to 100 percent (though in fact it does not matter which way the data is plotted, it can be rotated in any direction). Hierarchical agglomerative clustering by group average linkage has been used in this study. The different types of clustering and linkage methods available are described below.

Clustering techniques have been categorised (Cormack, 1971) as:
Hierarchical. Samples form groups which themselves form successively larger groups;
Optimising. Sample grouping are of set sizes and specified cluster distances are based on common features;
Mode-seeking. The number of clusters is set by the author and clustering is based on the proximity of samples and there density in n-dimensional [species] space;
Clumping. Samples can be placed in more than one cluster. Clusters are created by successively selecting different samples to be the centre of a cluster or;
Miscellaneous.

Hierarchical clustering was used in this study owing to its simplicity: the similarity data are not manipulated and cluster size, location or composition are not predetermined. Hierarchical dendrograms can be produced either by divisive or agglomerative methods (Clifford and Stephenson, 1975). Divisive clustering begins with one group (cluster) containing all samples and the progressive division of samples into smaller and smaller groups by classification of single attributes. This method is considered useful for large sample sizes because it begins with maximum information and groups remain stable with additional samples, but it is a strict yes/no method and may result in misclassification (Clifford and Stephenson, 1975).

Agglomerative clustering begins with single sample points, which are grouped by sample-local information; it therefore requires accurate sampling. It involves many computations (at least $(n-1)^2$), but when sample size (n) is small in comparison to the factors (species) it can be used productively, since the number of iterations required is relatively small whilst the quantity of information on which to make divisions is large. Most importantly [for ecological data] agglomerative clustering can be used successfully with data containing missing values (Clifford and Stephenson, 1975).

Hierarchical agglomerative clustering was chosen due to the points covered above, the availability of computational programmes and the ease of interpretation. In this method, samples are successively fused together, starting with the highest mutual Bray-Curtis similarity coefficient. Initial pairings are formed between samples above a specified similarity level. After the placement of the first points, the similarity matrix is recalculated with each group of samples classed as an individual cluster. Secondary matrices can be produced by a variety of methods. Similarity values for the groups created in the first step of agglomerative clustering may be calculated by either,

Single linkage (or nearest neighbour) clustering, which plots sample or group similarity as the maximum similarity of the paired samples;

Complete linkage (or furthest neighbour) clustering, which plots the minimum similarity between samples or;

Group-average similarity, which is calculated as the sum of sample similarities divided by the number of similarities.

Single linkage and complete linkage clustering produce a dendrogram identical to a dendrogram of rank similarity, and is effectively non-metric (Clarke and Warwick, 1994). However, the single linkage method tends to result in the 'chaining' of samples and the complete linkage method often produces few small groups. Group average clustering, on the other hand, produces distinct sample groups of an intermediate size, which are more useful for data interpretation. Therefore, for this study group-average weighting was used for new matrices. So, the similarity of A and B to say sample C is calculated as [S(A,C) + S(B,C)]/2.

Similarity matrices were calculated up to $n(n-1)/2$ times (for n number of samples), until all samples were placed by similarity in the dendrogram. Sequential pairs may or may not include the first, so the resulting dendrogram can theoretically have several groups of similar sites with different levels of similarity. The placement of points (samples) along the x-'axis' is random, by clusters, whilst similarity of samples and clusters is indicated against the y-axis as a joining line. The clustering procedure continues until all samples, including any isolated clusters, are joined to close the dendrogram leaving it unrooted.

ii Multi-Dimensional Scaling

Dendrograms can force samples into discrete groups that may be artificial, especially where communities are graded on a discrete basis (Field *et al.*, 1982). Also, following the fusion of samples into a cluster, their 'identity' is lost by the group-averaging method of subsequent clustering. Therefore, to complement cluster analysis, the data were also represented and analysed by non-metric Multi-Dimensional Scaling, nMDS, to produce spatial distance models (Davison, 1983). These are ordinations plotted in n-dimensional hyperspace, without axes, with distances based on the ranks of similarity between samples. Any gradient in community similarity is therefore retained in the positioning of samples within the ordination.

Non-metric MDS ordinations plot samples (points) in n-dimensional space as rank similarity distance. This is then compressed into 2-dimensions, with reference to the

original data matrix, for ease of interpretation (Field *et al.*, 1982). Rank ordination is used as opposed to percentage similarity values (as in metric MDS) since the range of similarity differences in the latter can produce a distorted ordination due to the complexity of sample placement. Also, metric MDS can be heavily skewed by zero values. The first step in the production of an ordinate map is to plot the pair of samples with the most similarity (Kruskal and Wish, 1978), their placement being random. The model starts a plot several times, in this case 10 restarts, and then plots the 2-D 'best fit' nMDS ordination, by repeating the similarity analysis taking the first pair of samples as a single replicate, and so on.

Ordinations also simplify or restrict the information held within the data set (at n-dimensions) in order to 'fit' it into the available 2-D 'space'. The ordinate distances, d_{jk}, may therefore deviate from the actual similarity distances, S_{jk}, between samples. The level at which a nMDS ordination deviates from the actual similarity between samples is termed stress (Eq.8). The source of stress (i.e. the similarity values most poorly represented in the plot) were located by plotting a shepard diagram (Kruskal and Wish, 1978). This is a plot of MDS distances d_{jk} against Bray-Curtis dissimilarity δ_{jk}. Stress is measured as the vertical distance, $\hat{d}_{jk}$, between the plot distances and the monotonic, non-metric regression-estimated distances, plotted against δ_{jk}. If the points are monotonic (the increase in $\hat{d}_{jk}$ perfectly matches the increase of delta d_{jk}) there is zero stress. Outliers (from the regression line) may result either from poor representation of stations or errors in the calculation of dissimilarity values (Clarke and Warwick, 1994).

Eq. 2.8. $$Stress = \sum_j \sum_k \left(d_{jk} - \hat{d}_{jk}\right)^2 \Big/ \sum_j \sum_k d_{jk}^2$$

$\hat{d}_{jk}$ = predicted distance from the fitted regression line, corresponding to dissimilarity, δ_{jk}

If, $\hat{d}_{jk} = \delta_{jk}$ for all $n(n-1)/2$ distances in the summation, stress is zero

Stress values	*Interpretation*
<0.05	No prospect of misinterpretation.
<0.1	Good ordination, no improved at higher dimensions.
<0.2	Sample ordination at higher levels of similarity may be unreliable.
>0.3	2-D ordination overly influenced by random placement of points.

Zero stress is rare and stress < 0.1 is commonly accepted, whilst stress >0.15 is often considered too high to produce a representative plot. Zero stress only occurs when similarity values perfectly match the actual difference between samples or when *n-1* dimensions are used, where *n* is the number of samples. Non-zero stress values occur when an insufficient number of dimensions are used. With the addition of further dimensions, an ordination increasingly represents the true relationship, in terms of proximity, between samples. Therefore, as the number of dimensions increases, the stress value will either decrease or remain constant, but never increase.

At some point, additional dimensions will merely act to describe 'noise' or sampling error in the data. Then the rate of reducing stress slows. Therefore, the 'true' dimensionality of the community data can be estimated by examining the rate of reducing stress with increasing dimensionality. This was demonstrated graphically by a scree plot, stress plotted against number of dimensions. In ecological data however, a distinct alteration in this rate of change is rare (Clarke and Warwick, 1994).

When large stress occurs, an ordination is not a good representation of the data and is distorting the relationships between sample positions. The number of ordinate dimensions are then not enough to represent the number of structuring factors (species) in the data. Stress occurs both evenly through all pairwise comparisons and within clusters in the plot, but is most likely between closely plotted samples. Stress located in tight cluster(s) was overcome by extracting the corresponding similarities for those points and plotting separate ordinations for each cluster. In this case, the first ordination identifies 'large scale' similarity between samples (points) and subsequent ordinations of selected clusters highlighted possible small-scale similarities between samples.

iii Community Composition

To test the significance of difference in community composition between sites (H_0 = No difference between sites) Pairwise Analysis of Similarities (ANOSIM; Clarke, 1993) was calculated. This is a measure of the distance between replicates, within and between sites, as rank similarities. It produces a single R statistic (Eq. 2.9) for

the observed values, which is constrained between –1 and +1 to give an indication of site and sample similarity. The significance of the R statistic is tested by random permutations of the pairwise analysis of similarity. The ANOSIM program rearranges the replicates between sites to produce a null distribution of R, assuming all samples are from the same population. If the calculated R-value occurs within this distribution, H_0 is accepted. H_0 is rejected at the significance level $100\ (t + 1) / (T + 1)$ %, if only t of the T simulated values of R are as large (or larger than) the observed R.

Eq. 2.9. $$R = \left(r'_B - r'_W\right)/\left(M/2\right)$$

r'_B = Averaged rank similarities of replicates within sites;

r'_W = Averaged rank similarities of paired replicates between sites;

M = n(n – 1)/2

n = number of samples.

If,

R <<0 – Similarities across sites > within sites (unlikely)

R = 0 –Similarities between and within sites equal

R = 1 – Similarity within sites > similarity between ANY replicates from other sites.

A similarity matrix of species was also created to produce a dendrogram and ordination of species relatedness, in terms of distribution between samples. The contribution of individual species to inter-group sample similarity was then computed by Similarity Percentages (SIMPER) (Clarke, 1993; Clarke and Warwick (1997). This estimates the consistency with which any one species contributes to similarity between samples as the ratio of dissimilarity (Bray-Curtis as above) and the standard deviation of similarity. SIMPER analysis in PRIMER produces a single index value, as percentage, for each species (Clarke and Warwick, 1994).

b *Comparing Faunal Data to Environmental Variables*

Environmental data are analysed following the methods described by Clarke and Ainsworth (1993). Environmental variables are plotted against each other as raw data to produce a draftsman plot. This was then used to determine which data transformation was necessary in order to approximate multivariate-normality for the statistical analyses. Normality is seen as linear pairwise relationships. Log transformation was used for concentrations, (right skewed), and reverse log transformation for salinity (and other variables that are left skewed) (Clarke and Warwick, 1994). When two variables were highly correlated (r >0.95) the variable

considered most independent, or previously shown to be influential to the distribution of benthic biota, was retained and the other excluded from further (multivariate) analysis.

To examine similarity between sampling sites by environmental data, the transformed environmental data were analysed by Bray-Curtis dissimilarity based on Euclidean distance (Clarke and Ainsworth, 1993). Increasingly complex combinations of environmental variables were compared so that, including univariate plots and the draftsman plot, the environmental variables were assessed singly, 2 at a time, 3 at a time and so on. The resulting triangular dissimilarity matrices were used to plot nMDS ordination of the sampling sites. These ordinations based on abiotic data were then compared to the ordination of species data (abundance and function groups; Clarke and Warwick, 1994). Multivariate analysis of environmental variables frequently involves factor analysis (Clarke and Ainsworth, 1993), such as Principal Component Analysis (PCA). However, this method eases the comparison of the biotic and abiotic ordinations (Clarke and Ainsworth, 1993). Equally, it is not appropriate to compute correlation-based (PCA or Euclidean distance) similarity of biotic data because correlation can be heavily weighted by joint absences, or zero counts, which often dominate biological data.

All combinations of environmental data are compared with the biotic community by rank correlation of the triangular similarity matrices. Each pair of triangular matrices (one biotic and one abiotic) is 'unpeeled' to give 2 vectors and each vector is then ranked (Fig. 2.5). Since biotic data is ranked by similarity and abiotic data by dissimilarity, the ranks are reversed for the abiotic data and rank correlation is then calculated. Rank correlation is chosen in preference to optical pattern matching (Procustes analysis; Gower, 1971) owing to the bias that is introduced when choosing the number of dimensions in which to optically compare ordinations. Spearman rank correlation (ρ_s, Eq. 2.10) is scaled by the number of terms in the similarity matrices (i.e. the number of samples) by down-weighting the rank differences by rank position (Eq. 2.11; (harmonic, weighted Spearman rank correlation, ρ_w). This reduces the sensitivity of the coefficient to distant pairs of samples (i.e. those samples with high dissimilarity).

Eq. 2.10.

$$p_s = 1 = \frac{6\sum_{i=1}^{N}(r_i - s_i)^2}{N(N^2-1)}$$

r_i $\{i=1,\ldots N\}$ = ranks of all the sample similarities for the biotic data

$s_i\{i=1,\ldots N\}$ = ranks of all the sample similarities for the abiotic data

$$N = n(n-1)/2$$

Eq. 2.11.

$$p_w = 1 - c\sum_{i=1}^{N}\frac{(r_i - s_i)^2}{(r_i + s_i)}$$

c, weights p_w between –1 and +1

$$c = \frac{6}{N(N-1)}$$

If,

p_w = -1, complete opposition of rankings, negative correlation.

p_w = 1, complete agreement of rankings, positive correlation.

p_w = 0, random, unrelated ranking of biotic and abiotic similarity matrices.

For each different combination of environmental data, the highest coefficients are tabulated. The most 'effective' combination (at each level of complexity) will have a maximum correlation, p_w, this increases with the number of variables to an optimum value. Beyond that maximum, it will decrease with the addition of further variables. The ordination of samples by biotic data is then displayed adjacent to the ordination by environmental variables with which they correlate most significantly. When the 2D ordinations had high stress values, they did not effectively describe this correlation, highlighting the need for vigour when testing correlation between similarity matrices (Davison, 1983).

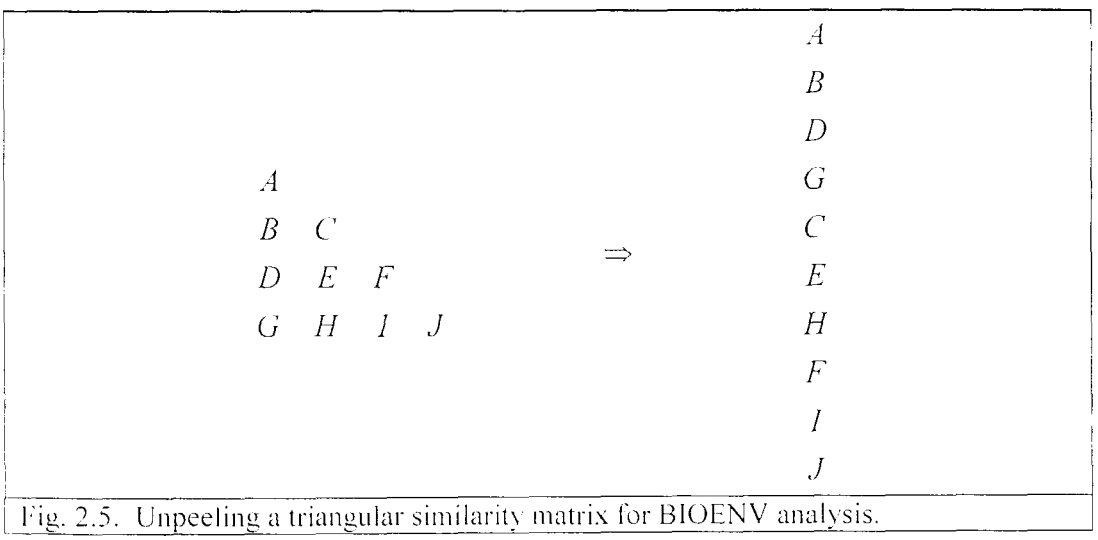


Fig. 2.5. Unpeeling a triangular similarity matrix for BIOENV analysis.

3 Physical and Environmental Parameters Along the Keyhaven-Lymington Lagoon System

3.1 Introduction

Brackish wetlands, or saltmarshes, have been recorded in the Solent since medieval times. Between 1600 and 1900 much of the Solent marshes were embanked to protect low-lying land from inundation by the sea, to provide pasture for cattle and to provide land for saltworks (Tubbs, 1999). During the same period the naturally occurring lagoons between Hurst Spit and Lymington, particularly between Keyhaven and Lymington, were expanded as saltpans (Tubbs, 1999; Fig 3.1), and for harbours and boatyards (Hodges, 2000). Archaeological evidence suggests that salt evaporation has been carried out here since the Iron Age, reaching peak production between the eleventh and sixteen centuries: In 1724, for example, 199 boiling pans were recorded in the Keyhaven and Lymington area (Tubbs, 1999).

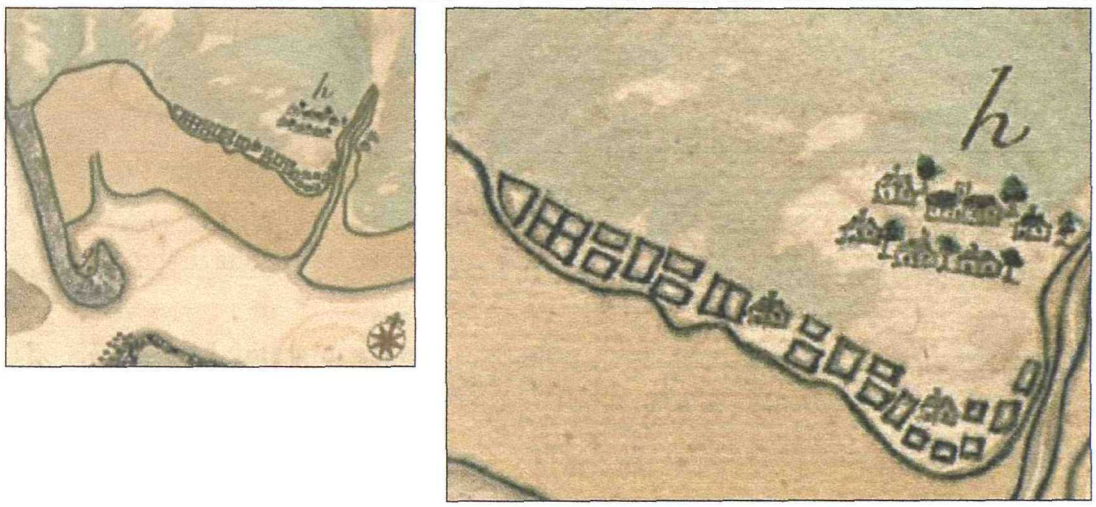


Fig 3.1. The Keyhaven-Lymington salterns (left), with detail (right).
Drawn by Drummer and Wiltshaw, 1698. Photographs by Norgate, J and Norgate, M, 2002. From material held by Hampshire CC Museums Service.

Sea water evaporation occurred in a series of pools, or pans, increasingly saline water passing down the pans until finally transferred to iron boiling pans for the production of a dry salt (Tubbs, 1999). From 1820 onwards, many of the salterns between Keyhaven and Lymington were drained (Tubbs, 1999) and others were adapted to form oyster beds (Lobb, 1867). Consequently, it has been suggested that the lagoons currently found between Keyhaven and Lymington are not salt pan relicts, but the product of later activity during sea wall repair (Tubbs, 1999). It is suggested,

however, that the position of the present sea wall corresponds with saltern embankment in the seventeen century (Tubbs, 1999). It is possible that this wall retains some relict salterns, which might be expected to show evidence of prior connection between them.

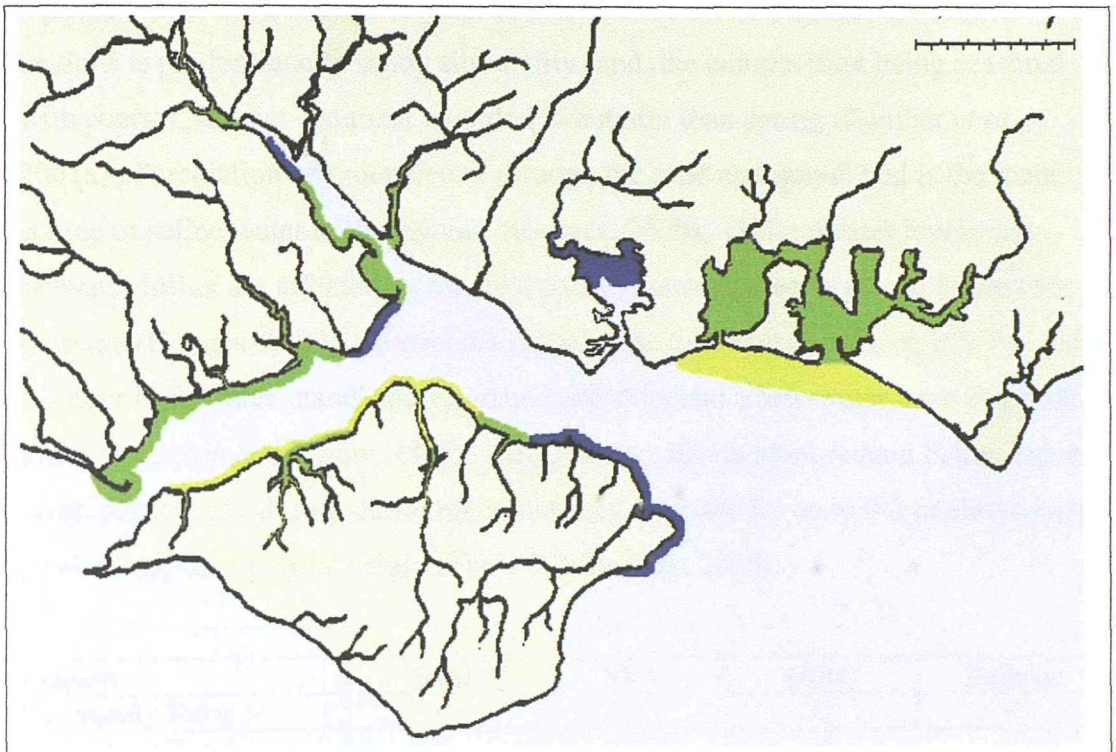


Fig. 3.2. Coastal locations in the Solent listed as Special Protection Areas (Blue), Special Areas of Conservation (Yellow) or both (Green). The scale bar represents 6 miles /10 km.

The Keyhaven-Lymington lagoon system has been managed by Hampshire County Council since 1973 (Fowler and Sheader, 1992), whilst adjacent marshland is used by local farms to graze cattle. The current coastal defences were built in 1990, between May and October, following storm damage to the previous sea wall by severe overtopping in winter 1989/90 (Sheader, 1990). The wall encloses 10 ponds which form a Site of Special Scientific Interest (SSSI) and of which the eastern-most 8 are included in the Solent and the Isle of Wight Special Area of Conservation (SAC) (Table 3.1 & Fig 3.2). There is a general trend of reducing salinity from east to west along the system as might be expected along a draining system of pans. However, Bamber (pers. com.) suggests that this indicates a lack of 'communication' between the lagoons, certainly the drainage dynamics between the three most easterly lagoons would not suggest they were linked as saltpans.

3.2 Site Details

3.2.1 Local Geology and Hydrology

The geology of the coast of Hampshire predominantly consists of chalk covered by silty clay and sand, topped by deposits of marine shingle and sand (Dixon and Moore, 1987). Above this, the surface sediment of the Keyhaven-Lymington lagoons is predominantly sandy silt or silty sand, the composition being seasonal with coarser, sandier sediment recorded in autumn than spring (Bamber *et al.*, 2001a). Percolation of groundwater through the sand and gravel bed is the main source of saline water to the lagoons (Hodges, 2000). Groundwater levels and seawater influx are affected by the tidal pattern, seasonal recharge and barometric pressure (Hodges, 2000). Mean tidal range in the Solent at Keyhaven is 1.5 m, with a 3 hour high-water 'stand' and shortened ebb flow and a low-water 'near stand' at low tide (Dixon and Moore, 1987). Groundwater levels often remain below lagoon level, particularly during the summer, but may fluctuate by up to 0.2 m above lagoon level in response to tidal height (Table 3.2: Hodges, 2000).

Lagoon	SSSI	SPA	cSAC	Ramsar
Normandy Farm	✓	✓	✓	✓
Eight Acre Pond	✓	✓	✓	✓
Salterns	✓	✓	✓	✓
Oxey	✓	✓	✓	✓
Pennington	✓	✓	✓	✓
Butts	✓	✓	✓	✓
Fishtail	✓	✓	✓	✓
Keyhaven	✓	✓	✓	✓

Table 3.1. Designations assigned to the Keyhaven-Lymington lagoons.

Ambient surface salinity in the Solent is approximately 34.4 ppt (Dixon and Moore, 1987). Groundwater salinity ranges from 36 ppt beneath Eight-Acre Pond and Salterns Lagoon[‡] to 0.8 ppt under Butts Lagoon (Hodges, 2000). It is affected by the rates and volume of seawater and freshwater input. An important source of freshwater to the system is runoff from adjacent marshland, owing to clay deposits in the gravel aquifer which reduce its permeability (Hodges, 2000). The catchment area

[‡] It should be noted that groundwater salinity has been recorded at only 1.7 ppt beneath Normandy Farm (Hodges, 2000), but it is likely that this reflects the landward position of that borehole, rather than a lack of seawater addition.

for freshwater runoff ranges from 2,746 m^2 into Eight Acre Pond lagoon up to 47,200 m^2 into the three Oxey Lagoons (Hodges, 2000). Rainfall and point sources, such as Lower Pennington stream and quarry drainage, are other sources of freshwater addition.

Lagoon volume and surface salinity are influenced by the sources and magnitude of freshwater input, marine water input, the rate of drainage and temperature (Bamber, 1997; Sheader, 1990; Bamber and Evans, 2003). Salinity therefore varies both along the system and with season (Bamber and Evans, 2003). Following construction of the current sea wall, salinity has generally reduced along the system, particularly at the western end in Keyhaven lagoon (Bamber *et al.*, 2001a). The previous sea wall allowed seawater to enter the lagoons at a number of locations, whilst the current wall was designed with flap valves that allow outflow, but restrict seawater inflow (Hodges, 2000). However, it was built above the gravel aquifer and percolation of saline groundwater into the lagoons has been recorded (Hodges, 2000). Stratification of the surface water has not been recorded in any of the lagoons (Bamber *et al.*, 2001b; Bamber and Evan, 2002).

Lagoon	NF	EAP	S	OS	P	B
Groundwater Level, m*	-0.2	0.4	1.2	-0.1	-0.1	0.2
Overlying S, ppt*	14.00	16.00	8.00	7.00	7.00	3.00
Groundwater Salinity, ppt*	1.70	36.00	36.00	33.00	31.80	0.80
Catchment area, m^{2}*	32745	2793	9746	47200	37400	14668
Lagoon Depth, m†	0.39	0.26	0.31	0.52	0.25	0.51
Groundwater seepage*	Y	N	Y	Y	Y	Y
†Lagoon surface area, ha†	4.468	2.48	1.691	1.156	3.003	0.9325

Table 3.2. Lagoon environment details provided by *Hodges (2000) and †Bamber *et al.* (2001b). Measurements by Hodges (2000) recorded in March 2000 and September 2001 by Bamber *et al.* (2001b). NF, Normandy Farm; EAP, Eight-Acre Pond; S, Salterns; OS, Oxey South; P, Pennington; B, Butts.

a *Normandy Farm*

Normandy Farm is the largest lagoon in the system at 4.468 hectares (ha) (Bamber *et al.*, 2001b). It was dug to supply gravel for the construction of the sea wall in 1990 and was developed as a lagoon to compensate for the loss of an adjacent lagoon area infilled during the same programme of work. It was 'seeded' with surface sediment salvaged from this earlier lagoon and connected to a surrounding drainage ditch by seawater inundation in November 1990 (Sheader, 1991). It is approximately 0.39 m

deep at it's northern edge (Hodges, 2000), increasing to a maximum depth of 3 m in the southern half of the lagoon (Bamber *et al.*, 2001a). Surface sediment grades from a soil-like substratum at the northern edge of the lagoon to a marine sediment in deeper water (Bamber *et al.*, 2001a). Sampling has shown that the lagoon is edged, and possibly lined, by clay with a covering of silt (pers. obs.).

There are four sluices in the lagoon, one in the eastern wall, two in either corner of the southern wall and one in the western wall. The westerly sluice allows seawater influx at high tide and drainage during flood periods and heavy rainfall (pers. obs.). Salinity in Normandy Farm has been recorded between 3 and 43 ppt, but this lagoon is generally regarded to be one of the more marine/estuarine environments (Bamber, pers. com.). Mean recorded salinity is 21.5 ppt. Freshwater addition is from the diffuse sources of rainfall and runoff from the surrounding catchment area (32745 m^2; Hodges, 2000).

b *Eight-Acre Pond*

Eight-Acre Pond covers an area of 2.48 ha (Bamber *et al.*, 2001b). The majority of the lagoon is shallow, with a recorded depth of 0.26 m (Hodges, 2000), although a maximum depth of 1.5 m has been recorded in central areas (Bamber *et al.*, 2001b). It has been managed for dinghy sailing since 1956, including the repeated drainage of the lagoon during winter to prevent sedimentation and bank erosion (Fowler and Sheader, 1992). Drainage ceased after the winter of 1984/85, but the lagoon bed remains a hard compacted gravel around its margins and over its northern end (Bamber *et al.*, 2001a). A muddier substratum is found in the deeper part of the lagoon, mainly restricted to the southern and eastern half (Bamber and Evans, 2002).

Drainage to seaward is managed via a single sluice in the southern corner of the lagoon, whilst a second sluice drains into the adjacent Salterns lagoon. Historically, Eight-Acre Pond has maintained higher salinities, records of surface water salinity ranging between 15[†] and 43 ppt (average 27 ppt). Groundwater salinity has been recorded at 36 ppt (Hodges, 2000). However, this is the only lagoon in the system into which groundwater inflow was not recorded: it is instead manually 'topped up'

[†] A record of 3.14 ppt listed in Hodges (2000) has been excluded as anomalous.

via the sluice (Hodges, 2000). There is also no direct freshwater input and the catchment area is relatively small at 2793 m^2 (Hodges, 2000), although flash streams on a private lane behind the lagoon may drain into it (pers. obs.).

c *Salterns*

Salterns lagoon is 1.691 ha in size (Bamber *et al.*, 2001b) with a maximum recorded depth of 0.31 m (Hodges, 2000), although Bamber (pers. com.) suggests the central area may be deeper. Sediments are characteristically fine and muddy, particularly in the shallower eastern corner (Bamber, 1997; Bamber *et al.*, 2001a). Groundwater beneath Salterns is approximately 36 ppt, whilst surface water salinity may vary between 4 and 36 ppt. Average recorded surface water salinity is 18.9 ppt. The lagoon drains to seaward via a single sluice. It receives freshwater from a stream at its north-western corner (Bamber *et al.*, 2001a) and as run-off from the adjacent marsh area (9746 m^2, Hodges, 2000). Additional drainage from Eight-Acre Pond, via an interconnecting sluice also enters Salterns at it north-western corner (Bamber, 1997).

d *Oxey South*

Oxey lagoon is composed of three small lagoons: Oxey South Lagoon is the largest at 1.156 ha in size (Bamber *et al.*, 2001b) and maximal depth of 0.52 m (Hodges, 2000). Oxey north is 0.6288 ha in size and Oxey East 1.019 ha. Oxey North lagoon has only recently been recognised as a brackish lagoon and historical information regarding the habitat or its fauna is not available (Bamber, 1997 notes, 'Oxey lagoon comprises two ponds connected by a surface stream...'). Oxey South is characterised by organically rich, fine anoxic mud, particularly at the seaward and southern sides of the lagoon (Bamber *et al.*, 2001a).

Each of the three Oxey lagoons is drained via its own sluice, although they are also connected by ground water percolation and a surface stream flowing from Oxey South in to Oxey East (Hodges, 2000). Due to the experimental lowering of the sluice flap valve in Oxey East in March 2000, Oxey North and Oxey South drained into Oxey East during 2000 (Hodges, 2000). Oxey South is also connected to Pennington lagoon by an underground pipe (Hodges, 2000), although flow through

the pipe has not been observed (Bamber *et al.*, 2001a). There may be reduced drainage through Oxey South sluice (Bamber, 1997), although this sluice is thought to allow tidal inflow (Hodges, 2000).

Groundwater salinity under the Oxey lagoons is near Solent ambient salinity at 33 ppt, but surface water salinity in Oxey South ranges between 0 and 48 ppt (0.7 to 32 ppt following the lowering of a flap valve in Oxey East). Average recorded salinity is 16.6 ppt. The only direct source of freshwater to Oxey Lagoons is a small stream running into Oxey North lagoon, but the overall catchment area from Oxey Marsh is large at 47200 m^2 (Hodges, 2000). Run-off from this catchment may substantially reduce lagoon salinity following heavy rainfall (Hodges, 2000).

e *Pennington Lagoon*

Pennington Lagoon is the second largest in the system at 3.003 ha (Bamber *et al.*, 2001b), but with a recorded maximum depth of only 0.25 m (Hodges, 2000), though Bamber (pers. com.) notes that the central and southern parts of the lagoon may be up to 1 m deep. Granulometry is relatively constant throughout the lagoon (Bamber *et al.*, 2001a), being predominantly firm mud and shingle, but with some softer mud at the westward end (Sheader, 1990).

Surface water salinity has a similar range to that in Oxey South Lagoon, between 0 and 40 ppt at the eastern end (average 15.4 ppt), but groundwater salinity under Pennington Lagoon is slightly lower at 31.6 ppt (Hodges, 2000). Freshwater input to the lagoon is from diffuse sources only, although the catchment area is relatively large at 37400 m^2 (Hodges, 2000). There is one sluice in the lagoon, at the western end, but this is blocked by shingle, preventing direct drainage to seaward (Hodges, 2000). Hodges (2000) noted drainage into Oxey South lagoon when the flap valve in Oxey East lagoon was lowered, but the relatively constant salinity throughout Pennington lagoon and a disparity in salinities between the two lagoons, supports the suggestion that water flow into Oxey is not frequent (Bamber *et al.*, 2001a).

f *Butts Lagoon*

Butts was the only lagoon surveyed west of the Pennington Sewer and the smallest studied. When measured by Bamber *et al* (2001b) the lagoon was 0.9325 ha in surface area and considered to be within its banks, but during flood periods it may cover a much wider area. Butts is approximately 0.51 m deep (Hodges, 2000), but may reach 0.8 m deep in some central areas (Bamber *et al.*, 2001a). It has a substratum similar to that found in Pennington Lagoon, being mainly soft mud, mixed with shingle and sand at its eastern end (Sheader, 1990).

There is a sluice connecting Butts to the bottom of Pennington Stream and then to the lower salinity Fishtail Lagoon. A pipe linking it to Pennington Lagoon under the Pennington Sewer was noted before the new sea wall was built, but this is now thought to be blocked (Sheader, 1990). There is no sluice to the adjacent Solent, although Butts receives large volumes of freshwater input. Surface water salinity ranges between 0 and 48 ppt, averaging 7.5 ppt. Groundwater salinity is only 0.8 ppt, possibly reflecting groundwater use by quarrying activities.

Direct sources of freshwater input are the Lower Pennington Stream (during periods of low rainfall the flow may reverse (Bamber, pers com.)), and discharge water from Efford Quarry[†] and a second gravel extraction to the north of Fishtail lagoon (Hodges, 2000). There is also significant drainage from the adjacent marshland (14668 m^2; Hodges, 2000). Consequent flooding following heavy rainfall can greatly reduce lagoon salinity (Sheader, 1990; Bamber *et al.*, 2001a).

[†] Efford quarry has operated westwards from Butts Lagoon since 1969. It moved directly to the north of Keyhaven Marsh around 1993. It removes groundwater from beneath Keyhaven Marsh for dewatering and discharges mine drainage back into the system (Hodges, 2001).

3.3 Long term data sets

3.3.1 Regional Data

a *Rainfall*

Meteorological Office rainfall data from the Southampton recording station, measured between 1899 and 1999 have been used as a baseline against which to compare rainfall during the sampling period (Fig. 3.3). Rainfall in the Southampton area follows a seasonal pattern of maximum monthly rainfall in winter (90.3 mm, December average from 1899 – 1999) and a minimum monthly rainfall during spring and summer (50 mm July and April average from 1899 – 1999). Whilst daily rainfall grouped by month has an approximately log normal frequency distribution, average monthly rainfall cannot be transformed to near-normality and therefore it has not been possible to statistically test monthly rainfall in 2000 against the baseline data set. However, graphical comparison identifies a divergence of the monthly rainfall pattern in 2000 from the average seasonal pattern.

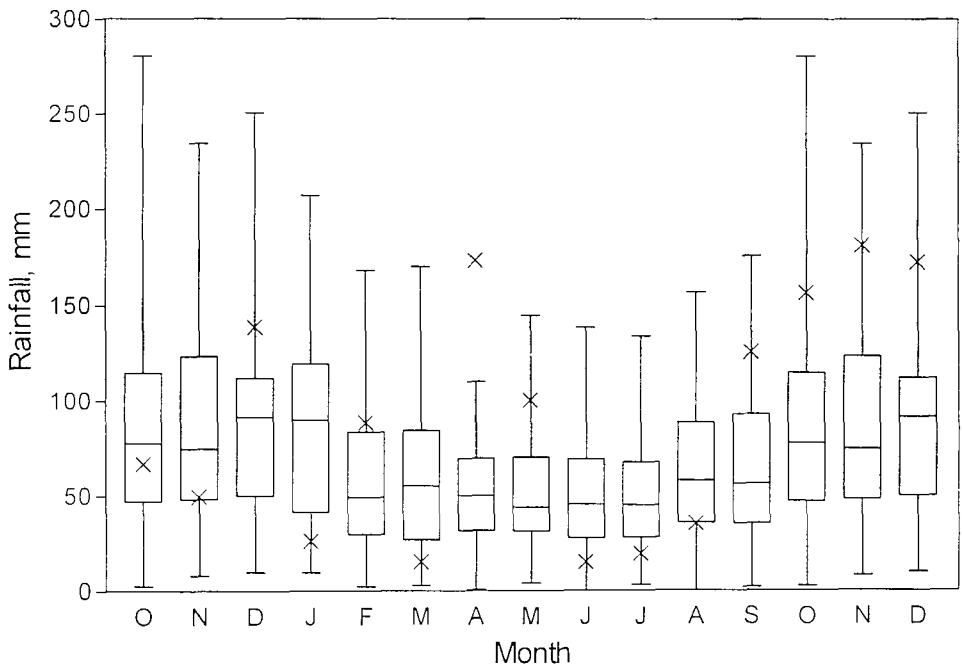


Fig. 3.3. Rainfall data from the Meteorological Office Southampton station.
Box and whisker plot of monthly rainfall measured between January 1899 – December 1999. Boxes represent the 25th and 75th quartile of measured values, with the mid-line representing the median value. The outlying lines indicated maximum and minimum values. Crosses represent monthly rainfall from October 1999 to December 2000 at the same station.

Overall, the monthly rainfall recorded in 2000 was within previously recorded values. Rainfall for all months from December 1999 to December 2000 were within the maximum and minimum recorded values for those respective months, with the exception of rainfall in April 2000. Rainfall in April 2000 was over 3 times the average recorded rainfall for the same period over the previous 100 years (173 mm in comparison to 50 mm on average, previous maximum 110 mm). Rainfall in May 2000 was also twice the previous month average (100 mm in comparison to 51 mm on average), but within recorded values (maximum May rainfall, 144 mm in 1932). Also from September 2000 onwards rainfall was again above average, but within recorded levels, in each case up to twice the average recorded rainfall.

b *Air Temperature*

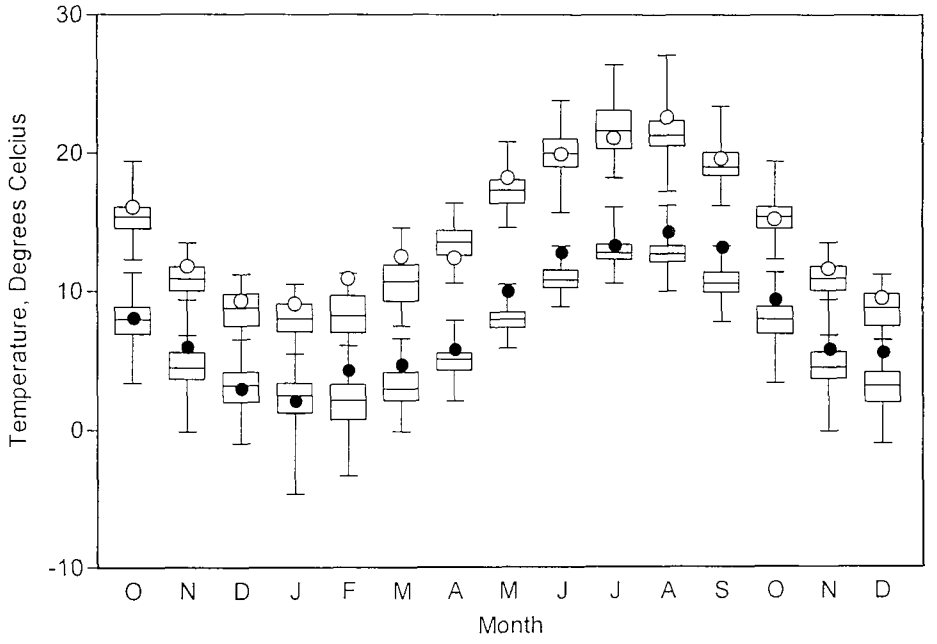


Fig. 3.4. Air temperature data from the Meteorological Office Southampton station. Box and whisker plot of monthly air temperature (maximum and minimum values) measured between January 1899 and December 1999. Boxes represent the 25th and 75th quartile of measured values, with the mid-line representing the median value. The outlying lines indicate maximum and minimum values. Minimum (solid circles) and maximum (open circles) monthly temperatures recorded from October 1999 to December 2000 at the same station are also shown.

The air temperature data from Southampton Meteorological Office recorded between 1899 and 1999 were also used as a baseline for comparison with air temperature

recorded at the same station during the sampling period (Fig. 3.4). The seasonal pattern of air temperature in the Southampton area has minimum monthly temperature in late winter (2.1°C average minimum temperature, February 1899 – 1999) and a maximum monthly temperature during summer (21.8°C average maximum temperature, July 1899 – 1999). Air temperature during the sampling period did not differ from that recorded in Southampton during the previous 100 years and followed the average seasonal pattern.

3.3.2 Lagoon Data

a *Surface Water Salinity*

Surface water salinity in the Keyhaven - Lymington lagoon system has been recorded intermittently since 1983 and at regular fortnightly intervals from 1999 onwards, subsequent to the establishment of the Life/Nature Program (Table 3.3 provides details of number of recordings at each lagoon, by month). Along the system, salinity ranges between 48 ppt and 0 ppt although the absolute range varies between the lagoons and with season (Fig. 3.5). Pennington and Oxey South lagoons have the most variable salinity, the highest (48 ppt, July 1990) and lowest (0 ppt, January 1998) recorded salinities having been recorded in them both. No salinity stratification has been recorded in these shallow environments (Bamber *et al.*, 2001a), although stratification has been recorded in the deeper ditch surrounding Normandy Farm lagoon (pers. obs.).

Plotting paired salinity values (i.e. salinity measurements taken on the same day) for each possible combination of lagoons shows that lagoon salinities are significantly correlated (Table 3.4). The greatest correlation is seen between the lower salinity lagoons and those that are connected, either by sluice or groundwater flow, although the salinity range and the pattern of salinity change may differ between neighbouring lagoons (Fig. 3.6). Pennington and Oxey south lagoons have the most similar salinity regimes (pearson's $r = 0.958$, $p < 0.0001$), probably reflecting drainage from Pennington into Oxey South lagoon and similar patterns of freshwater addition and groundwater exchange. There is also a highly significant correlation between salinity in Eight Acre Pond and Salterns lagoon (Pearson's $r = 0.812$, $p < 0.001$).

again the former lagoon drains into the latter.

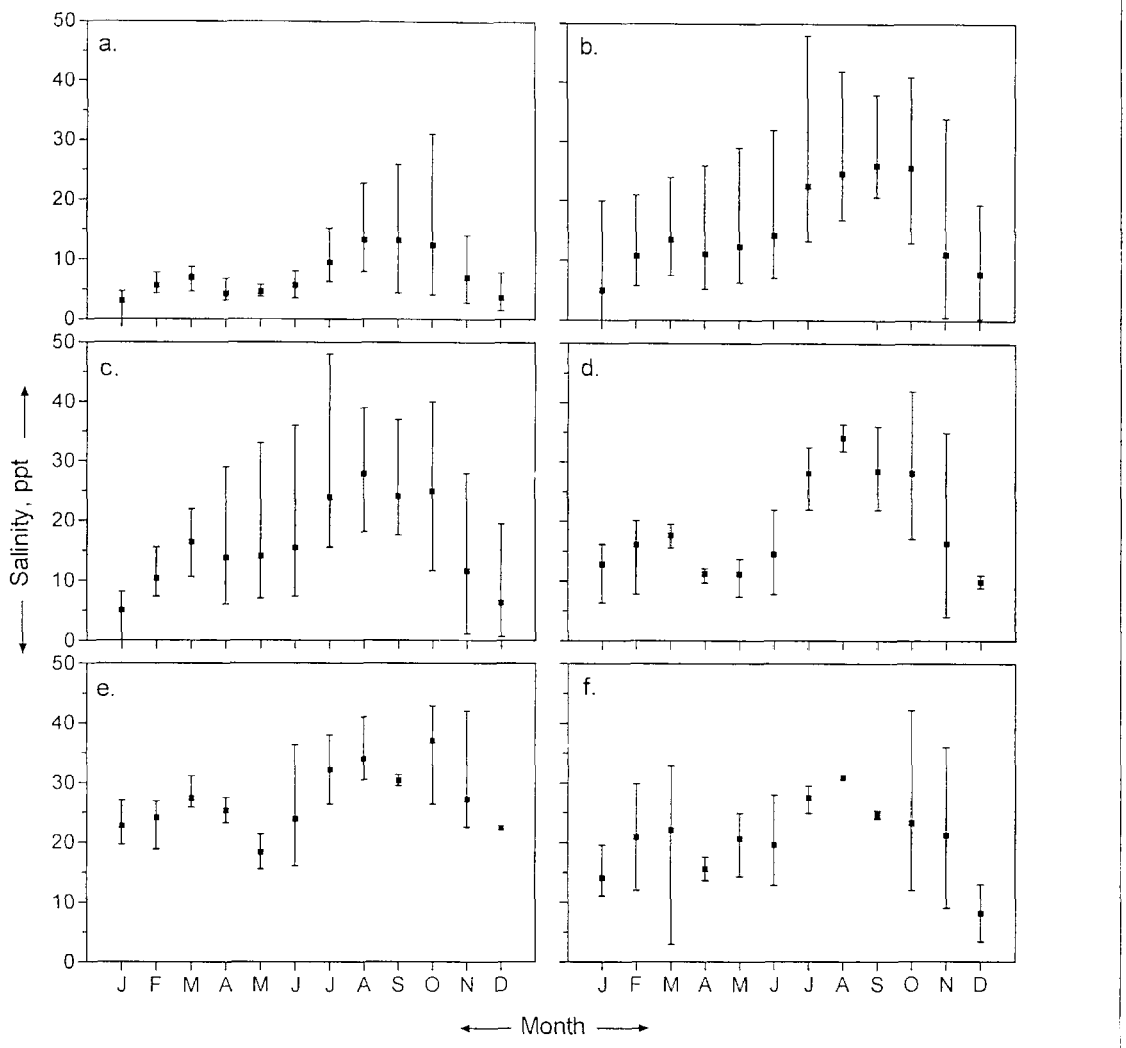


Fig. 3.5. Average monthly salinity recorded at each lagoon (solid dots). The outlying lines indicate maximum and minimum values. Records from 1983 to 2000. Lagoons: a, Butts; b, Pennington; c, Oxey South; d, Salterns; e, Eight-Acre Pond; d, Normandy Farm.

	Month											
Lagoon	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sept**	**Oct**	**Nov**	**Dec**
B	11	4	8	7	7	7	10	7	8	7	10	6
P	11	5	10	10	9	8	12	8	9	8	12	8
OS	11	4	9	11	9	8	13	10	9	9	11	8
S	4	4	4	3	3	4	5	2	3	3	5	2
EAP	5	3	4	3	4	4	6	3	3	3	6	2
NF	6	2	5	2	3	4	5	3	2	4	5	2

Table 3.3. Number of replicates available to calculate average monthly lagoon salinity. Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight-Acre Pond and; NF, Normandy Farm.

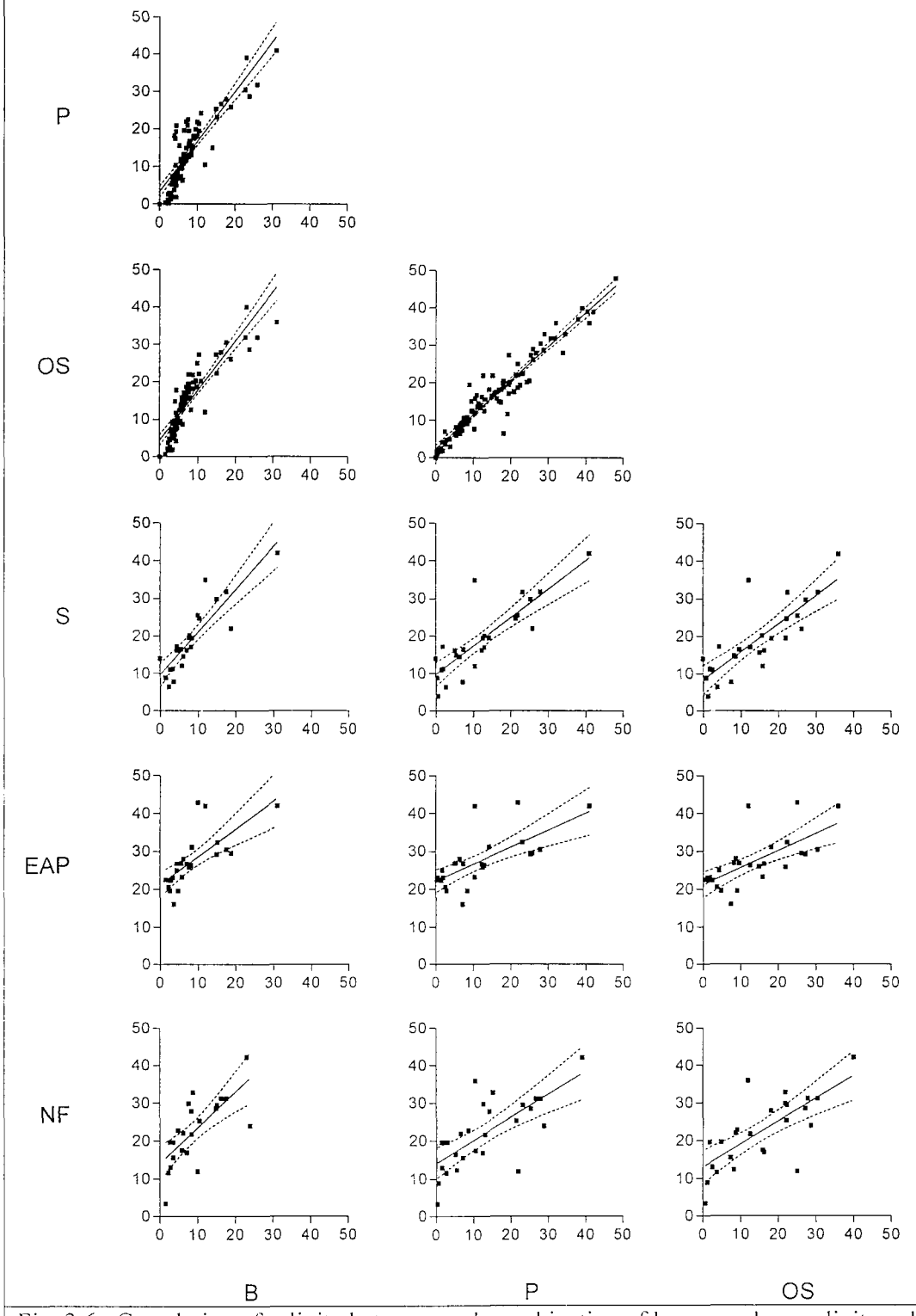


Fig. 3.6. Correlation of salinity between each combination of lagoon, where salinity values plotted are taken on the same day. x and y axes are both Salinity, ppt. Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns, EAP, Eight Acre Pond and NF, Normandy Farm.

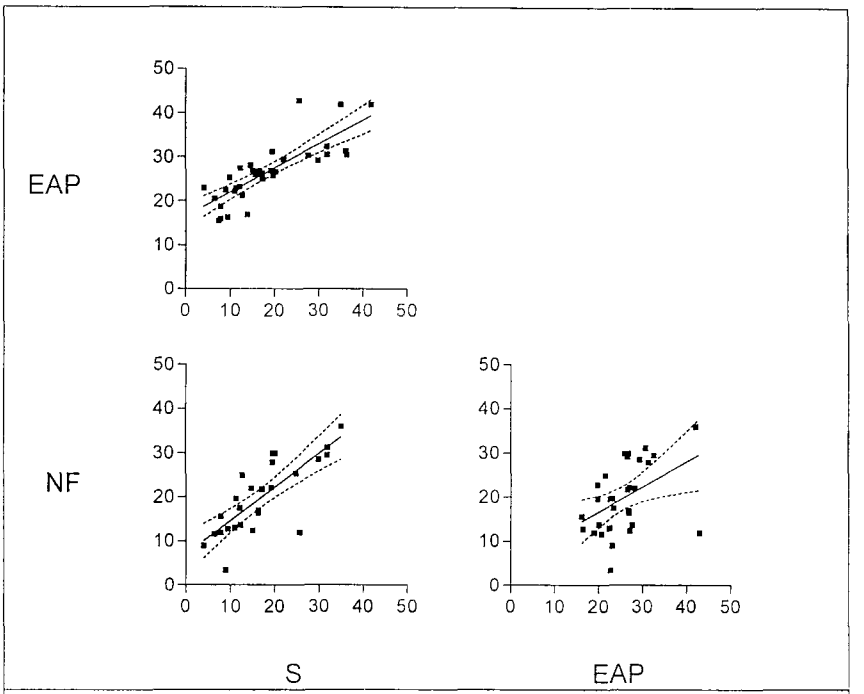


Fig. 3.6. Continued...

Lagoon	B	P	OS	S	EAP
P	0.865* (89)				
OS	0.882* (86)	0.958* (101)			
S	0.875* (23)	0.849* (26)	0.817* (26)		
EAP	0.556‡ (25)	0.689^{+} (26)	0.677^{+} (26)	0.812* (36)	
NF	0.713^{-} (23)	0.709* (27)	0.725* (26)	0.782* (26)	0.445† (20)

Table 3.4. Correlation, Pearson's r, between lagoon salinities. Salinity values recorded on the same day are compared for each paired correlation calculation. Values in brackets are the replicate number, n.
Significant level: * $p < 0.0001$, $^{+}p < 0.001$, $^{\ddagger}p < 0.01$, $^{\dagger}p < 0.05$.
Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight-Acre Pond and; NF, Normandy Farm.

The salinity regime in Butts lagoon is significantly correlated with that in Pennington, Oxey South and Salterns lagoons ($p < 0.0001$). However, Butts lagoon has a reduced salinity range and a more dramatic reduction in salinity in contrast to the other lagoons (the line of regression is steeper), possibly reflecting poor drainage from Butts. Whilst the salinity regimes in both Eight Acre Pond and Normandy Farm lagoons are highly significantly correlated to those in Pennington, Oxey South and Salterns lagoons ($p < 0.001$), the significance of similarity between each other ($p < 0.05$) and with Butts lagoon ($p < 0.01$ and $p < 0.001$, respectively) are reduced. It is likely that this reflects the greater freshwater addition to Butts lagoon and the more efficient drainage from Normandy Farm and Eight-Acre Pond, as well as the extensive management of Eight-Acre Pond.

b *The influence of rainfall on surface water salinity*

Owing to the small volume of point-source freshwater input to the system above Pennington sewer and the limited drainage to, and exchange with, the adjacent marine water body, it might be expected that rainfall would be an important factor controlling lagoon salinity. Comparison of monthly rainfall in 2000 with corresponding lagoonal salinities (Fig. 3.7) indicates that salinity in the whole system decreased rapidly and remained low in response to heavy rainfall (> 100 mm/mth: April and September to December 2000 inclusive). The largest salinity decline was recorded in Normandy Farm lagoon - 12 ppt decrease from March to April. Lagoon salinity is significantly correlated with rainfall in Pennington, Oxey South, Salterns and Eight Acre Pond lagoons ($p < 0.05$, in all cases; Fig. 3.8). Whilst there is a general trend of decreasing salinity with increasing monthly rainfall, there is considerable variability of salinity with rainfall in each lagoon. In the higher salinity lagoons salinity continues to fall, if only slightly, in the month following heavy rainfall. It is possible that this arises from continued freshwater addition from terrestrial drainage. Alternatively it may indicate a more rapid recovery in the lower salinity lagoons, although this is contrary to expectation owing to their poor drainage, particularly from Butts lagoon.

c *Water Quality*

Water quality analysis was conducted during the LIFE Nature project (Hodges, 2000). Groundwater samples were taken for chemical analysis in February 2000 from Normandy Farm, Eight Acre Pond and Salterns and surface water samples in March 2000 from Normandy Farm, Eight Acre Pond, Salterns and Oxey South (Tables 3.5 a and b respectively; Hodges, 2000). Biological Oxygen Demand (BOD) was higher in ground water than surface water in each of the lagoons assessed, but was relatively low throughout. BOD ranged from a maximum of 35.3 mgl^{-1} in groundwater to a minimum of 3 mgl^{-1} in surface water. This can be compared with the Fleet lagoon, Dorset, where the background BOD level has been recorded between 3 – 6 mgl^{-1} but may reach 168 mgl^{-1} owing to bird excrement and the drainage of human/agricultural waste (Johnston and Gilliland, 1999). Chemical Oxygen Demand (COD) was much higher than BOD in all the lagoons (30 mgl^{-1} BOD compared to 160 mgl^{-1} COD in Salterns lagoon, for example) and probably

reflects the magnitude of detrital addition with terrestrial runoff, low rates of lagoon flushing and fringing flora.

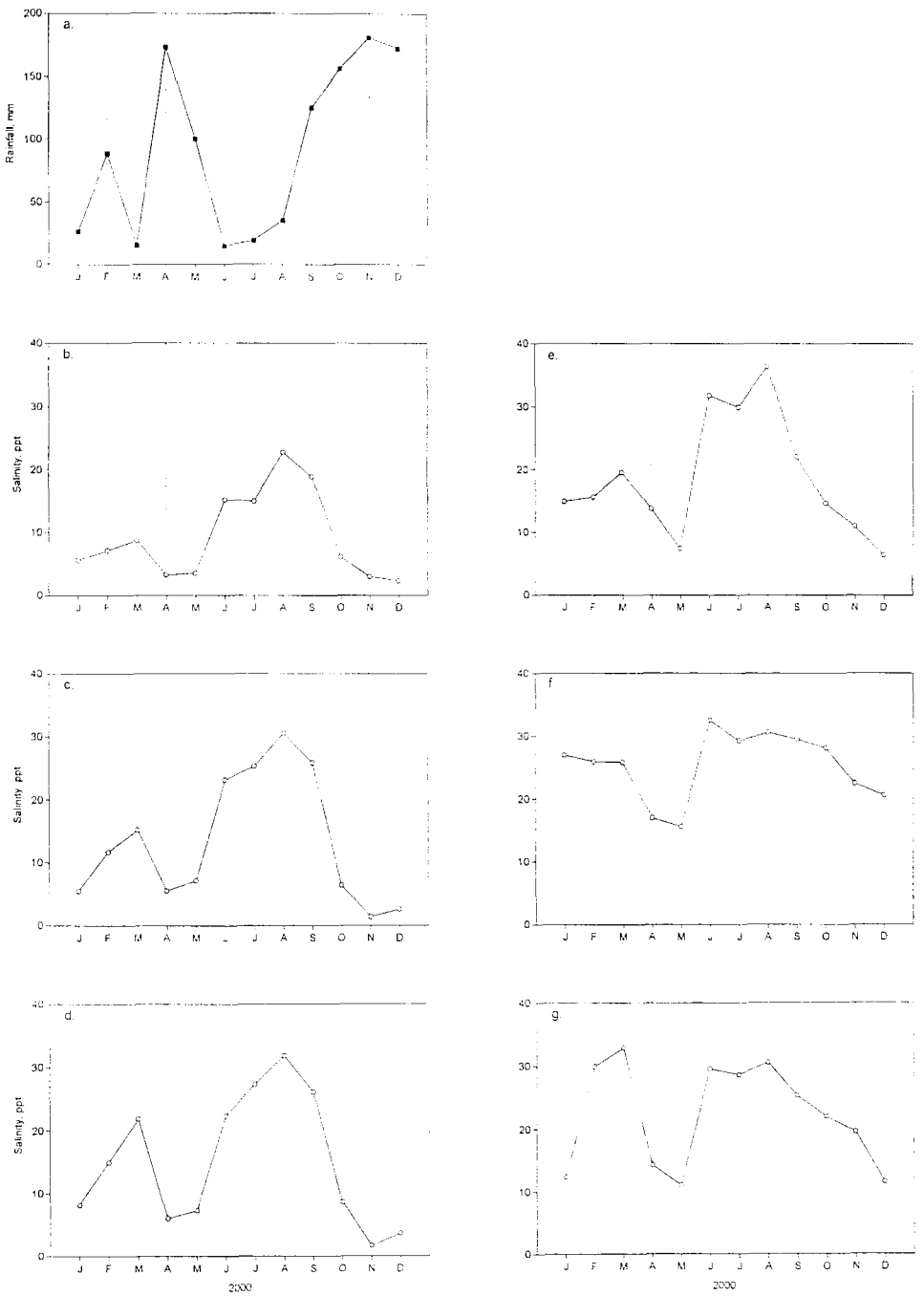


Fig 3.7. Comparison of monthly rainfall and lagoon salinity at month end.
A, Rainfall, mm; b – g, Salinity ppt. Dashed line indicates peak in rainfall. Lagoons: b, Butts; c, Pennington; d, Oxey South; e, Salterns; f, Eight Acre Pond; g, Normandy Farm.

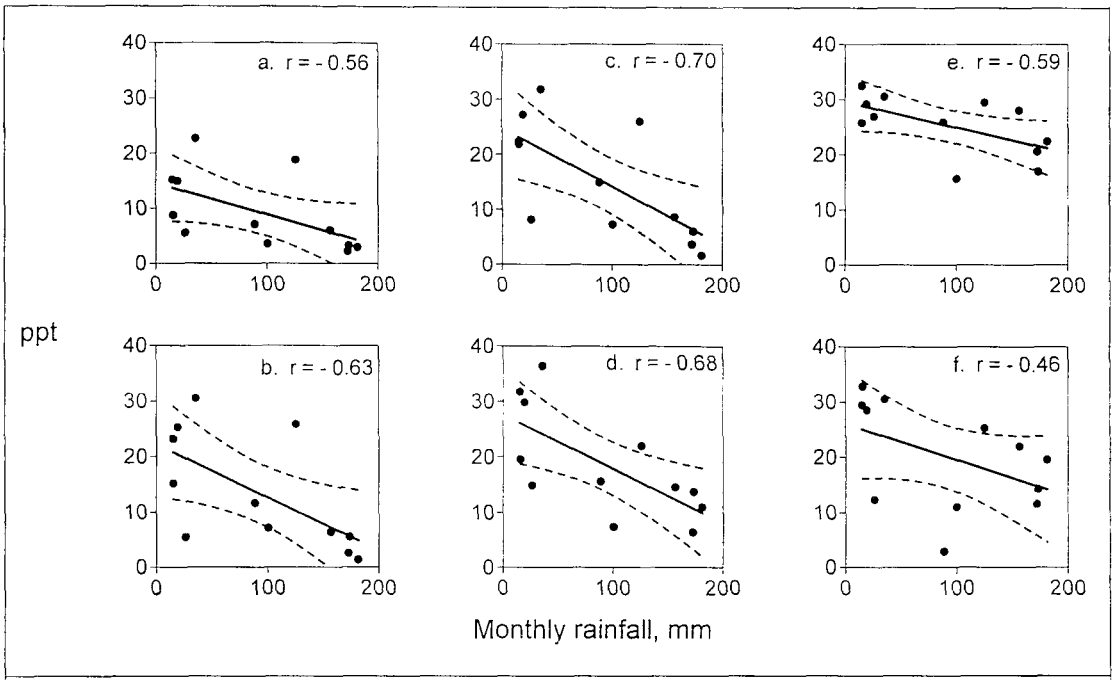


Fig. 3.8. Salinity correlation with rainfall for each lagoon (Pearson's r), with the Spearman's regression line and 95 % confidence interval. Lagoons: a, Butts; b, Pennington; c, Oxey South; d, Salterns; e, Eight Acre Pond and; f, Normandy Farm.

Groundwater in Eight Acre Pond had a high level of nitrate (11.6 mgl^{-1}) in comparison with Normandy Farm and Salterns, whilst surface water nitrogen levels were more similar throughout (0.9 – 1.6 mgl^{-1}). The surface water nitrate levels were similar to those recorded in estuaries. In the Tweed and Tamar estuaries, for example, nitrate has been noted to decrease linearly with salinity, reflecting input with freshwater and flushing rates (approximately 1.75 to 0.2 mgl^{-1}; Uncles *et al.*, 2002). In the lagoon system a relative lack of flushing and irregular freshwater addition are likely to contribute to the similarity of nitrate throughout.

The pH in the Keyhaven-Lymington lagoon system was also within recorded norms. Its recorded range is from 7.15 to 7.3 in groundwater and 7.75 to 8.10 surface water. This compares with average seawater pH between 7.5 to 8.5 (Duxbury and Duxbury, 1993) and a pH range in Solent Water of 7.89 to 8.26 (Bamber *et al.*, 1991). Data are also available on pH in another lagoon in the Solent system, Calshot Pond, in Southampton Water and from lagoons UK wide. In Calshot Pond pH was recorded between 7.22 and 8.62, generally increasing with increasing salinity (Bamber *et al.*, 1991), whilst UK wide pH in lagoons has been recorded between 7.01 and 9.32 (Bamber *et al.*, 1992). Lagoonal pH is expected to be more variable than fully-

marine water owing to freshwater addition and increased biological activity (Bamber *et al.*, 1991).

	Lagoon		
Ground water	**Normandy Farm**	**Eight Area Pond**	**Salterns**
PH	7.20	7.3	7.15
BOD, mgl^{-1}	30	35.3	30
Nitrate, mgl^{-1}	0.9	11.6	0.9
Ammonia as N, mgl^{-1}	< 0.5	< 0.5	2.06
Total Oxidised N, mgl^{-1}	< 1	11.6	< 1

Table. 3.5 a. Groundwater quality in the Keyhaven-Lymington System. Data from Hodges (2000).

	Lagoon			
Surface water	**Normandy Farm**	**Eight Area Pond**	**Salterns**	**Oxey South**
pH	7.75	8.1	7.65	7.75
BOD, mgl^{-1}	3	3	4	5.7
COD, mgl^{-1}	111	130	160	106
OC AS C, mgl^{-1}	9.71	4.89	10	18.5
Nitrate, mgl^{-1}	1.6	0.9	0.9	0.9
Ammonia as N, mgl^{-1}	< 0.5	< 0.5	< 0.5	< 0.5
Total Oxidised N, mgl^{-1}	1.7	< 1	< 1	< 1

Table 3.5 b. Surface water quality in the Keyhaven – Lymington lagoons. Data from Hodges, 2000.

3.4 Results

3.4.1 Univariates

a *Granulometry*

Due to the high silt fraction in the lagoon sediments, the methods previously described on page 40 did not allow a satisfactory description of sediment granulometry – the sediment samples were 'baked' resulting in solidification of the silt and clay fractions. Therefore, granulometric data from spring 2000 was kindly made available by Dr Roger Bamber (Bamber *et al.*, 2001a). These samples were processed according to the method describe in Holme and McIntyre (1971). The data are in the form of percentage gravel, sand, silt and clay (Fig. 3.9).

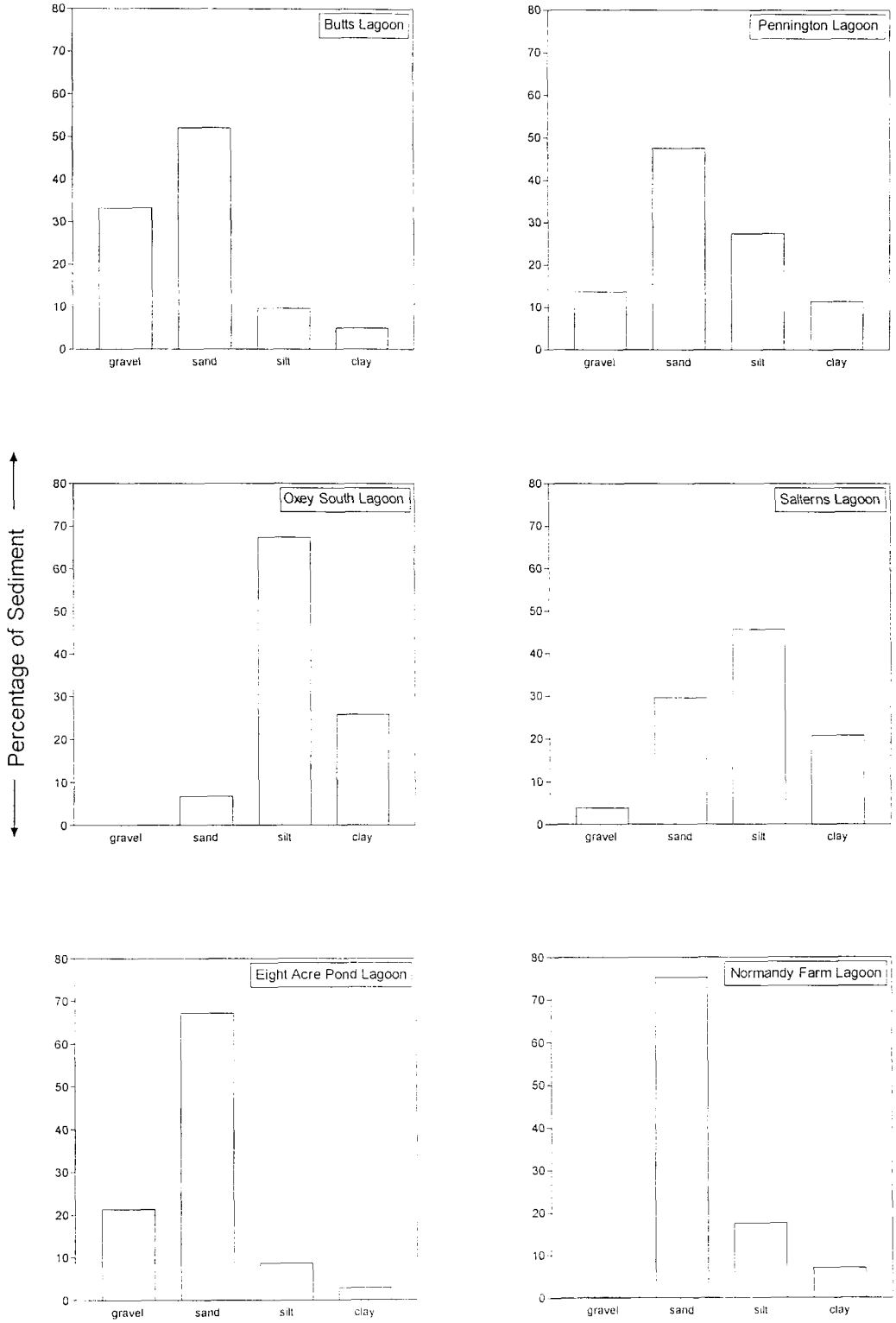


Fig. 3.9. Percentage distribution of sediment particle size fraction in each lagoon. Data from Bamber *et al* (2001a).

The percentage contribution of each fraction varies between lagoons, although combined sand/silt dominates all lagoon sediments. The surface sediment of Normandy Farm lagoon was dominated by sand (75 %) with smaller proportions of

silt (17 %) and clay (7 %). The surface sediments in Eight Acre Pond, Pennington and Butts lagoons were similarly dominated by the sand fraction (67%, 47 % and 52 %, respectively), with gravel being the next most predominant in Eight Acre Pond and Butts (21 % and 33 %, respectively), but silt being the next greatest component in Pennington (27 %). Clay was a minor component of the sediments in each of these lagoons. The surface sediments in Oxey South and Salterns lagoons differed, being composed predominantly of silt (67 % and 45%, respectively). Oxey South had finer sediment, 93 % being composed of silt and clay, whilst in Salterns 66 % of the sediment was silt and clay, and a further 29 % sand. This variability of sediment type represents a wide range of habitat type and may be compared to estuarine environments. In European estuaries, for example, sediment silt content has been recorded between 2 % and 96 % (Soetaert *et al.*, 1995). Equally, clay and silt content may not reflect the rate and volume of freshwater input (Montagne and Kalke, 1992). Overall, Pennington and Salterns had the most mixed, or heterogeneous, sediment and Normandy Farm had the most homogeneous sediment.

b *Sediment organic matter content*

Organic matter content was extremely variable between the lagoons, ranging from a minimum of 2.5 % of sediment dry weight in Eight-Acre Pond to 17.98 % in Oxey South (Fig. 3.10). The organic carbon content of the sediment in Eight-Acre Pond is similar to that of estuarine and coastal marine sediments (eg. St Lawrence Estuary, Quebec, Canada, 1.1 – 2.4 % organic matter; Tita *et al.*, 1999), owing the higher loss-on-ignition values identified in the other lagoons are less frequently found in marine environments, due to sediment resuspension and tidal flushing. The total range is, however, comparable to that found in other UK lagoons (2.9 – 24.6%; Bamber *et al.*, 1992*) and also the Baltic Sea, a deep land-locked basin with a marine to brackish/freshwater salinity range and where flushing by, and exchange with, adjacent marine water are also reduced. In the Baltic Sea organic carbon ranges from a minimum average of 2.77 % dry wt. to maximum average of 12.3 % dry wt (Duplisea, 2000).

* These data are from Table 4 of Bamber *et al.* 1992. Note their legend should read g/g rather than mg/g.

It might be expected that organic carbon content and granulometry would be significantly correlated, however, neither median particle diameter (phi), percent silt nor percent clay are significantly correlated with sediment organic carbon content ($r = 0.50$, $r = 0.68$ and $r = 0.70$, respectively; $p > 0.05$). It can been seen in fig. 3.10, however, that this is due to the high percentage content of organic carbon and large median grain size in Butts Lagoon. Excluding the Butts data from the regression analysis then shows organic carbon content and median sediment diameter to be significantly correlated ($r = 0.98$, $p < 0.01$ for median diameter v organic carbon). It is possible that the sediment in Butts lagoon has such a different organic carbon:median diameter ratio owing to the recent re-lining of the lagoon with coarse sediment during the rebuilding of the sea wall, followed by rapid addition of organic detritus during terrestrial flooding and subsequent settlement of that detritus into the lagoon owing to limited flushing. In comparison, the sediment in Eight Acre Pond is coarse owing to previously severe drainage activities, and has a reduced organic carbon content probably owing to limited terrestrial run off to the lagoon and manage drainage.

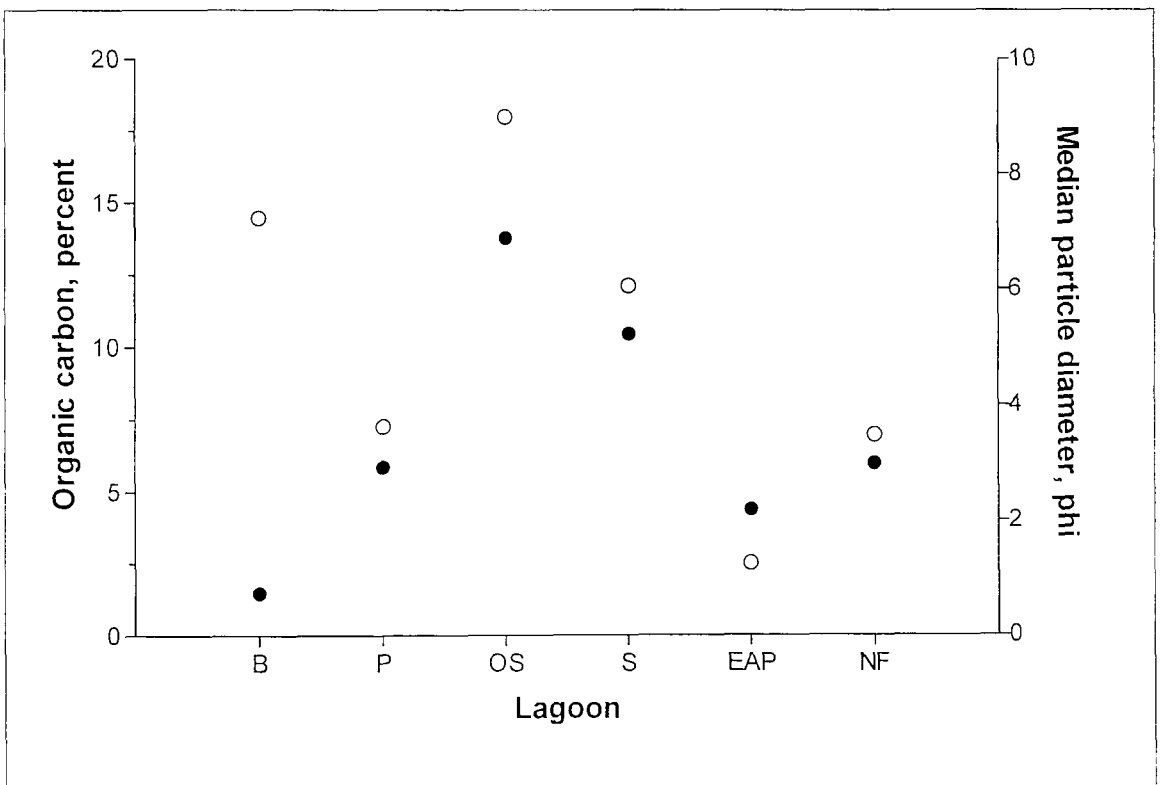


Fig. 3.10. Organic carbon content, as percentage from loss on ignition (open circles) and median particle diameter (closed circles) of the surface sediment in each lagoon. Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm. Adapted from Bamber *et al.*, 2001a.

c *Surface Sediment Pigments*

To ensure the most complete preservation of pigments, sediment samples were frozen at –70 °C until required (Lucas and Holligan, 1999). However, the freezer in which the samples were stored malfunctioned and it was necessary to transfer the samples to an available –20 °C freezer. Nevertheless, storing sediment samples for pigment analysis at this temperature has been proven to be sufficient to allow reliable pigment preservation (Wolfstein *et al.*, 2000). Also, malfunction of the –70 °C freezer was noted quickly and the room in which the freezer was located was dark, thus reducing the risk of bacteria growth in the sample material. The results of subsequent sediment pigment analyses are not, therefore, thought to have been unduly influenced by storage at the higher (but still very cold) temperature.

Benthic chlorophyll a concentration can be used as an indirect measure of microphytobenthos biomass (Garrigue, 1998) and therefore potential food sources for meiofauna. Mean surface sediment chlorophyll a concentration measured in April 2000 ranged from a minimum of 0.01 ng g^{-1} in Normandy Farm and Eight Acre Pond lagoons to 0.36 ng g^{-1} in Oxey South lagoon (Fig. 3.11). Mean phaeopigment

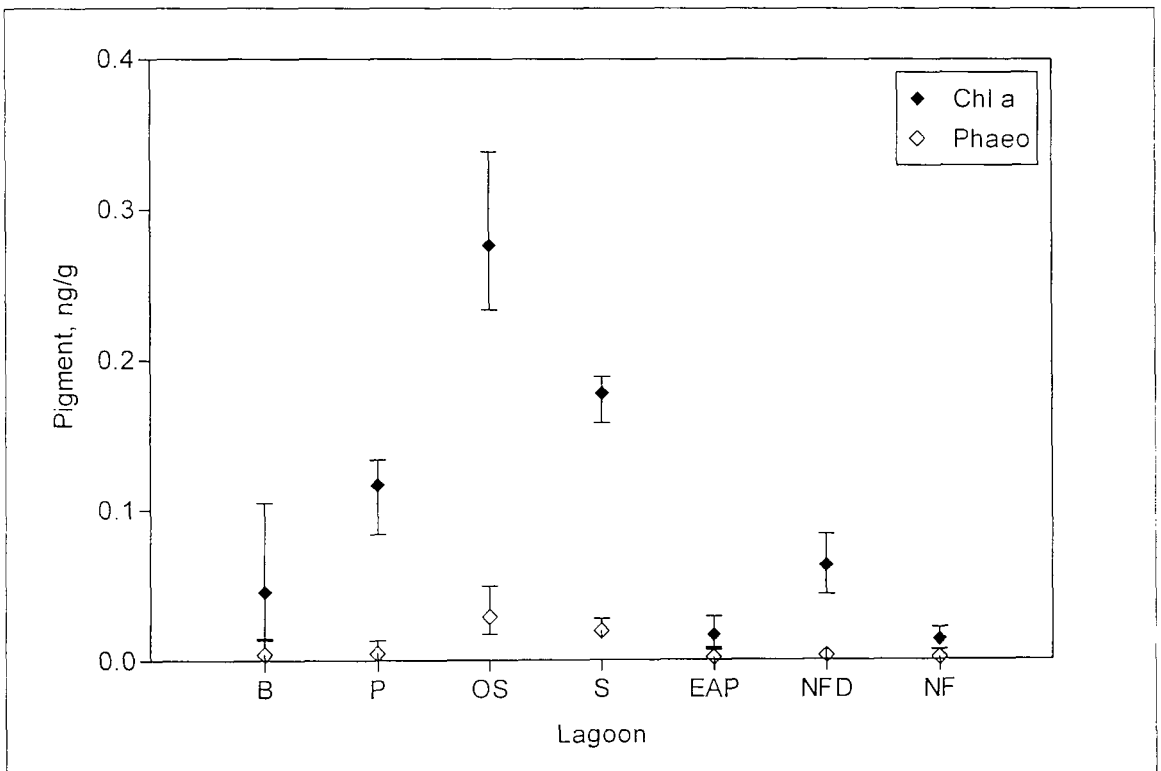


Fig. 3.11. Pigment concentrations in the top 1 cm of lagoon sediments. Outlying lines are maximum and minimum values.
Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NFD, Normandy Farm Ditch; NF, Normandy Farm.

concentration ranged from 0.00 ng g^{-1} to 0.05 ng g^{-1}. The variation in measured pigment concentrations between replicates per lagoons was small, whilst statistical analysis of pigment concentrations between lagoons (one-way ANOVA) identified a significant difference in Chlorophyll a ($r = 0.97$; $p<0.0001$) and phaeopigment ($r = 0.85$; $p<0.0001$) concentrations between lagoons.

A Tukey's test was also performed to identify which lagoons contributed the most to the difference between lagoon sediment pigment concentrations (Table 3.6 a and b). The majority of lagoons had significantly different sediment Chlorophyll a concentrations ($p <0.001$) – Oxey South compared to all other lagoons; Salterns to Normandy Farm, Normandy Farm Ditch, Eight Acre Pond, Oxey South and Butts and; Pennington to Normandy Farm. Significant difference was also identified between Pennington and Butts ($p < 0.05$).

Site	B	P	OS	S	EAP	NFD
P	*					
OS	***	***				
S	***	NS	***			
EAP	NS	***	***	***		
NFD	NS	NS	***	***	NS	
NF	NS	***	***	***	NS	NS

Table 3.6 a. Output of Tukey's Test comparing sediment Chlorophyll a concentration between lagoons. Significance Level; ***, $p < 0.001$; *, $p < 0.05$; NS, Not Significant. Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NFD, Normandy Farm Ditch; NF, Normandy Farm.

Sediment phaeopigment concentrations were only significantly different between Oxey South and Normandy Farm, Normandy Farm Ditch, Eight Acre Pond, Pennington and Butts and between Salterns and Normandy Farm, Normandy Farm Ditch, and Eight Acre Pond. The differences in sediment pigment concentrations identified between sites are likely to reflect differences in physical factors affecting photosynthesis and phytobenthic growth in each lagoon. These may include catchment area (and therefore addition of freshwater and nutrients, drainage rates, wind-induced wave formation, sediment type, salinity, water clarity and ambient water temperature.

Site	B	P	OS	S	EAP	NFD
P	NS					
OS	***	**				
S	NS	NS	NS			
EAP	NS	NS	***	*		
NFD	NS	NS	***	*	NS	
NF	NS	NS	***	***	NS	NS

Table 3.6 b. Output of Tukey's Test comparing sediment Phaeopigment concentration between lagoons. Significance; ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; NS, Not Significant. Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NFD, Normandy Farm Ditch; NF, Normandy Farm.

Phaeopigments are breakdown products from chlorophyll a and as such their concentration is likely to reflect initial chlorophyll a concentration, drainage rates, sediment burial rates, and also settlement of phytoplankton from the surface water. Consequently, there is a significant correlation ($r = 0.87$, $p < 0.0001$) between chlorophyll a and phaeophytin concentrations in the sediment samples (Fig. 3.12).

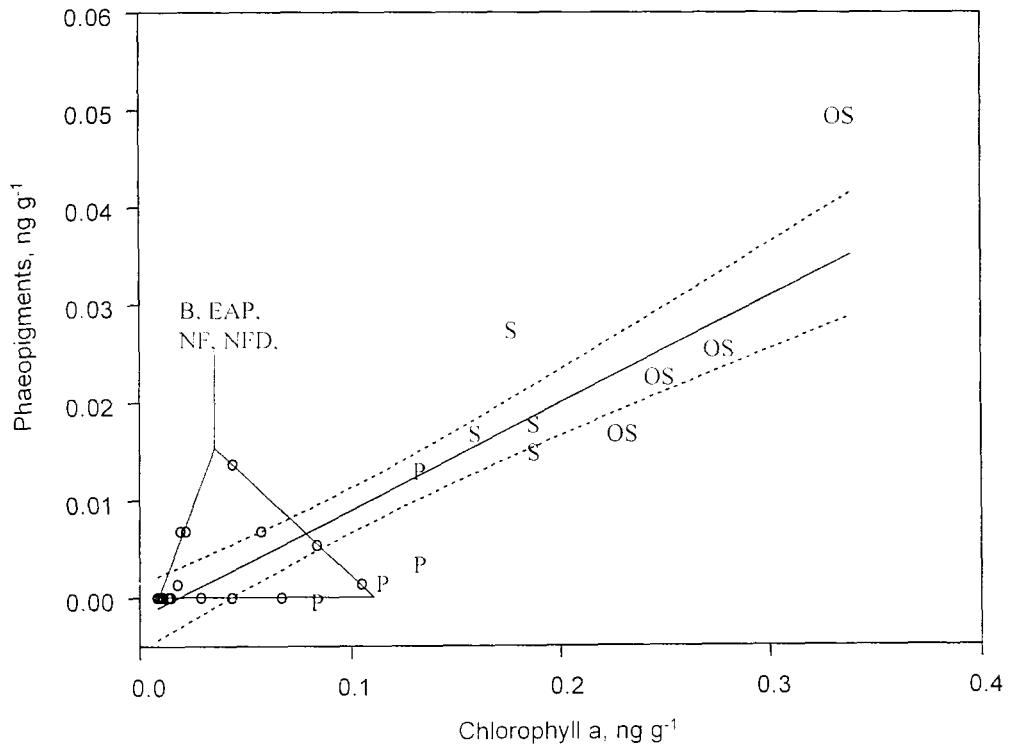


Fig. 3.12. Chlorophyll a and phaeophytin concentrations, with a line of linear regression and 95 % confidence interval. Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NFD, Normandy Farm Ditch; NF, Normandy Farm.

3.4.2 Multivariate analysis

Conventionally salinity and granulometry are considered to be the two most important variables influencing meiofaunal (nematode) distribution (Heip *et al.*, 1985), and as such they have been combined to assess the similarity of the lagoons in terms of these two variables. Average salinity was plotted against median sediment particle size for each lagoon, and lagoon similarity (as Euclidean distance) was also calculated (Fig. 3.13 a and b). To prevent bias towards larger values in the production of the similarity matrix data were transformed to a 0 – 1 scale by dividing all phi values by the maximum phi value and all salinity values by the maximum salinity. The analysis was then repeated with transformed data (Fig. 3.14 a and b).

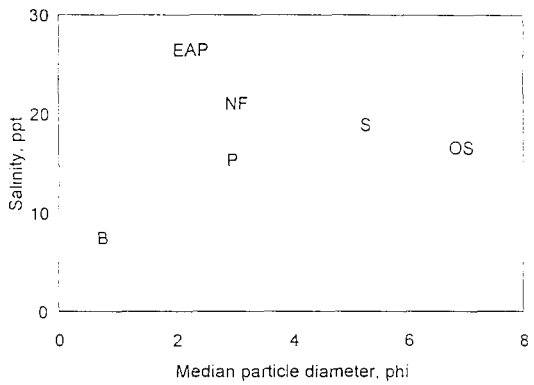


Fig. 3.13 a. Plot of average salinity (ppt) against median sediment particle size (phi).

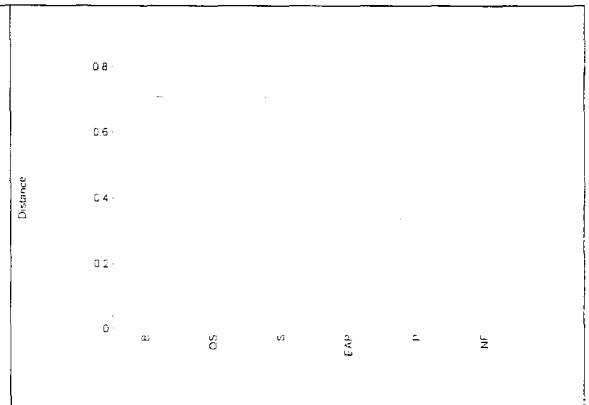


Fig. 3.13 b. Dendrogram of lagoon similarity by average salinity and median sediment particle size.

Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm.

Simply by plotting untransformed mean salinity against untransformed median particle size distinguishes two groups of sites, with Butts lagoon as an outlier. Oxey South and Salterns lagoons were most similar in terms of average salinity and with some difference in sediment type, although they both had very fine sediments. Normandy Farm, Eight-Acre Pond and Pennington lagoons were most similar in terms of granulometry, but with greater variability in salinity. Butts lagoon was isolated with coarse sediment and low salinity. This division of sites was confirmed by the Euclidean similarity dendrogram. Normandy Farm and Pennington lagoons had almost identical median particle diameter and as such were most similar, whilst Oxey South and Salterns had very similar average salinity and were also grouped separately. Following this division, the similarity calculation placed Eight-Acre

Pond with the Normandy Farm and Pennington group, probably again due to similar granulometry, and placed Butts lagoon as a separate group.

Plotting the data as inverse $\log_e$ salinity against $\log_e$ median particle diameter further acts to identify Butts lagoons as very dissimilar from all the others, probably reflecting the low salinity and coarse sediment at this site. In contrast, Eight-Acre Pond, the other site with coarse sediments, is more closely grouped with the sandy sites, but with a wide range over salinity. Similarity calculation based on the 0 – 1 scaled transformed data also serves to emphasis the similarity within two groups of lagoons, Normandy Farm and Pennington lagoons, and Oxey South and Salterns lagoons. Again Eight-Acre Pond is similar to the Normandy Farm and Pennington group, probably again due to similar granulometry, and places Butts lagoon as a entirely separate group.

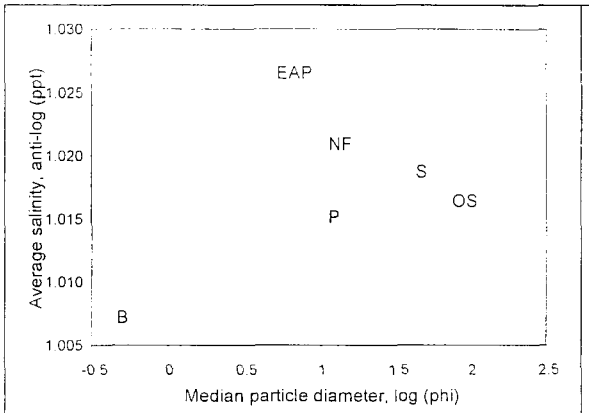


Figure 3.14 a. Plot of average salinity (anti-log) against median sediment particle size (log mm).

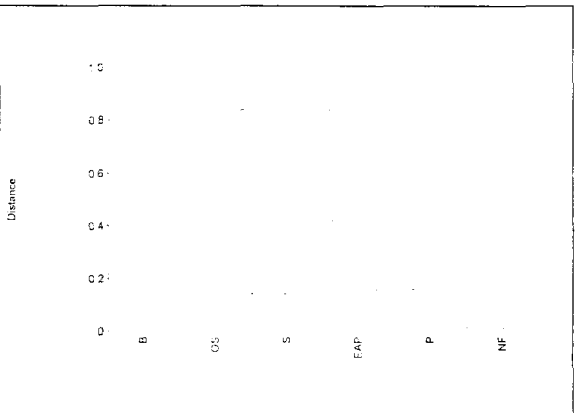


Figure 3.14b. Dendrogram of lagoon similarity by salinity (anti-log) and median sediment particle size (log mm).

Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm.

As discussed in the preceding results, the difference between the lagoons studied extends beyond the granulometry and salinity. Bamber *et al.* (1992), note that the environmental variables which exhibit most variability and therefore are likely to be most influential to the faunal community include, water temperature, salinity, pH, organic carbon content of the sediment and nutrient levels. Thus a preliminary analysis of site similarity was carried out using all environmental data available for the lagoons studied in combination with temperature values measured during sampling in April 2000. Temperature is included because it is likely to reflect a combination of other factors such as wave action, lagoon surface area, freshwater

addition, lagoon depth and stratification. These data have been analysed as untransformed values scaled to a 0 – 1 range (Table 3.7).

The separation of lagoons by similarity analysis of untransformed, scaled environmental data shows a bias towards granulometry but is very similar to that produced by analysis only the granulometric and salinity data. In fact, since the fauna studied are benthic infauna, biasing the analysis towards the benthic habitat is not unreasonable. The dendrogram separates the sites into coarse (Eight Acre Pond, Butts, Normandy Farm and Pennington) and fine (Oxey South and Salterns) sediment or low and higher phaeopigment concentrations (Fig. 3.15 a), whilst there is a gradient across the MDS plot of decreasing chlorophyll a concentration from left to right. Also there is a clear gradient of salinity in the coarse sediment group in the MDS ordination (Fig. 3.15 b), whilst the two fine sediment sites have brackish water.

	Recorded Values						Scaled Data					
Lagoon	**B**	**P**	**OS**	**S**	**EAP**	**NF**	**B**	**P**	**OS**	**S**	**EAP**	**NF**
Median sediment, phi	0.731	2.932	6.882	5.233	2.188	2.996	0.11	0.43	1.00	0.76	0.32	0.44
Organic Carbon, %	14.470	7.268	17.980	12.130	2.505	6.969	0.80	0.40	1.00	0.67	0.14	0.39
Salinity, Mean ppt	7.504	15.358	16.624	18.920	26.508	21.039	0.28	0.58	0.63	0.71	1.00	0.79
Temperature, °C	14.900	13.900	13.800	17.400	15.300	13.600	0.86	0.80	0.79	1.00	0.88	0.78
Chl a, mean, ng/g	0.045	0.117	0.276	0.178	0.017	0.014	0.16	0.42	1.00	0.64	0.06	0.05
Phaeop, mean, ng/g	0.004	0.005	0.029	0.019	0.002	0.002	0.14	0.16	1.00	0.67	0.06	0.06
Catchment area, m^2	14668	37400	15733	9746	2793	32745	0.39	1.00	0.42	0.26	0.07	0.88

Table 3.7. Environmental data available for lagoon similarity analysis and the scaled data used in calculations. Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm.

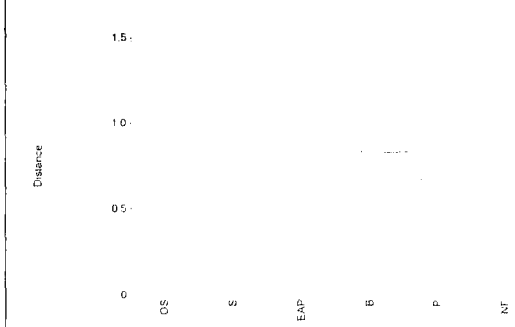


Fig. 3.15 a. Similarity dendrogram of lagoons based on all available environmental data.

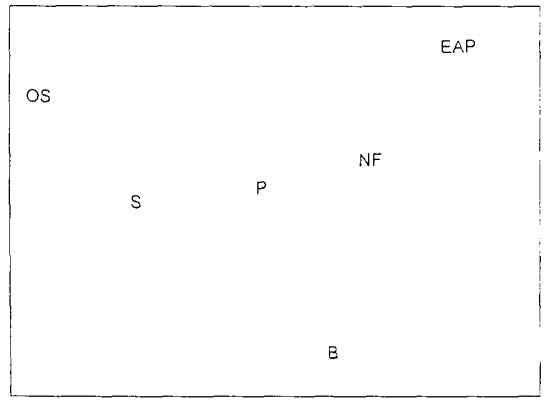


Fig. 3.15 b. MDS Euclidean distance ordination of lagoons based on all available environmental data.

Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm.

3.5 Summary and Conclusions

In terms of salinity regime, Keyhaven-Lymington lagoons are intermediate between estuarine environments and enclosed brackish water areas such as the Baltic Sea. The lagoons studied are, like estuaries, subject to seasonal salinity changes, which may occur rapidly in response to heavy rainfall, but are not subject to salinity changes on a tidal basis. The lagoonal habitat provided in the Keyhaven-Lymington system varied in terms of most environmental variables, particularly salinity, granulometry, food availability (measured as sediment organic carbon content and photosynthetic pigment concentration) and surface water nutrient concentrations.

It appears that the lagoons each represent distinct habitats, with some similarity between Oxey South and Pennington lagoons. The multivariate analysis suggests that, if the environmental variables studied are equally important habitat features for meiobenthic/nematode assemblage structure, there would be a correlation of faunal similarity between the brackish water sites with sediment type. Increased sediment heterogeneity is associated with higher species diversity and abundance due to an increased availability of sediment pore space and an increased diversity of space size. A separate similarity might be expected between Eight-Acre Pond and the sandiest lagoons and further similarity between Butts lagoon and the lower salinity sites.

4 Spatial Distribution of Nematoda in the Keyhaven-Lymington Lagoon System

4.1 Introduction

Lagoons are by definition extreme environments: Temperature can show a daily variation five times that of ambient; lagoons may freeze over; pH may vary and stratify on a daily basis; salinity may vary seasonally; and organic content and nutrient levels tend to be high and accumulate (Bamber *et al.*, 1992). However, marine Nematoda are known to be highly physiologically adapted to varying salinity conditions (Paetzold, 1955, 1958). They are the dominant meiofaunal taxon in most benthic environments, particularity in estuarine and brackish water (Elmgren, *et al.*, 1984; Hodda and Nicholas, 1986; Guidi-Guilvard and Buscail, 1995;Villano and Warwick, 1995; Vanaverbeke *et al.*, 2000) and under eutrophic/low oxygen conditions (Heip *et al*, 1988; Josefson and Widbom, 1988; Soetaert *et al.*, 1995; Moens *et al.*, 1999). In sheltered muddy sites nematodes are always the dominant taxon (Heip *et al.*, 1985).

Nevertheless, tolerance to salinity variation is not uniform throughout the nematode taxon (Foster, 1998), and a model has been devised to define estuarine salinity boundaries by marine and freshwater nematode species diversity (Riemann, 1966). In north-western Europe, it has been estimated that at least 155 nematode species predominantly occur in brackish water or are marine species recognised as tolerant to brackish water (Heip *et al.*, 1985). Eighteen nematode species have been recorded only in brackish water environments, whilst it is estimated that 50 species is an approximate maximum alpha diversity for brackish water sites (Heip *et al.*, 1985). Low or variable salinity may act to suppress nematode species number (Heip *et al.*, 1985) - in the Thames estuary, for example, Attrill (2002) found lowest sub-tidal diversity at 10 and 15 ppt (6 and 7 mean number of meiofauna species per core), and noted a significant correlation between species number and salinity range.

Gerlach (1953) divided brackish water nematodes into six groups according to salinity tolerance. Many species have been recorded in salinity ranging from 2 – 30 ppt (Brenning, 1973; Warwick and Gee, 1984; Soetaert *et al.*, 1995), however,

absolute tolerance is likely to relate to salinity range (Attrill, 2002), rate of change and length of exposure to non-ambient salinity (Forster, 1998). In fact, salinity, sediment particle size and temperature are considered to be the three primary physical factors controlling meiofaunal abundance and species composition (Coull, 1999). It has been suggested both that salinity tolerance may differ with other factors, including sediment type (Heip *et al.*, 1985), and that within a given tolerance range in salinity and temperature[1] other variables exert more importance on brackish water fauna (Vernberg and Vernberg, 1972; Newell, 1979; Little, 1986).

This survey quantified the nematode assemblages in Keyhaven-Lymington lagoon system and the results are discussed in terms of the lagoonal habitat. There is limited data available on meiofauna in UK lagoons, but that which is available suggests that meiofaunal abundance is reduced in comparison to marine and estuarine/brackish water environments (Bamber *et al.*, 1992). However, Bamber *et al.* (1992) collected meiofauna on a 90 μm mesh sieve, which will have excluded smaller meiofaunal species and juvenile life stages of larger species. This survey redressed that problem by used a 45 μm mesh sieve.

4.2 Results

Although every effort was made to take all samples at approximately 30 cm depth, it is possible that differences in the aspect of the sampling sites influenced the fauna sampled. Butts, Oxey South, and Salterns lagoons and Normandy Farm ditch each have a stepped edge, with an almost instant change from land to sub-tidal and associated fringing algae. However, the sites sampled in Normandy Farm and Eight-Acre Pond lagoons were gently sloping from terrestrial to sub-tidal, although effectively without an intertidal region owing to an almost complete lack of tidal influence behind the sea wall. The site sampled in Pennington lagoon was intermediate between these two regions, gently sloping into fine mud with gravel, and fringing algae approximately 10 m away. It is likely therefore that the sites experience different environmental conditions. The gently sloping sites may be exposed to wind-driven disturbance (wave formation was observed in Pennington

[1] Tolerance of salinity fluctuations and freezing are thought to be related, owing to the similarity of osmotic stress during these to processes – Farke *et al.*, 1984.

lagoon), whilst the more basin-like sites are likely to experience [more prolonged] hypoxic events owing to reduced disturbance.

4.2.1 Univariate Diversity Indices

a *Species number*

Where possible, species level identification was made; however if morphologically different individuals of the same genus could not be identified to species, they have been listed as putative species (A, B, C etc). In some cases morphologically different species fitting the same species description are listed separately. For example, although *Hypodontolaimus balticus* and *H. balticus sp B* each fit the same species description, *H. balticus sp B* had fewer pre-cloacal supplements than previously recorded. A total of 81 nematode species were identified (Table 4.1), the maximum number of species per lagoon was recorded in Normandy Farm lagoon (45 species - occurrence over three replicates). Species assemblage varied widely between the lagoons - of the 81 species recorded, only one (*Daptonema setosum*) was ubiquitous throughout the system, whilst 28 nematode species were unique to one of the seven sites. The greatest number of single-site species were recorded in the most saline lagoons (Eight-Acre Pond, 11 species; Normandy Farm, 8 species and; Normandy Farm ditch, 5 species). Only in Salterns lagoon was a single-site species not recorded.

Variation in species number between replicates was small in Pennington (15 ± 1; mean ± sd), Salterns (24 ± 2.65), Eight-Acre Pond (17.67 ± 2.52), and Normandy Farm (30.33, ± 1.15) and the drainage ditch site adjacent to Normandy Farm (29.67 ± 2.52). However, variation in species number between replicates was higher in Butts (9 ± 3.61) and Oxey South (18.67 ± 5.13) lagoons. Increased variation of species number between replicates may indicate a greater patchiness of species assemblages within a site. Overall, number of species per lagoon ranged from a minimum of 14 (average 9 species per replicate) in Butts lagoon to 45 (average 30.3 species per replicate) in Normandy Farm lagoon (Fig. 4.1). There was an increase in species number from west to east, with the exception of Eight-Acre Pond. ANOVA supports

Sites		B		P		OS		S		EAP		NFD		NF	
No.	Species	Mean	± s.d.	Mean	± s.d.	Mean	± s.d.	Mean	± s.d.	Mean	± s.d.	Mean	± s.d.	Mean	± s.d.
7	*Daptonema setosum*	168.81	105.01	139.57	174.32	435.94	370.98	230.89	244.07	6.10	5.29	22.09	38.26	43.39	28.92
6	*Daptonema procerum*	3.30	5.71	151.40	199.02	12.48	12.88	356.59	401.36	0.00	0.00	168.85	64.10	454.52	155.74
6	*Dichromadora sp A*	0.00	0.00	27.91	48.35	19.43	13.14	190.32	242.29	5.87	10.16	26.25	7.05	40.76	17.21
6	*Diplolaimella ocellata*	993.35	622.50	1254.35	291.62	72.61	63.59	10.99	19.04	44.38	28.17	6.35	11.00	0.00	0.00
6	*Thalassomonhystera sp Aa*	324.58	300.50	0.00	0.00	4.87	8.43	3.66	6.35	7.32	12.67	32.60	5.79	1.77	3.07
6	*Tripyloides sp A*	0.00	0.00	118.13	43.83	19.87	13.26	34.98	33.16	2.93	5.08	135.71	66.52	4.04	7.00
5	*Chromadoridae sp A*	0.00	0.00	0.00	0.00	10.58	9.25	203.34	237.16	5.87	10.16	37.60	40.03	18.36	5.12
5	*Daptonema sp B*	0.00	0.00	64.42	33.46	4.42	4.29	69.45	75.08	0.00	0.00	32.60	5.79	86.22	68.10
5	*Daptonema korneense*	0.00	0.00	0.00	0.00	1.56	2.71	191.76	61.30	7.32	12.67	226.45	172.26	72.88	58.56
5	*Sabatieria sp C*	0.00	0.00	22.55	21.12	0.78	1.35	508.80	542.92	0.00	0.00	137.36	73.19	4.96	8.60
5	*Thalassomonhystera sp indet*	119.66	43.95	0.00	0.00	4.87	8.43	3.37	5.84	0.00	0.00	43.64	20.43	32.82	23.90
4	*Aponema/Calmicrolaimus sp B*	7.99	13.85	0.00	0.00	2.86	4.95	0.00	0.00	6.10	5.29	39.26	39.85	0.00	0.00
4	*Chromadorita sp Bb*	28.78	38.07	0.00	0.00	0.00	0.00	13.00	22.52	3.17	5.49	0.00	0.00	23.90	31.48
4	*Daptonema oxycerca*	0.00	0.00	0.00	0.00	5.65	7.84	36.41	36.31	0.00	0.00	43.95	31.73	132.52	91.72
4	*Daptonema sp G*	0.00	0.00	0.00	0.00	10.52	16.23	23.70	14.52	0.00	0.00	24.06	26.91	13.89	19.64
4	*Monhystrella sp A*	7.99	13.85	0.00	0.00	0.00	0.00	0.00	0.00	7.32	12.67	11.05	19.13	4.04	7.00
4	*Ptycholaimellus ponticus*	0.00	0.00	0.00	0.00	12.08	15.24	34.40	12.51	7.32	12.67	17.71	30.67	0.00	0.00
4	*Rhabditis marina*	7.99	13.85	0.00	0.00	4.87	8.43	7.33	12.69	21.98	22.00	0.00	0.00	0.00	0.00
4	*Sabatieria pulchra sp A*	0.00	0.00	0.00	0.00	3.64	4.43	391.71	303.53	0.00	0.00	99.18	91.45	1.77	3.07
4	*Sphaerolaimus gracilis*	0.00	0.00	27.91	48.35	0.00	0.00	44.03	33.94	6.33	10.97	0.00	0.00	13.40	12.32
4	*Thalassomonhystera sp Ac*	0.00	0.00	27.91	48.35	0.00	0.00	83.73	44.66	0.00	0.00	82.59	25.61	20.49	18.90
4	*Thalassomonhystera parva*	0.00	0.00	8.60	14.89	9.73	16.86	0.00	0.00	0.00	0.00	95.60	25.72	30.91	4.98
3	*Anoplostoma sp A*	0.00	0.00	0.00	0.00	4.87	8.43	52.79	56.45	0.00	0.00	0.00	0.00	16.59	6.96
3	*Chromadora nudicapitata*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	693.46	449.99	28.44	34.12	22.05	19.37
3	*Chromadoridae sp B*	0.00	0.00	254.46	257.62	0.00	0.00	3.66	6.35	0.00	0.00	0.00	0.00	4.04	7.00
3	*Chromadorita sp Ba*	11.29	12.05	0.00	0.00	0.00	0.00	33.04	38.94	0.00	0.00	0.00	0.00	1.77	3.07
3	*Daptonema sp F*	0.00	0.00	0.00	0.00	4.87	8.43	16.66	20.11	0.00	0.00	104.99	28.19	0.00	0.00
3	*Daptonema sp K*	0.00	0.00	0.00	0.00	0.00	0.00	3.37	5.84	0.00	0.00	6.35	11.00	19.78	12.83
3	*Desmolaimus zeelandicus*	0.00	0.00	1372.48	181.51	5.65	7.84	7.33	12.69	0.00	0.00	0.00	0.00	0.00	0.00
3	*Dichromadora cephalata*	0.00	0.00	1421.71	596.79	0.00	0.00	100.48	82.85	0.00	0.00	37.29	25.37	0.00	0.00
3	*Halalaimus sp A*	0.00	0.00	0.00	0.00	0.00	0.00	3.66	6.35	0.00	0.00	6.35	11.00	8.51	7.67
3	*Hypodontolaimus balticus sp B*	0.00	0.00	56.95	65.79	0.00	0.00	3.37	5.84	0.00	0.00	0.00	0.00	5.81	6.07
3	*Hypodontolaimus sp B*	0.00	0.00	67.66	63.37	4.87	8.43	0.00	0.00	0.00	0.00	0.00	0.00	4.04	7.00
3	*Linhomoeous sp B*	0.00	0.00	0.00	0.00	8.51	6.13	7.33	12.69	0.00	0.00	0.00	0.00	11.70	15.88
3	*Sabatieria sp A*	0.00	0.00	0.00	0.00	0.78	1.35	62.12	82.71	0.00	0.00	118.45	158.28	0.00	0.00

Table 4.1. Average abundance of nematode species 10 cm^{-2} (± standard deviation), in the Keyhaven-Lymington lagoon system. Listed in order of frequency, most frequent first. Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

	Sites	B		P		OS		S		EAP		NFD		NF	
No.	Species	Mean	± s.d.	Mean	± s.d.	Mean	± s.d.	Mean	± s.d.	Mean	± s.d.	Mean	± s.d.	Mean	± s.d.
3	*Spilophorella paradoxa*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	38.80	8.92	47.80	12.86	4.96	8.60
3	*Terschellingia longicaudata*	0.00	0.00	0.00	0.00	543.09	430.90	201.34	124.33	0.00	0.00	1367.22	467.17	0.00	0.00
3	*Thalassomonhystera sp Ab*	712.79	81.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	34.79	33.26	6.74	7.55
3	*Thalassomonhystera sp C*	0.00	0.00	0.00	0.00	0.00	0.00	26.00	45.04	0.00	0.00	208.51	114.40	135.57	155.56
3	*Viscosia viscosa*	0.00	0.00	246.98	79.86	23.71	18.13	0.00	0.00	0.00	0.00	84.06	94.23	0.00	0.00
2	*Adoncholaimus fuscus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	60.19	57.39	6.74	7.55
2	*Axonolaimus cf paraspinosus*	0.00	0.00	0.00	0.00	20.32	22.07	0.00	0.00	0.00	0.00	0.00	0.00	82.02	44.54
2	*Calyptronema maxweberi*	0.00	0.00	0.00	0.00	0.00	0.00	3.66	6.35	0.00	0.00	56.34	26.27	0.00	0.00
2	*Cyatholaimus sp A*	0.00	0.00	8.60	14.89	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	38.21	43.04
2	*Hypodontolaimus balticus*	0.00	0.00	13.96	24.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.96	8.60
2	*Leptolaimus limicolus*	0.00	0.00	48.35	51.89	0.78	1.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2	*Leptolaimus papilliger*	0.00	0.00	73.02	18.56	11.30	15.68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2	*Paracyatholaimus cf pentadon*	0.00	0.00	55.83	63.96	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	37.71	31.79
2	*Sabatieria sp D*	0.00	0.00	0.00	0.00	0.00	0.00	42.38	64.83	0.00	0.00	25.40	43.99	0.00	0.00
2	*Syringiolaimus sp A*	0.00	0.00	0.00	0.00	0.78	1.35	0.00	0.00	3.17	5.49	0.00	0.00	0.00	0.00
2	*Terschellingia communis*	0.00	0.00	0.00	0.00	4.87	8.43	0.00	0.00	0.00	0.00	37.29	25.37	0.00	0.00
2	*Theristus acer*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	165.39	104.25	0.00	0.00	19.78	12.83
2	*Viscosia sp B*	7.99	13.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.04	7.00
1	*Adoncholaimus sp B*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.04	7.00
1	*Anticoma sp A*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	28.05	32.74	0.00	0.00	0.00	0.00
1	*Aphelenchoides sp A*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.93	5.08	0.00	0.00	0.00	0.00
1	*Atrochromadora parva*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	313.42	281.31	0.00	0.00	0.00	0.00
1	*Camacolaimus tardus*	7.99	13.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
1	*Cyatholaimus sp indet*	0.00	0.00	13.96	24.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
1	*Daptonema normandicum*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	61.53	46.59
1	*Daptonema sp H*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	31.56	50.12
1	*Daptonema sp indet*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.77	3.07
1	*Daptonema sp J*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.96	8.60
1	*Desmodoridae sp A*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	172.20	133.69	0.00	0.00
1	*Dichromadora geophila*	11.29	12.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
1	*Dichromadoridae sp A*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.04	7.00
1	*Diplolaimella sp A*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.85	15.33	0.00	0.00
1	*Enoplus aff brevis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	71.12	69.31
1	*Euchromadora vulgaris*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	67.55	41.69	0.00	0.00	0.00	0.00
1	*Metalinhomeous sp A*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	232.39	87.31	0.00	0.00
1	*Neochromadora poecilosomoides*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	46.12	18.76	0.00	0.00	0.00	0.00

Table 4.1. Continued....

	Sites	B		P		OS		S		EAP		NFD		NF	
No.	Species	Mean	± s.d.	Mean	± s.d.	Mean	± s.d.	Mean	± s.d.	Mean	± s.d.	Mean	± s.d.	Mean	± s.d.
1	*Chromadorella filiformis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	28.55	6.62	0.00	0.00	0.00	0.00
1	*Oncholaimus sp A*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	19.05	17.78	0.00	0.00	0.00	0.00
1	*Oncholaimus dujardinii*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	39.52	60.98	0.00	0.00	0.00	0.00
1	*Praeacanthoncus punctatus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.32	12.67	0.00	0.00	0.00	0.00
1	*Sabatieria sp indet*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.05	19.13	0.00	0.00
1	*Sphaerolaimus balticus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.77	3.07
1	*Teratorhabditis sp A*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	424.27	128.17	0.00	0.00	0.00	0.00
1	*Tylenchidae sp A*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.35	11.00	0.00	0.00
1	*Viscosia glabra*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.93	5.08	0.00	0.00	0.00	0.00
1	*Xyalidae sp A indet*	0.00	0.00	0.00	0.00	4.87	8.43	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Average no. of species	9.00	3.61	15.00	1.00	18.67	5.13	24.00	2.65	17.67	2.52	29.67	2.52	30.33	1.15
	Average no. of Inds. 10 cm^{-2}	2413.82	1079.43	5476.73	1392.22	1276.01	919.28	3005.69	2464.30	2012.53	1109.79	3937.22	1057.20	1616.47	738.87
	Total number of species	14		22		32		34		28		39		45	

Table 4.1. Continued....

this suggestion; species number was significantly different between sites ($r = 0.95$, $p < 0.05$). A Tukey's pair-wise comparison test identified that difference was significant between the lagoons most distant from each other or most isolated (Table 4.2).

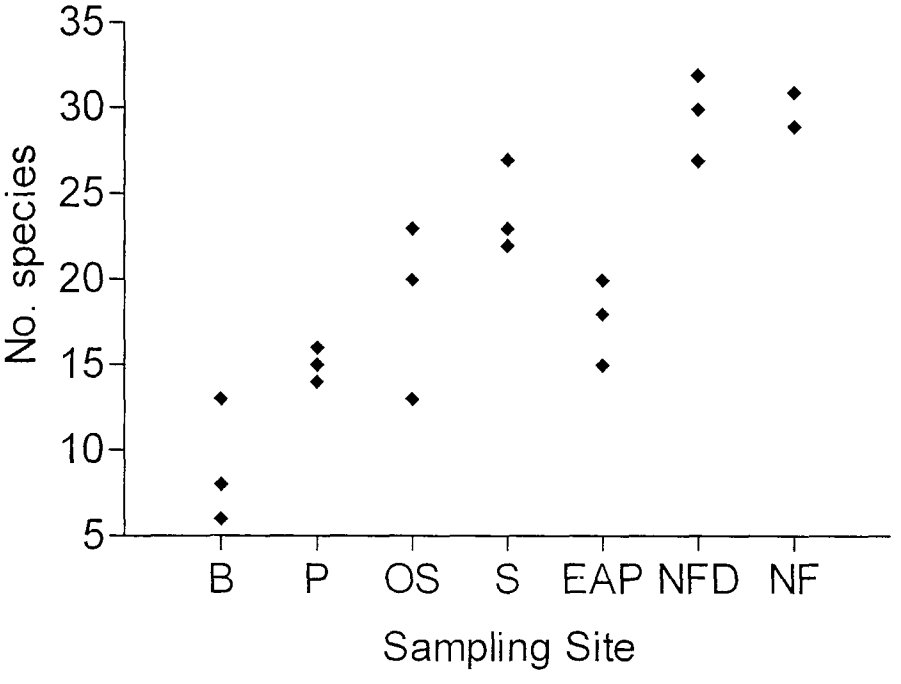


Fig. 4.1. Number of nematode species per site, three replicates per site, in the Keyhaven-Lymington lagoon system. Note that for Normandy Farm two points over-lie at 31 species.
Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

Sites	B	P	OS	S	EAP	NFD
P	ns					
OS	ns	ns				
S	0.001	0.05	ns			
EAP	0.05	ns	ns	ns		
NFD	0.001	0.001	0.01	ns	0.01	
NF	0.001	0.001	0.01	ns	0.01	ns

Table 4.2. Comparison of nematode species number between sites in the Keyhaven-Lymington lagoon system. Significance level, p, of the Tukey's pair-wise comparison test between site means of species number. Not significant = ns.
Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

b *Abundance*

Abundance ranged from a minimum of 351 individuals 10 cm^{-2} in Oxey South lagoon to a maximum in Pennington lagoon of 6280 individuals 10 cm^{-2} (Fig. 4.2). Within-site variation of abundance was high in Salterns lagoon (3005.69 inds. 10 cm^{-2} ± 2464.30; mean ± sd), but relatively low in the other sites [Butts (2413.82 inds. 10 cm^{-2} ± 1079.43), Pennington (5476.72 inds. 10 cm^{-2} ± 1392.22), Oxey South (1276.00 inds. 10 cm^{-2} ± 919.27), Eight-Acre Pond (2012.52 inds. 10 cm^{-2} ± 1109.79) and Normandy Farm (1616.46 inds. 10 cm^{-2} ± 738.87), and Normandy Farm ditch (3937.22 inds. 10 cm^{-2} ± 1057.20)]. The higher variability of abundance between replicates in Salterns lagoon may indicate an increased variability of habitat at this site in comparison to the other lagoons, sampling error, or that species/assemblage patchiness was sampled in Salterns. Notably, the species composition between the three replicates from Salterns was very similar.

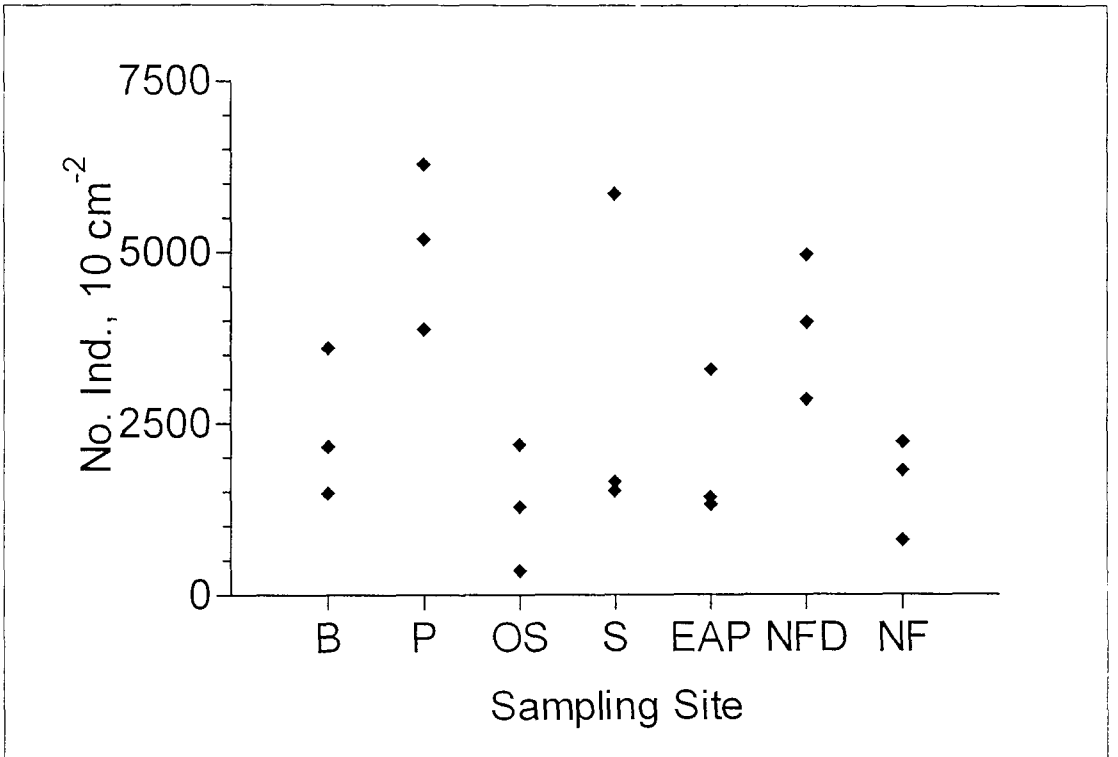


Fig. 4.2. Number of nematode individuals 10 cm^{-2} recorded at each site, three replicates per site, in the Keyhaven-Lymington lagoon system.
Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

It is possible that the low abundance recorded at Oxey South and Normandy Farm lagoons was owing to sedimentary conditions. Both had relatively fine substrates.

but Oxey South lagoon was predominantly flocculent and anoxic silt and clay, whilst the sediment sampled in Normandy Farm was compacted sand in clay and silt. Both these habitats might act to restrict the penetration of fauna into the sediment. However, it should be noted that the sediment in Normandy Farm ditch was similar to that in Oxey South lagoon (pers. obs.) and this site did not have a similarly reduced faunal abundance.

Owing in part to within-site variation of abundance no east-west pattern between sites was visible, nevertheless, ANOVA identified a significant difference between site abundances ($r = 0.78$, $p < 0.05$). The Tukey's pair-wise comparison test only identified a significant difference in abundance between Pennington and Oxey South lagoons, and between Pennington and Normandy Farm lagoons (Table 4.3). These differences were a result of relatively low nematode abundance in Oxey South and Normandy Farm lagoons, in contrast to the high mean abundance recorded in Pennington lagoon. Oxey South and Normandy Farm lagoons themselves differed significantly in number of species, Oxey South having a lower number of species.

Sites	B	P	OS	S	EAP	NFD
P	ns					
OS	ns	0.05				
S	ns	ns	ns			
EAP	ns	ns	ns	ns		
NFD	ns	ns	ns	ns	ns	
NF	ns	0.05	ns	ns	ns	ns

Table 4.3. Comparison of number of nematode individuals between sites in the Keyhaven-Lymington lagoon system. Significance level of the Tukey's pair-wise comparison test between site means of number of individuals. Not significant = ns. Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

c *Diversity Indices*

As with species number, the three diversity indices calculated each identified an increase in diversity from west to east, with the exception of Eight-Acre Pond. The gradient of that increase and the position of the intermediate sites varied with the diversity index.

i Shannon-Wiener

The range of Shannon-Wiener diversity values was low, a minimum of 1.24 $H'_{(loge)}$ was recorded in Oxey South lagoon and a maximum of 2.83 $H'_{(loge)}$ in Normandy Farm lagoon (Fig. 4.3). Highest Shannon-Wiener diversity was recorded in the Eastern-most sites - Normandy Farm lagoon ($H'_{(loge)}$ = 2.69 ±0.12; mean ± s.d), Normandy Farm ditch ($H'_{(loge)}$ = 2.63 ± 0.16) and Salterns lagoon ($H'_{(loge)}$ = 2.62 ± 0.11.). It was intermediate in Eight-Acre Pond ($H_{(loge)}$ = 2.02 ± 0.14), Pennington ($H_{(loge)}$ = 1.94 ± 0.16), and two replicates from Oxey South ($H_{(loge)}$ = 1.62 ± 0.33, total average), and it was lowest in Butts lagoon ($H'_{(loge)}$ = 1.42 ± 0.16) and one replicate from Oxey South.

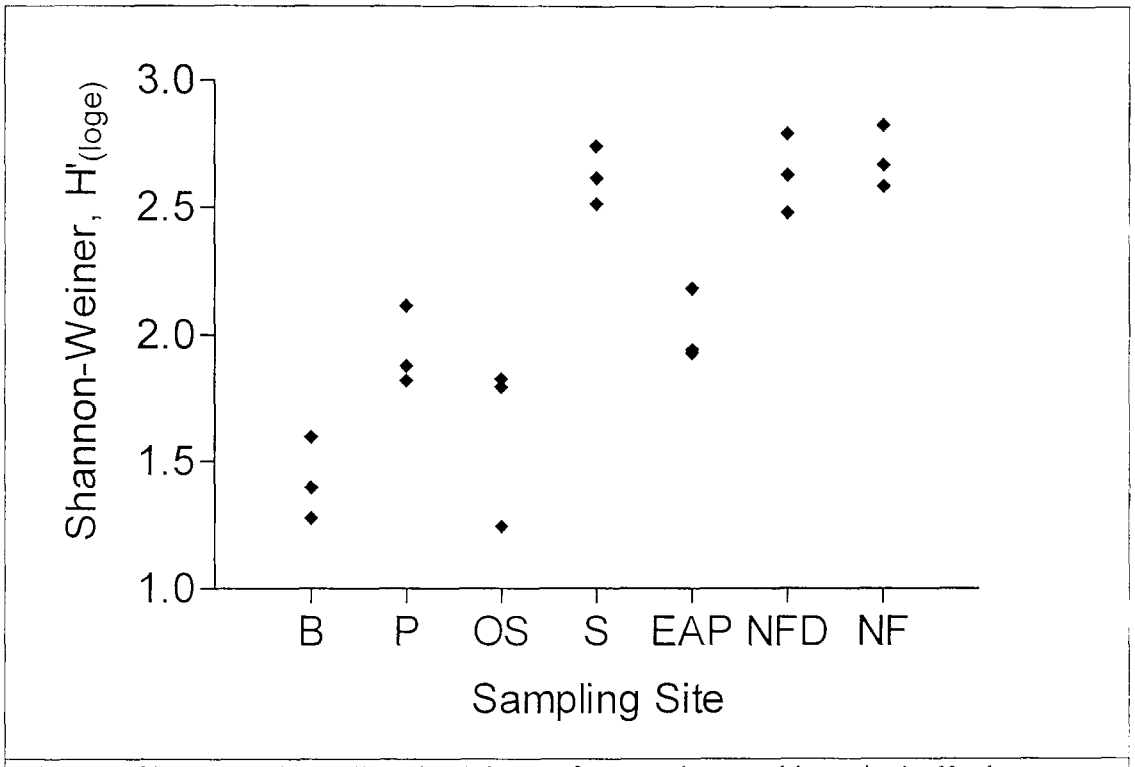


Fig. 4.3. Shannon-Wiener diversity, $H'_{(loge)}$, of nematode assemblages in the Keyhaven-Lymington lagoon system. Three replicates per site.
Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

Variability of Shannon-Wiener diversity (as standard deviation about mean values) was low at each site, except Oxey South lagoon, reflecting the pattern seen in species number within sites. The calculation of Shannon-Wiener diversity index is connected to the distribution of abundance amongst species, and as such the reduced $H'_{(loge)}$ in Oxey South reflects the dominance of two species in the nematode assemblage (*T. longicaudata*, 37.33 % ±25.44 and *D. setosum*, 37.11 % ± 15.45). However, the

generally high resolution of Shannon-Wiener diversity allowed for a highly significant result from ANOVA between sites ($r = 0.96$, $p < 0.0001$), whilst the Tukey's pair-wise comparison test confirmed that significant difference was between the sites most distant from each other and/or with grossly different sediment types (Table 4.4).

	B	P	OS	S	EAP	NFD
P	0.05					
OS	ns	ns				
S	0.001	0.01	0.001			
EAP	0.05	ns	ns	0.05		
NFD	0.001	0.01	0.001	ns	0.05	
NF	0.001	0.01	0.001	ns	0.01	ns

Table 4.4. Comparison of nematode Shannon-Wiener diversity between sites, in the Keyhaven-Lymington lagoon system. Significance level of the Tukey's pair-wise comparison test between site means. ns, not significant.
Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

ii Margalef's species richness

Margalef's diversity index, d, identified an almost linear progression of increasing average diversity from west to east (Minimum in Butts lagoon, 0.65 d; maximum in Normandy Farm lagoon, 4.49 d), although again with depressed diversity in Eight Acre Pond (Fig. 4.4).

As with the Shannon-Wiener diversity, within site variability (as standard deviation about mean values) was low at each site, except Oxey South lagoon, reflecting the pattern seen in species number. Margalef's diversity differed significantly between sites (ANOVA: $r = 0.93$, $p < 0.0001$), but the linear increase in diversity values from west to east prevented a clear division of the sites by Tukey's pair-wise test (Table 4.5). Although sites that were most distant or those with different sediments substrates were significantly different.

iii Pielou's evenness index

Pielou's evennes index, J', was used to identify the level of evenness or, conversely dominance, at each site (Fig. 4.5). The range of the evenness index between sites was very small; the highest Pielou's species evenness was recorded in Salterns lagoon (0.83 ± 0.01) and lowest in Oxey South (0.56 ± 0.06). However, ANOVA

identified a significant difference between sites ($r = 0.94$, $p < 0.001$), probably owing to the high resolution of evenness values at each site. The 'extreme' values from Salterns and Oxey south lagoon were identified by a Tukey's pair-wise comparison test as the main source of difference in evenness within the system, all other sites being similar (Table 4.6).

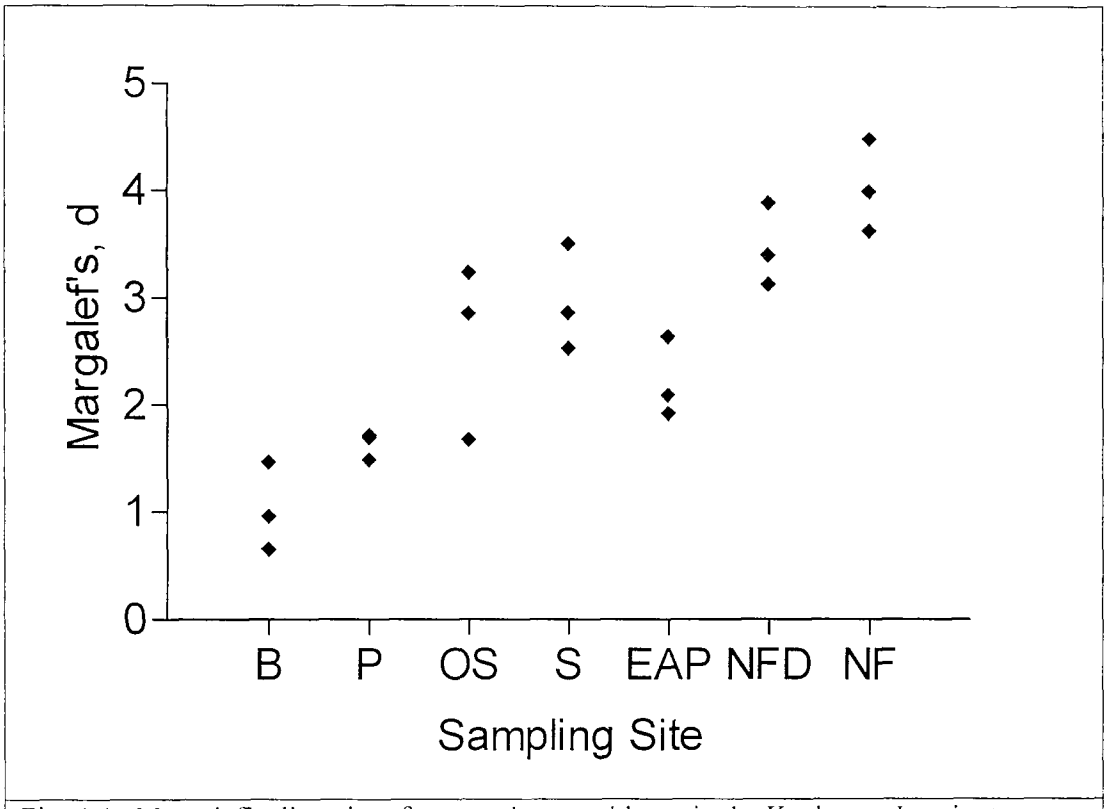


Fig. 4.4. Margalef's diversity of nematode assemblages in the Keyhaven-Lymington lagoon system. Three replicates per site.
Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

	B	P	OS	S	EAP	NFD
P	ns					
OS	0.05	ns				
S	0.01	0.05	ns			
EAP	ns	ns	ns	ns		
NFD	0.001	0.01	ns	ns	ns	
NF	0.001	0.001	0.05	ns	0.01	ns

Table 4.5. Comparison of nematode Margalef diversity between sites, in the Keyhaven-Lymington lagoon system. Significance level of the Tukey's pair-wise comparison test between site means. ns, not significant.
Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

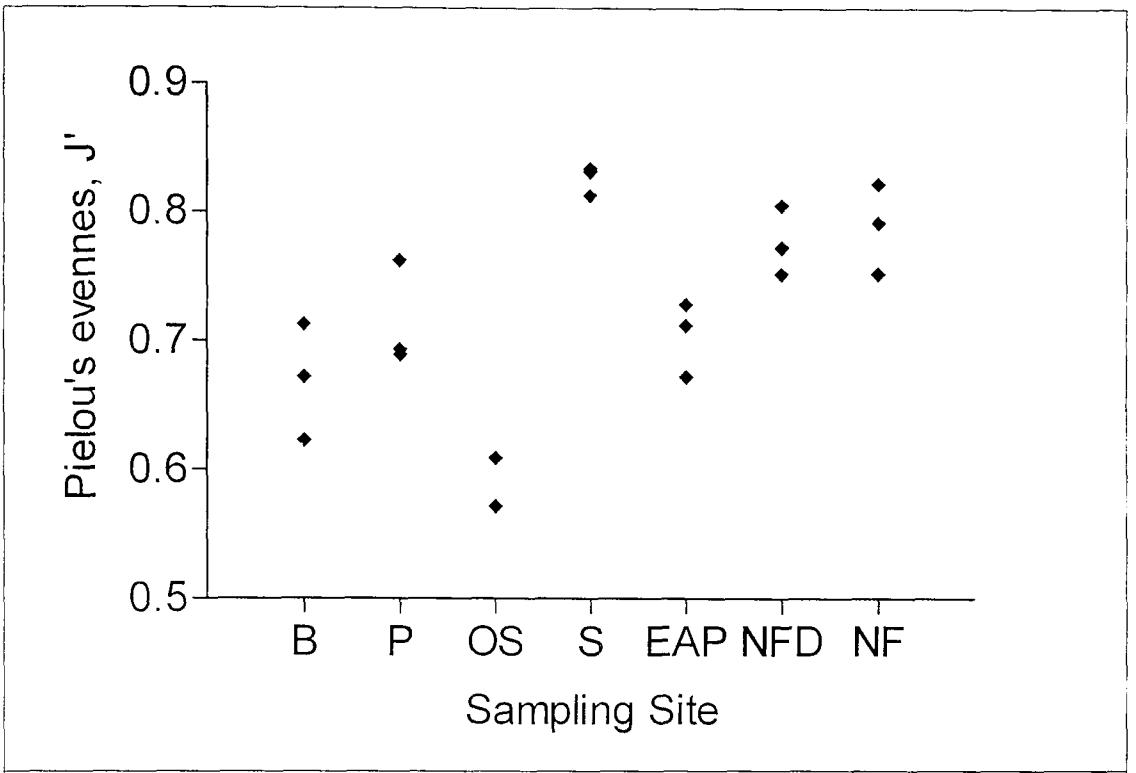


Fig. 4.5. Pielous' diversity of nematode assemblages in the Keyhaven-Lymington lagoon system. Three replicates per site.
Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

Sites	B	P	OS	S	EAP	NFD
P	ns					
OS	0.05	0.01				
S	0.01	0.05	0.001			
EAP	ns	ns	0.01	0.05		
NFD	ns	ns	0.001	ns	ns	
NF	0.05	ns	0.001	ns	ns	ns

Table 4.6. Comparison of nematode Pielous' diversity between sites in the Keyhaven-Lymington lagoon system. Significance level of the Tukey's pair-wise comparison test between site means. ns, not significant.
Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

d *K-Dominance Plots*

A K-dominance plot was produced in order to facilitate the discussion of species evenness and diversity (Fig. 4.6). All replicates had a low level of dominance, with average percentage of the dominant species per replicate over all sites of 35.02 % ± 11.84. Salterns lagoon had the lowest dominant species (*Sabatieria pulchra* sp B; 14.67 % ± 5.46), whilst the first four species (co-dominants) represented 50 % of the nematode abundance. This was also the case in Normandy Farm and Normandy

Farm Ditch, each had only one dominant species (Normandy Farm - *Daptonema procerum*, 29.56 % ± 4.73; Normandy Farm ditch – *Terschellingia longicaudata*, 34.22 % ± 4.68) accompanied by three other sub-dominant species accounting for 50 % of nematode abundance in total. Each of these sites had high diversity, the remaining 50 % of abundance represented by a suite of lesser abundant species (Normandy Farm, 41 species; Normandy Farm ditch, 35 species and; Salterns, 30 species).

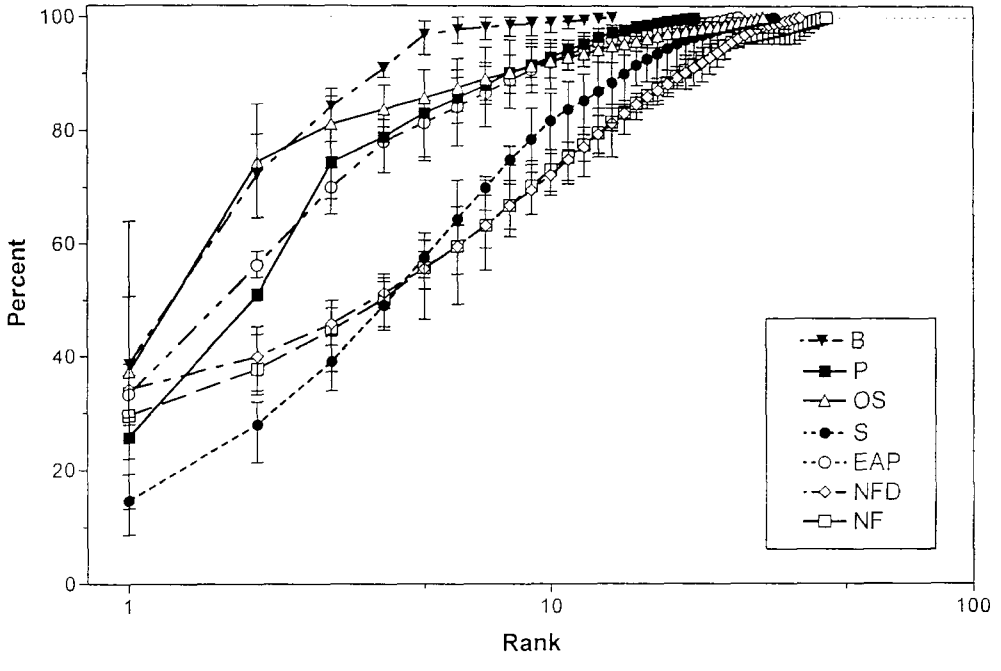


Fig. 4.6. K-Dominance plot of the nematode assemblages in the Keyhaven-Lymington lagoon system. Mean cumulative abundance with minimum and maximum values indicated by error bars.
Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

In each of Eight-Acre Pond, Oxey South, Pennington and Butts lagoons 2 species represented > 50 % of the total nematode abundance. In Eight-Acre Pond, Oxey South and Butts lagoons two species were co-dominant (Eight Acre Pond, *Chromadora nudicapitata*, 33.33 % ± 4.67 and *Teratorhabditis sp A*, 22.89 % ± 5.35; Oxey South, *Terschellingia longicaudata*, 37.33 % ± 25.44 and *Daptonema setosum*, 37.11 % ± 15.45; and; Butts, *Diplolaimella ocellata*, 38.67 %± 14.89 and *Thalassomonhystera sp Ab*, 33.56 % ± 15.27). In Pennington lagoon three species were co-dominant (*Desmolaimus zeelandicus*, 25.78 % ± 4.44; *Dichromadora cephalata*, 25.22 % ± 5.39 and; *Diplolaimella ocellata*, 23.56 % ± 5.55 %). A third

species represented > 10 % of the total nematode abundance in Eight-Acre Pond and Butts lagoons (Eight-Acre Pond, *Atrochromadora parva*, 13.78 % ± 5.09; Butts, *Thalassomonhystera sp Aa*, 12.00 % ± 6.11) and other species each represented < 10 % of the abundance (EAP, 25 species; Butts, 11). In Oxey South and Pennington all other species each represented < 10 % of the nematode abundance (30 species and 19 species respectively). Butts lagoon differed from the others in that it had a much lower overall diversity.

The division of sites in the K-dominance plot was similar to that by the Shannon-Wiener diversity index, essentially distinguishing the most diverse sites as those with the largest number of species and intermediate/low abundance. Since the K-dominance plots cross, the observed variation in site ranking between the univariate indices would be expected - the sites vary in terms of dominance, evenness and species number. Primarily, however, the plots crossed between species rank 1 and 2, with little crossing between the three groupings after rank 2/3 and the sites can be approximately divided into three groups: A. lowest dominance, highest diversity (Normandy Farm, Normandy Farm ditch and Salterns); B. increased dominance, intermediate diversity (Pennington, Oxey South and Eight-Acre Pond), and; C. increased dominance, low diversity (Butts).

e *Caswell's Neutral Model*

The species diversity recorded in each of the sites varied little from than predicted by Caswell's Neutral Model (if $-2 < V < 2$, no significant departure from neutrality). Only Salterns lagoon had significantly increased diversity to that predicted by the model ($V = 2.26 \pm 0.32$ sd), whilst Oxey South lagoon had lower than expected diversity, but not significantly so ($V = -0.96 \pm 0.44$ sd). The other lagoons had higher than predicted diversity, but again not significantly so (Fig. 4.7). Diversity higher than that predicted by the model may indicate increased biological interaction, whilst below that predicted by the model may indicate decreased biological interaction and increased importance of physical disturbance.

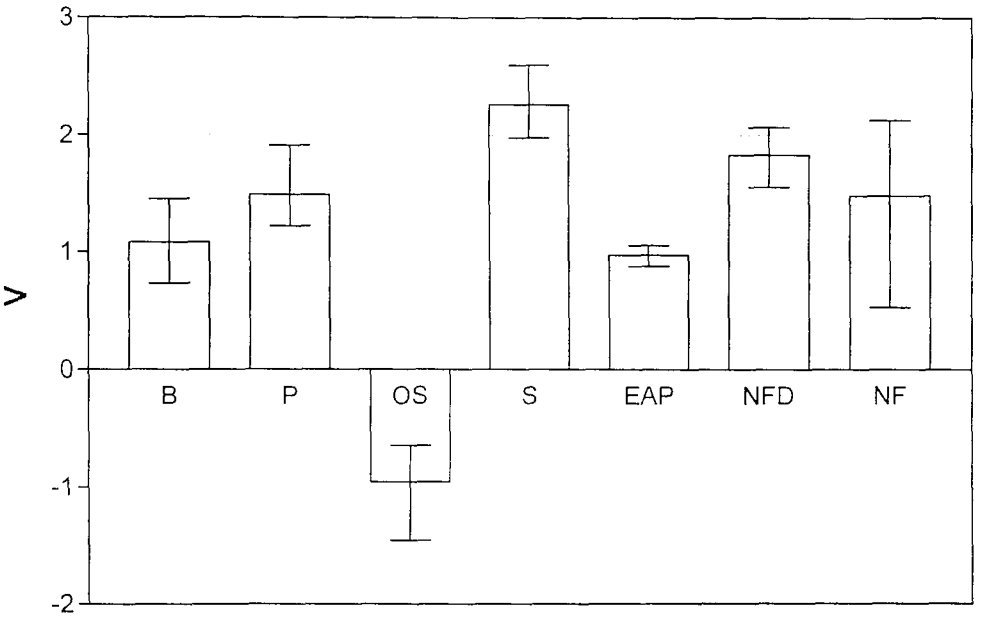


Fig. 4.7. Caswell's neutral model *V* statistic of nematode diversity along the Keyhaven-Lymington lagoon system. Bar chart of mean *V* stat value per site with, maximum and minimum values indicated as error bars.
Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

Salterns and Oxey South lagoons did not have significantly different numbers of species or individuals. Also, they did not differ in terms of Margalef's diversity, but did differ significantly in terms of both the Shannon-Wiener diversity index and the Pielou's evenness index ($p < 0.001$, in both cases). Hopper and Meyers (1967) have shown that this pattern may represent an increased dominance of fewer species as demonstrated by the crossing of the K-dominance plots for these sites. That Caswell's model indicates an increase in disturbance in Oxey South lagoon, may be borne out by the physical environment. Whilst the multivariate analysis of the environmental parameters in Salterns and Oxey South lagoons (Chapter 3) has shown that these two lagoons provided the most similar habitats in the system, it is possible that the slight differences in these parameters between the lagoons span critical tolerance levels for the nematode fauna. For instance, the sediments in both lagoons had a silt/sand fraction of > 60 %, but the sediment in Oxey South was more homogeneously silty whilst Salterns had a greater sand component. Also, both lagoons had a brackish/marine salinity regime, reaching an average summer peak in Salterns of 34.15 ppt and 29 ppt in Oxey South, but the overall salinity range in Oxey South lagoon was greater (0 – 48 ppt recorded, compared to 4 – 42 ppt in Salterns). Also, when comparing salinity over the sampling year in comparison to rainfall, it is

noticeable that salinity levels in Salterns were more sustained and declined at a slower rate in response to rainfall.

f *Correlation of univariate indices with environmental parameters*

The distribution of sites by univariate diversity indices can be related to available environmental data. Highest diversity was recorded in Salterns, Normandy Farm and Normandy Farm ditch, which had intermediate to higher salinity and silt/sand dominated sediment although nematode abundance was variable between sites. Eight-Acre Pond, Oxey South and Pennington lagoons on the other hand each had intermediate species number, but differed in habitat type: Eight-Acre Pond had coarse sediment and a polyhaline salinity regime, whilst Pennington and Oxey South lagoons had finer sediment and lower, variable salinity (poikilohaline). Finally, Butts lagoon had both a low, variable salinity and a coarse sediment substrate and had the lowest species number, but intermediate abundance.

Pearson's correlation, r, was calculated in a pair-wise fashion between each univariate index with each environmental parameter (Full list of environmental parameters given in Table 4.7). It was recognised that in repeating the test a number of times the risk of a type I statistical error was increased, consequently this analysis is used only as an indicator of possible correlation between environment and biota. A more detailed multivariate analysis of species assemblage data and environmental parameters follows (section 4.2.2.e). Percentage values (sediment granulometry and sediment organic carbon) were arcsine transformed before calculation of the correlation coefficients. Each univariate index was averaged across replicates, per site, to allow comparison with the single replicate environmental data available. Normandy Farm ditch was excluded from the analysis due to a lack of environmental data available from this site.

From all the available environmental data, only two parameters (Salinity skewness and percent sediment gravel) significantly correlated with only two measures of diversity (S and d; Table 4.8). It should be noted that both these parameters correlated with longitude ($r = -0.89$ and $r = -0.93$, respectively; $p < 0.05$) and each other ($r = 0.87$, $p < 0.05$). It is possible that salinity skewness and granulometry were

auto-correlated since a large skew of salinity will to some extent reflect infrequent, large changes in salinity, which may correspond with lagoon flushing. Flushing of a lagoon (either by water addition or artificial drainage) might also increase removal of fine sediment particles by their resuspension in the water column. It should be noted that the values of salinity skew between lagoons are predominately influenced by the relatively higher value for Butts lagoon.

		Lagoon					
Code	**Environmental variable**	**B**	**P**	**OS**	**S**	**EAP**	**NF**
A	Catchment area, m^2	14668	37400	47200	9746	2793	32745
B	Groundwater seepage, Y/N	1	1	1	1	0	1
C	Lagoon Depth, m	0.510	0.250	0.515	0.308	0.257	0.393
D	Organic carbon, arsine loi %	0.145	0.073	0.181	0.122	0.025	0.070
E	Pigment, mean chlorophyll a g^{-1}	0.045	0.117	0.276	0.178	0.017	0.014
F	Pigment, mean phaeopigment g^{-1}	0.004	0.005	0.029	0.019	0.002	0.002
G	Salinity maximum ppt, 2000	25.94	39.00	40.00	36.40	42.90	42.20
H	Salinity mean ppt, 2000	8.80	13.54	15.15	18.63	25.79	21.76
I	Salinity minimum ppt, 2000	1.50	0.40	0.70	4.00	15.60	3.40
J	Salinity median ppt, 2000	7.15	11.70	14.95	17.10	26.46	22.08
K	Salinity skew, 2000	1.28	0.65	0.43	0.54	0.42	0.05
L	Salinity kurtosis, 2000	0.67	-0.45	-0.71	-0.43	2.05	-0.26
M	Salinity range ppt, 2000	24.44	38.60	39.30	32.40	27.30	38.80
N	Salinity ppt, April sampling	3.00	7.00	7.00	8.00	16.00	14.00
O	Salinity maximum ppt, overall	31.00	48.00	48.00	42.00	42.90	42.20
P	Salinity mean ppt, overall	7.50	15.36	16.62	18.92	27.03	21.38
Q	Salinity minimum ppt, overall	0.00	0.00	0.00	4.00	15.60	2.93
R	Salinity skew, overall	2.11	0.87	0.71	0.67	0.79	0.20
S	Salinity kurtosis, overall	4.88	0.51	-0.06	-0.32	0.80	-0.47
T	Salinity range, overall	31.00	48.00	48.00	38.00	27.30	39.28
U	Sediment, arcsine clay %	0.050	0.114	0.261	0.209	0.029	0.070
V	Sediment, arcsine sand %	0.547	0.496	0.068	0.301	0.737	0.852
W	Sediment, arcsine silt %	0.097	0.278	0.739	0.475	0.086	0.177
X	Sediment, arsine gravel %	0.339	0.137	0.000	0.039	0.215	0.002
Y	Sediment, median diameter, phi	0.731	2.932	6.882	5.233	2.188	2.996
Z	Sluice flow, Y/N	0	0	1	0	0	0
AA	Sluice leakage, Y/N	0	0	1	0	0	0

Table 4.7. Environmental data used to correlate with nematode assemblage univariate indices. Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

The highest correlation ($r = -0.884$, $p < 0.055$) was recorded between species number and salinity skew overall and salinity skew in 2000. This negative correlation suggests that as salinity skew reduced nematode diversity, S, increases. Salinity skewness was also correlated with Margalef's species diversity, d (overall, $r = -0.869$; 2000, $r = 0.892$). A significant negative correlation was also found

between percentage gravel and species number, S ($r = -0.819$, $p < 0.05$) and Margalef's diversity, d ($r = -0.830$, $p < 0.05$) for all sites. Diversity indices were not similarly correlated with the sediment silt fraction. H' and J' were not significantly correlated with any environmental parameter.

		Univariate indices				
Code	**Environmental Parameter**	**S**	**N**	**d**	**J'**	**H'(loge)**
A	Catchment area, m^2	0.136	0.057	0.183	-0.478	-0.167
B	Groundwater seepage, Y/N	0.096	0.200	0.088	0.028	0.033
C	Lagoon Depth, m	-0.195	-0.597	-0.078	-0.583	-0.494
D	Organic carbon, arsine loi %	-0.241	-0.258	-0.166	-0.512	-0.439
E	Pigment, mean chlorophyll a g-1	-0.016	-0.014	0.025	-0.447	-0.191
F	Pigment, mean phaeopigment g-1	0.090	-0.258	0.150	-0.411	-0.120
G	Salinity maximum, 2000	0.650	-0.108	0.649	0.103	0.510
H	Salinity mean, 2000	0.655	-0.330	0.647	0.387	0.639
I	Salinity minimum, 2000	0.085	-0.271	0.083	0.176	0.178
J	Salinity median, 2000	0.647	-0.399	0.652	0.317	0.593
K	Salinity skew, 2000	**-0.884**	0.286	**-0.892**	-0.262	-0.706
L	Salinity kurtosis, 2000	-0.326	-0.204	-0.318	-0.001	-0.200
M	Salinity range, 2000	0.550	0.136	0.551	-0.057	0.334
N	Salinity, April sampling	0.618	-0.309	0.614	0.338	0.577
O	Salinity maximum, overall	0.371	0.224	0.360	-0.148	0.232
P	Salinity mean, overall	0.612	-0.243	0.602	0.306	0.587
Q	Salinity minimum, overall	0.134	-0.243	0.126	0.212	0.232
R	Salinity skew, overall	**-0.884**	0.124	**-0.869**	-0.337	-0.758
S	Salinity kurtosis, overall	-0.801	0.021	-0.780	-0.278	-0.696
T	Salinity range, overall	0.175	0.336	0.174	-0.258	0.005
U	Sediment, arcsine clay %	0.197	-0.073	0.230	-0.269	0.025
V	Sediment, arcsine sand %	0.225	-0.007	0.183	0.500	0.353
W	Sediment, arcsine silt %	0.184	-0.151	0.234	-0.394	-0.048
X	Sediment, arcsine gravel %	**-0.819**	0.188	**-0.830**	-0.150	-0.609
Y	Sediment, median diameter, phi	0.412	-0.216	0.454	-0.231	0.186
Z	Sluice flow, Y/N	-0.030	-0.438	0.083	-0.794	-0.410
AA	Sluice leakage, Y/N	-0.030	-0.438	0.083	-0.794	-0.410

Table 4.8. Pearson's correlation coefficient values, r, between univariate measures of the nematode assemblage and environmental parameters. When $n = 6$, ν (degrees of freedom) = 4, therefore at $p < 0.05$, $r_{min} = 0.811$. Where $r \geq 0.811$, it is highlighted as bold text.

4.2.2 Multivariate statistics

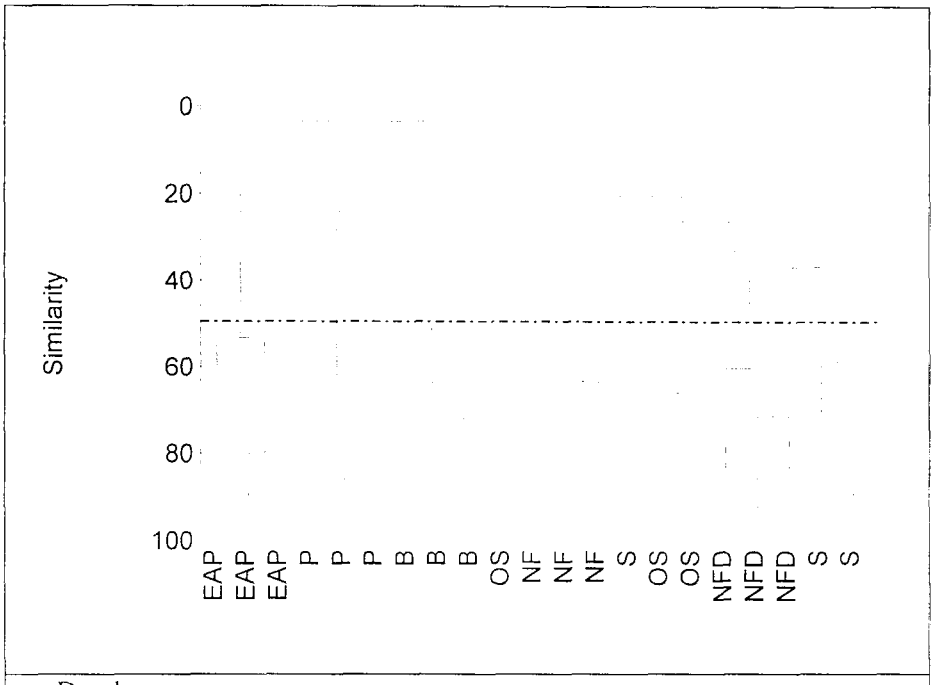
a *Site similarity*

Multivariate analysis of the untransformed species assemblage data by Bray-Curtis similarity identified both high within-site similarity of samples (> 50 % similarity)

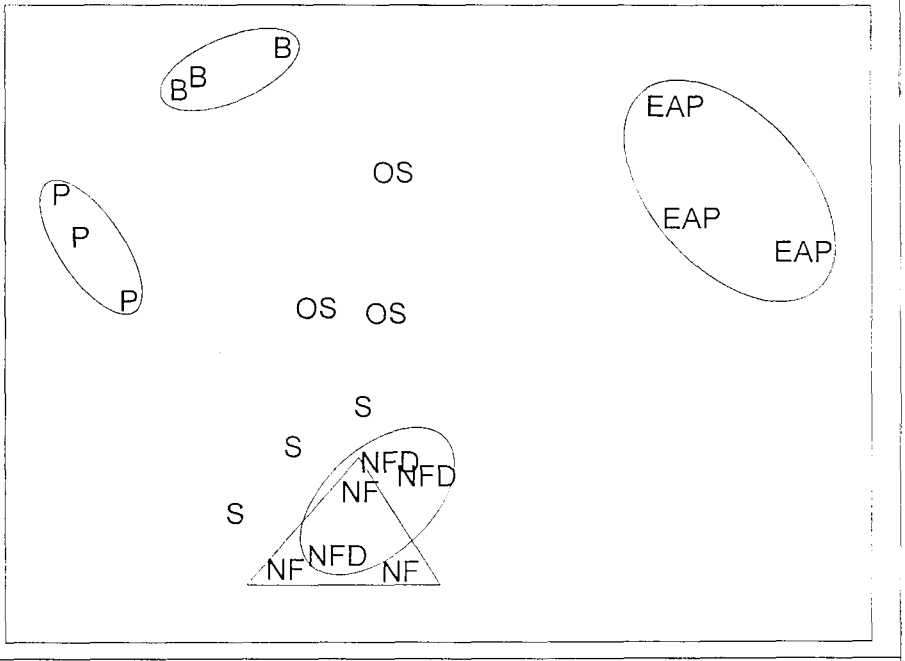
and separation of sites by species assemblages (< 40 % similarity) for most sites (Fig. 4.8.a). Samples from Eight-Acre Pond had > 50 % similarity, whilst being > 95 % dissimilar from each of the other sampling sites. Pennington and Butts lagoons each had > 60 % within site similarity, they were > 70 % dissimilar to each other and > 90 % dissimilar from all other sites. Normandy Farm ditch also had > 60 % within site similarity of samples, they were most similar to two samples from Salterns lagoon, but at < 40 % similarity. Samples from Normandy Farm also grouped together, but at ~ 49 % similarity only. Species assemblages were most variable in Oxey South and Salterns lagoons and this was identified by dispersal of replicates from these sites with the Normandy Farm and Normandy Farm ditch samples.

The pattern of similarity between sites was not well represented by a 2-D MDS ordination (Fig. 4.8.b). Definition was maintained between sites that were < 20 % dissimilar and replicates from the same site plotted together. The group of sites including Normandy Farm, Normandy Farm ditch, Salterns and Oxey South lagoons was not well represented – the plot had a stress of 0.15, which is at the limit for useful interpretation. Essentially, the analysis suggests these latter four sites have the most similar species assemblages and that Eight-Acre Pond, Butts and Pennington lagoons each represent alternate assemblage types.

By repeating the analysis with fourth-root transformed species assemblage data, site similarity by species composition could be assessed, with less influence of species abundance (Fig. 4.9.a). Within sites variability was reduced (> 50 % similarity in Oxey South, > 60 % similarity between samples within all other sites), suggesting that patchiness of species abundance was more responsible than species presence/absence for within site differences. Similarity between sites also increased for all sites, except between Butts and Pennington lagoons. Similarity of species composition was increased between Pennington and Oxey South lagoons, relative to Butts lagoon probably owing to a greater number of similar species in Pennington and Oxey South lagoons and a low total number of species in Butts lagoon. The different species assemblages in both Eight-Acre Pond and Butts lagoons in comparison to other sites were also emphasised. Similarity was high (relatively) between Normandy Farm ditch and Salterns lagoon (> 50 % similarity).



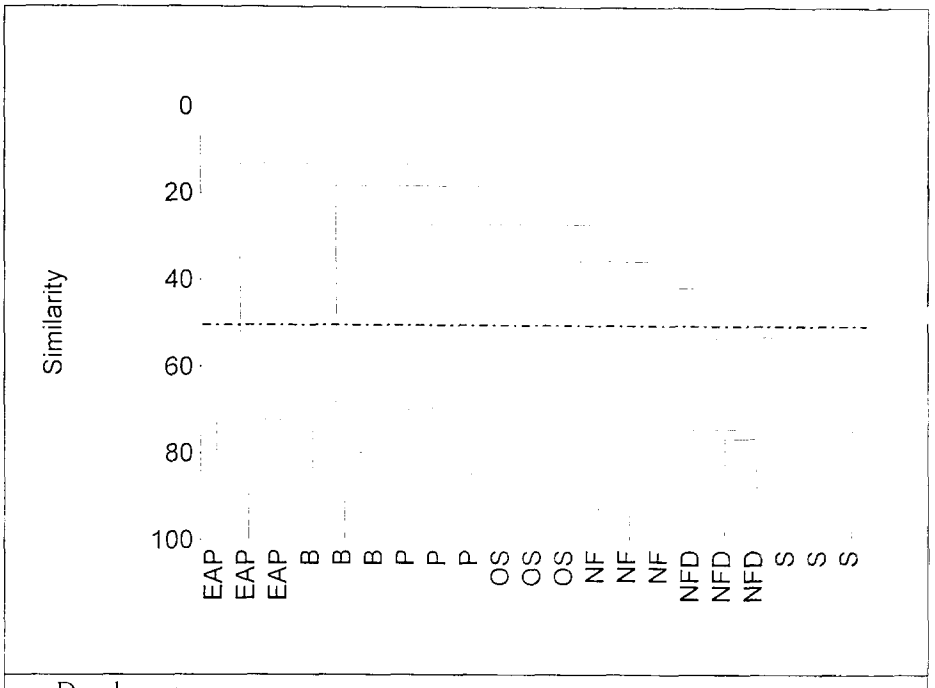
a. Dendrogram.



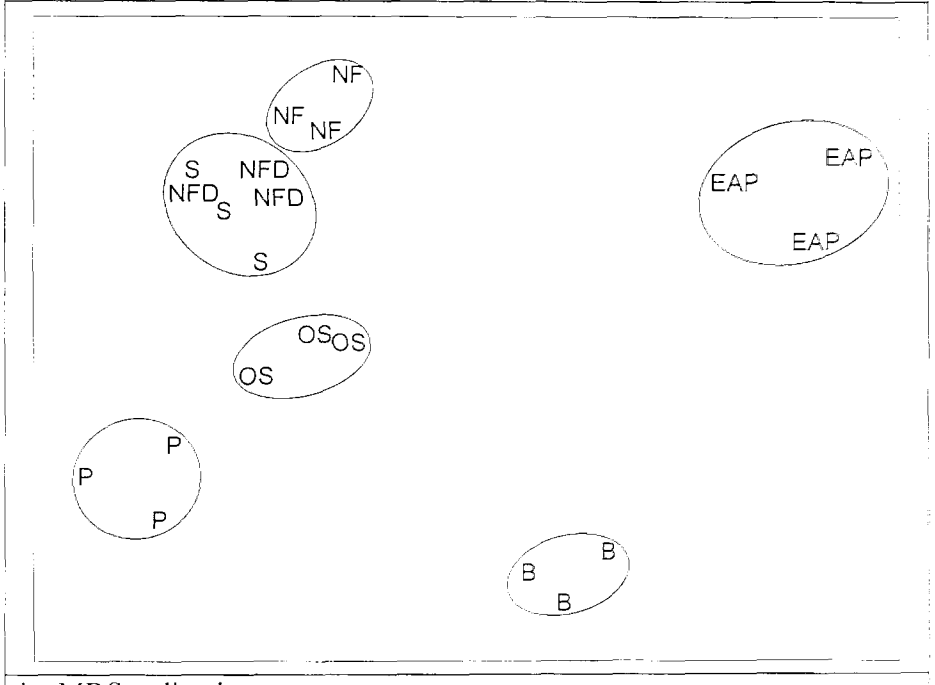
b. MDS ordination

Fig. 4.8. Bray-Curtis site similarity of the Keyhaven-Lymington lagoons based on untransformed nematode assemblage data. Stress = 0.15. Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

The MDS ordination of similarity between fourth-root transformed nematode assemblages distinguished all sites except Normandy Farm ditch and Salterns lagoon although stress was still high (stress = 0.12, Fig. 4.9.b). The species assemblages in Normandy Farm ditch and Salterns lagoon plotted in an intermediate position between Normandy Farm and Oxey South lagoons. Eight Acre Pond and Butts are



a. Dendrogram.



b. MDS ordination.

Fig. 4.9. Bray-Curtis site similarity of the Keyhaven-Lymington lagoons based on fourth-root transformed nematode assemblage data. Stress = 0.12.
Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

again isolated, but Pennington lagoon appears more similar to the group including Normandy Farm, Normandy Farm ditch Salterns and Oxey South. Within this latter group the site are distributed with highest average salinity sites at the top of the ordination and lowest average salinity at the bottom.

It should be noted that the high levels of stress recorded for both 2-D ordinations limit their usefulness, however, the results of the similarity analyses suggest that the sites divided into three groups by species assemblage and dominance: A. Eight-Acre Pond; B. Normandy Farm, Normandy Farm ditch, Salterns and Oxey South and; C. Butts lagoons. Pennington was similar to Oxey South lagoon in terms of species assemblage, and Butts lagoon in terms of species dominance and might therefore be considered intermediate between groups B and C.

Calculation of the ANOSIM R statistic for all pairs of sites confirmed that the nematode species assemblages between sites are significantly different for both untransformed and fourth-root transformed data (global $r = 0.976$, $p < 0.001$ and; global $r = 0.992$, $p < 0.001$, respectively). Difference between site assemblages by pair-wise comparison could not be tested - owing to the small number of replicates per site ($n = 3$), the significance level of this test was restricted to $p < 0.1$.

b *Similarity of species assemblages*

i Within sites, between replicates

Similarity of species assemblages between replicates and sites was estimated using Similarity Percentages (SIMPER) analysis. Within sites similarity of species assemblages was > 40 % for all sites (Table 4.9). Species assemblages were most variable in Oxey South and Salterns lagoons (< 45 % similarity between replicate assemblages) and least variable in Pennington lagoon (> 70 % similarity between replicates). The number of species accounting for 90 % of within site similarity varied between sites and appeared to decrease with increasing dominance. The percentage contribution to overall within site similarity of the species most similar between replicates was lowest in Salterns lagoon (18 %), which had the lowest dominance and the highest site evenness (J'), and highest in Butts lagoon (42 %), which had the highest dominance and lowest diversity. The species contributing the most to within sites similarity were the most dominant species at all sites, except Butts and Salterns lagoons. The second most abundant or co-dominant species were most similar between replicates in both these lagoons, reflecting greater patchiness of the dominant species, relative to the other abundant species.

Sites	Within site Similarity (%)	No. spp 90% of similarity	Species most similar between replicates, within site	Mean Abundance 10cm^{-2}	Contribution to site similarity (%)
Butts	66.53	4	*Thalassomonhystera sp Ab*	712.79	42.64
Pennington	72.56	5	*Desmolaimus zeelandicus*	1372.48	31.59
Oxey South	42.83	4	*Terschellingia longicaudata*	543.09	41.33
Salterns	43.88	12	*Sabatieria pulchra sp A*	391.71	18.09
Eight Acre Pond	62.12	6	*Chromadora nudicapitata*	693.46	34.50
Normandy Farm Ditch	63.99	16	*Terschellingia longicaudata*	1367.22	41.84
Normandy Farm	53.98	14	*Daptonema procerum*	454.52	40.21

Table 4.9. Similarity of nematode assemblages within sites between replicates in the Keyhaven-Lymington lagoon system, the number of species accounting for 90 % of that similarity, and the species most important to it. Untransformed abundance data, 10 cm^{-2}.

Recalculation of the SIMPER analysis with fourth-root transformed assemblage data increased the estimated similarity between replicates at all sites, except Pennington lagoon (Table 4.10). In each case the increase in similarity was < 10 %, whilst for Pennington lagoon the decrease was < 5 %. The decrease in similarity between replicates at Pennington was owing to co-dominance of three species (75 % of abundance), each with low variability of abundance between replicates, and a higher variability of rare species between replicates, the latter of which become more important in the analysis after fourth-root transformation of the data. At the other sites, most species had a similar variability between replicates.

The species contributing the greatest percentage to within site similarity remained the same for all sites, except Oxey South Lagoon, where *Daptonema setosum* replaced *Terschellingia longicaudata* as the most similar species between replicates. These species were co-dominant in Oxey South lagoon, but *D. setosum* had least variable abundance between sites. For each site, fourth-root transformation of the data set halved the percentage contribution to overall site similarity of the species most similar between replicates. This was with the exception of Normandy Farm and Normandy Farm ditch, in which the reduction was to almost 25 % of that of the contribution for untransformed data. Again, percentage contribution to overall site

similarity by the species most similar between replicates was lowest in Salterns lagoon and highest in Butts lagoon. Also the low percentage contributions to overall site similarity by the most similar species between replicates in Normandy Farm and Normandy Farm ditch reflected high evenness and diversity in these sites.

Sites	Within site similarity (%)	No. spp to 90% similarity	Species most similar between replicates, within site	Mean Abundance, $10cm^{-2}$	Contribution to site similarity (%)
Butts	72.12	5	*Thalassomonhystera sp Ab*	712.79	23.95
Pennington	69.88	11	*Desmolaimus zeelandicus*	1372.48	15.40
Oxey South	54.32	12	*Daptonema setosum*	435.94	17.66
Salterns	68.93	16	*Sabatieria pulchra sp A*	391.71	8.05
Eight Acre Pond	67.65	10	*Chromadora nudicapitata*	693.46	14.08
Normandy Farm Ditch	74.99	21	*Terschellingia longicaudata*	1367.22	8.92
Normandy Farm	65.62	21	*Daptonema procerum*	454.52	9.22

Table 4.10. Similarity of nematode assemblages between replicates within sites in the Keyhaven-Lymington lagoon system, the number of species accounting for 90 % of that similarity, and the species most important to it. 4^{th} root transformed abundance 10 cm^{-2}.

ii Between sites

Between sites, species assemblages were dissimilar (> 65 % dissimilarity) for all pair-wise comparisons of untransformed data (Table 4.11). Particularly, the species assemblage in Eight-Acre Pond was >95 % dissimilar from all other sites. Also, whilst species assemblages were dissimilar between Pennington and Butts lagoons (75 % dissimilarity), each were highly dissimilar from all other lagoons (89 – 98 % and 87 – 96 % dissimilarity, respectively). These values of dissimilarity reflect the shared species between site pairs (Table 4.12), and the relative abundance of species between sites.

The lowest percentage of shared species was recorded between Butts lagoon and all other sites (9.1 – 20 %), although this mainly reflects the low species diversity in Butts, whilst a low percentage of shared species between Eight-Acre Pond lagoon and all other sites (11.1 – 22.4 %) is more likely to be owing to the different species in Eight-Acre Pond. Equally, Normandy Farm ditch and Salterns lagoon were the

most similar sites but still at a relatively high dissimilarity (67 % dissimilarity), and of the 48 species recorded between them only 52 % occurred in both sites. This was also recorded between Salterns and Oxey South where of a total between site diversity of 44 species, 50 % were recorded in both (dissimilarity 77 %).

Site	B	P	OS	S	EAP	NFD
P	75.90					
OS	87.12	92.31				
S	94.23	89.71	77.45			
EAP	96.65	98.41	95.62	97.29		
NFD	95.24	91.16	74.19	66.95	96.28	
NF	94.78	91.84	89.28	74.28	95.54	78.92

Table 4.11. Percentage dissimilarity of nematode assemblages between sites in the Keyhaven-Lymington lagoon system. Based on untransformed species data, per 10 cm^{-2}. Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

Sites	B	P	OS	S	EAP	NFD
P	33 (9.1)					
OS	39 (17.9)	41 (31.7)				
S	40 (20.0)	43 (30.2)	44 (50.0)			
EAP	35 (20.0)	45 (11.1)	49 (22.4)	51 (21.6)		
NFD	45 (17.8)	50 (22.0)	49 (44.9)	48 (52.1)	55 (21.8)	
NF	49 (16.3)	50 (22.0)	59 (30.5)	55 (43.6)	61 (19.7)	61 (37.7)

Table 4.12. Summed nematode species diversity, S, between site pairs and the percentage of those species recorded in both sites (value in brackets). Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

For each pair-wise comparison of sites, the species cumulatively representing 50 % of the measured dissimilarity were good representatives of that dissimilarity. Beyond 50 % cumulative species contribution to site dissimilarity, within site variability of species abundance reduced the discriminatory effectiveness of species (measured by mean similarity ÷ standard deviation of similarity). For each pair-wise comparison of species dissimilarity between sites, 50 % of dissimilarity was accounted for by no more than 6 species, whilst 90 % of dissimilarity was accounted for by a maximum of 29 species (between Normandy Farm and Normandy Farm ditch) and by a minimum of 6 species (between Oxey South and Butts lagoon). Many species contributed to the difference between Normandy Farm and Normandy Farm ditch, owing to the high evenness and diversity at these sites. In contrast, few species contributed to the difference between Oxey South and Butts lagoons owing

to the relatively high dominance in each and low diversity between them.

Overall, a total of 18 species accounted for 50 % of all pair-wise calculations of between site dissimilarity, these included the 14 most dominant species throughout the system (70.78 % total abundance), species occurring in only one site (*A. parva*, *Metalinhomoeus sp A* and *M. viviparum*) and one species (*Chromadoridae sp A*) which occurred in all sites east from and including Oxey South lagoon (Table 4.13). Maximum percentage contribution to pair-wise site dissimilarity by any one species ranged between 12 and 30 %. However, from the 21 pair-wise comparison, only 5 species were contributed most to between site dissimilarity. This was owing to the relatively high abundance and dominance of these species in one (or in the case of *D. ocellata*, two) sites in comparison to the others (*D. ocellata*, Butts/Pennington; *D. zeelandicus*, Oxey South; *Sabatieria pulchra* sp B, Salterns; *C. nudicapitata*, Eight-Acre Pond and; *T. longicaudata*, Normandy Farm ditch). Only Normandy Farm was not represented in this manner, owing to high species diversity and evenness, but low abundance.

As with other analyses, fourth-root transformation of the data reduced the estimate of dissimilarity between all site pairs, although dissimilarity remained high for site pairs including Eight-Acre Pond or Butts lagoons (Table 4.14). Again, this indicates the disparity of species in Eight Acre Pond and Butts lagoons relative to the other sites. Normandy Farm Ditch and Salterns were most similar (47 % dissimilarity), followed by Normandy Farm and Salterns (57 % dissimilarity). Salterns and Oxey South (58 % dissimilarity) and Normandy Farm and Normandy Farm ditch (60 % dissimilarity). Pennington lagoon is least dissimilar to Butts in terms of untransformed data, and least dissimilar to Oxey South lagoon in terms of fourth-root transformed data analysis. The number of species contributing to dissimilarity between sites increased and their percentage contributions to that dissimilarity became more evenly distributed following fourth-root transformation of the data. However, the discriminatory effectiveness of each species was low (dissimilarity mean / sd < 0.5 or less).

	B		P		OS		S		EAP		NFD	
P	*D. zeelandicus:*	23.41										
	D. cephalata:	23.27										
	Thalass sp Ab:	12.32										
OS	*D. ocellata:*	28.06	*D. zeelandicus:*	22.57								
	Thalass sp Ab:	24.72	*D. cephalata:*	22.34								
			D. ocellata:	19.57								
S	*D. ocellata:*	20.29	*D. zeelandicus:*	19.01	*T. longicaudata:*	15.38						
	Thalass sp Ab:	16.26	*D. cephalata:*	17.80	*S. pulchra sp B:*	13.23						
	S. pulchra sp B:	8.54	*D. ocellata:*	17.30	*S. pulchra sp A:*	11.41						
	S. pulchra sp A:	7.22			*D. setosum:*	10.71						
EAP	*D. ocellata:*	21.46	*D. zeelandicus:*	19.09	*C. nudicapitata:*	21.98	*C. nudicapitata:*	15.28				
	Thalass sp Ab:	18.03	*D. cephalata:*	18.93	*T. longicaudata:*	16.63	*Teratorhabditis sp A:*	9.93				
	C. nudicapitata:	15.82	*D. ocellata:*	16.79	*Teratorhabditis sp A:*	14.59	*S. pulchra sp B:*	8.95				
							S. pulchra sp A:	7.63				
							A. parva:	6.60				
							D. procerum:	6.15				
NFD	*T. longicaudata:*	22.58	*D. zeelandicus:*	16.19	*T. longicaudata:*	21.96	*T. longicaudata:*	25.89	*T. longicaudata:*	23.90		
	D. ocellata:	15.79	*T. longicaudata:*	15.91	*D. setosum:*	10.29	*S. pulchra sp B:*	6.63	*C. nudicapitata:*	11.24		
	Thalass sp Ab:	11.65	*D. cephalata:*	15.80	*Metalinhomeous sp A:*	5.99	*S. pulchra sp A:*	5.74	*Teratorhabditis sp A:*	7.48		
			D. ocellata:	14.71	*D. korneense:*	5.89	*Metalinhomeous sp A:*	5.25	*A. parva:*	5.12		
					Thalass sp C:	5.66	*Thalass sp C:*	4.50	*Metalinhomeous sp A:*	4.05		
					M. viviparum:	4.22	*D. procerum:*	4.47				
NF	*D. ocellata:*	25.02	*D. zeelandicus:*	21.51	*T. longicaudata:*	19.78	*S. pulchra* sp B:	12.43	*C. nudicapitata:*	18.77	*T. longicaudata:*	30.98
	Thalass sp Ab:	19.90	*D. cephalata:*	21.28	*D. procerum:*	18.21	*D. procerum:*	11.09	*D. procerum:*	13.58	*D. procerum:*	6.60
	D. procerum:	12.08	*D. ocellata:*	19.65	*D. setosum:*	14.15	*S. pulchra sp A:*	10.73	*Teratorhabditis sp A:*	12.72	*Metalinhomeous sp A:*	5.24
							T. longicaudata:	7.89	*A. parva:*	8.30	*D. korneense:*	4.09
							D. setosum:	4.50			*M. viviparum:*	3.71
							Chromadoridae sp A:	4.47				

Table 4.13. The percentage contribution of nematode species accounting for 50 % of between site dissimilarity in the Keyhaven-Lymington lagoon system. SIMPER analysis of untransformed species data. *Thalass - Thalassomonhystera.
Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

Sites	B	P	OS	S	EAP	NFD
P	81.52					
OS	76.43	67.7				
S	84.25	70.57	57.96			
EAP	84.85	91.54	84.10	88.62		
NFD	83.82	75.43	64.50	47.13	86.03	
NF	82.73	77.63	70.51	56.61	85.21	59.95

Table 4.14. Dissimilarity of nematode assemblages (as a percentage) between sites in the Keyhaven-Lymington lagoon system. Based on fourth root transformed species data. Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

c *Dominant Species*

The full species list for the Keyhaven-Lymington lagoon system is given in Table 4.15 as average percentage abundance for all samples combined and average percentage abundance per site. Although a total of 81 species were recorded in the system, 50 % of the total system abundance was represented by only 8 species, and 90 % of abundance by 31 species (9.88 % and 38.27 % of the system diversity, S, respectively). There were two co-dominant species in the system that together accounted for only 22 % of the total number of nematode individuals. These were accompanied by 4 species which each accounted for 5 – 10 % of the total system abundance and 19 species which each accounted for 1 – 5 % of the total system abundance. The ten most abundant species were *Diplolaimella ocellata* (12 %), *Terschellingia longicaudata* (10 %), *Dichromadora cephalata* (7.9 %), *Desmolaimus zeelandicus* (7.0 %), *Daptonema procerum* (5.8 %), *Daptonema setosum* (5.3 %), *Thalassomonhystera sp Ab* (3.8 %), *Chromadora nudicapitata* (3.8 %), *Sabatieria pulchra sp B* (3.2 %) and, *Daptonema kornoeense* (2.5 %).

Of the ten most abundant species *Terschellingia longicaudata, Dichromadora cephalata, Daptonema procerum, Daptonema setosum, Chromadora nudicapitata, Sabatieria pulchra* group, *Daptonema kornoeense* and, *Desmolaimus zeelandicus* have been recorded in European estuaries (Soetaert *et al.*, 1995). Also, *Daptonema setosum, Desmolaimus zeelandicus, Chromadora nudicapitata, Dichromadora cephalata*, and *Daptonema procerum* have been recorded in the Baltic Sea (Brenning, 1973), whilst *D. ocellata* has been record in the Venice Lagoon, Italy (Villano and Warwick, 1995). Species identification of the *Thalassomonhystera* genus was not possible due to a paucity of 'good' males, but these species probably

Average percent abundance	All sites	B		P		OS		S		EAP		NFD		NF	
	Average	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD
Diplolaimella ocellata	12.07	38.67	14.89	23.56	5.55	6.67	4.00	0.67	1.15	2.89	2.34	0.22	0.38	0.00	0.00
Terschellingia longicaudata	10.70	0.00	0.00	0.00	0.00	37.33	25.44	11.11	10.55	0.00	0.00	34.22	4.68	0.00	0.00
Dichromadora cephalata	7.90	0.00	0.00	25.11	5.39	0.00	0.00	3.33	0.67	0.00	0.00	0.89	0.38	0.00	0.00
Desmolaimus zeelandicus	7.02	0.00	0.00	25.78	4.44	0.44	0.38	0.44	0.77	0.00	0.00	0.00	0.00	0.00	0.00
Daptonema procerum	5.81	0.22	0.38	2.67	3.06	1.78	1.68	10.00	4.00	0.00	0.00	4.22	1.02	29.56	4.73
Daptonema setosum	5.30	6.67	1.15	2.22	2.78	37.11	15.45	6.89	3.67	0.44	0.38	0.44	0.77	3.33	2.40
Thalassomonhystera sp Ab	3.82	33.56	15.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.89	0.77	0.44	0.38
Chromadora nudicapitata	3.77	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	33.33	4.67	0.67	0.67	1.11	1.02
Sabatieria pulchra sp B	3.42	0.00	0.00	0.44	0.38	0.22	0.38	14.67	5.46	0.00	0.00	3.78	2.14	0.22	0.38
Daptonema kornoeense	2.53	0.00	0.00	0.00	0.00	0.44	0.77	8.44	4.68	0.22	0.38	5.78	3.85	3.78	2.78
Sabatieria pulchra sp A	2.51	0.00	0.00	0.00	0.00	0.44	0.38	13.33	1.15	0.00	0.00	2.22	1.68	0.22	0.38
Teratorhabditis sp A	2.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	22.89	5.35	0.00	0.00	0.00	0.00
Thalassomonhystera sp Aa	1.90	12.00	6.11	0.00	0.00	0.22	0.38	0.22	0.38	0.22	0.38	0.89	0.38	0.22	0.38
Thalassomonhystera sp C	1.87	0.00	0.00	0.00	0.00	0.00	0.00	0.44	0.77	0.00	0.00	5.56	3.36	6.89	6.19
Viscosia viscosa	1.80	0.00	0.00	4.44	0.38	2.67	2.40	0.00	0.00	0.00	0.00	2.00	2.40	0.00	0.00
Tripyloides sp A	1.60	0.00	0.00	2.22	0.77	1.56	0.38	1.56	2.14	0.22	0.38	3.56	1.68	0.22	0.38
Atrochromadora parva	1.59	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	13.78	5.09	0.00	0.00	0.00	0.00
Dichromadora sp A	1.57	0.00	0.00	0.44	0.77	2.00	1.15	4.89	3.36	0.44	0.77	0.67	0.00	2.89	1.39
Chromadoridae sp A	1.40	0.00	0.00	0.00	0.00	0.67	0.67	5.56	4.23	0.44	0.77	0.89	1.02	1.33	0.67
Chromadoridae sp B	1.33	0.00	0.00	4.22	3.91	0.00	0.00	0.22	0.38	0.00	0.00	0.00	0.00	0.22	0.38
Daptonema sp B	1.30	0.00	0.00	1.11	0.38	0.67	0.67	2.00	0.67	0.00	0.00	0.89	0.38	5.56	3.08
Metalinhomeous sp A	1.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.78	1.02	0.00	0.00
Daptonema oxycerca	1.11	0.00	0.00	0.00	0.00	0.44	0.38	1.11	0.38	0.00	0.00	1.11	0.77	8.22	3.15
Thalassomonhystera sp Ac	1.09	0.00	0.00	0.44	0.77	0.00	0.00	3.56	2.69	0.00	0.00	2.22	1.02	2.00	2.40
Thalassomonhystera sp indet	1.04	6.00	3.53	0.00	0.00	0.22	0.38	0.22	0.38	0.00	0.00	1.11	0.38	1.78	1.02
Theristus acer	0.94	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.00	0.67	0.00	0.00	1.11	0.38
Sabatieria sp A	0.92	0.00	0.00	0.00	0.00	0.22	0.38	1.56	1.39	0.00	0.00	2.67	3.06	0.00	0.00

Table 4.15. Nematode species list for the Keyhaven-Lymington lagoon system as average percentage abundance for all samples combined and mean (and sd) percentage abundance per site.
Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

Average percent abundance	All sites	B		P		OS		S		EAP		NFD		NF	
	Average	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD
Desmodoridae sp A	0.87	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.00	3.06	0.00	0.00
Thalassomonhystera parva	0.73	0.00	0.00	0.22	0.38	0.44	0.77	0.00	0.00	0.00	0.00	2.67	1.33	2.22	1.02
Daptonema sp F	0.64	0.00	0.00	0.00	0.00	0.22	0.38	0.44	0.38	0.00	0.00	2.67	0.00	0.00	0.00
Axonolaimus cf paraspinosus	0.52	0.00	0.00	0.00	0.00	1.11	1.02	0.00	0.00	0.00	0.00	0.00	0.00	5.56	2.52
Paracyatholaimus cf pentadon	0.47	0.00	0.00	0.89	1.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.22	1.54
Sphaerolaimus gracilis	0.46	0.00	0.00	0.44	0.77	0.00	0.00	1.56	1.02	0.44	0.77	0.00	0.00	1.11	1.02
Spilophorella paradoxa	0.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.22	1.02	1.33	0.67	0.22	0.38
Leptolaimus papilliger	0.43	0.00	0.00	1.33	0.00	0.89	0.77	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hypodontolaimus sp B	0.39	0.00	0.00	1.33	1.15	0.22	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.38
Anoplostoma sp A	0.38	0.00	0.00	0.00	0.00	0.22	0.38	1.56	0.77	0.00	0.00	0.00	0.00	1.11	0.38
Daptonema sp G	0.37	0.00	0.00	0.00	0.00	0.67	0.67	0.89	0.38	0.00	0.00	0.67	0.67	0.89	1.02
Ptycholaimellus ponticus	0.36	0.00	0.00	0.00	0.00	1.11	1.02	1.56	1.02	0.22	0.38	0.44	0.77	0.00	0.00
Enoplus aff brevis	0.36	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.78	2.52
Chromadorita sp Bb	0.35	0.89	1.02	0.00	0.00	0.00	0.00	0.22	0.38	0.22	0.38	0.00	0.00	1.11	1.39
Sabatieria sp D	0.34	0.00	0.00	0.00	0.00	0.00	0.00	0.89	1.02	0.00	0.00	0.89	1.54	0.00	0.00
Euchromadora vulgaris	0.34	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.33	1.33	0.00	0.00	0.00	0.00
Adoncholaimus fuscus	0.34	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.78	2.04	0.44	0.38
Hypodontolaimus balticus sp B	0.34	0.00	0.00	1.33	1.76	0.00	0.00	0.22	0.38	0.00	0.00	0.00	0.00	0.44	0.38
Daptonema normandicum	0.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.56	2.14
Calyptronema maxweberi	0.30	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.38	0.00	0.00	1.56	1.02	0.00	0.00
Aponema/Calmicrolaimus sp B	0.28	0.22	0.38	0.00	0.00	0.22	0.38	0.00	0.00	0.44	0.38	1.11	1.02	0.00	0.00
Leptolaimus limicolus	0.25	0.00	0.00	1.11	1.39	0.22	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cyatholaimus sp A	0.24	0.00	0.00	0.22	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00	2.40
Neochromadora poecilosomoides	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.44	0.77	0.00	0.00	0.00	0.00
Chromadorita sp Ba	0.23	0.44	0.38	0.00	0.00	0.00	0.00	0.89	0.38	0.00	0.00	0.00	0.00	0.22	0.38
Rhabditis marina	0.21	0.22	0.38	0.00	0.00	0.22	0.38	0.44	0.77	1.33	1.76	0.00	0.00	0.00	0.00
Terschellingia communis	0.21	0.00	0.00	0.00	0.00	0.22	0.38	0.00	0.00	0.00	0.00	0.89	0.38	0.00	0.00
Oncholaimus aff. dujardinii	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.33	1.76	0.00	0.00	0.00	0.00
Daptonema sp H	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.56	2.14

Table 4.15. Continued...

Average percent abundance	All sites	B		P		OS		S		EAP		NFD		NF	
	Average	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD
Monhystrella sp A	0.15	0.22	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.38	0.22	0.38	0.22	0.38
Daptonema sp K	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.38	0.00	0.00	0.22	0.38	1.11	0.38
Chromadorella filiformis	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.78	1.02	0.00	0.00	0.00	0.00
Anticoma sp A	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.11	0.77	0.00	0.00	0.00	0.00
Linhomoeous sp B	0.14	0.00	0.00	0.00	0.00	0.67	0.00	0.44	0.77	0.00	0.00	0.00	0.00	0.67	0.67
Oncholaimus sp A	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.11	1.39	0.00	0.00	0.00	0.00
Hypodontolaimus balticus	0.10	0.00	0.00	0.22	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.38
Halalaimus sp A	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.38	0.00	0.00	0.22	0.38	0.67	0.67
Cyatholaimus sp indet	0.07	0.00	0.00	0.22	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Viscosia sp B	0.06	0.22	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.38
Dichromadora geophila	0.06	0.44	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sabatieria sp indet	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.38	0.00	0.00
Diplolaimella sp A	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.38	0.00	0.00
Camacolaimus tardus	0.04	0.22	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Praeacanthoncus punctatus	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.38	0.00	0.00	0.00	0.00
Tylenchidae sp A	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.38	0.00	0.00
Daptonema sp J	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.38
Xyalidae sp A indet	0.02	0.00	0.00	0.00	0.00	0.22	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Adoncholaimus sp B	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.38
Dichromadoridae sp A	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.38
Syringolaimus sp A	0.02	0.00	0.00	0.00	0.00	0.22	0.38	0.00	0.00	0.22	0.38	0.00	0.00	0.00	0.00
Aphelenchoides sp A	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.38	0.00	0.00	0.00	0.00
Viscosia glabra	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.38	0.00	0.00	0.00	0.00
Daptonema sp indet	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.38
Sphaerolaimus balticus	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.38

Table 4.15. Continued...

equate to the Monhysteridae recorded in other European brackish water environments (Olafsson and Elmgren, 1997; Soetaert *et al.*, 1995; Bouwman, 1983).

The distribution of the ten most abundant and dominant species between the lagoons is given in Fig. 4.10. a and b. The two co-dominant species in the system, *Terschellingia longicaudata* and *Diplolaimella ocellata*, each occurred in high relative abundance (>20 % of individuals) in two lagoons. *D. ocellata* was most abundant in sites with low average salinity, regardless of sediment type, but also occurred in all sites excluding Normandy Farm lagoon. It was most dominant in Butts lagoon, although it was most abundant (as absolute numbers) in Pennington lagoon, with abundance and dominance rapidly decreasing from west to east. The genus *Diplolaimella* Allgén, 1929 has been documented as tolerant of brackish water and fluctuating salinity (Warwick *et al.*, 1998; Villano and Warwick, 1995), whilst *D. ocellata* was found to be the most dominant species in association with green alga (*Ulva rigida* Agardh) and absent/rare in non-Ulva areas in the Venice lagoon (Villano and Warwick, 1995).

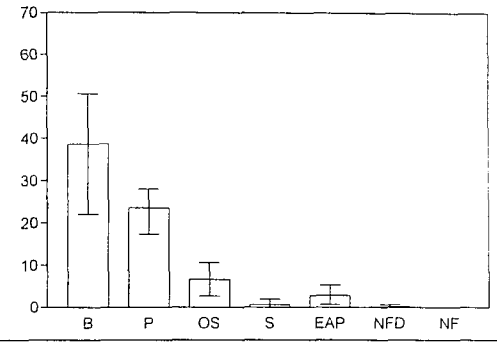
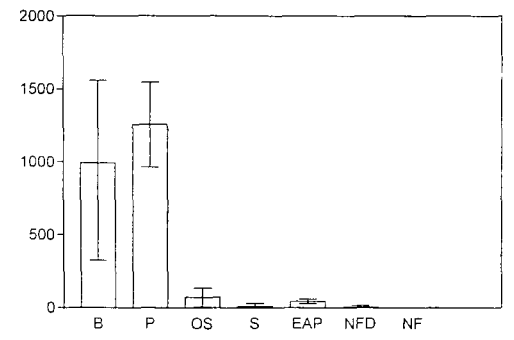
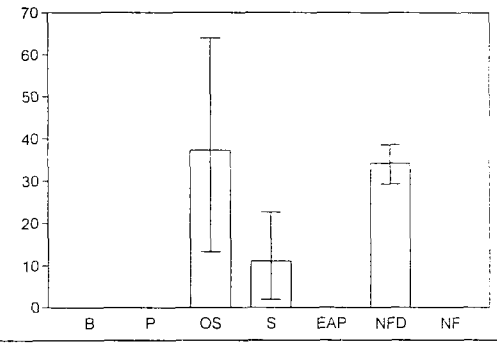
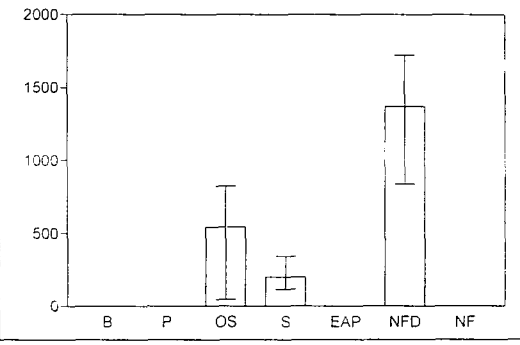
Terschellingia longicaudata (10 % of all individuals in the system) was limited to sites with silt/sand sediments, over any salinity range. It was most dominant in Oxey South lagoon, but most abundant (as absolute number of individuals) in the ditch adjacent to Normandy Farm. It was also recorded in lower abundance in Salterns lagoon. These three sites each have brackish to marine salinity (total range 0 – 48 ppt), similar to Pennington and Normandy Farm lagoons, but in combination with predominantly silty sediment. (Although data is not available, the sediment in Normandy Farm ditch was very similar to that in Salterns and Oxey South, pers. obs.). It would seem, therefore, that *T. longicaudata* is restricted in the system by availability of suitable substrate. Certainly Warwick *et al.* (1998) noted that UK records of this species are predominantly in muddy substrates with variable exposure and salinity (intertidal, subtidal and estuarine mudflats), whilst a survey of European estuaries quantified the range of *T. longicaudata* between 20 – 30 ppt but limited to sediment between 8 - 33 μm median particle size (Soetaert, *et al.*, 1995).

C. nudicapitata, *D. zeelandicus*, *D. cephalata* and *Thalassomonhystera sp Ab* were each dominant in one lagoon and were only recorded (in much lower numbers) in

lagoons with similar or higher average salinities, but not in lagoons with lower average salinity. The third and fourth most abundant species in the system, *D. cephalata* and *D. zeelandicus*, were co-dominant species in Pennington lagoon (25.11 % ± 5.39 and 25.78 % ± 4.44, respectively) with *D. ocellata* (23.56 % ± 5.55). Total nematode abundance was highest in Pennington lagoon, and averaged across replicates, *D. cephalata* occurred in a greater density than any other species in the system (1421.71 ± 596.79 inds 10 cm^{-2}) at this site. *Thalassomonhystera sp Ab* was almost entirely restricted to Butts lagoon (33.56 % ± 15.27), whilst *C. nudicapitata* was recorded in the 3 most easterly sites, but in much greater abundance in Eight-Acre Pond.

Daptonema procerum and *Daptonema setosum* were more evenly distributed, in terms of number of individuals, throughout the system. *D. procerum*, the fifth most abundant species, was dominant in Normandy Farm lagoon (29.56 % ± 4.73). It occurred in the marine/brackish water sites with silt/sand sediment, also being abundant in Normandy Farm ditch and Salterns lagoon, though in reduced dominance. *D. setosum* was relatively evenly distributed between the low to intermediate brackish lagoons, but with highest abundance and dominance (37.11 % ± 15.45) in Oxey South lagoon. *D. setosum* has been previously recorded as the dominant species in tidal freshwater in the Elbe estuary (Riemann, 1966) and in association with *Sabatieria pulchra* in or adjacent to cyanobacterial mats which create hypoxic sedimentary environments (Vopel and Arlt, 1995).

Sabatieria pulchra sp B and *Daptonema kornoeense*, were evenly distributed in the intermediate to high salinity range, but in low abundance and dominance. *S. pulchra* sp B had highest abundance in Salterns lagoon, whilst *D. korneense* had high abundance in Normandy Farm ditch, although both accounted for a higher proportion of individuals in Salterns lagoon. The distribution of these latter two species may indicate a preference to fine sediments and brackish/marine salinity, similar to *T. longicaudata* but with less tolerance to either salinity fluctuation (size of range) or high silt content due to their absence from Oxey South lagoon.

Percentage dominance	Abundance 10 cm^{-2}
1. *Diplolaimella ocellata*	
	
2. *Terschellingia longicaudata*	
	
3. *Dichromadora cephalata*	

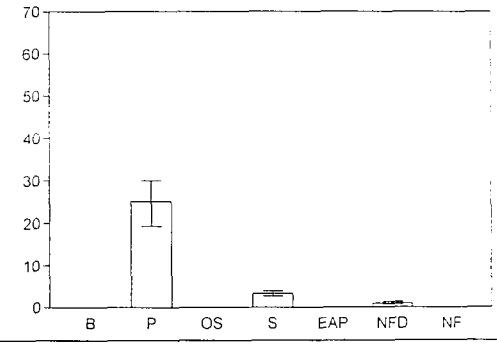
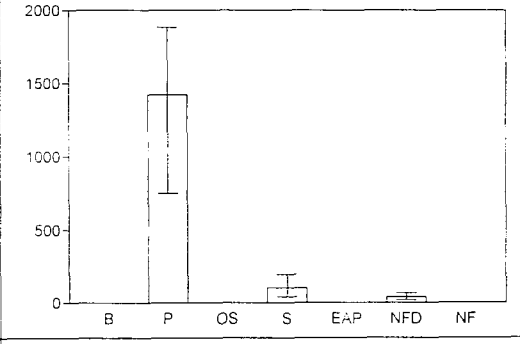
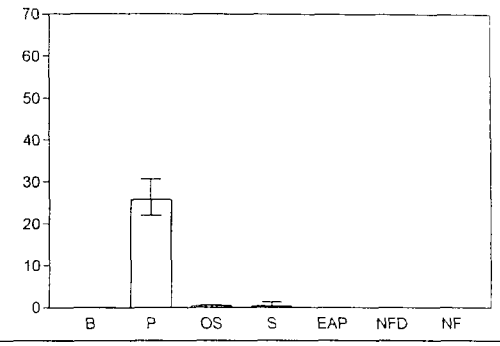
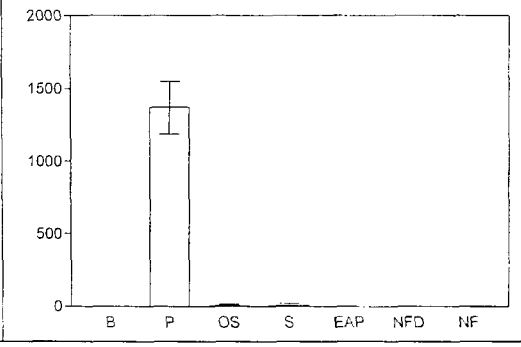
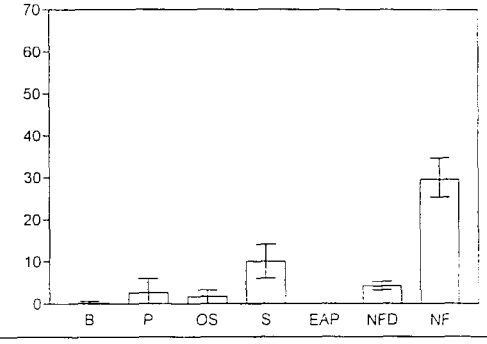
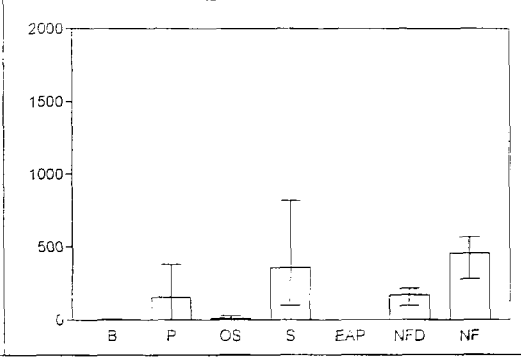
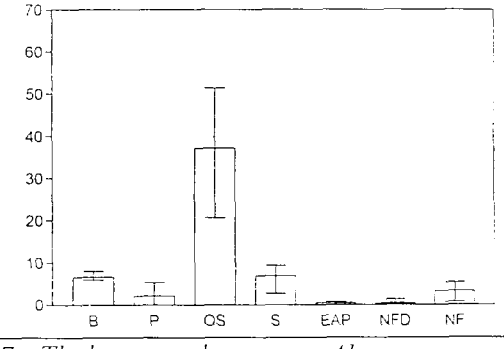
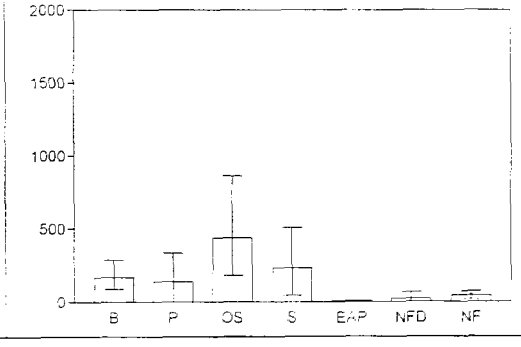

	

Fig. 4.10.a. Site Dominance. Bar graphs of mean percentage abundance, error bars are maximum and minimum values.	Fig. 4.10.b. Abundance distribution. Bar graphs of mean abundance 10cm^{-2}, error bars are maximum and minimum values .

Fig. 4.10. The ten most abundant nematode species in the Keyhaven-Lymington lagoons. Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

Percentage dominance	Abundance 10 cm^{-2}
4. *Desmolaimus zeelandicus*	
	
5. *Daptonema procerum*	
	
6. *Daptonema setosum*	
	
7. *Thalassomonhystera sp Ab*	

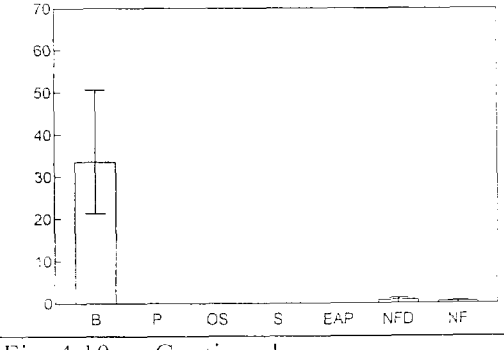
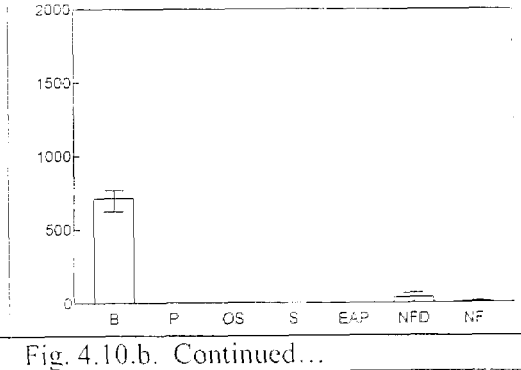
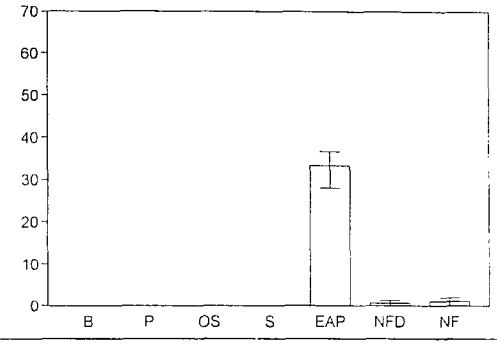
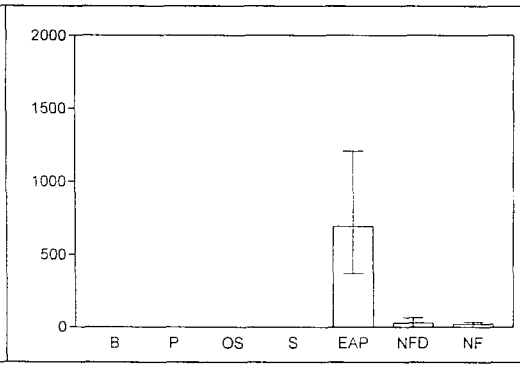
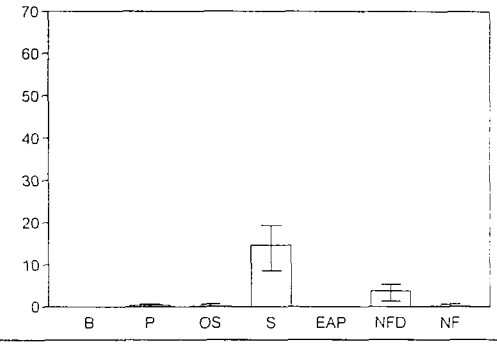
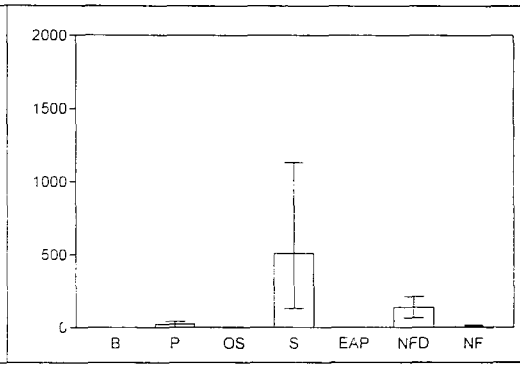

	

Fig. 4.10.a. Continued...	Fig. 4.10.b. Continued...

Percentage dominance	Abundance 10 cm^{-2}
8. *Chromadora nudicapitata*	
	
9. *Sabatieria pulchra sp B*	
	
10. *Daptonema kornoeense*	

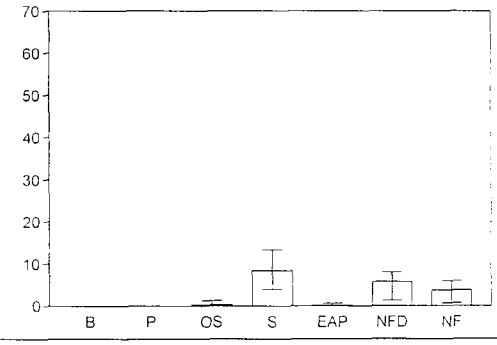
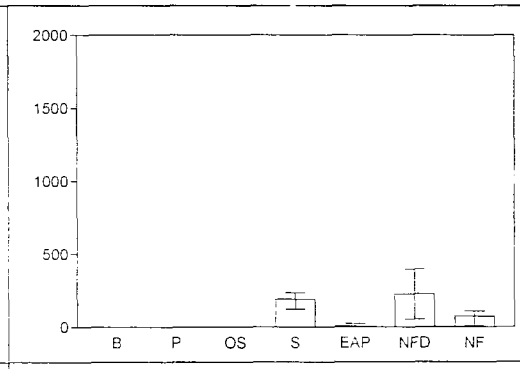

	

Fig. 4.10.a. Continued...	Fig. 4.10.b. Continued...

d *Species similarity (distribution between samples)*

Bray-Curtis similarity between species assemblages was calculated using both untransformed and fourth-root transformed data. Only Bray-Curtis similarity dendrograms are presented since the stress of forcing the Bray-Curtis similarity data into a 2-dimensional nMDS ordination was high (stress = 0.17, untransformed data; 0.16, fourth-root transformed data) making nMDS ordinations almost meaningless for data interpretation. Owing to this high level of stress, the similarity analyses were repeated including only species that accounted for 90% of nematode abundance throughout the system (31 species) but this reduced the available information rather than reducing the complexity of the analysis. The nMDS plots of these analyses also

had high stress values (0.17 and 0.15, respectively), which suggested that the stress was caused by the complexity of species distributions rather than 'noise' from rarer species.

The Bray-Curtis similarity dendrogram of untransformed species data (Fig. 4.11) loosely divided the species into six groups, each are rooted at very low similarity between species sub-groups. High similarity (> 60 %) of distribution is predominantly only recorded between pairs or triplicates of species. However, the abundance distribution of species within each group is similar (Fig. 4.12). They are:
Group A consists of species predominantly or only recorded in Eight-Acre Pond;
Group B represents rare species, predominantly recorded in one of either Normandy Farm, Normandy Farm ditch, or Butts (i.e. possibly species at a tolerance limit);
Group C species predominantly found in the western sites (Butts and Pennington), with limited abundance in the higher salinity sites;
Group D species with low abundance, predominantly recorded in the higher salinity, sandy sediment in Normandy Farm, with lower abundance in other fine sediment sites;
Group E similar to Group B, but represented only 3 species (All Thalassomonhystera sp) that are found throughout the system, but being most abundant in Butts lagoon.
Group F the largest number of species and those with the greatest abundance. Species most abundant in meso/polyhaline conditions, tolerant of wide salinity fluctuations and fine sediments (Normandy Farm and Salterns). Low abundance in the similarly polyhaline Eight-Acre Pond, may either be due to competition with more successful species which cannot tolerate wide variations in salinity or the coarser substrate. Also, species in Group F are less abundant in Oxey South lagoon, although the substrate is similar to Normandy Farm ditch and Salterns. It is possible also that these species are less able to tolerate the more variable conditions in Oxey South lagoon.

The distribution of *Terschellingia longicaudata* between sites was distinct from the other species, although most similar to the species in Group F. Its distribution was very discrete, having been recorded in only the three, fine sediment lagoons (Normandy Farm ditch, Salterns lagoon and Oxey South lagoon), and with abundance declining with decreasing salinity and increasing salinity range.

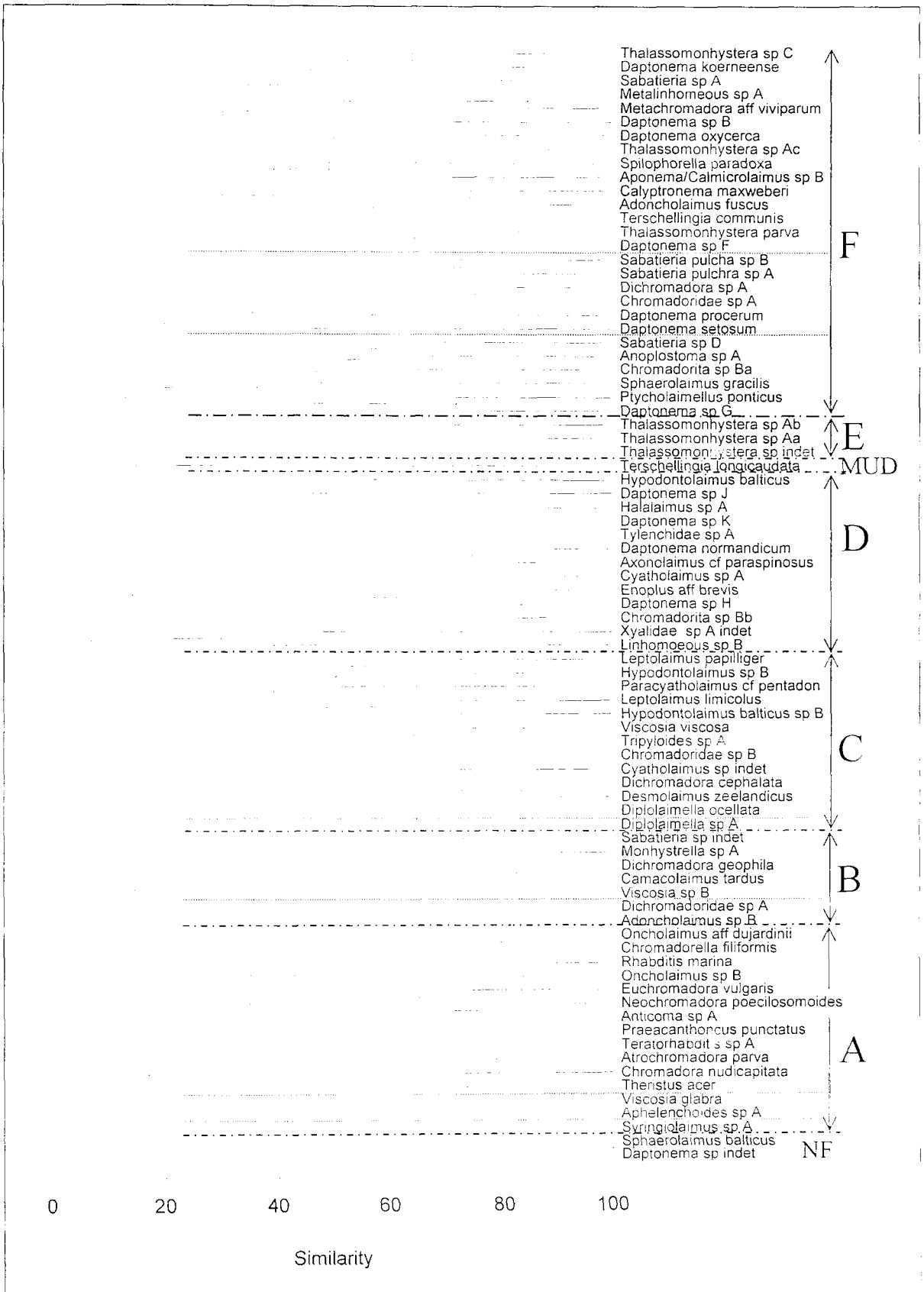


Fig. 4.11. Bray-Curtis similarity dendrogram of nematode species by occurrence in the Keyhaven-Lymington lagoon system (Untransformed species data).

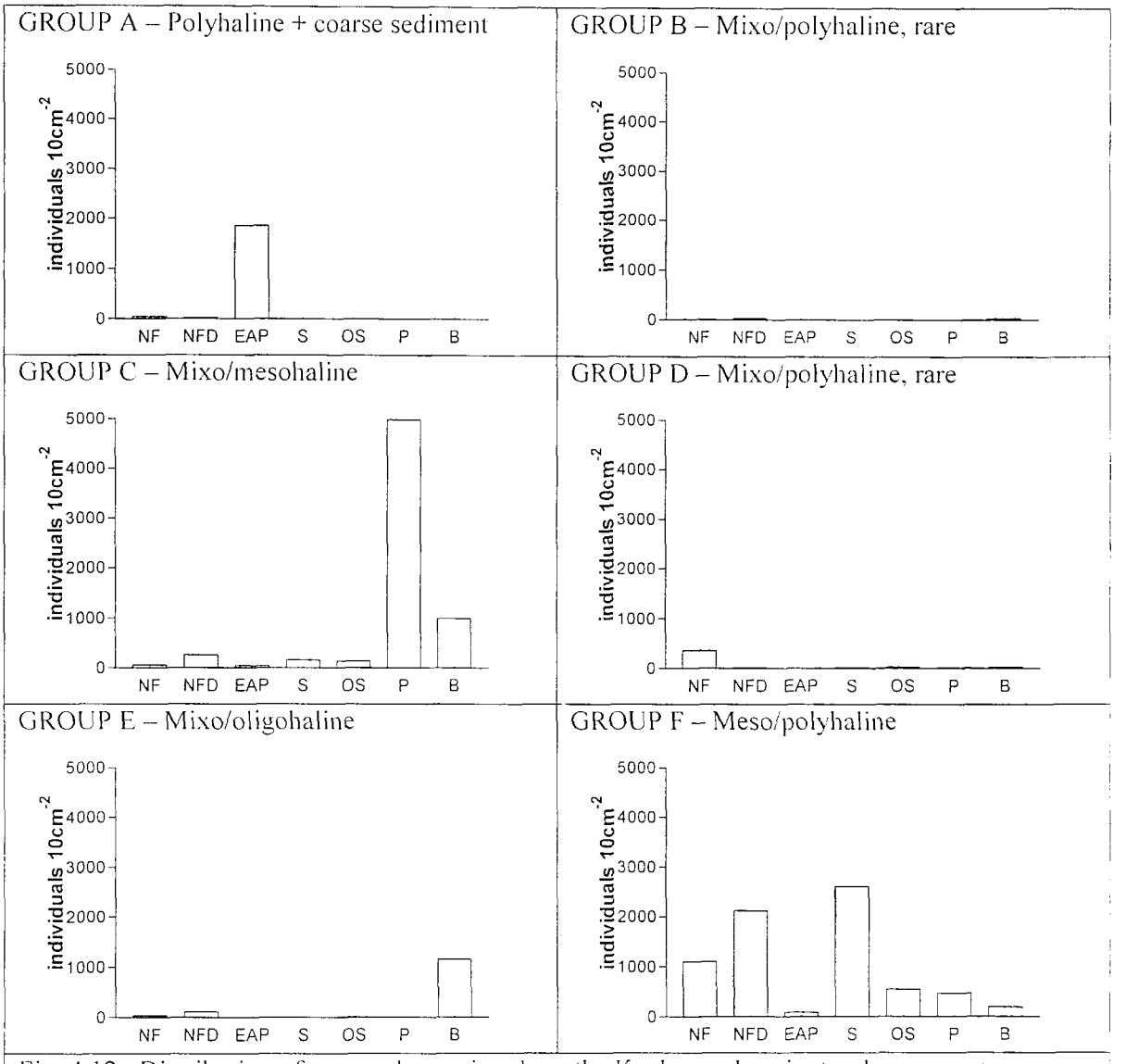


Fig. 4.12. Distribution of nematode species along the Keyhaven-Lymington lagoon system, grouped as indicated in Fig. 4.11 (Bray-Curtis similarity analysis of untransformed species assemblage data). Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

The species predominantly or solely occurring in Eight-Acre Pond were least similarly distributed to all other species in the system. The UK records predominantly list each in sand/gravel or seaweed substrates (Platt and Warwick, 1988), whilst, *Teratorhabditis* sp A is likely to be a terrestrial or plant-associated species (the sampling site was edged by over-hanging trees and leaf litter was visible in/on the lagoon bed). In contrast, the sites westwards from Normandy Farm ditch each had relatively fine sediments, but very variable salinity (poikilohaline: 1 – 40 ppt), although with slightly different ranges in each. It is likely, therefore, that whilst salinity records indicate that Eight-Acre Pond was polyhaline (14 – 40 ppt), the over-

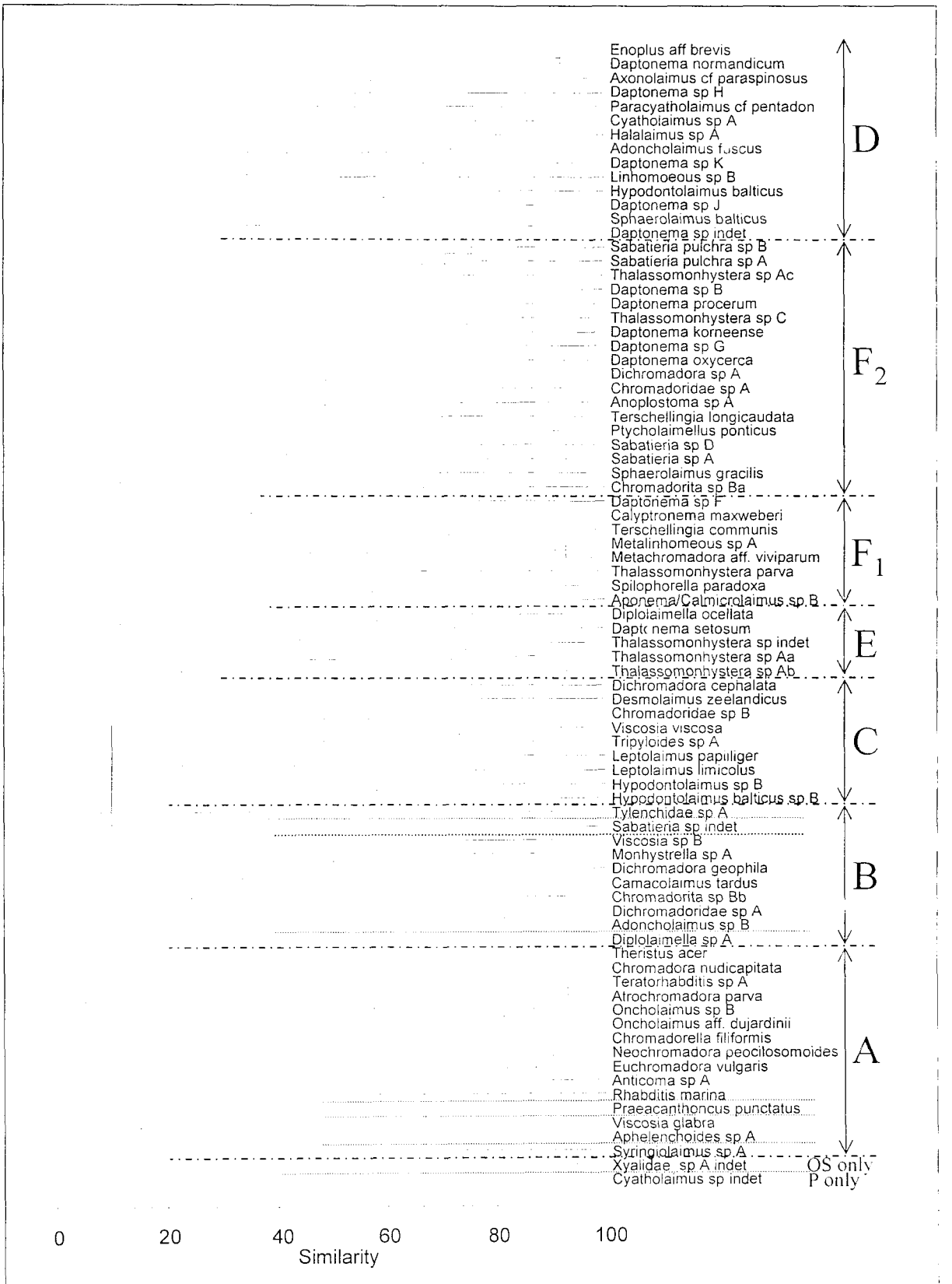


Fig. 4.13. Bray-Curtis similarity dendrogram of nematode species by occurrence in the Keyhaven-Lymington lagoon system (fourth-root transformed species data).

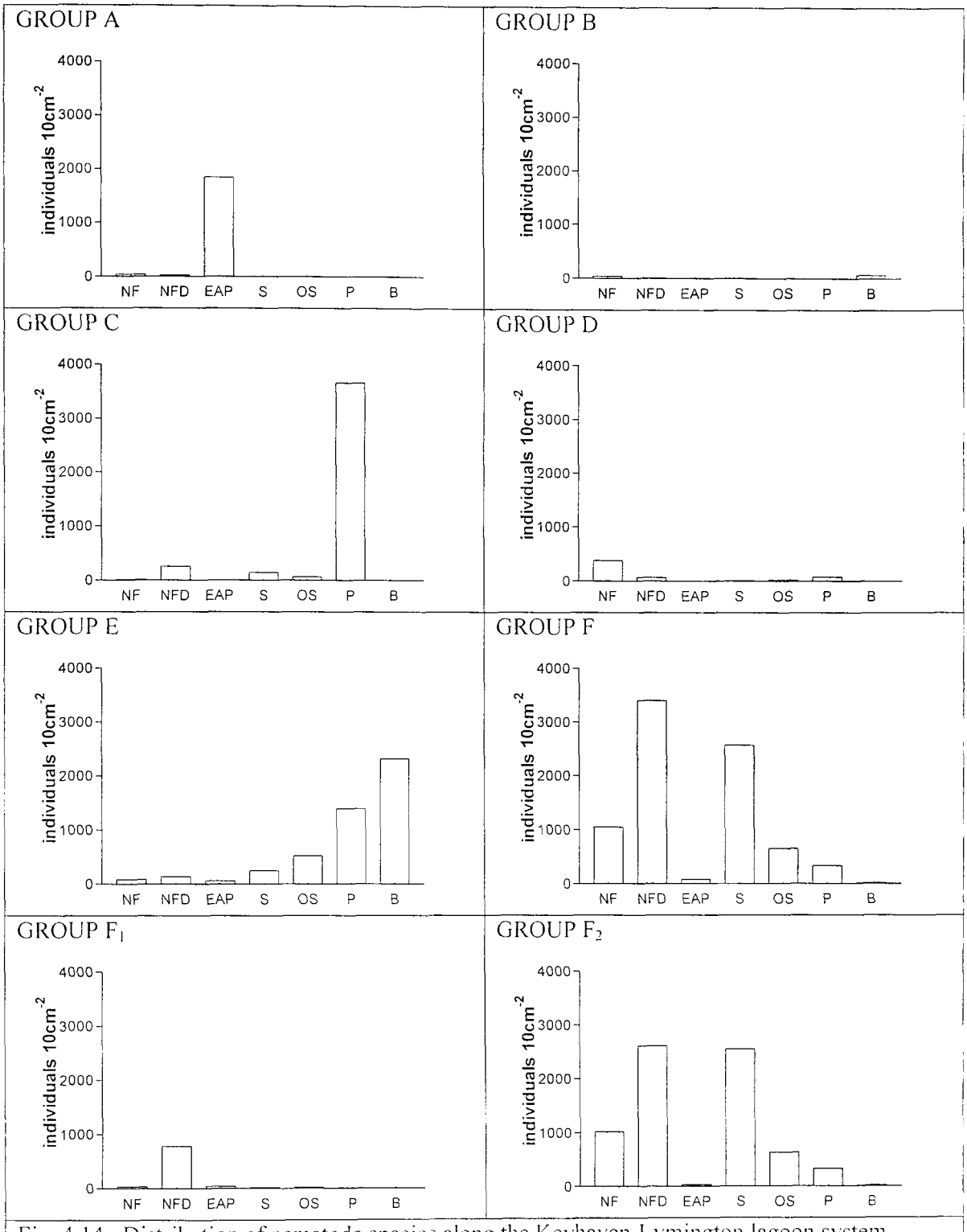


Fig. 4.14. Distribution of nematode species along the Keyhaven-Lymington lagoon system, grouped as indicated in Fig. 4.13 (similarity analysis of fourth-root transformed species assemblage data). Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

riding factor influencing the nematode assemblage was the sediment substrate. The greater variability of salinity in the other lagoons is likely to be most influential to the species assemblages, particularly in Butts lagoon where salinity is lowest (1 – 25

ppt). The larger percentage sand content in Normandy Farm sediments may explain the reduced abundance at this site relative to other fine sediment sites.

Repeating the similarity analysis with fourth-root transformed species assemblage data divided the species in a similar manner to that by untransformed data analysis (Fig. 4.13). The six groups remained approximately the same (Fig. 4.14), although Group C contained no species recorded in Butts lagoon, whilst *D. ocellata* and *D. setosum* were grouped with the *Thalassomonhystera* species in Group E as species being most frequent in the more westerly sites. Also group F divided into F_1 and F_2. F_1 included species most abundant in Normandy Farm ditch, but also recorded in low density in all sites except Pennington and Butts lagoons, whilst F_2 included species most abundant in Normandy Farm ditch and/or

Salterns lagoon with declining abundance through the system to Butts lagoon and also in reduced abundance in Normandy Farm and rare in Eight-Acre Pond. *Terschellingia longicaudata* grouped with these species.

e *Comparing Faunal Data with Environmental Variables*

Site similarity based on both untransformed and fourth-root transformed species assemblage data (as average abundance 10 cm^{-2} per sites) was compared with the site similarity based on the environmental data available (Table 4.7) by Spearman's rank correlation. Owing to a lack of environmental data from Normandy Farm ditch, this site was excluded from the analysis. Environmental variables expressed as percentage values - gravel, sand, silt, clay, and organic carbon – were arcsine transformed and then values for all parameters were standardised by (x – mean)/sd. Clarke and Warwick (1994) advise that in order not to bias the correlation analysis between species assemblage and multivariate environmental similarity matrices towards any one environmental parameter, only non-correlating (Pearson's $r < 0.95$) environmental parameters should be included in the multivariate BIOENV comparisons. Therefore, matrix of correlation between each variable is given in Table 4.16. However, due to the low replicate number for environmental data, the BIOENV analysis was carried out with all environmental data available, the intention being to assess the output to identify any cross-correlation of environmental parameters.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z
B	0.60																									
C	0.37	0.47																								
D	0.42	0.67	0.81																							
E	0.52	0.43	0.29	0.73																						
F	0.39	0.36	0.40	0.76	**0.96**																					
G	-0.32	0.02	0.43	0.24	-0.34	-0.34																				
H	0.23	-0.41	-0.50	-0.53	0 05	0.04	-0.87																			
I	-0.34	-0.69	-0.54	-0.69	-0.30	-0.19	-0.64	0.81																		
J	-0.70	**-0.97**	-0.50	-0.69	-0.48	-0.37	-0.10	0.42	0.79																	
K	-0.30	-0.69	-0.48	-0.66	-0.30	-0.18	-0.62	0.81	1.00	0.79																
L	-0.27	0.17	0.31	0.39	-0.03	-0.08	0.90	-0.92	-0.78	-0.26	-0.79															
M	-0.75	-0.89	-0.27	-0.58	-0.66	-0.57	0.40	0.00	0.42	0.87	0.43	0.18														
N	0.85	0.47	-0.04	0.11	0.47	0.36	-0.75	0.59	0.08	-0.48	0.08	-0.66	-0.77													
O	-0.29	0.08	0.41	0.36	-0.14	-0.16	**0.97**	-0.91	-0.73	-0.17	-0.72	**0.98**	0.30	-0.72												
P	-0.25	-0.69	-0.51	-0.78	-0.45	-0.36	-0.56	0.81	**0.97**	0.76	**0.97**	-0.78	0.46	0.11	-0.70											
Q	0.56	-0.04	-0.40	-0.14	0.51	0.39	-0.83	0.81	0.35	-0.02	0.34	-0.66	-0.40	0.80	-0.74	0.32										
R	-0.25	-0.69	-0.60	-0.68	-0.20	-0.12	-0.70	0.88	**0.98**	0.77	**0.98**	-0.80	0.37	0.16	-0.76	**0.95**	0.50									
S	-0.69	**-0.96**	-0.55	-0.71	-0.45	-0.34	-0.17	0.47	0.82	**1.00**	0.82	-0.31	0.83	-0.43	-0.23	0.79	0.04	0.80								
T	0.90	0.65	0.10	0.40	0.69	0.53	-0.49	0.26	0.33	-0.73	-0.33	-0.26	-0.88	0.89	-0.38	-0.32	0.70	-0.21	-0.68							
U	0.50	0.49	0.27	0.70	**0.97**	**0.96**	-0.47	0.11	-0.20	-0.49	-0.21	-0.17	-0.74	0.54	-0.29	-0.37	0.51	-0.12	-0.45	0.69						
V	-0.38	-0.41	-0.36	-0.80	**-0.97**	-0.93	0.12	0.17	0.44	0.47	0.45	-0.21	0.55	-0.25	-0.10	0.60	-0.32	0.35	0.45	-0.91	-0.91					
W	0.57	0.43	0.32	0.69	**0.98**	**0.97**	-0.48	0.18	-0.16	-0.45	-0.16	-0.22	-0.69	0.58	-0.31	-0.31	0.57	-0.07	-0.41	-0.90	-0.90	-0.90				
X	-0.55	-0.34	0.03	-0.14	-0.52	-0.55	0.90	-0.65	-0.36	0.25	-0.36	0.81	0.68	-0.85	0.87	-0.29	-0.70	-0.41	0.19	-0.68	-0.68	0.30	-0.68			
Y	0.49	0.29	0.15	0.50	0.89	0.91	-0.69	0.41	0.11	-0.27	0.11	-0.46	-0.63	0.63	-0.54	-0.05	0.67	0.19	-0.22	-0.82	-0.82	-0.77	**0.96**	-0.82		
Z	0.65	0.20	0.58	0.67	0.79	0.81	-0.23	0.18	-0.17	-0.30	-0.11	-0.16	-0.40	0.44	-0.14	-0.22	0.45	-0.09	-0.30	0.75	0.75	-0.74	0.83	-0.44	0.75	
AA	0.65	0.20	0.58	0.67	0.79	0.81	-0.23	0.18	-0.17	-0.30	-0.11	-0.16	-0.40	0.44	-0.14	-0.22	0.45	-0.09	-0.30	**1.00**	**1.00**	-0.74	0.83	-0.44	0.75	**1.00**

Table 4.16. Matrix of Pearson's correlation between paired environmental variables. High correlation between variables (Pearson's r > 0.95) is highlighted by bold text. See Table 4.7 for coding of parameters.

The output from the analysis of untransformed species assemblage data gave four alternative combinations of environmental parameters with the best Spearman's Rank fit (r = 0.918) to the nematode assemblage similarities (Table 4.17). Each best-fit included five of the seven parameters listed, of which salinity minimum 2000 and salinity mean overall were significantly positively correlated (r = 0.97), and median salinity 2000 and groundwater seepage were significantly negatively correlated (r = -0.97). Both these pairs of parameters occurred together in one of more of the best-fit estimates. Also, between the four best-fits the substituting parameters were different measures of salinity. Therefore the analysis was repeated, firstly only including salinity measures from the sampling year (2000) and then only including overall salinity measures.

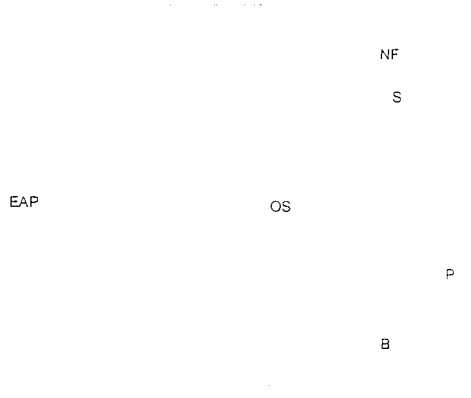
Parameters	Fit 1	Fit 2	Fit 3	Fit 4
Groundwater seepage	✓	✓	✓	✓
Organic carbon, %	✓	✓	✓	✓
Salinity, median 2000	✓	✓	✓	✓
Salinity, minimum 2000	✓	✓		
Salinity range 2000	✓		✓	
Salinity mean overall		✓	✓	✓
Salinity range overall				✓

Table 4.17. The four combinations of environmental parameters providing the best Spearman's rank fit of site similarity with the site similarity of untransformed nematode assemblage data (r = 0.918).

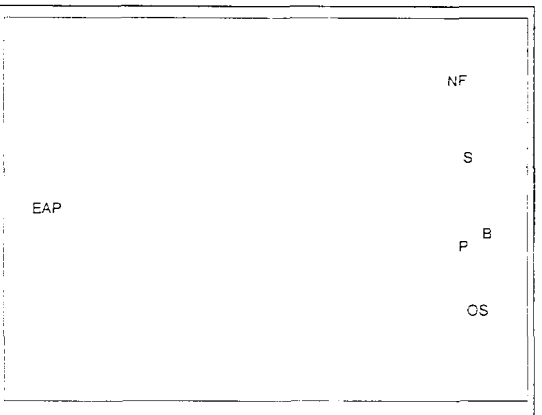
Calculation of the best-fit environmental data including only salinity data from 2000 identified the same set of environmental parameters as the original analysis (Fit 1 in Table 4.17) and at the same level of rank correlation (r = 0.918). However, with the overall salinity data the rank correlation of the best-fit parameters decreased (r = 0.893). This may indicate that more recent salinities gave a better indication of nematode assemblages than long term salinity records (nematoda have a relatively short life span and many species have almost continual reproduction so this is not unexpected). However, it is perhaps more likely that the current nematode assemblage is a product of both recent and past environmental condition, long term conditions influencing the current species suite and current environmental conditions influencing their relative abundances.

The inclusion of groundwater seepage in the best fit output and its high correlation with salinity minimum were predominantly due to a skew effect in the data – only

Eight-Acre Pond lagoon did not receive groundwater seepage. To confirm this, the BIOENV analysis was repeated for a fourth time, excluding overall salinity data and excluding groundwater seepage data. In this instance the same set of environmental parameters gave the best-fit similarity matrix (obviously excluding groundwater seepage), but at a lower rank correlation (r = 0.889). MDS ordinations of site similarity by untransformed species data (averaged per site) and by the best-fit environmental parameters are given in Fig. 4.15a and b. The skew of sites by the best-fit environmental parameters owing to Eight-Acre Pond is visible in Fig. 4.15.b.



a. MDS ordination of site similarity by averaged nematode species assemblage data (untransformed). Stress = 0.00



b. MDS ordination of site similarity by the best-fit environmental parameters (Fit 1). Stress = 0.01

Fig. 4.15. Spearman's rank correlation between plots, r = 0.918. Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm.

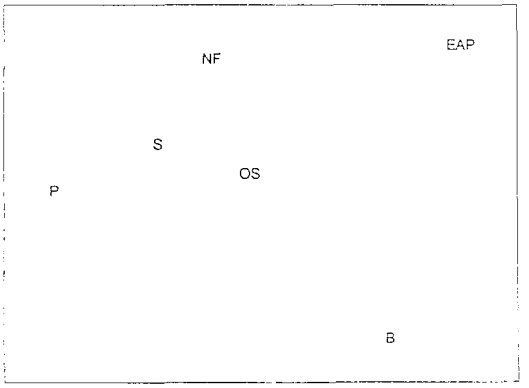
Repeating the BIOENV analysis with fourth-root transformed nematode assemblage data and all environmental data gave only one set of 'best-fit' environmental parameters, although with a lower Spearman's rank correlation between similarity matrices (r = 0.829). The four next best-fit environmental parameters again substituted between different measures of salinity (Table 4.18). In this case, groundwater seepage and salinity were again included in the best-fit parameters, but with lagoon depth. Highly correlating parameters did not occur in any of the sets of best-fit parameters. The MDS ordinations of site similarity by four-root transformed species data (averaged per site) and by the best-fit environmental parameters are given in Fig. 4.16 a and b.

Owing to a concern that the significantly different fauna in Eight-Acre Pond skewed the BIOENV analyses, they were repeated excluding salinity variables (as the

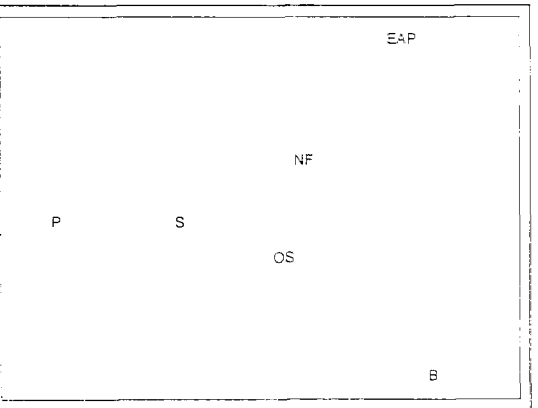
parameters contributing the most to site distributions). When all salinity variables were excluded the best-fit correlation to site similarity by untransformed nematode data was given by groundwater seepage alone (r =0.818), confirming a high bias by Eight-Acre Pond in the analysis. However, when the correlation was repeated with fourth-root transformed data excluding salinity parameters, the best-fit was given by groundwater seepage, lagoon depth and percentage gravel but at a low rank correlation (r = 0.671).

Parameters	**Fit 1**	**Fit 2**	**Fit 3**	**Fit 4**	**Fit 5**
Spearman's correlation, r	0.829	0.825	0.825	0.825	0.825
Groundwater seepage	✓	✓	✓	✓	✓
Lagoon depth	✓	✓	✓	✓	✓
Salinity maximum, 2000	✓				
Salinity kurtosis, 2000	✓	✓		✓	
Salinity April sampling	✓		✓		✓
Salinity median, 2000		✓	✓		
Salinity maximum, overall		✓	✓	✓	✓
Salinity range overall				✓	✓

Table 4.18. The four combinations of environmental parameters providing the best Spearman's rank fit of site similarity with the site similarity of fourth-root transformed nematode assemblage data.



a. MDS ordination of site similarity by averaged nematode species assemblage data (4^{th} root transformed). Stress = 0.00



b. MDS ordination of site similarity by the best-fit environmental parameters. Stress = 0.00

Fig. 4.16. Fourth-root transformed nematode data: Spearman's rank similarity of plots = 0.829 Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm.

The analyses were therefore repeated again with all environmental parameters, but excluding Eight-Acre Pond. The best-fit environmental parameters were again dominated by salinity parameters (Tables 4.19 and 4.20), in combination with lagoon depth and clay for untransformed nematode assemblage data and lagoon depth and/or

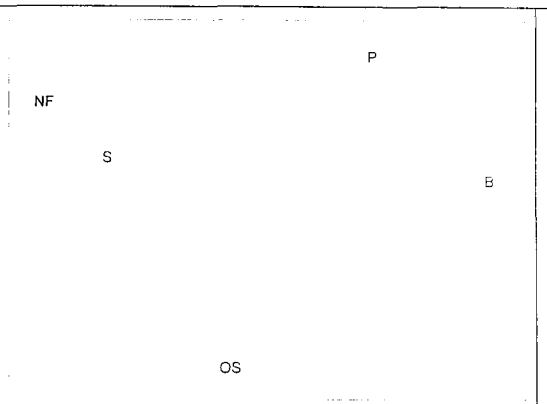
silt or gravel for fourth- root transformed nematode assemblage data. High rank correlations were recorded between similarity matrices for the best-fit environmental parameters and both the untransformed and fourth-root transformed nematode assemblage data (r = 0.903 and r = 0.964, respectively). Several of the best-fit combinations were equivalent, only salinity parameters differing between '2000' and 'overall' measures. Whilst each of the best-fit groups had the same rank correlation of sites similarity with the nematode assemblage data, visual inspection of the site ordinations by each of the data sets suggest that one 'best-fit' had the best overall match for each analysis. These MDS ordinations are given in Figs. 4.17 a and b and Fig 4.18 a and b (untransformed and fourth-root transformed nematode data, respectively).

Parameters	**Fit 1**	**Fit 2**	**Fit 3**
Lagoon depth	✓	✓	✓
Salinity mean, 2000	✓	✓	✓
Salinity median, 2000	✓	✓	✓
Salinity minimum, 2000	✓		
Sediment % clay	✓	✓	✓
Salinity minimum, overall		✓	
Salinity range, overall			✓

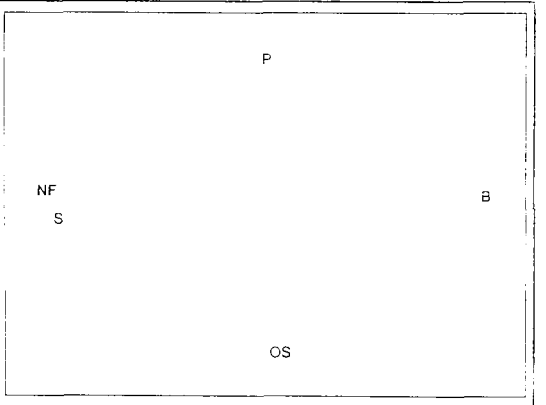
Table 4.19. The three combinations of environmental parameters providing the best Spearman's rank fit of site similarity with the site similarity by untransformed nematode assemblage data, when Eight-Acre Pond from the analysis (r = 0.903). Where best-fit combinations are separated by a dotted line they are the same except for exchange between salinity parameters 2000 and equivalent salinity overall.

	Best–fit combinations									
Parameters	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Lagoon depth	✓	✓	✓	✓	✓	✓	✓	✓	✓	
Salinity kurtosis, overall	✓									✓
Salinity mean, 2000	✓	✓	✓	✓	✓					
Salinity median, 2000	✓	✓	✓			✓	✓	✓	✓	
Salinity maximum, 2000		✓								
Salinity skew, 2000				✓		✓	✓			
Sediment % gravel			✓							✓
Salinity range, overall				✓	✓					
Salinity skew, overall					✓			✓	✓	
Salinity range, 2000						✓		✓		
Salinity mean, overall							✓		✓	✓
Organic Carbon										✓

Table 4.20. The ten combinations of environmental parameters providing the best Spearman's rank fit of site similarity with the site similarity by fourth-root transformed nematode assemblage data, Eight-Acre Pond excluded (r = 0.964).



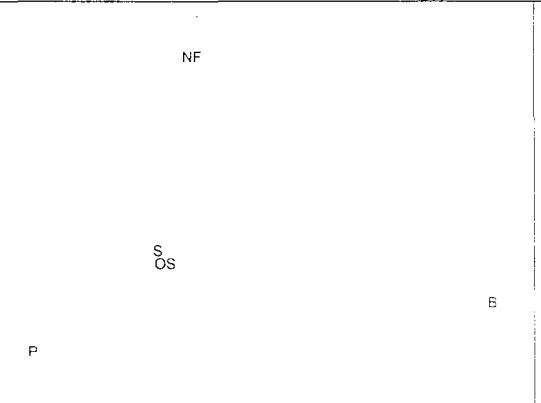
a. MDS ordination of site similarity by averaged nematode species assemblage data (untransformed). Eight-Acre Pond excluded. Stress = 0.00



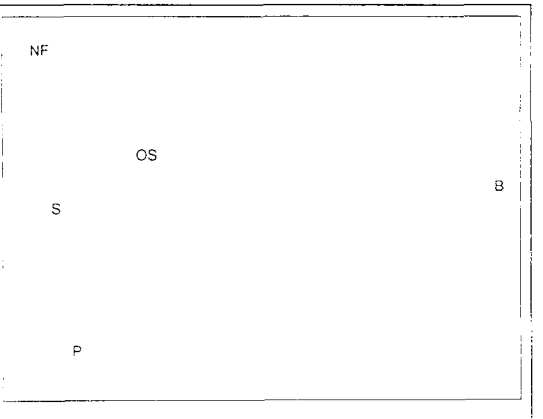
b. MDS ordination of site similarity by the best-fit environmental parameters. Fit 1. Stress = 0.01

Fig. 4.17. Spearman's rank correlation between plots, r = 0.903
Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

The BIOENV analyses identified few environmental parameters that were correlated significantly with the nematode assemblages. Those parameters included in the best-fits were groundwater seepage, current and historical salinity (mean, median, maximum, minimum, range, skew and kurtosis), lagoon depth, percentage organic carbon and percentage sediment gravel. Each is likely to represent different influences on nematode assemblage dynamics.



a. MDS ordination of site similarity by nematode species assemblage data (fourth-root transformed). Eight-Acre Pond excluded. Stress = 0.00



b. MDS ordination of site similarity by the best-fit environmental parameters. (Fit 3) Stress = 0.00

Fig.4.18. Spearman's rank similarity between plots = 0.964
Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm; NFD, Normandy Farm Ditch.

Groundwater seepage segregates Eight-Acre Pond lagoon as the only location

without the addition of freshwater as groundwater, which may result in a more marine habitat at this site and therefore may also influence salinity. The salinity parameters will together influence species distributions in terms of tolerance to salinity fluctuation (range, frequency and time duration) and the abundance of species, dependent on their success in the current ambient salinity.

Percentage composition of organic carbon may influence both habitat type and food availability. Decomposition of organic matter is likely to result in increased biological oxygen demand in surface sediments and may influence the position of the RDP layer in sediments, as well as the sediment type. Although some studies suggest that levels of organic loading do not influence nematode diversity (Gee *et al.*, 1985), percentage organic carbon in the sediment is likely to correlate with anoxia/hypoxia (owing to increased biological oxygen demand) and therefore may influence vertical distributions of species in the sediment and restrict the physical size of the hospitable habitat. Normandy Farm ditch, Salterns lagoon and Oxey South lagoon, for example, each have fringing macroalgae that would provide both food and substrate. Also all sites excluding Normandy Farm ditch and Eight-Acre Pond, received additional organics from grazing cattle, whilst further sources may arrive to all sites via land-drainage.

The inclusion of groundwater seepage and lagoon depth may indicate longer-term influences to the faunal assemblage. Lagoon depth may be important for the provision of refugia when shallower areas are disturbed, by a rapid reduction in salinity following heavy rainfall, for example (Bamber *et al.*, 2001c). The applicability of this hypothesis to meiofaunal sized animals is difficult to determine, however, since rates of recolonisation have proved very variable between habitats (Sherman, *et al.*, 1983; Guidi-Guilvard and Buscail, 1995; Travizi, 2000). However, a significant correlation was not recorded between lagoon depth and nematode species diversity (See Table 4.8), and lagoon depth was not correlated ($r < 0.95$) with any of the other measured environmental variables, and its significance to nematode assemblages is therefore difficult to quantify.

4.3 Discussion

The nematode abundance values recorded throughout the system suggest that the survey by Bamber *et al.* (1992) may have underestimated the abundance of nematode fauna in lagoonal habitats. They took samples from muddy sites in Pennington (near to the sampling location for this survey) and Eight-Acre Pond lagoons with a high organic content and recorded 622.8 ind. 10 cm^{-2} and 911.4 ind. 10 cm^{-2}, respectively. In contrast, the present survey recorded 5476.7 ± 1392.2 ind. 10 cm^{-2} in Pennington lagoon, and 2012.52 ± 1109.8 ind. 10 cm^{-2} in Eight-Acre Pond. These differences may result from underestimation by Bamber *et al.* (1992) owing to the large mesh size used (90 μm instead of 45 μm), or variability of habitat type either as spatial patchiness or change over time.

The overall nematode abundance recorded in the present study is comparable to that recorded in other sub-tidal, brackish water systems. In the Mersey estuary, for example, nematode abundance has been recorded between 162.03 ± 68.81 (2 ppt) and 508.75 ± 89.90 (30 ppt) ind. 10 cm^{-2} (Ferrero *et al.*, 1997), whilst Warwick and Price (1979) recorded up to 12,460 ind. 10 cm^{-2} in the Lynher estuary. A study of European estuaries also noted an increase in abundance with salinity, abundance ranging from 100 to 11,500 ind. 10 cm^{-2}, abundance increasing in an approximately logarithmic manner from 2 to 30 ppt (Soetaert *et al.*, 1995). Also, abundance may change with seasons, in the Baltic Sea for example, Olafsson and Elmgren (1997) recorded on average a range between 2000 and 4250 ind. 10 cm^{-2} throughout a year (fine sediment; 3 – 7 % organic carbon; stable salinity, 7 ppt).

Nematode diversity recorded in the Keyhaven-Lymington lagoon system was also comparable to that recorded in other brackish water systems. A total of 81 nematode species or putative species were recorded throughout the system, ranging from 14 species in Butts lagoon to 45 species in Normandy Farm. Warwick and Gee (1984), for example, recorded an increase in species number per site from fresh to brackish to marine locations (30, 32 and 46 species respectively). Also, Villano and Warwick (1995) recorded a total of 72 nematode species from 42 stations in the Palude Della Rosa, Venice Lagoon (brackish water). The low diversity in Butts lagoon may be comparable to polluted estuaries. Ferrero *et al* (1997), recorded a total of 163 nematode species in the Mersey estuary, ranging from an average of 8.3 species per

core at a polluted site (8 ppt) to 45.0 species per core (30 ppt) at the mouth of estuary. Although it is difficult to separate the stresses of 'pollution' and reduced salinity, it is noticeable that at the site furthest up the estuary (2 ppt). Ferrero *et al.* (1997) recorded an average of 29.8 species per core, although salinity might be more stable there also.

The nematode assemblages also differed between the lagoons in the Keyhaven-Lymington system. The site sampled in Normandy Farm lagoon had the highest nematode diversity, but low abundance and a high number of unique species. Normandy Farm ditch had a similar number of species, but higher abundance, whilst Salterns lagoon had fewer species and variable abundance. These latter two sites had the most similar nematode fauna. Westwards from Salterns lagoon, reducing diversity and increasing species dominance were recorded. Oxey South and Pennington lagoons had similar fauna, with increased dominance of fewer species relative to Salterns lagoon, however, abundance was low in Oxey South and high in Pennington lagoon. Diversity was on average lowest in Butts lagoon where brackish to freshwater species dominated. Eight-Acre Pond lagoon had an almost entirely different nematode assemblage to all other sites, with intermediate abundance and diversity. The species assemblage in Salterns lagoon was representative of both the adjacent estuarine/brackish and low salinity sites. Salterns had no site-specific species and the lowest single-species dominance of abundance.

Black anoxic muds were observed at the sediment surface in Butts, Pennington, Oxey South and Salterns lagoons and the ditch adjacent to Normandy Farm, whilst an RDP layer was noted in Normandy Farm at ~ 5 - 10 mm depth and at > 1 cm depth in Eight-Acre Pond. The extent of anoxia varies throughout the year, but predominantly black muds suggest that fauna may be restricted to the upper centimetre of sediment in these lagoons (McLachlan, 1978; Jensen, 1983, 1987b). Nevertheless, in Normandy Farm ditch, Salterns and Pennington lagoons species abundance was high, although it was lower in Butts and Oxey South lagoons. It is possible that this reflects other environmental stress in these lagoons. Certainly in Butts lagoon the low average salinity is likely to be the main factor leading to a reduced nematode abundance and diversity, but in Oxey South conditions were similar to both Pennington and Salterns.

Multivariate analysis of the environmental parameters has shown that Salterns and Oxey South lagoons have the most similar habitats in the system. Sediment granulometry and salinity regimes are considered to be the two most important factors structuring free-living marine nematode communities (Gerlach, 1953; Reimann, 1966; Heip *et al.*, 1985; Coull, 1999) and each are found to be similar between Oxey South and Salterns. However, although the sediments in both lagoons had a silt/sand fraction of > 60 % , the sediment in Oxey South was more homogeneously silt whilst Salterns had a greater sand component. Also, both lagoons had brackish/ poikilohaline salinity regimes, but salinity reached an average summer peak of 34.15 ppt in Salterns and 29 ppt in Oxey South, whilst the overall salinity range was greater in Oxey South lagoon (0 – 42 ppt, compared to 4 – 42 ppt in Salterns). Also, when comparing salinity over the sampling year with rainfall, it is noticeable that salinity levels in Salterns were more sustained and declined at a slower rate in response to rainfall.

These findings were generally in agreement with conclusions reached regarding the relative 'merits' of the macrofauna populations. Pennington, Oxey and Salterns lagoons have a high diversity of macrofaunal species, with all specialist and scheduled lagoonal species recorded there (Bamber *et al.*, 2001a), whilst Bamber (1997) concluded that Salterns lagoon supported a 'community superior to that of Oxey'. Equally the macrofauna has been described in Butts lagoon as 'impoverished', and in Normandy Farm as characteristically lagoonal (i.e. similar to Salterns and Oxey South), but with a distinct set of dominant species (Bamber *et al.*, 2001a). Also, Bamber *et al.* (2001a) note that infaunal polychaetes were lacking from Eight-Acre Pond, although the epibenthic fauna were similar to Normandy Farm.

The differences in the nematode assemblage between the seven sites can be largely attributed to differences in habitat type between the lagoons. Nematode assemblages were correlated with salinity, sediment type and lagoon depth. Salinity may be divided into average salinity, salinity range and frequency of change, as well as sources of freshwater (i.e. groundwater), whilst sediment type was mainly correlating in terms of percentage contribution of the 'extreme' fractions (i.e. clay or gravel) and

percentage composition of organic carbon.

Five habitat types/species assemblages are identified in the Keyhaven-Lymington lagoon system. These are defined by the habitat and dominant and associated nematode species (> 10 % and 5 – 10 % of individuals, respectively). Essentially these are;

A. Polyhaline salinity, sand/gravel dominated sediment - Eight-Acre Pond;

Dominant species:	*Chromadora nudicapitata*
	Teratorhabditis sp A
	Atrochromadora parva
Associated species:	*Theristus acer*

B. High meso-/polyhaline salinity, sand dominated sediment – Normandy Farm;

Dominant species:	*Daptonema procerum*
Associated species:	*Daptonema oxycerca*
	Thalassomonhystera sp C
	Daptonema sp B
	Axonolaimus paraspinosus

C. Poikilo- (poly) haline salinity, silt dominated sediment, high percentage content organic carbon - Normandy Farm ditch, Salterns, Oxey South;

Dominant species:	*Terschellingia longicaudata*
Dominant/Associated:	*Daptonema setosum*
	Sabatieria pulchra sp B
	Daptonema procerum
Associated species:	*Daptonema korneense*

D. Poikilo- (poly-) haline, sand dominated sediment – Pennington

Dominant species:	*Diplolaimella ocellata*
	Dichromadora cephalata
	Desmolaimus zeelandicus
Associated species:	*Viscosia viscosa*
(4 %)	*Chromadoridae* sp B

E. Poikilo- (meso-) haline salinity, sand dominated sediment - Butts

Dominant species:	*Diplolaimella ocellata*
	Thalassomonhystera sp Ab
	Thalassomonhystera sp Aa
Associated species:	*Daptonema setosum*

This division of the sites broadly be more simply defined as - Normandy Farm supporting a reduced estuarine/marine intertidal nematoda (fine sand), Eight-Acre Pond also supporting a reduced estuarine/marine intertidal nematoda (coarse sand), Oxey South, Salterns and Normandy Farm ditch supporting a range of estuarine to oligohaline, muddy substrate nematoda, and Butts and Pennington supporting a range of estuarine to oligohaline sand substrate nematoda.

As well as physical/chemical constraints, lagoonal populations may be regulated by isolation and frequency of species addition/replenishment. All the nematode species recorded in the Keyhaven-Lymington system are thought to have been recorded in other marine and brackish water locations in Europe and to a greater extent the UK. However, nematodes lack a pelagic larval phase (Gerlach, 1977) and (re)colonisation is considered to be dependent on horizontal migration through the benthos or resuspension into the water column with sediments (Palmer and Gust, 1985). That the system is now isolated behind a seawall may therefore limit species addition/exchange by horizontal migration between the lagoons and with the adjacent Solent has effectively been removed, whilst wind/wave generated sediment movement into these sheltered habitats is much restricted relative to open coasts and 'natural' lagoons. However, two instances of macrofaunal colonisation provide evidence of continued 'communication' either between the lagoons, or with the adjacent Solent Water. Firstly, the polychaete *Desdomona ornata* was first recorded in the Solent in 1997 (Smith *et al.*, 1999) and has been observed in the Keyhaven-Lymington lagoons system since 2000 (This survey; Bamber *et al.*, 2001a). Also, after the flooding of the newly dug Normandy Farm lagoon in 1990, a rapid colonisation by lagoonal species such as the lagoonal specialist *Nematostella vectensis* was recorded (Sheader, 1991). This latter example may also provide an indication of meiofaunal dispersal into/ within the system, since Normandy Farm

shares similar nematode species with the other sites in the system as well as having a number of rare and unique nematode species (relative to other sites in the system), which are recorded in UK estuaries. These two examples suggest that the lagoons and their inhabitants may be neither isolated nor relict.

Following from this survey it would seem that the collation of more detailed information regarding Normandy Farm ditch would be appropriate. As a high diversity community in fine sediments it may become apparent that this site is either;

A. A low diversity estuarine community, or:

B. A high diversity lagoonal community.

The similarity of the fauna in Normandy Farm ditch, Salterns lagoon and Oxey South lagoon suggest that at the very least this site may prove to be an important source of fauna for Normandy Farm lagoon, where a lagoonal macrofaunal population continues to become more established following the flooding of the lagoon in 1990 (Bamber, *et al.*, 2001a).

5 Comparison of Macrofaunal and Nematode Assemblages in the Keyhaven-Lymington Lagoon System

5.1 Introduction

Macrofaunal assemblages in the Keyhaven-Lymington system are distinct between lagoons, with only small within-lagoon variation, although diversity tends to be low (7 to 19 species), and density high (usually 1,000 – 150,000 individuals per m^2) (Bamber *et al.*, 2001a). The lagoons east of Pennington Sewer, up to and including Salterns, support typical English lagoonal communities with a high diversity of specialist and scheduled species, whilst Normandy Farm and Eight-Acre Pond also support these together with marine and/or estuarine species (Bamber, 1997; Bamber *et al.*, 2001a). The lagoons west of Pennington Sewer are considered to be adversely affected by freshwater input: salinity may remain below 10 ‰ for extended periods and, although plant or sediment niches are similar to other lagoons in the system, macrofaunal diversity is reduced, dominated by low salinity and freshwater species, particularly chironomids (Bamber *et al.*, 2001a). The macrofauna species divide into 3 generalised groups, i. characteristic lagoon species (either phytal or benthic); ii. species characteristic of the western lagoons and tolerant to low salinity, and; iii. species ubiquitous throughout the lagoons.

The Keyhaven-Lymington lagoon system is included in the Solent Lagoons SAC primarily owing to the presence of 'good' populations of lagoonal specialist macrofauna, particularly *Nematostella vectensis* (starlet sea-anemone), *Gammarus insensibilis* (lagoon sand shrimp), and *Armandia cirrhosa* (lagoon sand worm) (Sheader and Sheader, 1989). Also, a lagoonal specialist flora is abundant, including *Ruppia* spp (tasselweed, *Ruppia maritima* and *Ruppia cirrhosa*) found throughout the system, *Chaetomorpha linum* (floating alga), which occurs east of Pennington Sewer, and *Lamprothamnium papulosum* (foxtail stonewort), which is only found consistently in Normandy Farm and transiently in Eight-Acre Pond (Bamber *et al.*, 2001a; Bamber and Evans, 2002). The system was chosen for study owing to the presence of this abundant and diverse lagoonal biota, an availability of historical data and continued regular monitoring of the biota and environmental variables at several sites (Bamber and Evans, 2003).

5.1.1 Site descriptions

a *Normandy Farm*

This site was newly built in 1990. Initially it had a reduced lagoon community, predominantly comprised of fauna associated with weed that was thought to have arrived from the adjacent coastal zone or from a relatively undisturbed (eastern) area of ditch (Sheader, 1991). It now has a diverse, lagoonal community, including all local lagoonal specialists except *Ventrosia ventrosa*, in association with higher-salinity-tolerant estuarine/marine species. It may be divided into a deeper (3 m) southern half with a dense lagoon assemblage and associated marine species (eg. *Abra tenuis*, *Caulleriella zetlandica* and *Arenicola marina*) and a shallow northern half with coarser sediment and a reduced lagoonal community. This division reflecting both the more soil-like substratum in the northern half and the possibility of stratification in the deeper half, which would act as a refuge during low salinity periods (Bamber *et al.*, 2001a).

b *Eight-Acre Pond*

Historically, Eight-Acre Pond has supported a diverse and characteristically lagoonal community including *A. cirrhosa*, with associated estuarine/marine species tolerant of higher salinities. Dense beds of *Ruppia* spp occur in the deeper area and *L. papulosum* is found at the northern end. However, winter drainage activities have resulted in a coarse and compacted sediment in shallow areas, and consequently a reduced abundance of sublittoral lagoonal specialist fauna and the loss of *A. cirrhosa* (Fowler and Sheader, 1992; Bamber *et al.*, 2001a). Nevertheless, a muddier substratum in the deeper areas supports a low density lagoonal specialist community (Bamber *et al.*, 2001a).

c *Salterns*

Reconstruction of the sea wall was also followed by an extension of the specialist community into Salterns (Bamber *et al.*, 2001a). This lagoon supports dense beds of *Ruppia* spp, *Ulva lactuca* and *Chaetomorpha* and associated macrofauna, including *N. vectensis*, which are thought to have dispersed from Eight-Acre Pond via an inter-connecting sluice (Bamber, 1997). A dense bed of *N. vectensis* has been recorded on

the north western bank, furthest from the sea wall (Bamber, pers. com., observed during mapping of the system in 2001), although it is seasonally patchy (Bamber *et al.*, 2001a). Also, annelid dominance is reduced (Bamber *et al.*, 2001a).

d *Oxey South*

Oxey South Lagoon is characterised by dense beds of *Ruppia* and *Chaetomorpha* with an associated specialist weed community and a diverse, abundant benthic community, particularly in the deep, organically rich anoxic mud at its southern end. On the seaward side adjacent to the *Ruppia* beds, an abundant *N. vectensis* population occurs in the fine mud (Bamber *et al.*, 2001a). However, Oxey Marsh to Keyhaven lagoons have shown a recent reduction in the specialist community, more so to the west of Pennington Sewer (Bamber *et al.*, 2001a; Bamber and Evans, 2002).

e *Pennington Lagoon*

Pennington lagoon also has dense beds of *Ruppia* and *Chaetomorpha* and an associated specialist weed community. However, although a successful lagoonal community has previously occurred in this lagoon (the highest density of *N. vectensis* - 40,000 to 70,000 m^2 - in mainland Britain was recorded here, for example [Sheader, 1990]), the benthic community is now dominated by the oligochaete, *Heterochaeta costata* and chironomid larvae (Bamber *et al.*, 2001a). Lagoonal specialists inclulding *N. vectensis* and *G. insensibilis* are now rare (Bamber, 1997) and it is possible this reflects the lack of a deeper refuge as recorded in Eight Acre Pond and Normandy Farm.

f *Butts Lagoon*

Butts Lagoon was the only lagoon surveyed west of the Pennington Sewer. The flora of Butts lagoon is similar to that found in Pennington Lagoon, but there is a much reduced diversity of macrofauna and an absence of many lagoonal specialists, including *N. vectensis* (Sheader, 1990; Bamber, 1997). It is also has a similar configuration to Pennington lagoon, but receives freshwater input from Pennington stream and does not have a sluice to seaward (Bamber *et al.*, 2001a). Consequently

salinity is reduced relative to the other lagoons and may decrease rapidly in response to freshwater input. Due to a blocked sluice preventing freshwater run-off, declining species abundance and diversity had been noted before the new sea wall was built (Sheader and Sheader, 1989). However, the shallow infauna may actually be temporary as a result of freshwater flooding, which can greatly increase the size of the lagoon boundary: at deeper sites (~0.8m) infaunal diversity and abundance is increased relative to the shallow sites, and includes *V. ventrosa*, possibly indicating a permanent deep infauna (Bamber *et al.*, 2001a).

5.1.2 Macro/Meio-fauna Interaction

Meiofaunal diversity is maintained largely by feeding specialisation on particles of different size, shape and food quality, whilst macrofauna diversity is thought to be influenced more by spatial segregation of species (Warwick, 1984). Thus physical disturbance is likely to have a greater impact on macrofaunal communities, whilst meiofaunal assemblage dynamics are more stable over a range of temporal scales (Heip, 1980; Herman and Heip, 1986). Nematodes in particular may be more sensitive to slight changes in sediment composition owing to their specialised feeding types (Govaere *et al.*, 1980).

Nematodes are known to be abundant and diverse in habitats where macrofauna are limited owing to either natural, physical or anthropogenic stress (Lorenzen, *et al.*, 1987; Hendelberg and Jensen, 1993), and whilst macrofaunal diversity becomes more variable owing to stress, meiofaunal communities usually remain more stable (Warwick *et al.*, 1990). This pattern of response is seen over a variety of habitat ranges. For example, nematodes are usually present even when macrofaunal communities are absent such as in hypoxic sediments (Josefson and Widbom, 1988; Hendelberg and Jensen, 1993). Equally, with increasing water depth to 1000 m (and decreasing temperature and median grain size) macrofaunal densities decline whilst meiofaunal densities (90 % nematodes) remain relatively constant (Flach *et al.*, 1999).

Nematodes are usually the dominant taxon in muddy sediments with a high organic matter component (Van Damme *et al.*, 1980; Josefson and Widbom, 1988; Lorensen

et al., 1987; Hendelberg and Jensen, 1993). Their dominance in estuarine sediments, for example, has been attributed to variety in burrowing capacity, tolerance to environmental stress and diversity of feeding types (Bouwman, 1983). However, meiofauna are also known to utilise oxygen drawn into the sediment from macrofaunal burrows in order to maintain an anaerobic/aerobic life style (Reise, 1981; Ferrero, 1992). Reise (1981), for example, noted an increased depth penetration by Nematoda and other meiofauna around the vertical shaft of *Arenicola marina* burrows where oxygen diffuses into the surrounding sediment. However, around the horizontal gallery and at the funnel and mouth of burrows where physical disturbance was greatest some meiofauna, including nematodes, were reduced (Reise, 1981; Jensen, 1987a). Meiofauna may also be attracted to macrofaunal burrows by enhanced bacterial densities (Reise, 1981). Therefore, if meiofauna were dependent on this oxygen or food source one might expect reduced meiofaunal densities with declining macrofaunal densities. In stressful habitats were macrofaunal diversity is reduced but density is maintained by the dominance of few successful species, meiofauna may continue to benefit from this aeration and maintain relatively higher diversity (presuming there is not an associated shift in feeding behaviour of the macrofaunal component).

There is also considerable debate as to whether macrofauna influence nematode abundance and diversity by the imposition of predation pressure. There is evidence to support a significant role of meiofauna as a food source to macrofaunal species; however, copepods are most often the dominant or only prey items. A review by Coull (1990), listed 53 feeding studies, including predator exclusion experiments, gut content analyses and mesocosm experiments, of which only 4 studies noted nematodes to be the most abundantly eaten prey item. In fact, some predator species are thought to selectively feed on copepods rather than nematodes because copepods have an epibenthic life style, making them easier to find (Ellis and Coull, 1989). However, nematodes may be digested within 1 hour and may be undetectable in the gut of predator species after 6 hours, which limits the usefulness of gut content studies (Coull, 1990). Camera footage of *Nematostella vectensis* has recorded feeding on larger nematodes, for example (Pearson, pers. com.). It may also be difficult to determine whether meiofauna are a significant food source to larger predators owing to their high abundance. Predation may not appear to significantly

reduce prey populations, unless in combination with abiotic disturbance and seasonal environmental parameters (Glassom and Branch, 1997).

Meiofaunal activity may also stimulate bacterial growth by increasing rates of geochemical fluxes, particularly oxygen diffusion, enlarging the volume of sediment in which aerobic metabolism may occur (Aller and Aller, 1992). Mucus secreted by nematodes can also stabilise sediments and provide a source of food to bacteria (Warwick, 1981). Yet although meiofauna are thought to predominantly feed on bacteria, they may reduce bacterial standing stock by as little as 3 % (Giere, 1993). However, predatory nematodes are thought to influence mortality rates of juvenile macrofauna, and other meiofauna, whilst nematode scavenging activity may aid carrion decomposition/recycling rates. We (Ferrero and Barnes) have observed larger nematodes with mandibles that have smaller (sometimes not that much smaller!) nematodes at various stages of digestion in their gut, and also the undigested crotchets/chaetae of much larger oligochaetes. The latter example probably indicates scavenger feeding.

5.2 Results

5.2.1 Univariate Diversity Indices

a *Species number*

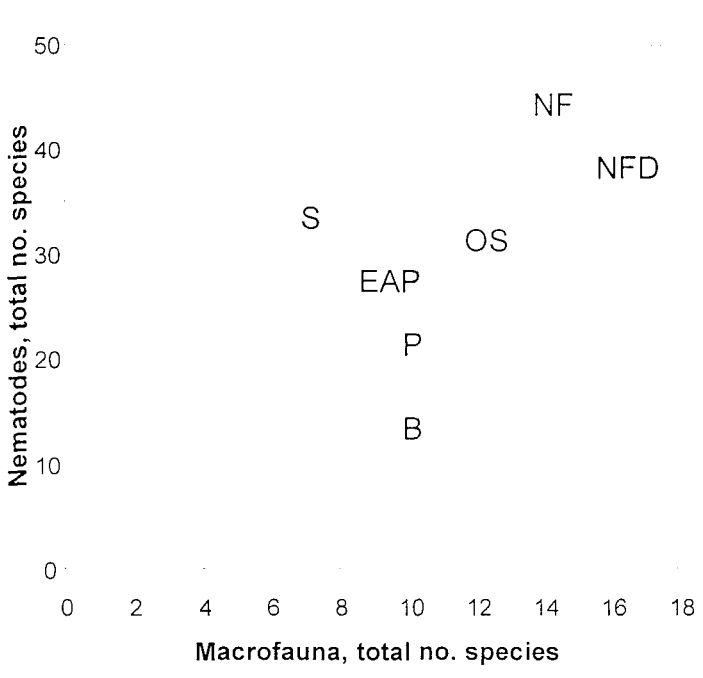
A total of 21 putative macrofauna species were identified (Table 5.1), although a maximum number of species were recorded in Normandy Farm ditch (16 species - occurrence over four replicates). The macrofaunal species assemblage was similar through the system, only 3 species (Chironomids, *C. volutator* and Oligochaetes) were ubiquitous throughout the system, but only 4 species (*Polydora cornuta*, *Abra tenuis*, *C. insidiosum* and *Idotea chelipes*) were unique to one of the seven sites. Within-site between replicate variation of species number was also low.

No immediate pattern was visible in values of species number, however, the two most easterly sites, Normandy Farm and Normandy Farm ditch had the highest species number. The lowest number of macrofaunal species was recorded in Eight-

	Sites	B		P		OS		S		EAP		NFD		NF	
No.	Species	Mean	± s.d.	Mean	± s.d.	Mean	± s.d.	Mean	± s.d.	Mean	± s.d.	Mean	± s.d.	Mean	± s.d.
7	Chironomids	4419.5	1769.1	6208.4	2072.7	105.2	210.5	20098.2	12059.6	315.7	631.4	1894.1	876.2	10207.0	2210.6
7	*Corophium volutator*	105.2	210.5	420.9	343.7	105.2	210.5	1157.5	867.7	315.7	403.0	2104.5	1417.0	14731.7	13560.7
7	Oligochaeta	32199.3	14374.6	7681.5	1661.6	13153.3	11641.0	10943.5	11398.2	315.7	403.0	90073.8	23573.2	10733.1	4642.7
6	*Capitella capitata*	631.4	1262.7	0.0	0.0	420.9	595.3	13574.2	1209.0	210.5	243.0	2630.7	4459.4	16099.6	9551.1
6	*Hydrobia ventrosa*	23886.4	28564.5	13469.0	6681.7	5577.0	8951.1	0.0	0.0	3788.2	2173.5	105.2	210.5	0.0	0.0
4	*Desdomona ornata*	0.0	0.0	631.4	729.0	210.5	420.9	0.0	0.0	0.0	0.0	1894.1	806.0	1578.4	1052.3
4	*Hydrobia ulva*	105.2	210.5	0.0	0.0	210.5	243.0	0.0	0.0	0.0	0.0	105.2	210.5	105.2	210.5
4	*Pygospio elegans*	0.0	0.0	315.7	403.0	315.7	631.4	0.0	0.0	0.0	0.0	315.7	403.0	6524.0	6055.8
4	*Microdeutopus gryllotalpa*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	210.5	420.9	105.2	210.5	420.9	841.8
4	*Nereis diversicolor*	0.0	0.0	4419.5	4044.5	315.7	403.0	0.0	0.0	0.0	0.0	1473.2	2104.5	0.0	0.0
3	Ostracoda	105.2	210.5	0.0	0.0	11259.2	7516.6	0.0	0.0	105.2	210.5	0.0	0.0	0.0	0.0
3	*Sphaeroma rugicauda*	631.4	420.9	210.5	243.0	0.0	0.0	0.0	0.0	0.0	0.0	105.2	210.5	0.0	0.0
2	*Arenicola marina*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	105.2	210.5	631.4	543.4
2	*Caulleriella zetlandica*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10207.0	4129.4	1367.9	867.7
2	*Chaetozone setosa*	0.0	0.0	0.0	0.0	0.0	0.0	315.7	631.4	0.0	0.0	0.0	0.0	105.2	210.5
2	*Manayunkia aestuarina*	0.0	0.0	1367.9	403.0	105.2	210.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2	*Nematostella vectensis*	0.0	0.0	0.0	0.0	0.0	0.0	947.0	867.7	0.0	0.0	1788.8	933.3	0.0	0.0
2	*Polydora ligni*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	105.2	210.5	6208.4	3338.6
1	*Abra tenuis*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	736.6	631.4
1	*Corophium insidiosum*	105.2	210.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
1	*Idotea chelipes*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	210.5	243.0	0.0	0.0	0.0	0.0
	Average no. species	5.0	1.6	7.5	2.1	5.5	1.0	4.5	1.3	3.8	1.0	9.5	1.3	10.0	0.8
	Average no. individuals	62188.8	38600.2	34724.7	41336.0	31778.4	14082.0	47036.2	16317.4	5471.8	15409.6	113013.2	27933.5	69449.4	26435.6

Table 5.1. Average abundance of macrofauna species 1 m^{-2} (± s.d.) along the Keyhaven-Lymington lagoons system. Listed in order of frequency, most frequent first. Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NFD, Normandy Farm Ditch; NF, Normandy Farm.

Acre Pond, in which all species were found in low abundance and the infauna was reduced (Fig. 5.1 a). There was no significant correlation between the number of macrofauna and nematode species along the system (Fig. 5.1 b). The two Normandy Farm sites had both the highest number of macrofaunal and nematode species.



Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NFD, Normandy Farm Ditch; NF, Normandy Farm.

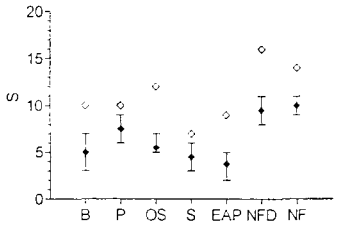
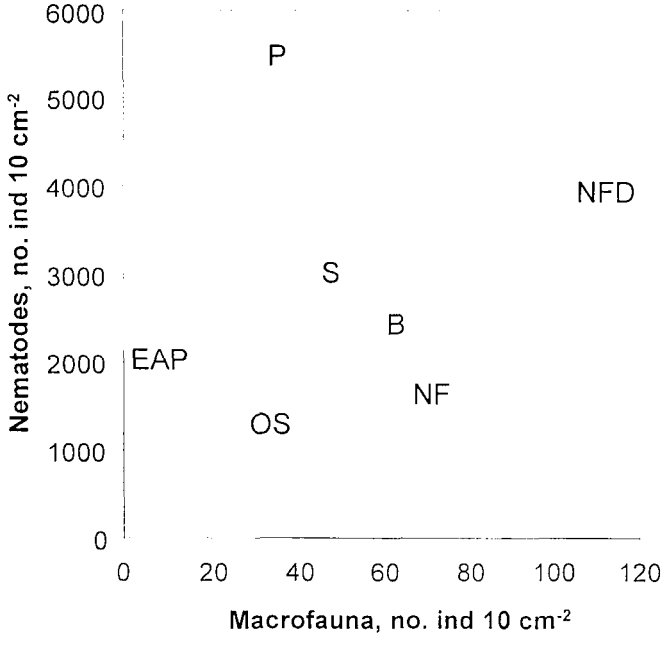


Fig. 5.1

TOP:
a. Number of macrofaunal species, S, per site along the Keyhaven-Lymington lagoon system..
Solid diamonds; mean number of species, error bars are minimum and maximum values.
Open diamonds; total number of species per site.
LEFT:
b. Correlation of nematode and macrofauna species number along the Keyhaven-Lymington lagoons system ($r^2 = 0.29$).

b *Abundance*

Macrofaunal abundance ranged from a minimum of 5,893.7 inds 1 m^{-2} Eight-Acre Pond lagoon to a maximum in Normandy Farm ditch of 145,633.3 inds 1 m^{-2} (Fig. 5.2 a). Within-site variation (± 1 s.d.) of abundance was high in Normandy Farm lagoon (69,449.4 inds 1 m^{-2} ± 26,435.6.), Eight-Acre Pond (5471.8 inds 1 m^{-2} ± 15,409.6), Pennington (34,724.7 inds 1 m^{-2} ± 41,336.0), and Butts (62,188.8 inds 1 m^{-2} ± 38600.2), but relatively low in the other sites [Oxey South (31,778.4 inds 1 m^{-2} ± 14,082.0), Salterns (47,036.2 inds 1 m^{-2} ± 1,6317.4), and Normandy Farm lagoon (113,013.2 inds 1 m^{-2} ± 27,933.5)]. No correlation was found between macrofaunal and nematode abundance, nor was there a correlation between polychaete and nematode abundance (Fig. 5.2 b).



Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NFD, Normandy Farm Ditch; NF, Normandy Farm.

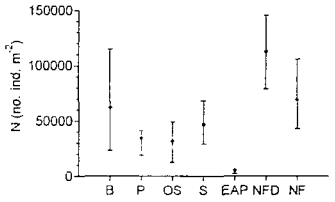


Fig. 5.2

TOP:
a. Mean number of macrofaunal individuals per site along the Keyhaven-Lymington lagoon system. Error bars are minimum and maximum values.

LEFT:
b. Correlation of nematode and macrofauna abundance along the Keyhaven-Lymington lagoon system, ($r^2 = 0.05$).

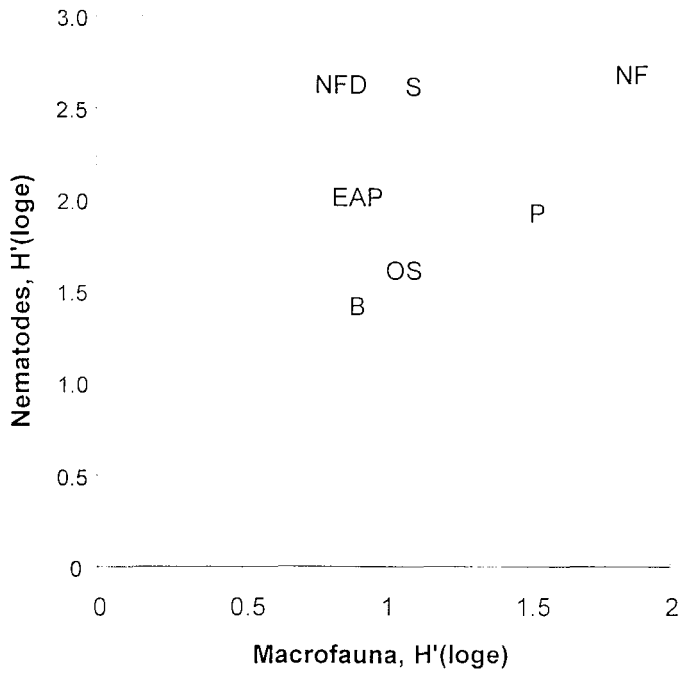
c *Diversity Indices*

i Shannon-Wiener

Shannon-Wiener diversity values were low at all sites. A maximum diversity was recorded in Normandy Farm lagoon ($H'_{(loge)} = 1.85 \pm 0.15$); all other lagoons had a Shannon-Weiner diversity of approximately 1, except Pennington lagoon which also had a slightly higher diversity ($H'_{(loge)} = 1.53 \pm 0.10$) (Fig. 5.3 a). No correlation was seen between macrofauna and nematode species diversity, although the site with highest macrofaunal Shannon diversity also had highest nematode Shannon diversity (Fig. 5.3 b). The lower salinity (greater salinity range) sites (Butts, Pennington and Oxey South) had a relatively greater reduction in nematode diversity than macrofaunal diversity.

ii Margalef's

Macrofaunal diversity measured by Margalef's diversity index was < 1 at all sites (Fig. 5.4 a). It had an almost identical pattern between sites as species number and did not correlate with Margalef's diversity of the nematode assemblage (Fig. 5.4 b).



Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NFD, Normandy Farm Ditch; NF, Normandy Farm.

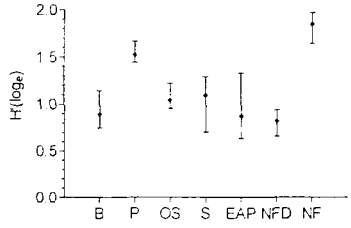


Fig. 5.3

TOP:

a. Average Shannon-Wiener diversity, $H'_{(loge)}$ of macrofauna species assemblages along the Keyhaven-Lymington lagoon system.
Error bars are minimum and maximum values.

LEFT:

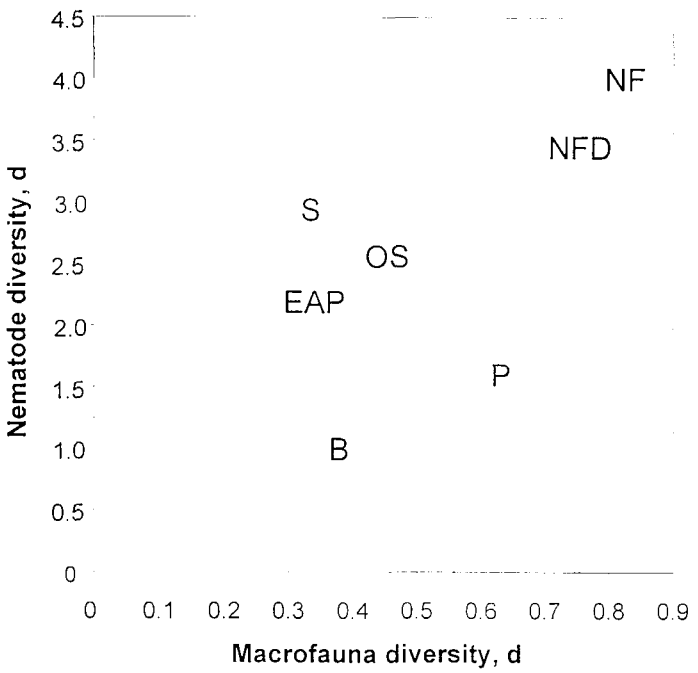
b. Correlation of nematode and macrofauna Shannon-Weiner diversity along the Keyhaven-Lymington lagoon system.($r^2 = 0.11$).

iii Pielou's evenness index, J'

Pielou's evenness was low (< 1) at all sites, and was between 0.5 and 0.75 for all sites except Normandy Farm ditch, where evenness was < 0.5 J' (Fig. 5.5 a). The relatively reduced evenness in the macrofaunal assemblage from Normandy Farm ditch resulted from the high dominance of oligochaetes at this site. The other sites tend to have at least 2 co-dominant species. Again no correlation is seen between the distribution of sites by macrofaunal and nematode evenness (Fig. 5.5 b).

d *K-Dominance Plots*

Although species number is low, clear distinctions can be seen between k-dominance plots for each site (Fig. 5.6). Normandy Farm ditch is distinct from the other sites in that 79 % of individuals are represented by oligochaetes, and the resultant k-dominance plot is very shallow. The other sites divide into two groups, firstly Normandy Farm and Pennington lagoons with lowest dominance. These two sites were both exposed to wind disturbance and had similar sediment characteristics, but different salinity regimes, and the macrofauna assemblage at these sites were very



Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NFD, Normandy Farm Ditch; NF, Normandy Farm.

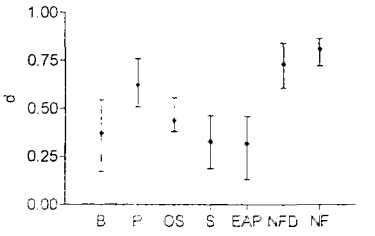
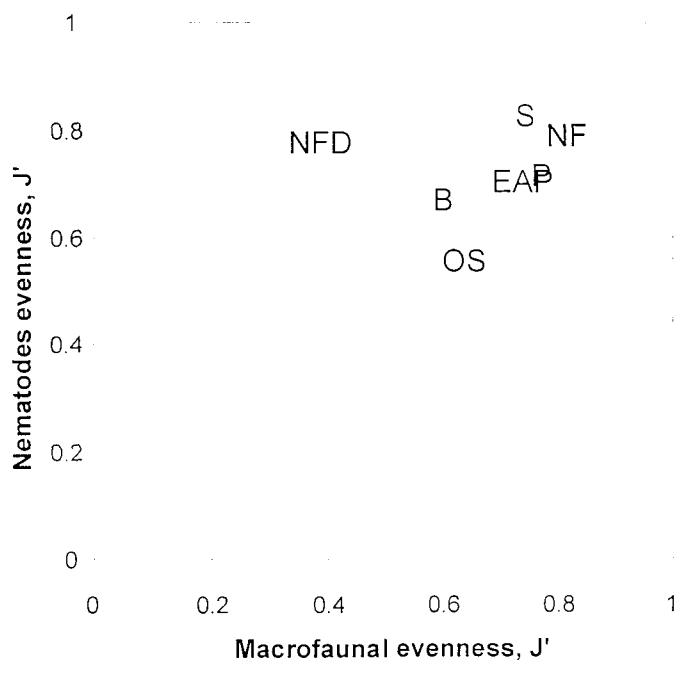


Fig. 5.4

TOP:
a. Average Margalef's diversity, d, of macrofauna species assemblages along the Keyhaven-Lymington lagoon system.
Error bars are minimum and maximum values.
LEFT:
b. Correlation of nematode and macrofauna diversity (Margalef's d) along the Keyhaven-Lymnington lagoon system, ($r^2 = 0.34$).



Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NFD, Normandy Farm Ditch; NF, Normandy Farm.

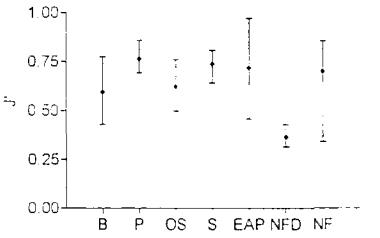


Fig. 5.5

TOP:
a. Average Pielous evenness index, d, of macrofaunal assemblages along the Keyhaven-Lymington lagoon system.
Error bars are minimum and maximum values
LEFT:
b. Correlation of nematode and macrofauna assemblage evenness (Pielous J') along the Keyhaven-Lymington lagoon system, ($r^2 = 0.01$).

different. Pennington supports a macrofauna reduced in diversity and abundance, whilst Normandy Farm supports a (relatively) diverse and abundant assemblage. The second group contains the other four intermediate sites (Normandy Farm ditch, Eight Acre Pond, Salterns, and Oxey South). These sites have intermediate diversity and species number, except Normandy Farm ditch which had a greater number of species, but high abundance and dominance.

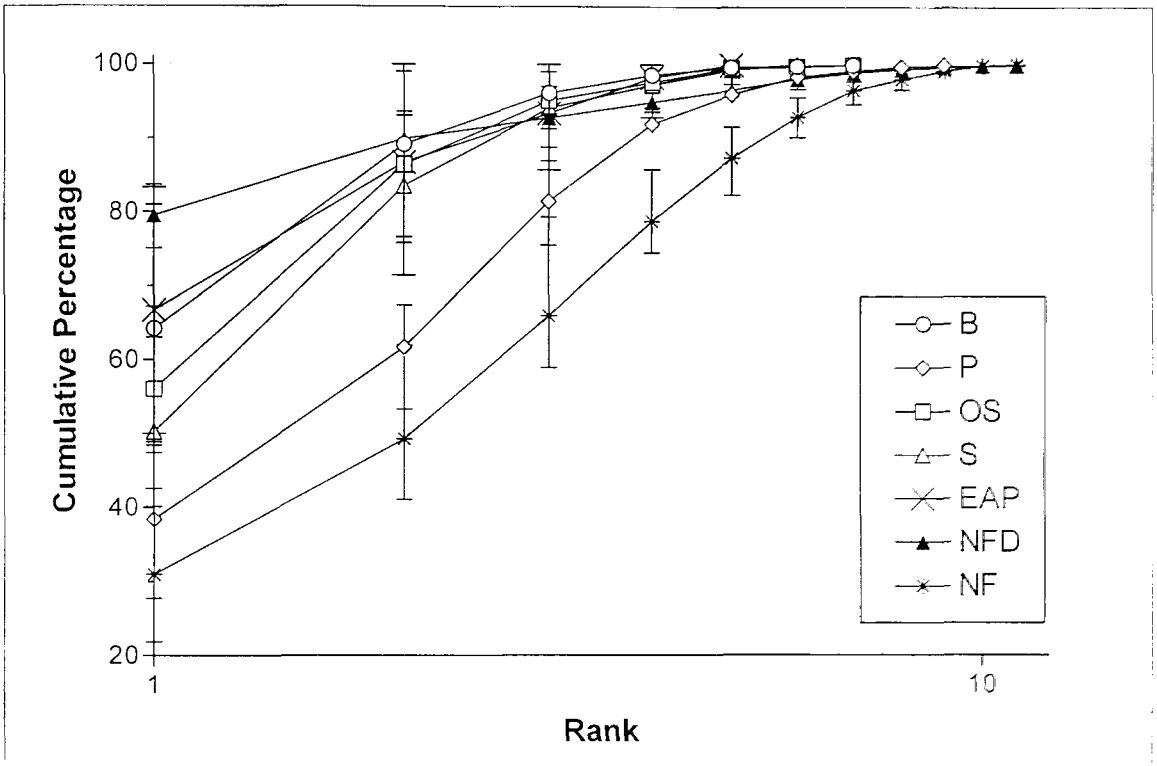


Fig. 5.6. K-Dominance plots of the macrofaunal assemblages along the Keyhaven-Lymington lagoon system. Mean cumulative abundance with minimum and maximum values indicated by error bars. Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NFD, Normandy Farm Ditch; NF, Normandy Farm.

e *Dominant Species*

The species with the greatest percentage dominance are listed below; their distributions throughout the system are shown in Fig. 5.7:

1. Oligochaetes dominated the system (45 % of all individuals), predominantly owing to higher percentage dominance in Normandy Farm ditch (79.6 %) and Butts lagoon (58.9 %), although recorded at all sites. The bimodal distribution of oligochaetes is probably explained by the presence of three species, *Tubificoides benedii*, *T. pseudogaster* and *Heterochaeta costata*, the latter of which prefers lower salinities (Bamber and Evans, 2003).

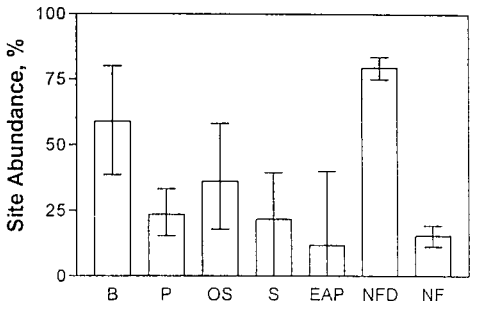
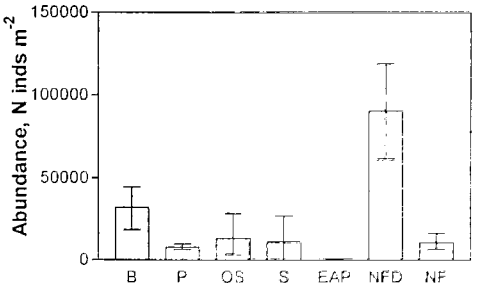
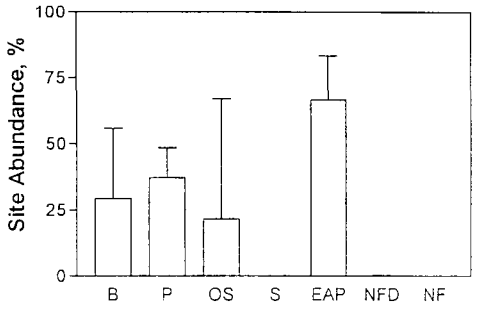
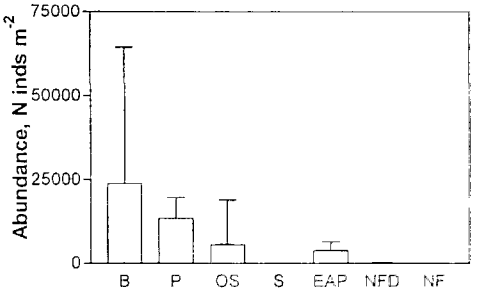
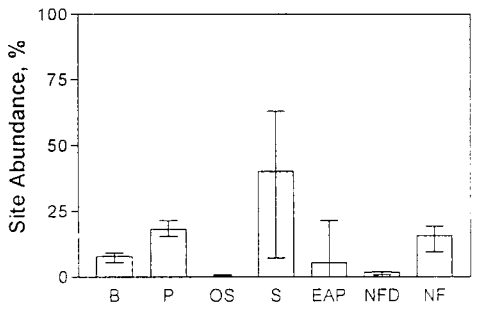
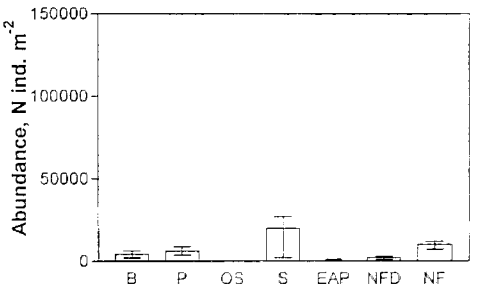
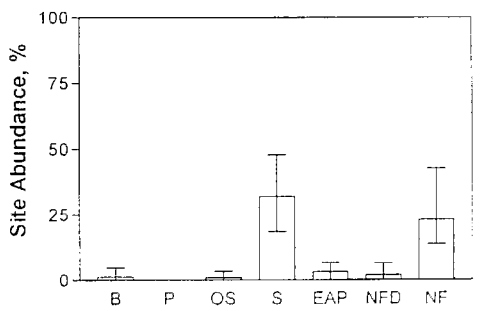
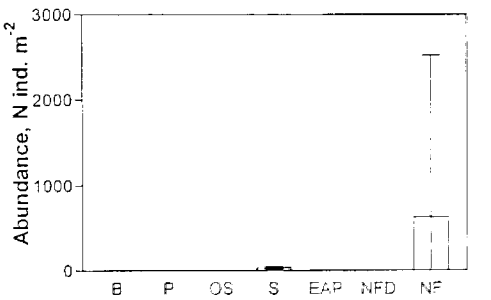
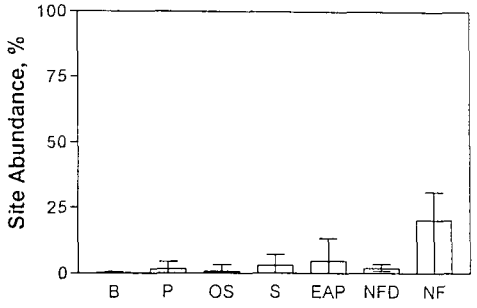
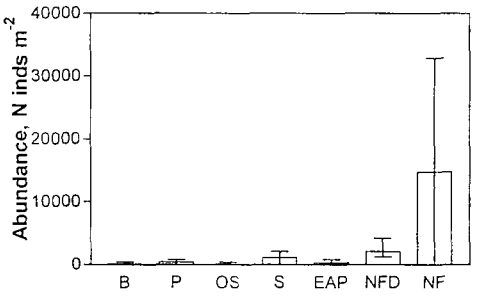
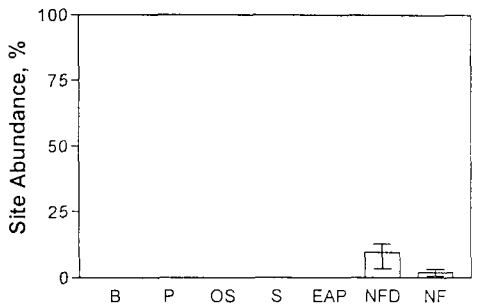
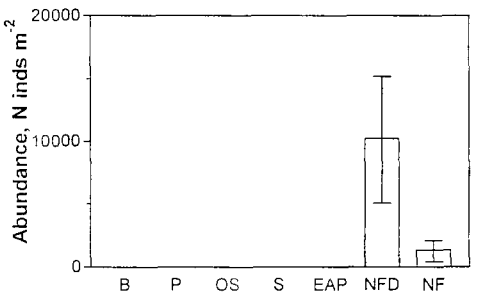
Percentage dominance	Abundance 10 cm^{-2}
1. Oligochaeta	
	
2. *Hydrobia ventrosa*	
	
3. Chironomids	
	
4. *Capitella capitata*	
	
a. Macrofaunal percentage dominance. Mean percentage abundance, error bars are maximum and minimum values.	b. Macrofaunal abundance distribution. Mean abundance 1 m^{-2}, error bars are maximum and minimum values. Note differing scale on Y axis.

Fig. 5.7. Distribution of macrofaunal species accounting for 90 % of total abundance along the Keyhaven-Lymington lagoon system. Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NFD, Normandy Farm Ditch; NF, Normandy Farm.

Percentage dominance	Abundance 10 cm^{-2}
5. *Corophium volutator*	
	
6. *Caulleriella zetlandica*	
	
7. Ostracoda	

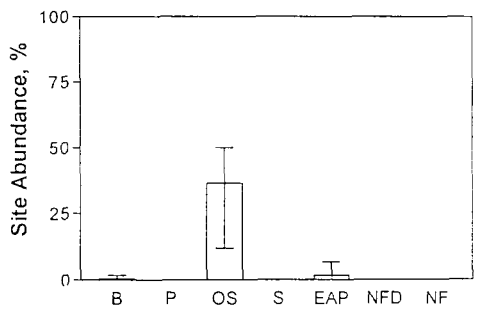
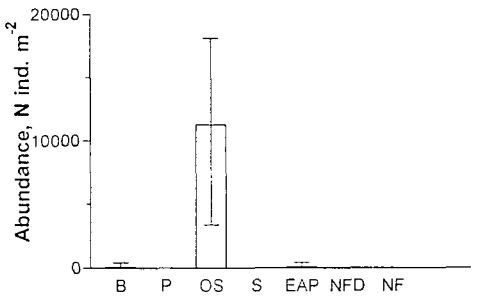

	

Fig. 5.7.a. Continued...	Fig. 5.7.b. Continued...

2. *Ventrosia ventrosa* 12.9 % of individuals counted, predominantly owing to high abundance in Butts lagoon, and was the only species to show a clear preference for lower salinity. However, it was the most dominant in species Eight Acre Pond (66.7 %) and Pennington (37.2 %) lagoons owing to relatively low total abundance at these sites. Absent from Salterns.
3. Chironomids 11.9 % of all individuals counted, due to a relatively high abundance throughout the system (recorded at all sites) with a peak of 20,000 ind. m^{-2} in Salterns lagoon. Most dominant (40.1 %) in Oxey South lagoon where total abundance was low.
4. *Capitella capitata* 9.2 % of individuals counted, recorded in all sites except Pennington. Most abundant in Salterns and Normandy Farm where it also

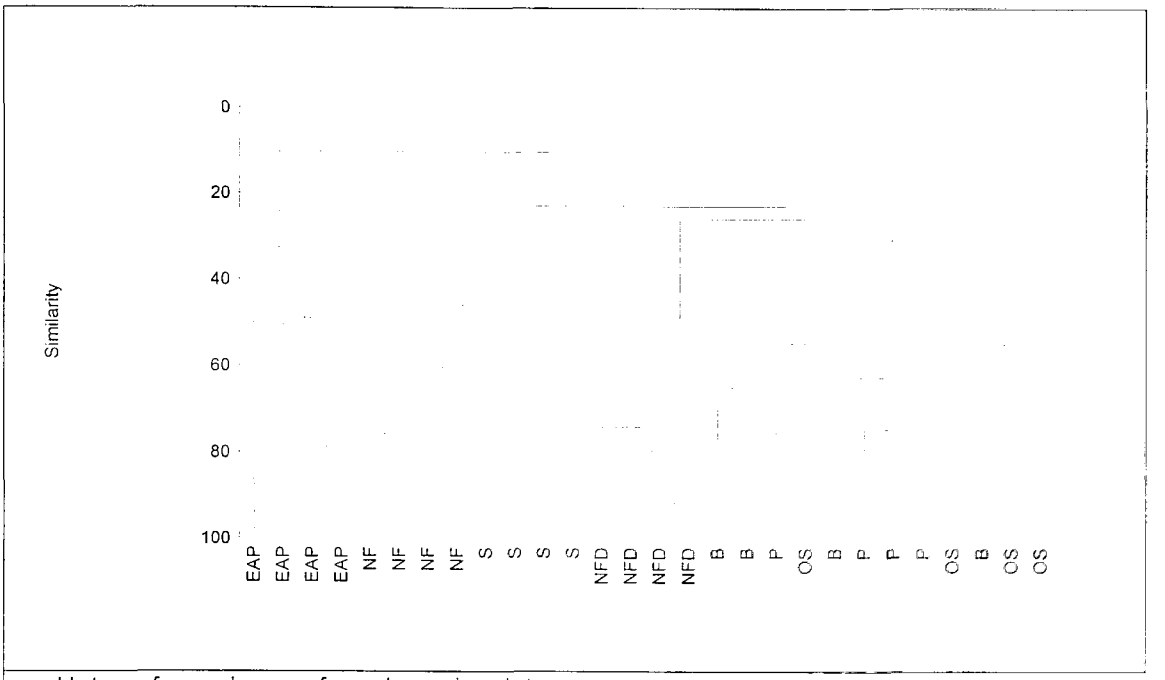
represented the greatest percentage of individuals (32.1 % and 23.1 %, respectively).

5. *Corophium volutator* 5.2 % of individuals counted, although recorded in all sites but at a relatively low abundance. Most abundant in Normandy Farm lagoon, where it is co-dominant (20.3 % of individuals).
6. *Caulleriella zetlandica* 3.2 % of individuals counted, although only recorded in the two Normandy Farm sites. Second most dominant in Normandy Farm ditch (9.6 % of individuals).
7. Ostracods 3.2 % of individuals counted, due to a high dominance (36.5 % of individuals) in Oxey South lagoon. Only also recorded in Butts and Eight Acre Pond.

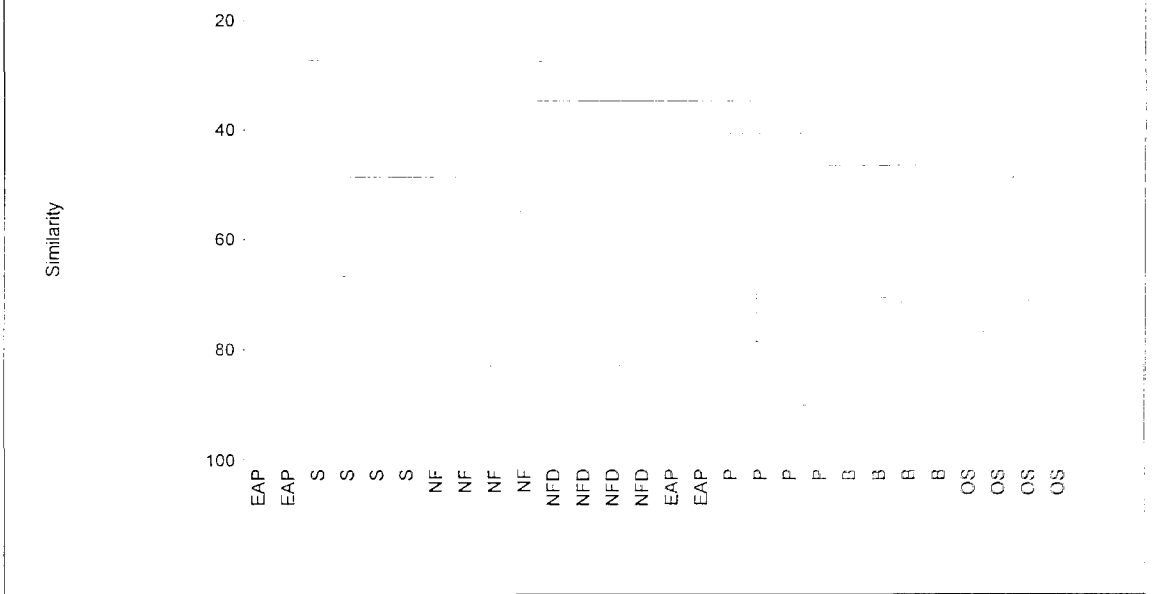
5.2.2 Multivariate statistics

a *Site similarity*

Although the macrofaunal assemblage was reduced in diversity and abundance relative to nematodes, the dendrogram of Bray-Curtis site-similarity based on untransformed macrofaunal data (Fig. 5.8 a) distinguished same-sites replicates from Normandy Farm, Normandy Farm ditch and Salterns at > 50 % similarity and samples from Eight-Acre Pond at > 30 % similarity. Replicates from Pennington, Oxey South and Butts lagoons did not clearly differentiate. However, calculation of site similarity with fourth-root transformed macrofaunal data (Fig. 5.8 b) distinguished each set of site replicates as a separate group for all sites except Eight-Acre Pond. Samples from Salterns, Normandy Farm, Normandy Farm ditch, Pennington and Butts each had > 60 % within-site similarity, indicating a relative homogeneity of species assemblage between replicates. Samples from Oxey South were > 40 % similar (dividing into two sample pairs, each with > 60 % similarity), indicating some variability of species dominance and occurrence between replicates. The separation of replicates from Eight-Acre Pond within the similarity dendrogram of fourth-root transformed data compared to that of untransformed data indicates patchiness of rare species between sites but a similarity of dominants. This is also confirmed by the ANOSIM test, which gave a significant difference between sites (untransformed data, $r = 0.864$, $p < 0.1$; fourth-root transformed data, $r = 0.83$, $p < 0.1$).



a. Untransformed macrofaunal species data.



b. Fourth-root-transformed macrofaunal species data.

Fig. 5.8. Dendrograms of Bray-Curtis site similarity based on macrofaunal assemblage data. Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NFD, Normandy Farm Ditch; NF, Normandy Farm.

Similarity analyses of sites by macrofauna and nematode assemblages defined sites in a relatively similar manner, each creating two site groupings. The sites with the most similar macrofauna and nematode species (fourth-root transformed dendrograms) were Normandy Farm, Normandy Farm ditch and Salterns, whilst for the macrofauna a second group of similar sites included Oxey South, Pennington and Butts. In terms of the nematode assemblage this latter group of sites were

increasingly dissimilar from the first group. For each faunal group Eight Acre Pond is distinct from the other sites, although, less so for the macrofaunal samples. Essentially then, the two analyses split the site assemblages by higher salinity (and higher diversity) in the former group and lower salinity (and lower diversity) in the latter group.

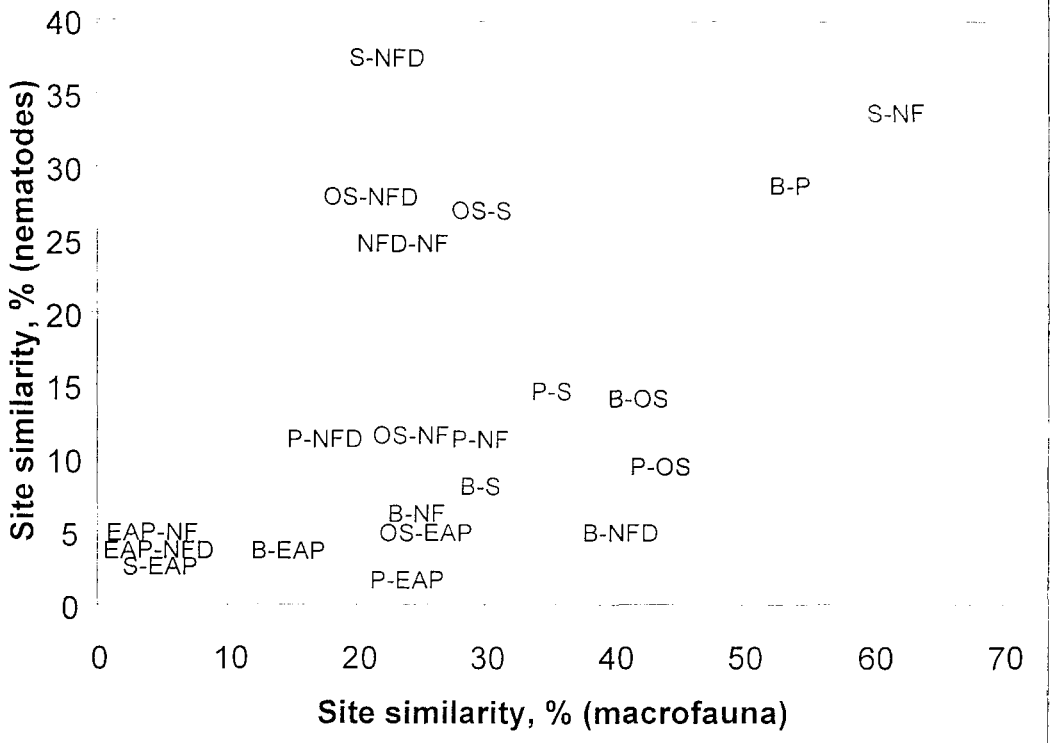
There was no correlation between site similarity calculated from macrofaunal and nematode species data, predominantly owing to differences between the nematode and macrofauna assemblages in Normandy Farm ditch (Fig. 5.9 a. untransformed data; b. fourth-root transformed data). At this site, evenness in the macrofauna assemblage was half that of the nematode assemblage, although diversity was still high. Also, site similarity between Salterns and Oxey South was much higher for the nematode assemblage than for the macrofaunal assemblage, predominantly due to a greater diversity in the nematode assemblage in Salterns lagoons, which included the lower salinity brackish water species occurring in the more westerly lagoons. The macrofaunal assemblage in Salterns included those species only found in the more saline sites. However, if these outliers are excluded, correlation of site similarity by macrofauna and nematode assemblages is significant ($r = 0.862$, $p < 0.001$) for untransformed data, but not for fourth-root transformed data ($r = 0.02$, $p > 0.05$).

It was also possible that the inclusion of epibenthic macrofaunal species in the comparison between macrofauna and nematode might have biased the analyses so the Bray-Curtis similarity of sites was recalculated including only burrowing macrobenthic species. However, this did not increase the correlation of site similarities calculated from these two groups ($r = -0.43$ for untransformed data; $r = -0.31$ for fourth-root transformed data).

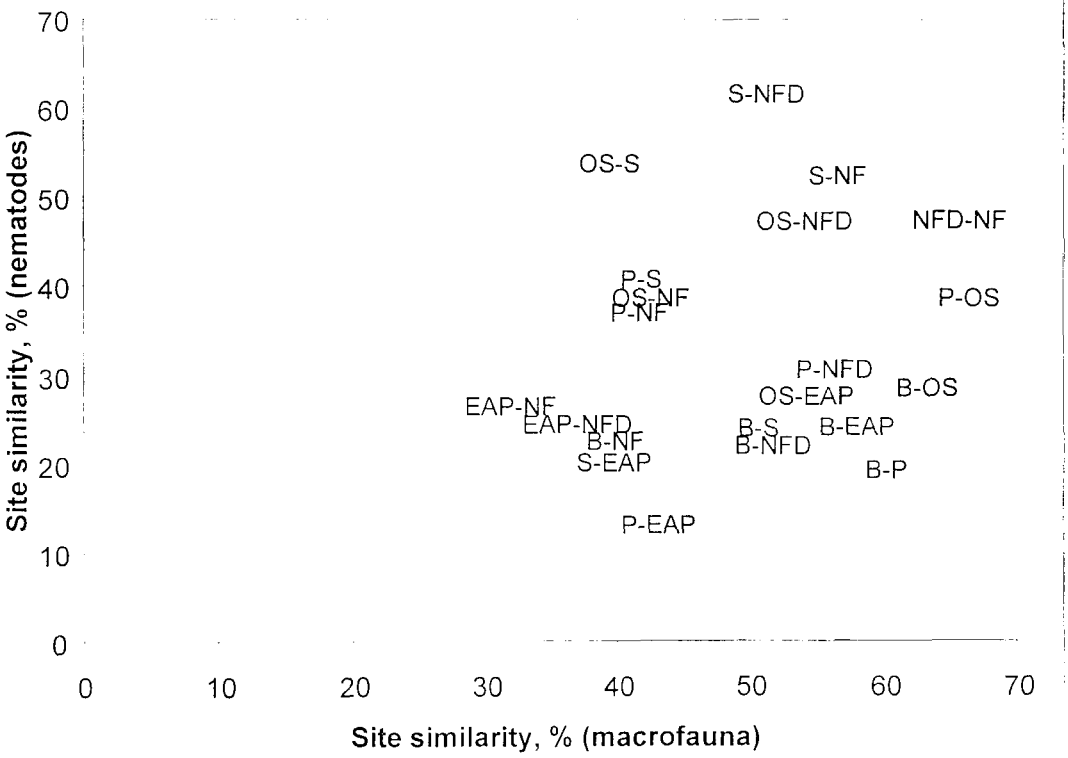
b *Similarity of species assemblages*

i Within sites, between replicates

All sites except Oxey South and Eight-Acre Pond had high (> 50 %) within-site similarity (Table 5.2), whilst high dominance in all sampling sites resulted in a high percentage contribution by only one species in all sites, except Pennington and Normandy Farm where diversity was highest. Recalculation of the SIMPER analysis



a. Untransformed macrofauna data (r = 0.47).



b. Fourth-root transformed macrofauna data (r = 0.18).

Fig. 5.9. Correlation of site similarity values calculated from macrofaunal and nematode data. Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NFD, Normandy Farm Ditch; NF, Normandy Farm.
Eg. B-P, similarity of nematode assemblage between Butts and Pennington plotted against similarity of macrofaunal assemblage between Butts and Pennington.

Sites	Within site Similarity (%)	No. spp 90% of similarity	Species most similar between replicates, within site	Mean Abundance 1 m^{-2}	Contribution to site similarity (%)
Butts	55.05	3	Oligochaeta	32199.3	71.52
Pennington	69.08	4	*Hydrobia ventrosa*	13,469.0	36.96
Oxey South	41.43	2	Ostracoda	11,259.2	48.82
Salterns	65.80	3	*Capitella capitata*	13,574.2	42.99
Eight Acre Pond	45.88	2	*Hydrobia ventrosa*	3,788.2	89.50
Normandy Farm Ditch	78.85	2	Oligochaeta	90,073.8	84.32
Normandy Farm	62.00	6	*Capitella captitata*	16,099.6	22.45

Table 5.2. Similarity of macrofaunal assemblages between replicates within sites in the Keyhaven-Lymington lagoon system, the number of species accounting for 90 % of that similarity and the species most important to it. Untransformed species data .

Sites	Within site similarity (%)	No. spp to 90% similarity	Species most similar between replicates, within site	Mean Abundance, 10cm^{-2}	Contribution to site similarity (%)
Butts	71.85	3	Oligochaeta	32199.28	40.43
Pennington	82.20	6	*Hydrobia ventrosa*	13468.98	21.43
Oxey South	56.83	3	Ostracoda	11259.23	38.57
Salterns	74.72	4	*Capitella capitata*	13574.21	35.66
Eight Acre Pond	46.16	4	*Hydrobia ventrosa*	3788.15	70.66
Normandy Farm Ditch	78.14	7	Oligochaeta	90093.81	29.55
Normandy Farm	80.34	8	*Capitella capitata*	16099.64	15.07

Table 5.3. Similarity of macrofaunal assemblages between replicates within sites along the Keyhaven-Lymington lagoon system, the number of species accounting for 90 % of that similarity, and the species most important to it. Fourth-root transformed species data.

with fourth-root transformed assemblage data (Table 5.3) increased between-replicate similarity for all sites, and reduced the percentage contribution of the most similar species by approximately one third, except in Normandy Farm ditch where the contribution was reduced by two thirds. Fourth-root transformation of the data identified homogeneity of rare species within this site as well as that of the dominant oligochaetes (Table 5.3).

The species contributing the most to within-site similarity were the most dominant species in all sites, except Salterns where the abundance of the most dominant species (*Capitella capitata*) was most variable between replicates. At this site the second most dominant species contributed the most to within site similarity. The species contributing the most to within site similarity remained the same for all sites, whether the data was untransformed or fourth-root transformed, probably owing to the heterogeneity of species composition between replicates and the relatively high dominance of few species at each site.

ii Between sites

Between sites, dissimilarity of the untransformed macrofaunal species data was > 55 % for all pair-wise comparisons (Table 5.4). The macrofaunal assemblage in Eight-Acre Pond is > 90 % dissimilar from the other three higher salinity sites (Normandy Farm, Normandy Farm ditch and Salterns), and therefore more similar to the lower salinity sites due to the reduced infaunal diversity. All sites are > 50 % dissimilar, probably owing to the low diversity in the system; small differences in species abundance between sites will effectively be more important, than in a sample with a larger diversity. The species accounting the greatest proportion of between site dissimilarity for each pair-wise comparison (SIMPER analysis of untransformed species data) are listed in Table 5.5.

Site	B	P	OS	S	EAP	NFD
P	56.46					
OS	65.04	66.71				
S	72.82	72.93	83.69			
EAP	87.06	76.08	84.28	95.93		
NFD	60.49	83.69	80.94	79.10	98.01	
NF	75.07	71.38	83.51	53.99	96.76	78.49

Table 5.4. Percentage dissimilarity of macrofaunal assemblages between sites in the Keyhaven-Lymington lagoon system. Based on untransformed species data. Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NFD, Normandy Farm Ditch; NF, Normandy Farm.

Fourth-root transformation of the data decreased dissimilarity between all sites (Table 5.6). Dissimilarity decreased by over 20 % between Butts and Eight-Acre Pond, Oxey South and Eight-Acre Pond, Pennington and Normandy Farm ditch, Salterns and Normandy Farm ditch and Normandy Farm lagoon and Normandy Farm ditch, whilst dissimilarity decreased by less than 5 % between Butts and Normandy

	B	P	OS	S	EAP	NFD
P	Oligochaeta 44.39 *H. ventrosa* 32.73					
OS	Oligochaeta 37.09 *H. ventrosa* 30.58	Ostracods 24.75 *H. ventrosa* 24.56 Oligochaeta 18.73				
S	Oligochaeta 29.53 *H. ventrosa* 24.80	Chironomids 26.24 *C. capitata* 24.03	Chironomids 29.71 *C. capitata* 21.61			
EAP	Oligochaetes 59.17	*H. ventrosa* 29.77 Oligochaeta 25.08	Oligochaeta 35.20 Ostracods 35.12	Chironomids 36.90 *C. capitata* 28.95		
NFD	Oligochaetes 56.62	Oligochaetes 66.06	Oligochaetes 65.95	Oligochaetes 62.49	Oligochaetes 76.99	
NF	Oligochaetes 21.89 *H. ventrosa* 20.64 *C. capitata* 16.27	*C. capitata* 21.45 *C. volutator* 18.48 *H. ventrosa* 18.39	*C. captitata* 18.6 *C. volutator* 16.63 Ostracods 13.38 Chironomids 12.56	Chironomids 22.82 *C. volutator* 21.36 Oligochaetes 13.13	*C. captitata* 21.74 *C. volutator* 19.10 Chironomids 14.40	*Oligochaetes 55.63*

Table 5.5. The percentage contribution of macrofaunal species accounting for 50 % of between site dissimilarity in the Keyhaven-Lymington lagoon system. SIMPER analysis of untransformed species data.
Lagoons: B, Butts.; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NFD, Normandy Farm Ditch; NF, Normandy Farm.

Farm ditch and Salterns and Normandy Farm. A large reduction in dissimilarity with fourth-root transformation of the data may indicate a greater similarity of rare rather than dominant species between lagoons. Little change in dissimilarity indicated a dominance of few species and a reduced number of rare species in one or both lagoons in a combination.

Sites	B	P	OS	S	EAP	NFD
P	40.65					
OS	53.15	54.27				
S	56.87	62.68	72.57			
EAP	60.38	64.50	64.38	76.71		
NFD	58.55	50.67	65.94	52.60	81.24	
NF	65.98	60.46	72.05	50.33	83.71	45.04

Table 5.6. Percentage dissimilarity of macrofaunal assemblages between sites in the Keyhaven-Lymington lagoon system. Based on fourth root transformed species data. Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NFD, Normandy Farm Ditch; NF, Normandy Farm.

c *Species similarity (by distribution between samples)*

Bray-Curtis similarity between species assemblages was calculated using untransformed macrofaunal data and then fourth-root transformed macrofauna and nematode data combined. The low similarity values between species and species groups in the similarity dendrogram of untransformed macrofaunal data (Fig. 5.10) is common in macrofaunal lagoonal studies due to the inconsistency of species occurrence (Bamber *et al.*, 2001). Nevertheless, the species groupings can be defined in much the same way as the nematode groups were defined in chapter 4:

1. *I. chelipes* was recorded only in Eight-Acre Pond (nematode Group A);
2. *N. diversicolor* and *M. aetuarinea* were recorded in Pennington and Oxey South (N. diversicolor also in Normandy Farm ditch), but most abundant in Pennington (nematode Group C).
3. *C. insidiosum*, *H. ulva* and *S. rugicaudata* were each most abundant in Butts lagoon although the latter two are recorded in the western lagoons also (nematode group E).
4. Oligochaeta, *H. ventrosa* and Ostracoda were each most abundant in a different lagoon, Oligochaeta and *H. ventrosa* were found throughout the system.
5. *C. setosa* was most abundant in Salterns

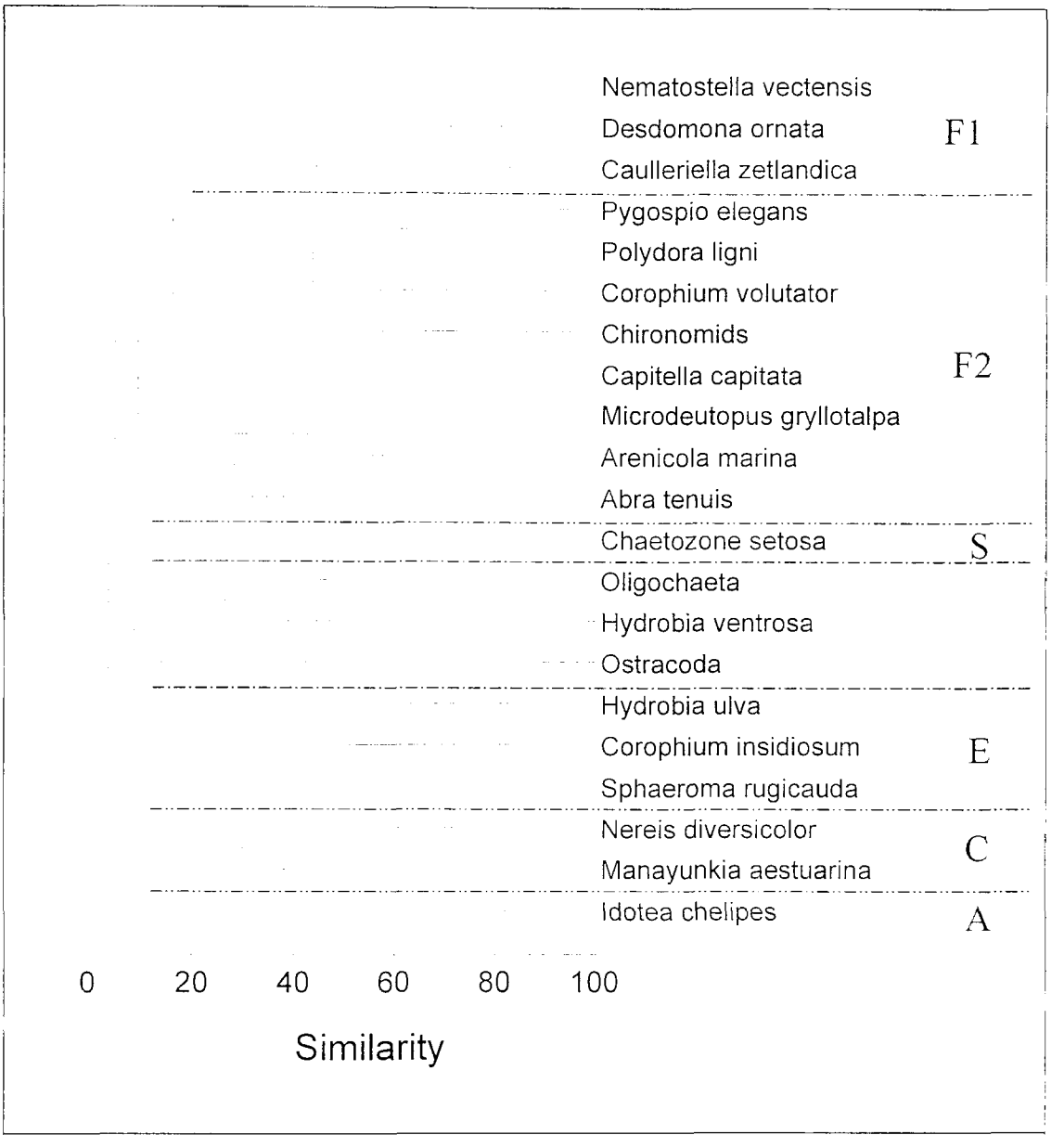


Fig. 5.10. Bray-Curtis similarity dendrogram of macrofaunal species by occurrence along the Keyhaven-Lymington lagoon system (Untransformed species data). Nematode groups from chapter 4 are indicated.

6. Species in the group *A. tenuis* to *P. elegans* were each most abundant in Normandy Farm lagoon (nematode Group F2?)
7. *C. zetlandica*, *D. ornata* and *N. vectensis* were each found in low abundance, predominantly in the higher salinity sites (nematode Group F1).

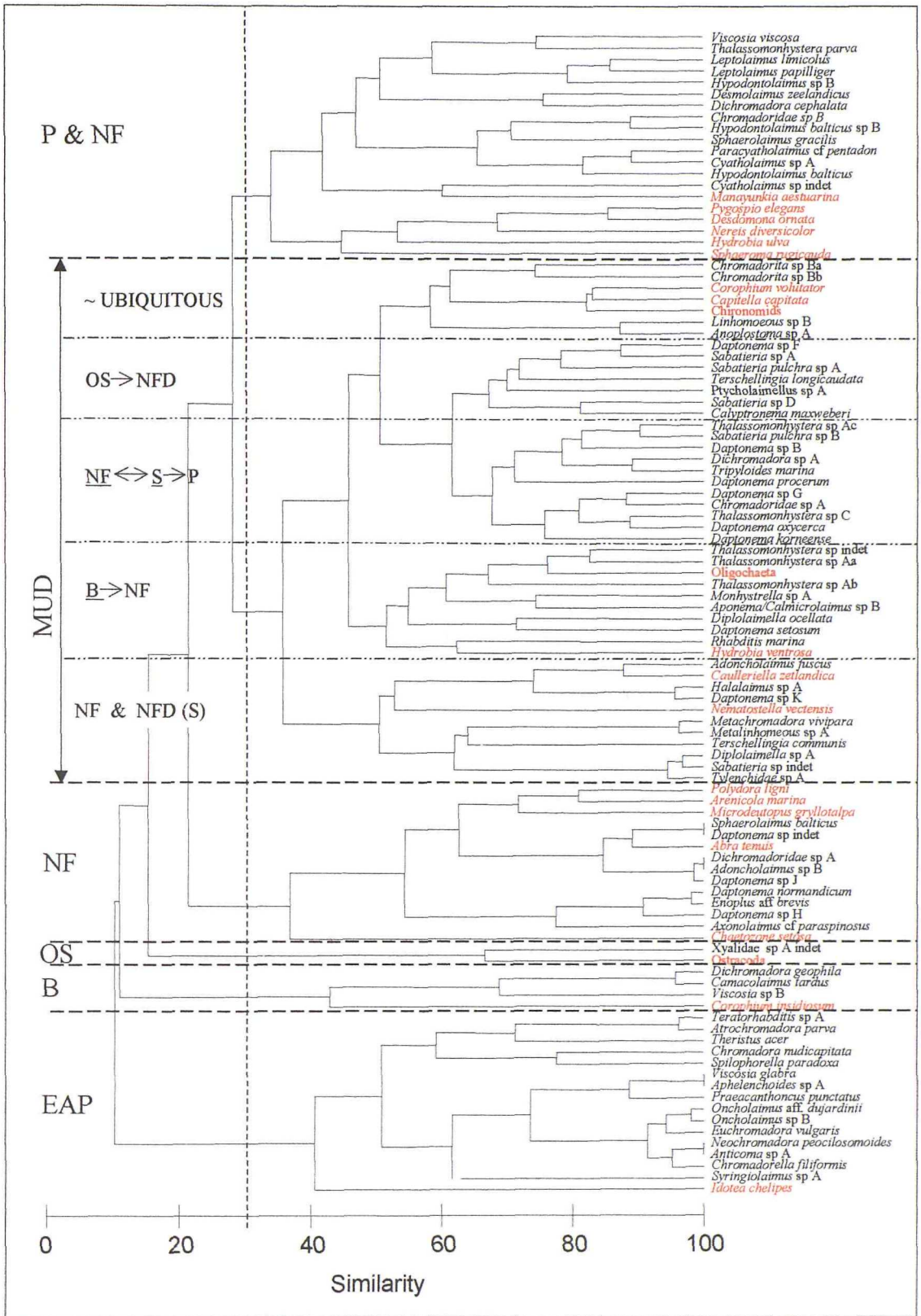


Fig. 5.11. Bray-Curtis similarity dendrogram of macrofauna and nematode species by occurrence along the Keyhaven-Lymington lagoon system (fourth-root transformed species data). Species in red are macrofauna.
Division of groups is made at the 30 % similarity level, with sub-division of the 'mud' group were appropriate. Groups are also defined by sites at which the species are most abundant.

This distribution of species is purely an indication of species sampled during this survey, the core sizes were standard for macrofaunal sampling, but were small in comparison to the 0.05 m^2 Petersen grab usually used by Bamber *et al.* (eg. 2001a, 2002). Consequently some species are likely to have been under-sampled. For example, although an increasing abundance of *H. ventrosa* was recorded from east to west as noted by Bamber (1997), other species such as *N. vectensis*, *I. chelipes* and *C. insidiosum*, which are usually recorded in declining abundance from east to west (Bamber, 1997) were each recorded at only a limited number of sites.

Nevertheless, although the data set is limited by the number of individuals sampled, a combined species similarity analysis of macrofauna and nematodes (fourth-root transformed data to reduced the disparity of abundance between the two groups) produced a dendrogram of species that could be interpreted in terms of species habitat preferences (Fig. 5.11). The species are essentially divided into six groups;

1. species predominantly occurring in sandy sediments in Pennington and Normandy Farm lagoons over a range of salinity;
2. species predominantly occurring in muddy sediments, dividing into those most abundant in the more saline lagoons, those occurring at intermediate salinity (Salterns, Oxey South and Pennington) and those most dominant in the lower salinity in Butts lagoon;
3. species most dominant in Normandy Farm (postulated by Bamber (pers. com.) to have the greater water exchange with the Solent);
4. species occurring in Oxey South;
5. species only occurring in Butts lagoon and;
6. species only or predominantly found in Eight Acre Pond, epibenthic macrofauna and epifaunal or predatory nematodes.

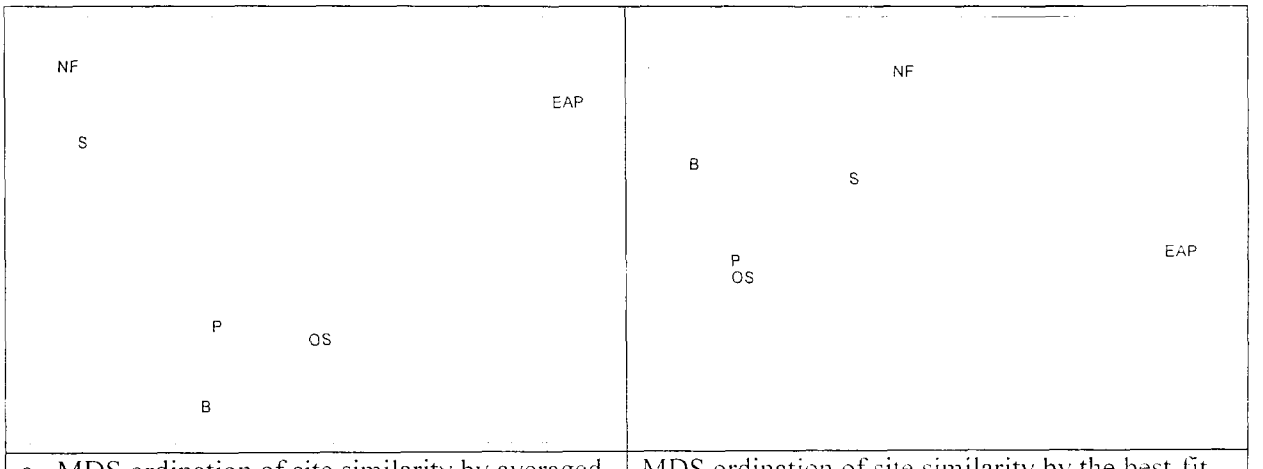
d *Comparing Faunal Data to Environmental Variables*

Pearson's correlation, r, between univariate indices and environmental parameters (full list of environmental parameters given in Table 4.7; Chapter 4) was insignificant for all pair-wise comparisons. However, BIOENV analysis of the macrofaunal data indicated that their distributions were most correlated with the

same salinity parameters (median, minimum and range) as the nematode assemblages. Median salinity and groundwater were the best fit parameters to site similarity of the untransformed macrofauna data, and catchment and salinity were the best fit parameters with fourth-root transformed macrofaunal data, but with a low Spearman's rank correlation (Table 5.7). The plots of site distribution by untransformed macrofauna assemblage data and best fit parameters are give in Fig. 5.12.

Macrofauna data	Untransformed	4th-root transformed
Best Fit Parameters	0.868 Groundwater seepage Salinity Median, 2000 (*0.779, Salinity minimum, 2000*)	0.429 Catchment area Salinity median, 2000 Salinity minimum, 2000 Salinity, minimum overall Salinity, range overall (*0.428, Salinity minimum overall*)

Table 5.7. The combinations of environmental parameters providing the best Spearman's rank fit of site similarity with the site similarity of macrofauna assemblage data (untransformed and fourth root transformed).



a. MDS ordination of site similarity by averaged macrofauna species assemblage data (untransformed). Stress = 0.00

MDS ordination of site similarity by the best-fit environmental parameters. Stress = 0.00

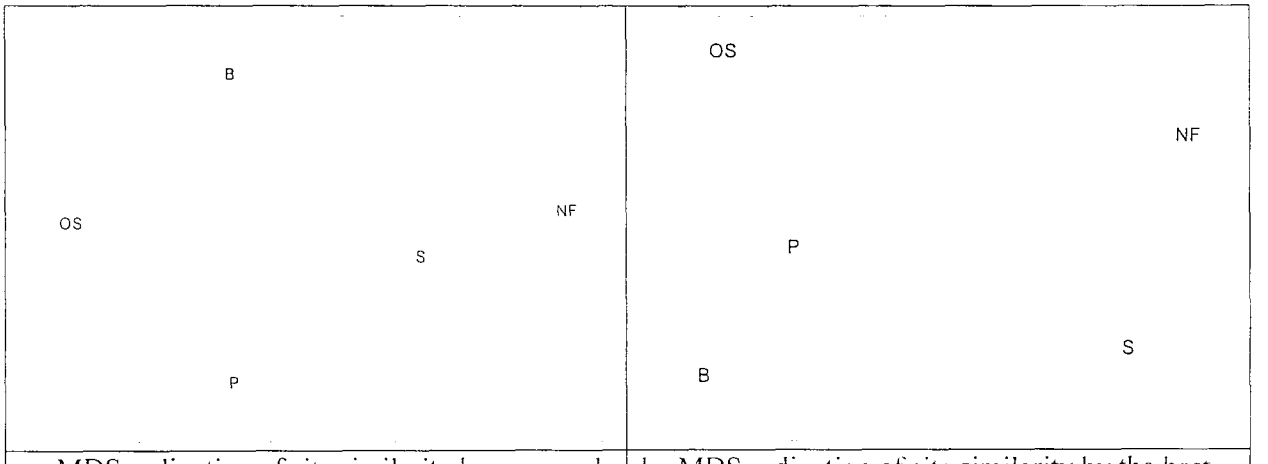
Fig. 5.12. Plots of site similarity by untransformed macrofauna assemblage data and best fit environmental parameters. Spearman's rank correlation between plots, r = 0.868
Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm.

However, these measures of correlation appeared to be skewed by the data from Eight-Acre Pond - its exclusion indicated that other, different, parameters may also influence the assemblages of nematoda and macrofauna (Table 5.8; Fig. 5.13). With the exclusion of Eight-Acre Pond, the best fit environmental parameters for the macrofaunal analysis, lead to the inclusion of catchment area and organic carbon for untransformed data and only catchment area for fourth-root transformed data. This is

in contrast to the BIOENV analysis with the nematode data which included sediment granulometry (clay when biotic data untransformed, gravel and organic carbon when fourth-root transformed) and lagoon depth. Salinity remains the parameter most correlated with species assemblage.

Best Fit Parameters	Macrofauna data – no EAP	
Environmental data	Untransformed	4^{th}-root transformed
All	0.939 Catchment area Organic carbon Salinity mean, 2000 Salinity median, 2000 Salinity range, overall	0.855 Catchment area Salinity median, 2000 Salinity kurtosis, 2000 Salinity, minimum overall, Salinity range, overall
Best single	0.842 Salinity median, 2000	0.774 Salinity minimum, overall

Table 5.8. The combinations of environmental parameters providing the best Spearman's rank fit of site similarity with the site similarity of macrofaunal assemblage data (EAP [Eight-Acre Pond] excluded).



a. MDS ordination of site similarity by averaged macrofaunal species assemblage data (untransformed), excluding EAP. Stress = 0.00

b. MDS ordination of site similarity by the best-fit environmental parameters. Stress = 0.00

Fig. 5.13. Plots of site distribution by untransformed macrofauna assemblage data and best fit environmental parameters, excluding EAP. Spearman's rank correlation between plots, r = 0.939. Lagoons: B, Butts; P, Pennington; OS, Oxey South; S, Salterns; EAP, Eight Acre Pond; NF, Normandy Farm.

Catchment area may be correlated to the unmeasured parameters of land drainage and associated nutrient input. The inclusion of granulometric parameters may reflect differences in feeding and life history strategies adopted by the two size classes, particularly the infauna. The results indicate that the physical attributes of the sedimentary environment within the range studied here were less important to macrofaunal assemblage dynamics than to the nematode assemblages. Thus the nematodes may be used to define the lagoons more clearly both by their salinity regimes and by the sedimentary habitat.

5.3 Discussion

At the most saline sites diversity and abundance patterns of the macrofaunal and nematode assemblages were similar, but there was no correlation between the two size classes west of Eight-Acre Pond. Macrofauna and nematodes were most diverse in Normandy Farm lagoon, probably owing to both the surface water exchange with the Solent and a salinity regime that is tolerated by marine as well as brackish water fauna. Both macrofauna and nematodes were reduced in diversity at Eight-Acre Pond relative to the other high salinity sites. Macrofaunal diversity was relatively poor in all sites, reaching a minimum in Salterns, whilst nematode diversity, although higher, declined significantly from east to west. The macrofauna probably did not suffer the same decline in species diversity with salinity as recorded for nematode, owing to the presence of low-salinity tolerant species (*Heterochaeta costata*, *Hydrobia ventrosa*, and chironomids. In the nematodes, however, as a percentage of the total species count few species were low-salinity tolerant, of the 14 nematode species recorded in Butts lagoon only two, *Diplolaimella ocellata*, and *Thalassomonhystera sp*, were most abundant there.

Although diversity and abundance of macrofauna and nematodes were equally reduced in Eight-Acre Pond, macrofauna showed an increased patchiness of species. This is likely to reflect inclusion of mobile epifauna in the data and the loss of macro-infauna owing to the coarse compacted sediments at this site. The reduced abundance and diversity of the nematode assemblage in Eight-Acre Pond is likely also to have resulted from the granulometric environment, since the majority of species will probably inhabit a narrow surface layer of flocculent material. However, the nematode species recorded in Eight-Acre Pond were an assemblage of sites specific species, rather than a reduced selection of those species occurring in the other sites. Therefore, it is important to note that, whilst the abundance of macro-infauna was reduced in Eight-Acre Pond, particularly in its shallow margins (Bamber *et al.*, 2001a), this site significantly increased the nematode diversity in the system as whole and might therefore represent an important habitat resource in the system.

Both the macrofaunal and nematode assemblages were variable in Oxey South. The coincidence of patchiness in both faunal groups may suggest that at the time of sampling this site was structurally diverse resulting in a close proximity of epifauna,

infauna and epiphytic fauna and an associated variability of abundance within and between each. Also, this site had black, anoxic mud which would reduce the penetration of fauna into the sediment. Finally, in Salterns nematode diversity was higher than macrofaunal diversity relative to other sites and nematode abundance and species composition was more variable between replicates. The variability of the nematode assemblage may indicate a patchiness of the granulometric environment, to which the macrofauna are less sensitive. However, the reduced diversity of macrofauna (only robust infauna such as oligochaetes, *C. capitata*, and chironomids and epifauna were abundant) may also suggest that the sedimentary habitat was disturbed. That the nematodes were not comparably reduced in diversity may suggest that this disturbance was selectively interacting on the fauna at a physiological level. The sediment at this site was black and anoxic. It is possible that oxygen limitation prevented the settlement of many macro-infaunal species and reduced the depth to which those few surviving could burrow, and it is known that nematodes are frequently abundant in anoxic or reduced sediments were macrofauna are absent or reduced (Hendelberg, and Jensen, 1993).

Although univariate measures of the macrofaunal and nematode assemblages did not correlate, the assemblage dynamics of both groups are most influenced by salinity variation within in each site. However, the nematode assemblages are also influenced by granulometric parameters on a fine scale, whilst macro-infaunal species differ only in response to coarse changes in sediment type. In this respect, each lagoon has a distinct nematode assemblage dependent on the local environmental parameters - even the two sites with the most similar nematode assemblages, Normandy Farm ditch and Salterns, only share 52 % of their joint species count. The macrofaunal assemblages however, although different between sites, are more similar (eg. Pennington and Oxey South share 69 % of their joint species count) and essentially represent four species groups; estuarine/marine species, euryhaline species, freshwater-tolerant species and lagoonal species (Bamber and Evans, 2003).

Nevertheless, although the lagoon macrofaunal assemblages are less diverse and less distinct than the nematode fauna, and are at a relatively low diversity in comparison to other brackish water habitats (eg estuaries), the characteristic lagoonal

macrofaunal species are endemic to these and other sheltered, relatively isolated brackish water habitats. Conversely, the species recorded in the nematode assemblages in the lagoon system are also recorded in estuarine brackish water habitats. This raises two issues, why are estuarine nematodes abundant in the lagoon system, when estuarine macrofauna are restricted to Normandy Farm where seawater influx is most regular, and; why were lagoonal specialist nematodes not found?

6 Discussion

The nematode and macrofaunal assemblages in the Keyhaven-Lymington lagoon system were structured differently in response to salinity, granulometry and isolation. Both nematodes and macrofauna were limited by salinity conditions, in general the nematode assemblages gradually declined in diversity with decreasing salinity, whilst the macrofaunal assemblages had low diversity throughout the system, although further reduced in Salterns and Eight Acre Pond. Equally, nematode assemblage dynamics differed between lagoons due to small changes in sediment granulometry, whilst the macrofaunal assemblages were relatively constant between sites. Even between sites with large differences in sediment type where the nematode assemblages were distinct, the macrofaunal assemblages remained comparable. Yet, whilst lagoonal macrofaunal assemblages are distinct from other brackish water habitats, having characteristic lagoonal specialist species, the nematode assemblages were formed of species recorded frequently in estuarine habitats.

The influence that salinity fluctuation and granulometry may have on macrofauna and nematodes at both the species and individual level are well recorded. Macrofaunal species tend to have a reduced tolerance to osmotic stress and assemblages are reduced in abundance and diversity under such conditions. Nematode assemblages, on the other hand, are generally more sensitive to granulometric changes, owing to their interstitial or micro-infaunal life style (as opposed to the macro-infaunal burrowing life style). However, that macrofauna and nematodes vary in terms of species composition resulting from lagoonal variation is perhaps unexpected. Although hydrological surveys indicate that water exchange between the lagoons in the Keyhaven-Lymington system and the adjacent Solent Water is limited (Hodges, 2000), a macrofaunal species, *Desdomona ornata* Banse, recently introduced to Southampton Water (Smith *et al.*, 1999) has been recorded in the Keyhaven-Lymington lagoons since 2000. Also oligochaetes, which do not have dispersive propagules and have been shown to take over ten years to reach ambient densities in disturbed or created salt marshes (Craft and Sacco, 2003), were recorded in Normandy Farm shortly after this lagoon was created. Whilst seeding from salvaged sediment may have provided a source of viable individuals, it would not

explain the apparently fast rate of dispersal throughout the lagoon. Nevertheless, the difference in levels of isolation between the macrofauna and nematode populations was emphasised by the greater diversity of the nematode assemblage as opposed to the low diversity, lagoon specific macrofaunal community.

6.1 Dispersal Mechanisms

Lagoonal specialist macrofauna are aplanktonic, which in combination with a closed lagoonal system is thought to increase their genetic isolation from marine assemblages. Dispersive larvae reduce the capability of species to adapt to local conditions (Strathmann *et al*, 1981; Bertness, 1989), which is perhaps one reason why marine species are less successful in the variable habitats provided by lagoons. Also species inhabiting such disparate biotopes would be disadvantaged by the length of time their dispersive larvae would require to reach other suitable habitat (Crisp, 1974; Jablonski and Lutz, 1983; Pechenik, 1999). Equally, the limited depth and water movement in lagoons would increase the rate at which planktonic larvae settle out of the water column, resulting in increased competition for space and food and therefore high rates of larval mortality. Thus the energy expenditure that would be required to produce enough larvae to ensure dispersal success would be prohibitive. Also, it has been suggested that planktonic development is a trait that has evolved due to competition and predation pressure (Highsmith, 1985; Pechenick, 1999), factors that are reduced for lagoonal fauna. Endemism and reduced species number relative to number of families reflect increased survivorship of lagoonal species (Myers, 1997).

It is thought that in dynamically shifting environments, organisms will attempt to migrate (due to behavioural or autonomic cues) in order to remain in their optimum species-specific habitat (Walter and Hengeveld, 2000). Yet, whilst species with dispersive propagules may be able to track their preferred habitat between generations, those with a non-dispersive larval phase, for which migration is a passive and random/chaotic event, will not exhibit such a rapid population response to environmental changes. For example, in estuaries frequent and regular tidal movement exposes individuals to relatively short (hours) periods of non-optimum salinity, whilst, in a lagoon salinity may change gradually with season, but may

remain at sub-optimal levels for a longer period of time (days/weeks). Thus estuarine species are more able to move with the most optimal environment (e.g. vertical diurnal migration; Boaden, 1968) and only encounter salinities close to their optimal range, whilst in lagoonal environments individuals must be more able to remain successful (ie. find food and produce viable offspring) over a greater range of environmental conditions.

Although isolation and habitat specificity is associated with speciation, migration between lagoons, either by active or passive means, must be important in order to maintain the genetic diversity of lagoonal species (Bamber *et al.*, 1992). However, the most commonly suggested method of transport - when attached to filamentous algae wrapped around birds feet, which dates back to Darwin (Barnes, 1987) – is not supported by field observations. Adjacent lagoons used by waders and wildfowl do not have similar macrofauna (Barnes, 1988a). Nevertheless, there is experimental and field evidence for the transport of adult benthic fauna in association with marine plants and in the water column or on the surface water film following sediment disturbance, species with hydrophobic exoskeletons being most successful (Highsmith, 1985). Species of amphipod, polychaete and bivalve have been recorded rafting on eel grass and tanaiids have been noted to float at the water's surface - adults, up to 65 hours; juveniles, up to 120 hours (experimental evidence from *Leptochelia dubia*; Highsmith, 1985).

Lagoonal species in the Venice lagoon are recorded in association with algae (Verhoeven, 1980), particularly following storms (Fava and Volkman, 1975). Within UK lagoons, rafting might occur in the floating algae *Chaetomorpha*. This would facilitate the transport of species between habitat patches, and also act to transport introduced species from the point of entry. For passive dispersers the sheltered nature of lagoons will be a limiting factor to migration frequency due to limited sediment disturbance and associated suspension in the water column. Dispersal is likely to be a stochastic event occurring at either local or region and spatial or temporal scales. Sediment type and frequency and force of water movement will influence the extent of sediment disturbance, and dispersal into the Keyhaven-Lymington lagoons will probably be most dependent on strong winds or

storm events that will increase the rate of water movement and therefore sediment disturbance.

However, nematodes also have aplanktonic larvae. Although species with an aplanktonic larval phase are more likely to form genetically isolated populations, even low rates of genetic exchange may prevent major evolutionary change (Peterson, 1996; Grant and da Silva-Tatley, 1997). The small size of nematodes means that they may be more readily dispersed into the water column than larger macrofaunal species. They are known to raft over long distances (Gerlach, 1977b; Giere, 1993; Heip *et al.*, 1985) and over shorter distances may be suspended in the water column (Jensen, 1981). Even in low (tidal-) energy subtidal environments wind-driven disturbance and freshwater inflow may significantly reduced infaunal meiofauna abundance (Guidi-Guilvard and Buscail, 1995). Yet, taxa-specific migration into the sediment as a response to water movement has been recorded in infaunal species (Boaden, 1968). Nematodes tend to have a reduced percentage abundance in the water column relative to initial sediment concentrations (Palmer, 1984; Guidi-Guilvard and Buscail, 1995), due to burrowing away from disturbance (Palmer, 1984).

In fact, two species recorded in the Keyhaven-Lymington lagoons, *Chromadorella filiformis* and *Monhystera parva*, have been recorded in drifting Sargassum in other areas (Micoletzky, 1922). Even limited water input from the adjacent marine area might be enough to add many nematode individuals. Speciation would then be unlikely since nematodes are tolerant of a greater range of environmental stresses than macrofauna. Within lagoons sufficient sediment disturbance to suspend small (and therefore lightweight) organisms such as nematodes may be frequent. Sediment disturbance may be created by the swimming activity of fish such as flounder and eel[*], bird feeding and movement, macrofaunal burrowing, agal decay and associated bacterial activity (which may include gaseous bubbling), cattle grazing (where present), leisure usage, and even frequent scientific investigation. In situ video footage would be required to assess rates of sediment disturbance.

[*] There have been observations of pelagic species in the Keyhaven-Lymington lagoons, but a quantitative survey has not been undertaken.

6.2 Nematode diversity

It is possible that nematode species found in lagoons are 'pre-adapted' to the whole-habitat environmental fluctuations that occur in lagoons. A lack of nematode lagoon specialists may result from their short generation times which affords them the capacity to quickly recover high abundances following disturbance events (Josefson and Widbom, 1988; Heip *et al.*, 1988). Physiological tolerance to salinity change (Forster, 1998), temperature (Farke *et al.*, 1984) and oxygen variability (Jensen, 1986) are also likely to be important to the abundance of nematodes in lagoons. For example, the species of Monhysteridae recorded in the Keyhaven-Lymington system were all deposit feeders (species with an unarmed buccal cavity), either non-selective (eg. *Daptonema*) or selective (eg. *Diplolaimella*, *Thalassomonhystera*). An increased dominance of selective deposit feeders was observed at Butts lagoon. Also, the average nematode length:width ratio was high (long and thin) at this site in comparison to the average across the system. In contrast, the species in Eight-Acre Pond tended to have a reduced length:width ratio (short and fat) and were mainly predators/scavengers (armed buccal cavity). It has been observed that selective deposit feeders tend to be sedentary and have an associated low oxygen consumption, whilst predators and scavengers tend to be active and have a high oxygen consumption (Wieser and Kanwisher, 1961). It is possible, therefore, that there is a correlation between oxygen availability and feeding type (and therefore species assemblage).

It is also known that species in decreased salinity habitats may have a high body length:width ratio. High length:width ratio correlates to high surface-area:volume ratio which may increase the ability to cope with water uptake due to rapidly decreasing salinity (Forster, 1998). All lagoons in the Keyhaven-Lymington system, except Normandy Farm and Eight-Acre Pond, had black anoxic mud at least during part of the sampling year and it is possible that salinity and oxygen availability have an additive influence to morphological distribution.

Although distinct lagoonal specialist nematode species were not recorded in the lagoon system, some morphological variability within species was recorded. For example, male *Hypodontolaimus balticus* typically have 22 - 23 precloacal supplements (Platt and Warwick, 1988) and whilst specimens fitting this description

were found, they were recorded along with specimens that had only 16 supplements in Normandy Farm. Also, variability in the hirsuteness of *Daptonema setosum* was recorded as well as a variable gubernaculum length in males. It is thought that this species may be represent by two ecological morphotypes throughout other brackish water systems (Ferrero, pers. com.). Another example includes variation in female *Daptonema procerum* - vulva position is typically at 45 – 48 % of total body length (Warwick *et al.*, 1998), but in all specimens from the Keyhaven-Lymington system vulva position was approximately 65 % of total body length. Although morphological plasticity in the Nematoda is common, variation is most often seen in tail length, amphid position and number of supplements. Comparative measurements have been taken throughout the lagoon system and measurements of animals from samples taken on the adjacent estuarine mud flats may provide further information of local variability of each species.

The morphological variations noted in nematodes from the Keyhaven-Lymington system are limited, but equally the lagoonal cockle, *Cerastoderma glaucum*, is predominantly distinguished from the edible cockle, *C. edule*, by its more elongate shell (Boyden, 1969). However, *C. glaucum* has a different reproductive pattern to *C. edule* (Barnes, 1980) and probably it would be necessary to take similar observations of the nematode fauna in lagoons. There is also the possibility of differential tolerance between populations of the same species due to physiological acclimatisation or inherited tolerance (Millward and Grant, 1995).

6.3 Conclusions

The habitat that is provided by each lagoon in the Keyhaven-Lymington system is variable. This variability is reflected in the distribution of macrofaunal assemblages throughout the system, but is more clearly defined by the nematode fauna. The nematode and macrofaunal assemblages are both influenced by salinity and granulometry, but the nematode fauna is more robust in terms of abundance and species diversity, it more sensitively delineates the difference between lagoons. Functional groups of the nematode assemblage may also be useful characters in defining the lagoonal habitat.

Although a distinct lagoonal specialist nematode fauna has not been identified, the distinct nematode assemblages found between each lagoon make the Nematoda a useful monitoring tool. The small size of nematodes reduces the need for large samples and would reduce any deleterious impact cause by sampling activity, whilst providing a statistically appropriate number of replicates.

It is possible that the increased maintenance of lagoons in the UK by the construction of sea walls has limited or even removed dispersal opportunities between lagoons (Barnes, 1994). It may be that we have yet to see a loss of genetic diversity both in the macrofaunal specialist and the nematode assemblage. The size difference between lagoonal macrofauna and the nematodes may mean that nematode populations retain a viable population in the system for longer than the macrofauna, due to differences in the dispersal opportunities. Essentially it is dispersal opportunity and stress tolerance that are most important factors influencing the diversity and abundance of lagoon communities, both the specialist macrofauna and the meiofauna. Species assemblages do not correlate to any one environmental factor: salinity, sediment type, latitude, lagoonal area, and proximity of other lagoons will all influence species composition (Barnes, 1988; Barnes, 1989; Bamber *et al.*, 1992).

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