

Using Macrophytes for the Environmental Assessment of Rivers: The Role of Sediment Nutrients

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Using Macrophytes for the Environmental Assessment of Rivers: The Role of Sediment Nutrients

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This report is intended to develop better understanding of the role of sediments in determining macrophyte community composition, in order that sediment-macrophyte relationships may be incorporated into methods using macrophytes as tools for the biological assessment of pollution.

Keywords

River; sediment; macrophyte; phosphorus; nutrient; biological assessment.

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EXECUTIVE SUMMARY

A study of the inter-relationship between submerged aquatic macrophytes and sediment characteristics in lowland British rivers is described. The research was focused on the variability of nutrient concentrations in river sediments, in which macrophytes are rooted, and the relationship between macrophyte species and sediment characteristics. The overall research aim was to further develop understanding of the role of sediments in determining macrophyte community composition in order that sediment-macrophyte relationships may be incorporated into methods using macrophytes as tools for the biological assessment of pollution.

A review of the role of abiotic factors controlling and determining macrophyte growth and community composition is presented with particular reference to river sediments. The role of sediments in macrophyte nutrition and flowing water nutrient dynamics is described. This review of research in the fields of macrophyte ecology, sediment chemistry and hydrology concludes that the study of sediment nutrients and the relationship with macrophytes in flowing waters has been neglected.

Seventeen lowland rivers in England were visited and sediment samples were collected from beneath macrophyte stands and unvegetated areas. The sediment samples were analysed for total phosphorus, inorganic phosphorus, total nitrogen, organic carbon, silt/clay content and organic matter content. Variability of these nutrient concentrations and sediment characteristics both within river reaches and between rivers were explored. The relationships between these physical and chemical sediment variables were considered through the use of linear regression and principal components analysis.

Sediments were found to exhibit a high degree of variability both within 100m river reaches and between the different rivers. Sediment phosphorus concentrations were found to differ greatly between rivers yet sediment nitrogen and organic carbon contents were similar for all rivers, with the exception of particularly organic-rich sediments. Total and inorganic phosphorus concentrations were closely related in all sediments although the relationship was not linear. There were also significant relationships between total nitrogen and organic carbon, both of which were related to the organic matter content of the sediment. Relationships between mean values for sediment parameters and mean water chemistry parameters indicated that the relationship between water column and sediment nutrient concentrations is complex and is not apparent from time- and space-integrated samples.

The significance of the sediment variables as a control on macrophyte community structure was investigated graphically and through the use of canonical ordination (redundancy analysis) and discriminant analysis. Macrophyte species showed broad tolerances to all sediment variables and it was difficult to separate the influence of sediment nutrients from other sediment parameters or differences between rivers. Ordination indicated that Base Flow Index (which reflects catchment geology), the degree of channel shading and sediment total nitrogen concentrations (possibly a surrogate for organic matter content which was closely related to total nitrogen and organic carbon) were important in explaining the variability in macrophyte species distributions. Discriminant analysis indicated that macrophyte species were not well distinguished by the sediments upon which they were growing.

Finally, the results of this study are discussed with reference to more general questions concerning the role of different abiotic and biotic factors on the distribution and ecology of submerged aquatic macrophyte species. Suggestions are made for further research and for future methodological advances.

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1. INTRODUCTION

This report summarises the key findings and outputs of a PhD research project jointly funded by Queen Mary, University of London and the Environment Agency (Clarke, 2000). The research focused on the spatial variability of nutrients associated with bed sediments in lowland English rivers and the tolerances of submerged rooted macrophyte species to these sediments. The research is presented here in a wider context which considers the application of submerged rooted macrophytes as a means of assessing and monitoring trophic status in rivers. The term *macrophyte* is used throughout this report to describe any vascular aquatic plant and the term *nutrient* to describe any element that in sufficient supply may enhance the growth of macrophytes and/or freshwater algae.

1.1 Biological Assessment of Water Quality

The concept of using living organisms to identify, monitor and assess pollution is well established and many bodies responsible for the monitoring of water quality regularly employ methods utilising invertebrates, algae and plants (see for example Hellawell, 1986). Biological assessment has a number of distinct advantages over conventional abiotic chemical monitoring. It gives a better indication of the bioavailability of pollutants and their likely ecological effect. Furthermore, biological assessment is less dependent upon the time and place of sampling. Organisms respond to continuous pollution and also to pulses of pollution and may be considered to present a time, and to a lesser extent, space integrated record of the water quality at a particular site (Hellawell, 1986; Wright, 1995). Additionally, the assessment of pollution through the use of biota may monitor a wider range and lower concentration (through bioaccumulation) of substances than can feasibly be measured in water and/or sediment samples (Whitton and Kelly, 1995). Conversely, biological methods may respond only to substances that produce a detectable effect on the test organism(s). In this way, the use of invertebrates would not necessarily detect, for example, the presence of phytotoxicological substances or plant macronutrients. Biological monitoring is therefore most usefully employed when a range of organisms are monitored, each for specific purposes, and in combination with traditional abiotic chemical assessment of water and/or sediment (Nixon *et al.*, 1996).

Biological assessment may be particularly applicable to running waters as pollution loads may be episodic (especially from diffuse sources) and rapidly dispersed and may be undetected through the chemical analysis of regularly collected water and/or sediment samples. Examples of the use of biological assessment in water quality monitoring include the use of:- invertebrates (Wright, 1995); diatoms (Kelly and Whitton, 1995); algae (Whitton *et al.*, 1981; Whitton, 1984; Whitton and Kelly, 1995); and macrophytes (Harding, 1981) (Holmes and Newbold, 1984, see Section 1.1.1).

1.1.1 The use of macrophytes in biological assessment

The Environment Agency are currently interested in developing schemes that use aquatic macrophytes as bioindicators or biomonitors of trophic status in rivers. This is driven by a need to monitor nutrient enrichment in natural waters to comply with the legislative requirements of the European Union Urban Waste Water Treatment Directive (UWWTD, 91/271/EC). The UWWTD was adopted by the British Government in May 1991 and concerns minimising the impact of waste water discharges to freshwaters, estuaries and coastal waters.

There are several advantages to using macrophytes as the basis for bioindication or biomonitoring schemes: macrophytes are stationary so absence is easily ascertained; they are by definition visible to the naked eye; there are relatively few species within any one region; many are rooted and thus reflect both water and sediment quality; they are relatively long-living and therefore can integrate seasonal or disturbance factors (Carbiener *et al.*, 1990); monitoring is rapid and requires little or no subsequent laboratory identification; and tissue samples can be easily dried and stored for future reference (Whitton *et al.*, 1981). Additionally, macrophytes may encompass a broad taxonomic base (Kelly and Whitton, 1998) increasing the likelihood of detecting a variety of pollution effects. Macrophytes may have their greatest potential as a tool complementary to macroinvertebrate methods as plants will respond differently to pollutants. The disadvantages of macrophytes as monitoring tools include: marked seasonal variations in community composition and species abundance with many species dying back during winter; many freshwater systems have sparse vegetation due to adverse physical factors (limited light attenuation, high water velocity, drought); or, in rivers where macrophyte growth is prolific, cutting may be employed as a management practice; and finally, the ecology of many macrophyte species and the response to both water and sediment-associated pollutants is not well documented (Department of the Environment, 1987).

There is currently considerable interest in utilising macrophyte-based bioindication and biomonitoring techniques to identify, assess and inform management policy on the anthropogenic nutrient enrichment (eutrophication) of freshwater systems (e.g. Carbiener *et al.*, 1995; Grasmück *et al.*, 1995; Holmes, 1995; Tremp and Kohler, 1995; Kelly and Whitton, 1998). In this application, macrophytes would seem to be the obvious organism for biological assessment as they can respond directly and indirectly to increases in nutrient concentrations and they are intimately involved in stream nutrient dynamics, particularly in shallow, low gradient running-waters where conditions favour abundant macrophyte growth (cf. Sand Jensen, 1997).

At present, the most widely employed method utilising macrophytes in the trophic assessment of rivers is the Mean Trophic Rank (MTR) (Holmes, 1995). The Environment Agency has recently commissioned the development of the MTR scheme (Holmes *et al.*, 1999) as a bioindication tool to aid the implementation and monitoring of the European Union UWWTD (see Dawson *et al.*, 1999a). A complementary tool based on benthic diatom taxa – the Trophic Diatom Index (TDI) was developed at the same time (Kelly *et al.*, 1995). Full details of the development and assessment of the two schemes is given in Dawson *et al.* (1999a). The research described in this report has in part originated from an Agency initiative to further develop the MTR to include information on other factors responsible for the distribution of macrophytes in rivers – in this case the role of sediments.

A major evaluation of the performance of the MTR has just been completed by the Natural Environment Research Council (NERC) Centre for Ecology and Hydrology (CEH) - (Dawson *et al.*, 1999b). Analysis of 5281 macrophyte surveys from Britain and Ireland, and associated water chemistry data where available, indicated that aquatic macrophyte flora have a spectrum of tolerances to nutrient enrichment and that the performance of the MTR system was sufficient to warrant its use as a tool in the assessment of eutrophication (Dawson *et al.*, 1999b). Relationships between MTR and phosphate and nitrate were general, but MTR did decline with increasing concentrations of these nutrients in the water column. The relationships between the logarithm of the nutrient concentration and MTR were stronger for phosphate than nitrate (Dawson *et al.*, 1999b). The evaluation recognised the possible influence of temporal and spatial variation upon plant communities and MTR was significantly correlated with a number of physical characteristics of the

rivers surveyed – mean depth, cross-sectional area, mean substrate size, river slope, source altitude, flow category, solid geology coding and geographical location (Dawson *et al.*, 1999b). The authors recommended that the highest priority in further development of the method was to determine the influence of these physical variables on the MTR and that this could be achieved through the incorporation of a predictive element to the system leading to a 'PLANTPACS' (Institute of Freshwater Ecology, 2000) similar in approach to the established RIVPACS (Wright, 1995).

The performance of the MTR has also been assessed independently through a series of macrophyte surveys at twenty-three sites on the River Welland, East Anglia (Demars and Harper, 1998). MTR was significantly but weakly associated with soluble nitrate and phosphate. The authors concluded that, although MTR has been shown to differentiate between sites upstream and downstream of nutrient inputs at a catchment scale, stream size was an overriding factor and relationships between MTR and water quality were obscured by site factors such as land-use, shade, and localised disturbance.

There are examples of other approaches investigating the link between macrophytes and trophic status and a brief review is provided by Kelly and Whitton (1998). Early work sought to associate particular species with trophic levels (e.g. work of Kohler, 1975; Kohler and Schiele, 1985; Tremp and Kohler, 1995) and others have adopted a phytosociological approach, relating community assemblage to trophic status (cf. Meriaux, 1982; Carbiener *et al.*, 1995). In lake research the DOME system has been developed to assess trophic status through the macrophyte community (Palmer, 1992; Palmer *et al.*, 1992). Recent work has also related plant attributes to trophic status in rivers by considering plants within functional groups rather than as taxonomic units (Ali *et al.*, 1999).

Haury and Peltre (1993) compared a number of macrophyte-based methods in five rivers of Northern France. A phytoecological index based on the work of Ellenberg (1973); Harding's plant score method (Department of the Environment, 1987); the Trophic Index of Holmes and Newbold (1984), which has been developed into the MTR; and Haslam's (1987) damage rating method were found to give convergent results predicting the water quality of the five rivers. However, the authors concluded that the method of Harding and that of Holmes and Newbold were simpler than the other methods and provided a good diagnosis of water chemistry (Haury and Peltre, 1993).

Frequently, the relationship between macrophytes and trophic status of running-waters has been obscured by the presence of other physical and chemical factors operating at the reach and catchment scale. Wiegand (1981) found that vegetation samples from Lower Saxony, Germany, were more related to the physico-chemical type of the water course (acidic or base-rich) than to water quality. Multivariate analysis of vegetation and water chemistry data from the Alsace Rhine floodplain and the Northern Vosges, France was used to develop a 'reference system' for running waters (Robach *et al.*, 1996). The analysis showed that the response of macrophyte communities to nutrient enrichment was different in acidic and calcareous systems (Robach *et al.*, 1996). A similar approach found that the macrophyte communities of 21 streams in the Lorraine region, France, could be classified into five classes where the first two classes were sites with a high percentage of bare bed and steep slopes, a third class was defined by water chemistry variables, and the remaining class was defined by light availability (Grasmück *et al.*, 1995). Another study of macrophyte communities in the Alsace, France, did, however, indicate a gradient of trophic status from oligotrophic communities through to eutrophic communities (Carbiener *et al.*, 1990).

1.1.2 Conclusions on using macrophytes as bioindicators

It is clear from both the evaluation of the MTR project and other attempts at using macrophytes for biological assessment that the influence of other factors (physical and chemical) frequently overrides or confounds that of nutrient concentrations. A number of factors control the distribution of organisms in running waters – flow velocity, stability of water depth (spates and droughts), light and temperature regimes, substrate condition (physical and chemical) and stability, dissolved oxygen availability and water quality (acidity, hardness, turbidity, salinity and nutrient concentrations) (Hellawell, 1986). Consequently, the use of macrophytes as bioindicators must acknowledge and account for these other influences. The range of factors that are important in structuring macrophyte communities also means that whilst some species will respond to and reflect the trophic level of the water others will indicate abiotic characteristics to differing degrees – these may be considered environmental descriptors, for example, *Nuphar lutea* which is restricted to deep, slow-flowing channels (Grasmück *et al.*, 1995).

It may be concluded that successful bioindication of trophic status using macrophytes can only be realised if there is a good understanding of how species and communities vary and respond to the many other factors that are important in governing river flora distribution. The use of macrophytes as indicators of river nutrient status has a further complication which is expressed in Kelly and Whitton's question (1998) –

“what is being measured by a complex community of organisms which derive nutrients to varying extents from both water and sediment?”

Rooted macrophytes can potentially derive nutrients from both water column and sediment (see Section 1.3.1) and macrophytes can therefore be expected to reflect the trophic status of the water *and* sediments (Carbiener *et al.*, 1995). This should be considered an advantage as eutrophication involves the entire system and trophic status is the result of complex interactions between all component parts of the system. Therefore, any organism which reflects only the trophic status of the water column will underestimate the nutrients available in the system. Much of the unexplained variance in the relationships between MTR and water concentrations of phosphate and nitrate may be the result of the influence of sediment concentrations of these nutrients. Thus, sediment nutrient concentrations should be considered if the MTR and other bioindication schemes are to accurately reflect eutrophication –

“underpinning research on the relationship between river macrophyte communities and nutrients, including the influence of sediment chemistry is urgently required to support some of the contentions within this project”

Workshop held at Lancaster 7-8 March 1996 (Dawson *et al.*, 1999a, point 3.11.3, p. 7)

1.1.3 Further development of the MTR and other bioindicator methods using macrophytes

The future application of macrophyte-based methods for bioindication of trophic status and eutrophication requires that this background information on the principal factors controlling macrophyte distribution (other than trophic status) is incorporated. The use of a particular organism or group of organisms in biological assessment must be supported by a detailed understanding of the ecology of the bioindicators and knowledge of what may control distributions in a particular environment. Section 1.3 reviews the current understanding of the ecology of riverine macrophyte communities with a particular emphasis on the role of sediments as a source of nutrients. First, Section 1.2 presents a brief review of the role of sediments in freshwater nutrient dynamics. The emphasis of the review is on the inter-relationship between macrophytes and phosphorus in the sediment–water system. This emphasis reflects the strong bias in the literature towards phosphorus and the view that phosphorus is the nutrient most likely to be limiting plant growth in running freshwater systems. In the evaluation of the MTR, Dawson *et al.*, (1999b) also focused on phosphorus on the assumption that phosphorus was more limiting, but acknowledged that in some locations nitrate may be limiting, for example, in shallow eutrophic lakes where denitrification rates are high (Golterman, 1976).

1.2 Nutrients in Freshwater Sediments

The future use of macrophytes in the biological assessment of eutrophication in rivers is dependent upon greater understanding of the importance of sediment nutrients to macrophyte nutrition. This implies and requires an understanding of the behaviour of phosphorus and nitrogen within riverbed sediments and the importance of the sediment component in flowing-water nutrient dynamics.

Most research on nutrients in sediments has focused on lakes (Williams *et al.*, 1976; Ostrovsky, 1987; Arshad *et al.*, 1988; Reddy *et al.*, 1988; Forsberg, 1989; Eckerrot and Petterson, 1993) and there have been few studies of nutrient concentrations or dynamics within riverbed sediments. Exceptions include work undertaken by Chambers *et al.* (1992) on riverbed chemistry in the Pembina River, Canada, and by House and Denison (1998) who investigated phosphorus dynamics in the River Wey, England.

The behaviour of phosphorus and nitrogen within freshwater sediments is complex but the state of current understanding is briefly outlined below. The review deals mainly with research on lake sediments. General reviews of phosphorus and nitrogen cycles within freshwater environments are given by Holtan *et al.* (1988) and Heathwaite (1993) respectively. Work dealing specifically with nutrient forms in freshwater sediments includes a review of phosphorus in sediments (Pettersson *et al.*, 1988) and work on nitrogen in lake sediments (Reddy *et al.*, 1988).

1.2.1 Phosphorus in freshwater sediments

The phosphorus within the sediments of a waterbody has its source in settled particulate phosphorus, dissolved phosphorus that has adsorbed to the surficial sediments, phosphorus which has accumulated within the interstitial water or phosphorus derived from the underlying geology. The propensity of phosphorus to adsorb to both inorganic and organic particles has the result that a large proportion of the phosphorus within a system will ultimately end up in the sediments; this may

be as much as 70% (Golterman *et al.*, 1983). Thus, the sediments of rivers and lakes may be viewed as an important sink for phosphorus and, as the phosphorus may ultimately be re-released to the water column, also as an important source. This release of sedimentary phosphorus has been observed following reductions in water column levels due to the equilibrium between water and sediment concentrations and has been termed secondary eutrophication (Martinova, 1993; Pitt *et al.*, 1997).

Phosphorus undergoes various transformations once in the sediment but characteristically occurs in mineral forms or adsorbed to particle surfaces within the sediment. Organic phosphorus in the sediment is to a large extent transformed to mineral phosphorus (Pettersson *et al.*, 1988). The total phosphorus content of river and lake sediments is therefore the sum of phosphorus in interstitial water, phosphorus adsorbed to clay particles, inorganic phosphorus bound to metals and organic phosphorus (De Groot and Golterman, 1990).

The relative proportions of different phosphorus forms in the sediment vary considerably and available knowledge is governed by the extraction schemes used to separate total sediment phosphorus. Consequently, all definitions are operationally derived as the phosphorus extracted may not necessarily correspond to the fraction supposedly targeted by the extraction. A complete review of sequential extractions schemes for the determination of sediment phosphorus is given in Chapter Three of Clarke (2000). However, it is possible to determine the different components of sediment phosphorus on an analytical basis.

Inorganic phosphorus in sediments is generally associated with iron, aluminium, manganese and calcium, and these elements are clearly of great importance in sediment phosphorus diagenesis (Holtan *et al.*, 1988). Acidic sediments predominantly have phosphorus combined with iron and aluminium whilst, in neutral and calcareous sediments, phosphorus combined with calcium is most important (Hesse, 1973). The presence of organic matter in sediments is important as it will be a potential source of metals that may become complexed with phosphorus (Stone and English, 1993). Analysis suggests that a large proportion of phosphorus in the sediment of freshwater systems may be organic (De Groot and Golterman, 1993). However, known organic compounds of phosphorus constitute a very small part of the total organic phosphorus in the sediment and most attempts to fractionate sediment phosphorus calculate the organic fraction as a residual after mineral fractions have been determined. Thus, the present understanding of sedimentary organic phosphorus is poor although organic phosphorus may potentially constitute in excess of 50% of total phosphorus in some sediments (De Groot and Golterman, 1993).

Sequential fractionation of sediment phosphorus from various lakes has indicated that iron- and aluminium-bound phosphorus constitutes a significant fraction of sediment phosphorus, comprising up to 62% of total phosphorus particularly in sediments with a high humus or peat content. However, in some lakes, calcium-bound phosphorus is the largest fraction, and residual phosphorus (mainly organic phosphorus) is often in excess of 50% of total phosphorus in sediments. Labile (or loosely-bound) phosphorus is generally present in low (0.4-7.6%) concentrations (Pettersson *et al.*, 1988). The differences between lakes are important. In lakes where calcite precipitations formed, almost all adsorbed phosphorus was inorganically bound (Gonsiorczyk *et al.*, 1998). The calcium bound fraction has been found to be the most variable sediment phosphorus fraction in temporal studies (Williams *et al.*, 1976) and organic phosphorus the least variable (Williams *et al.*, 1976; Ostrovsky, 1987). Intercorrelations between phosphorus species in the sediments of a number of North

American lakes suggested there are relatively constant relationships between forms of phosphorus regardless of lake trophic status or alkalinity, and it was concluded that the presence of iron had a greater influence on sediment phosphorus concentration than either trophic status or alkalinity (Ostrovsky, 1987).

The importance of different phosphorus forms will also vary with the physical structure of the sediment. Measurements of exchangeable phosphorus in sediments of the Pembina River, Canada, found that the highest concentrations were in the finest sediments, with the lowest in sandy sediments (Chambers *et al.*, 1992). Levels in cobbles were also high, but this may reflect phosphorus associated with finer particles within the interstices of the cobble matrix. Stone and English (1993) investigated the geochemical composition of suspended and bed sediments with particles of various sizes. Within the sediment fraction less than 63µm total phosphorus concentrations decreased with increasing particle size; calcium contents were similar across all size fractions and it was concluded that phosphorus in the smallest size fractions must be associated with iron and aluminium oxides. The relationship between sediment phosphorus fractions and sediment particle size is not expected to be universal as some systems will contain large particles with a high propensity for phosphorus adsorption.

The volume of interstitial or porewater in sediments can be a significant proportion of the total volume of a shallow lake, and the phosphorus contained within the interstitial water may be the most freely-available to the roots of submerged macrophytes. The concentrations of phosphorus in the interstitial water are approximately 5-20 times higher than those in overlying waters (Boström *et al.* (1982) quoted in Enell and Löfgren, 1988) and, in the Pembina River, soluble phosphate and ammonium in the interstitial water were consistently higher than values in the open water (Chambers *et al.*, 1992). Yet phosphorus in interstitial water generally only constitutes a small proportion (perhaps <1%) of the total phosphorus associated with the sediment (Boström *et al.*, 1988a; Enell and Löfgren, 1988). For example, in the carbonate sand sediments of *Zostera* sp. beds in Bermuda, the total phosphorus pool in the top 20cm of the sediment was 500 times larger than the interstitial water phosphorus pool (Jensen *et al.*, 1998). Clearly, relative to the water column, interstitial water concentrations of phosphorus (and possibly other solutes) are significant but are only a small component of the total sediment phosphorus concentration; this highlights the major importance of sediments as a store and source of phosphorus.

Interstitial phosphorus is the sediment fraction most sensitive to environmental conditions and has a higher chemical mobility than phosphorus associated with the sediment particles (Syers *et al.*, 1973). Consequently, interstitial phosphorus concentrations are important in regulating phosphorus release from sediments and other phosphorus cycling processes. This sensitivity and chemical mobility ensures that interstitial phosphorus concentrations are subject to large spatial and temporal variation, the latter being particularly pronounced in shallow and eutrophic systems with upper layers of sediment seeing daily variations (Enell and Löfgren, 1988).

Spatial variability of sediment phosphorus and cycling between sediment and water

Existing data suggest that the concentration and forms of nutrients within the sediments of lakes and rivers are highly variable both spatially and temporally. Spatial variability in sediment concentrations of phosphorus is related to the degree of spatial heterogeneity in freshwater substrates, and the physical and chemical characteristics of the sediment are important to both sediment and interstitial

water concentrations. The profiles of phosphorus in the sediments of lakes and rivers are influenced by catchment characteristics and hydrodynamics. On a dry weight basis, phosphorus concentrations in lake and river sediments generally decrease with depth (cf. Lijklema, 1998). Increased concentrations at the surface are the result of: the higher concentrations in the recently settled material; delays in mineralisation due to high sedimentation rates; and an accumulation of phosphorus from diffusion in deeper sediment.

Transformations and dynamics of sedimentary phosphorus are largely controlled by the environmental conditions within and directly above the sediment. Of particular importance are pH and redox potential (eH). Martinova (1993) states that the main phosphorus transformation processes in the top 20-30cm of freshwater sediments are related to the decomposition of organic phosphorus and the subsequent adsorption of the orthophosphate produced.

A number of studies have looked at spatial and temporal variability in lake sediments, although there have been few investigations of this kind in flowing water environments. Investigations in a subtropical lake indicated that there was a high degree of spatial variability in sediment chemistry, although seasonal variation in sedimentary phosphorus was minimal (Arshad *et al.*, 1988). Similarly, fractions of sediment phosphorus varied with depth and season in two coastal lagoons although the sum of fractions for a given depth varied little in the course of a year (Moutin *et al.*, 1993). Spatial variability may also influence the distribution of sediment phosphorus fractions – Gonsiorczyk *et al.* (1998) found that the amount of soluble phosphorus increased while adsorbed phosphorus decreased with depth, and the authors suggested that there was desorption of phosphorus in deeper lake layers where pH decreased.

The dynamics and cycling of phosphorus within lakes is now fairly well understood. However, this understanding may not be applicable to running water systems. The behaviour of phosphorus in the environment, and particularly its propensity for binding to soil and sediments, results in a cycle which operates over a much longer temporal scale than the cycles of elements such as nitrogen. The tendency towards forming mineral compounds and adsorption to sediment particles also means that sediments of lakes and rivers could be expected to play a far more important role in the cycling of phosphorus than in the cycling of nitrogen and carbon. A key process in the cycling of phosphorus within freshwaters is the decay of organic matter resulting in a transport of phosphorus to the sediment and the subsequent release of phosphorus from the sediments into the water column in a form available for biological uptake.

1.2.2 Nitrogen in freshwater sediments

Nitrogen is more soluble and mobile than phosphorus (Heathwaite *et al.*, 1996) and thus is not associated with the sediment to the same degree. Consequently the behaviour of nitrogen within freshwater sediments is poorly understood. However, the importance of nitrogen to plant nutrition and the suggestion that some macrophytes may be nitrogen rather than phosphorus limited due to the usually high concentrations of phosphorus in interstitial waters (Barko *et al.*, 1991) justifies further study of nitrogen behaviour in freshwater sediments.

Owing to its greater solubility in water, nitrogen does not bind to the sediment surfaces in the same manner as phosphorus. Consequently less attention has been given to nitrogen in sediments and little is known about forms and cycling of nitrogen in sediments. It is likely that due to the soluble nature of

nitrogen forms interstitial water may be an important component of the sediment nitrogen cycle and the interstitial water nitrogen concentration is usually much higher than the concentrations within the overlying waters (Keeney, 1973). Most sediment nitrogen is organic (Martinova, 1993) although the predominant forms will depend on the trophic level of the freshwater system, microbial action and the pH of the system (Heathwaite *et al.*, 1996). Organic nitrogen within the sediments has its source in settled organic material whilst inorganic forms accumulate as adsorbed nitrogen and nitrogen fixed within the clay lattice (Martinova, 1993). However, nitrogen chemistry within the sediments will largely be determined by the microbial actions which govern denitrification and nitrification processes.

The dynamic nature of nitrogen has ensured that many studies have considered total nitrogen or divided this into organic and inorganic nitrogen. Bonetto *et al.* (1988) attempted to develop a fractionation scheme to determine bioavailable nitrogen in the soils of rice paddies but the results suggested that rice plants do not obtain all required nitrogen from one well-defined chemical fraction. It was concluded that nitrogen occurs in the soil as many different compounds which are less well-defined than those for phosphorus (Bonetto *et al.*, 1988). This suggests that sequential fractionation approaches to nitrogen determination in sediments are inappropriate.

Nitrogen dynamics

Cycling and transformations of nitrogen within freshwater systems are largely a result of biologically-mediated interactions with the gas phase (Howard-Williams, 1985). Five processes may be identified within the nitrogen cycle: nitrogen fixation, nitrification, denitrification, ammonification/mobilisation and assimilation. A detailed account of these processes is given by Heathwaite (1993), the importance of these processes within the sediments is briefly considered here.

Nitrification and denitrification are both vital steps in releasing nitrogen from the sediments to the overlying water column. Nitrification occurs in well oxygenated conditions, and as such may be an important process in well oxygenated river gravels and at the sediment surface in oxygenated streams. Even in low oxygen sediments ammonia may diffuse to the overlying water where nitrification may take place. Denitrification, which represents a loss of nitrogen from the system, requires nitrogen available as nitrate, anaerobic (or near anaerobic) conditions and the presence of readily-degradable organic matter (Faafeng and Roseth, 1993). Thus, it may be expected that denitrification is an important process at depth in river sediments and near the sediment surface within dense macrophyte stands. As these conditions do not favour nitrification ammonia may accumulate in these zones. Garcia-Ruiz *et al.* (1998) showed that denitrification rates in 31 rivers in north-east England were strongly and positively related to the water content of sediments, percentage carbon and nitrogen of the sediments, percentage of particles less than 100µm and river water conductivity, alkalinity, nitrate and phosphate.

Much of the nitrogen in sediments is present in forms that are not available for biotic uptake and, consequently, the transformations of sedimentary nitrogen are important controls on nitrogen availability to organisms. The turnover of ammonium is faster in the water column than in the sediments, whilst for nitrate the opposite is true (Wetzel, 1983). A series of sequential processes are involved in the transport of nitrogen from the sediment. Initially, ammonification must occur and then the ammonium produced diffuses to the water column. Soluble organic nitrogen may also diffuse to

the water column from interstitial water pools and ammonification may occur within the water column (Reddy *et al.*, 1988). The mobility of sediment nitrogen will be influenced by the sediment concentrations of ammonium as, when this concentration falls, the concentration gradient is reduced (Reddy *et al.*, 1988). In flowing waters, this concentration gradient will be maintained, and thus transfers from sediment to the water column may be faster and more significant than in standing waters. However, aerated water overlying anaerobic sediments will limit nitrogen release from the sediments (Heathwaite, 1993), and so oxygenated streams may have lower sediment denitrification rates. Clearly, the influence of flow upon the nitrogen cycle may have a number of outcomes, and it is difficult to extrapolate the understanding gained in standing water systems to rivers and streams.

1.2.3 Nutrient dynamics in flowing waters

Much of the current understanding of processes regulating nutrient transformations and movements within freshwater systems is based on research undertaken in lake environments. Whilst chemically rivers and lakes are closely aligned, there are distinct physical and structural differences. Consequently, paradigms of nutrient cycling developed through lake studies are unlikely to be directly transferable to running-water systems. It is to be expected that nutrient processes operating within lake sediments may also be evident in river sediments. However, transfer of knowledge between the two systems must consider the influence of flow, greater sediment heterogeneity, coarser sediments, and increased dominance of mineral sediment in rivers.

The presence of an overall unidirectional flow within rivers is likely to be of significance as in lakes wave action and seasonal water movements play a role in nutrient cycling. In recognition of this the concept of nutrient spiralling has been proposed for running water systems (Newbold *et al.*, 1981). Spiralling occurs because each cycle of nutrients will be displaced downstream from the previous cycle. The model developed by Newbold *et al.* (1981) defined the length of a spiral as the distance an atom travels downstream between biological assimilations. Spirals of nutrients will be influenced by physico-chemical controls such as precipitation and sorption of nutrients to sediments (dependent on the chemical state of the sediment-water interface), the hydrology and geomorphology of the stream (nutrients accumulate at low flows due to increased contact area to channel volume ratio), and biological uptake (cf. Meyer, 1979).

Nutrient behaviour in flowing waters will also differ from that in lakes due to the nature of the sediment and sediment-water interface. Turbulence in streams ensures thorough oxygenation of the interface and therefore in flowing waters anaerobic conditions are likely to be restricted to marginal areas, dead zones, and within dense macrophyte stands. This has important implications for the exchange of nutrients between sediments and the water column. The presence of flow also results in a high degree of sediment and habitat heterogeneity in streams providing greater potential for nutrient retention and storage. Sediment transport processes such as scour and fill will also lead to areas of nutrient depletion and accumulation in the riverbed. Furthermore, in shallow streams macrophyte biomass may be extensive and thus, plants may play a more central role in nutrient dynamics than in lakes where plants may be restricted to the littoral zone.

There have been few studies of riverine nutrient dynamics or the spatial variability of riverbed nutrient concentrations. A study by Chambers *et al.* (1992) of sediment and interstitial water phosphorus concentrations in the Pembina River, Canada, found that interstitial water chemistry varied with depth and time. At one Pembina site with fine sediments, SRP (soluble reactive phosphorus) in the interstitial

water of the top 5cm varied 400-fold over a year, although interstitial water chemistry in sand showed very little vertical variation. Similarly, sediment chemistry varied over time, with the sand site displaying the greatest annual variability and the fine sediment site the least (Chambers *et al.*, 1992). This temporal variability was related to discharge on an interannual scale, but not over shorter time-scales. However, the study does indicate that riverbed chemistry is very dynamic, with changes occurring at depths of 20-25cm below the surface (Chambers *et al.*, 1992), and that this dynamism results in a high degree of spatial (vertical and horizontal) and temporal variability in sediment chemistry. Four return visits to a number of sites on the River Wey, Hampshire, by House and Denison (1998), indicated that spatial differences in sediment chemistry were related to differences in sediment particle size. There was also an increase in sediment total phosphorus concentrations from winter to summer, associated with phosphorus coprecipitation with calcite during summer and sediment loss through scouring during winter (House and Denison, 1998).

1.3 Relationships Between Macrophytes and Sediments

The influence of sediment upon macrophyte community structure has been included in many studies of macrophyte ecology. For example, Pearsall (1920) concluded that the nature of the substratum was the primary control on the distribution of aquatic plants in the lakes of the English Lake District and that plant succession was accompanied by changes in the substratum through increasing organic matter content. Although Butcher (1933) considered flow velocity as the most important factor in determining the macrophyte vegetation of British rivers given similar chemical and physical conditions, once he had classified rivers according to their source, further subdivisions were made on the basis of the substratum and the water chemistry composition from acidic through to highly calcareous streams. Additionally, two vegetation types were recognised within rivers; silted and non-silted communities, distinguished by flow type and underlying substrate (Butcher, 1933). Haslam (1978) also considered substrate, along with flow, river channel geometry and drainage order, as the most important physical variables and the availability of light, nutrients and dissolved gases as other important controlling factors in riverine macrophyte communities. Thus, there is some evidence that sediments may be an important controlling variable in macrophyte ecology. The importance of sediment nutrients and the physical structure of sediments is further considered in the following sections.

1.3.1 Sediments as a source of nutrients for submerged rooted macrophytes

The sediments of flowing water systems are a potential source of nutrients for rooted macrophyte species. However, whether submerged, rooted macrophytes obtain nutrients from the water column (through shoots), sediment (through roots) or from both of these sources has been the focus of some debate. Early work on these plants noted vascular reduction and many suggested that as this would limit the capacity for solute movement (cf. Olsen, 1953; Sutcliffe, 1959; Seddon, 1972) shoot uptake prevailed. This view was supported by the observation that the roots of submerged macrophytes are reduced, accounting for 10% or less of plant biomass in comparison with to 20-40% for herbaceous terrestrial species (Agami and Waisel, 1986). Providing evidence for or against this view has been the subject of numerous laboratory and *in situ* experiments. Two-chamber laboratory experiments have been employed with plants rooted in sediment isolated from the water column (for example, Best and Mantai, 1978) and several workers have utilised radioactive isotopes of phosphorus (^{32}P) and nitrogen (^{15}N) to trace the movement of nutrients through the plants (cf. Nichols and Keeney, 1976; Bole and Allan, 1978; Pelton *et al.*, 1998). Others have conducted

experiments in field situations to investigate root or shoot uptake of nutrients in lakes (Carignan and Kalff, 1980; Chambers and Kalff, 1987; Rattray *et al.*, 1991). A comprehensive review of these experiments is given in Clarke (2000).

There are sound theoretical reasons for expecting macrophytes within flowing water systems to rely largely on the water column for nutrients. First, sediments in rivers are generally coarser than lake sediments and may have reduced capacity for nutrient retention. Secondly, flowing water ensures continual replacement of water and associated solutes reducing the likelihood of localised nutrient depletion within the water column. Although there have been few studies investigating the role of sediment nutrients in flowing waters there is some evidence to suggest that sediment nutrients may also be of importance. Biomass and shoot density of *Potamogeton crispus* grown in the South Saskatchewan River, Canada, were consistently greater in high-nutrient sediments than low-nutrient sediments regardless of water column character (Chambers *et al.*, 1989). Similarly, observations in the river indicated that macrophyte biomass and sediment phosphorus were log-linearly related (though sediment nitrogen did not display this relationship) (Carr and Chambers, 1998). Nutrient addition experiments in artificial streams confirmed the results with *Potamogeton pectinatus* biomass being greatest on sediments enriched with nitrogen and phosphorus, and increasing with phosphorus concentration (Carr and Chambers, 1998). In contrast, relationships between the sediment, water and plant tissue phosphorus concentrations of *Elodea nuttallii*, *Elodea canadensis* and *Callitriche obtusangula* growing in flowing waters in the Rhine floodplain indicated that the plants were more effective in obtaining phosphorus from the water rather than sediment (Robach *et al.*, 1995). Studies of macrophyte standing crop, sediment, water and tissue concentrations of nitrogen, phosphorus and potassium in 19 Mid-Jutland streams in Denmark found no correlation between maximum standing crop and water concentrations of phosphate, nitrate or potassium, or between tissue concentrations and sediment concentrations of these nutrients. However, there was a correlation between tissue concentrations and water concentrations suggesting stream water was the main source of nutrients for the macrophytes (Kern-Hansen and Dawson, 1978).

Conclusions on the source of nutrients for submerged rooted macrophytes

Laboratory and *in situ* experiments indicate that rooted submerged macrophytes obtain nutrients from both sediment and water. It is difficult to draw firm conclusions from the literature because the wide variations in species and techniques employed prevent direct comparisons between studies. A review of the role of sediments in community dynamics and macrophyte growth by Barko *et al.* (1991) concluded that sediment was the primary source of nitrogen, phosphorus, iron, manganese and micronutrient uptake whereas calcium, magnesium, sodium, potassium, sulphate and chloride were obtained from the water. This is evidently in conflict with studies that have found that sediment nitrogen does not correlate with measures of plant uptake (cf. Carr and Chambers, 1998). Despite the obvious problems in reaching a definitive conclusion regarding the source of nitrogen and phosphorus, the experiments have discovered a number of interesting aspects to nutrient uptake and some general conclusions can be made.

Evidence suggests that sites of nitrogen and phosphorus absorption depend on a variety of factors including: morphology (therefore species and phenotypes may differ in response) (Denny, 1972); relative concentrations in water and sediment (Carignan and Kalff, 1980; Rattray *et al.*, 1991); presence and type of organic matter (Barko and Smart, 1983); water column pH (Schuurkes *et al.*, 1986); and sediment density (Barko *et al.*, 1991). Macrophytes may also undergo morphological

adaptations in response to sediment nutrient concentrations and induce chemical changes in the sediment affecting nutrient availability. Many results have indicated an increase in root:shoot ratio to compensate for poor sediment fertility by increasing the root uptake area (Best and Mantai, 1978; Idestam-Almquist and Kautsky, 1995). Additionally, macrophytes have the potential to alter the physical and chemical nature of the sediment in which they are rooted thus affecting the availability of sediment nutrients for uptake (see Section 1.3.3).

The importance of sediment nutrient concentrations to rooted macrophytes will also depend on the relative concentrations in the sediment of nutrient forms that are *available* to plants for uptake and use. Little is known about the forms of sediment phosphorus that are available to macrophytes, though there have been a number of algal bioassay experiments which have considered the availability of sediment phosphorus to phytoplankton of the overlying water (cf. Golterman, 1976; Williams *et al.*, 1980). However, with respect to nitrogen compounds macrophytes are expected to take ammonium from the sediment in preference to nitrate as plants need to expend energy to reduce the latter form of nitrogen (Agami and Waisel, 1986). As ammonium concentrations are generally low in well-oxygenated waters (for example, most shallow flowing waters), the greatest pool of ammonium will be in anaerobic sediments (Agami and Waisel, 1986). This would support the view that sediments are the principal source of nitrogen (cf. Barko *et al.*, 1991). Studies have indicated that nitrogen limitation may be significant in macrophyte communities (McCreary, 1991) as nitrogen is depleted more rapidly from the sediment than phosphorus (Barko *et al.*, 1991). A temporal study of macrophyte-colonised and uncolonised sediments in Lake Memphremagog, Canada, provided evidence of this potential limitation; interstitial SRP concentrations varied less than ammonium concentrations, which the author suggested was due to phosphate being buffered by a larger exchangeable pool than ammonium (Carignan, 1985).

In conclusion, the source of nutrients for submerged, rooted macrophytes has not been clearly defined despite considerable effort over almost 100 years. Sediments evidently have an important role in the nutrition of these plants but there are obvious species differences, and other environmental and biological factors will play a role in determining the principal source of nutrients. Research is thus needed if the preferences and tolerances of specific macrophytes to sediment character and composition are to be better understood.

1.3.2 Sediment as a habitat for submerged rooted macrophytes

Bed sediments have a dual importance to the ecology of submerged rooted macrophyte species, as a source of nutrients and as a means of anchorage within the channel. Thus, it may be expected that different macrophyte species (or groups of species) will express different preferences and tolerances for both physical and chemical sediment conditions. This also implies that there is potential for interactions among both individual plants and species related to the sediment environment (competition, niche partitioning). Plants may be expected to respond to the physical structure (particle size) and the chemical nature (fertility, pH, redox potential) of the sediment.

Barko *et al.* (1991) summarised the effect of sediment density and organic matter content in a review of sediment-macrophyte interaction studies. It was suggested that macrophyte growth declines with increasing organic matter content and showed a unimodal response to sediment density (as organic matter and sand have opposing effects on sediment density) with greatest growth on sediments with a density of 0.8–1.0 g ml⁻¹ (Barko *et al.*, 1991). Macrophyte growth was reduced

on low density organic sediments due to the long distances over which nutrients must diffuse (Barko *et al.*, 1991). This reflected earlier work that had demonstrated that the presence of organic matter in the sediment could potentially limit nutrient uptake by macrophytes (Barko and Smart, 1983; Barko and Smart, 1986). These hypothetical relationships between plant growth and sediments were investigated through experiments with *Myriophyllum spicatum* and *Potamogeton pectinatus* by Wertz and Weisner (1997) who found no relationship between macrophyte biomass and sediment density, and no significant difference in the average growth of either species between sandy and non-sandy sediments. In practice, it is difficult to determine a sediment density effect upon macrophyte growth as density and fertility are intrinsically linked; therefore macrophytes may be expected to respond to a combination of both.

Evidence of competition in submerged macrophyte communities

It is generally accepted that competition plays a much less important role in riverine macrophyte communities than in terrestrial plant communities (Haslam, 1978). This view is supported by the observations that macrophytes seem to be largely influenced by abiotic factors, for example, shade, flow, water chemistry, sediment fertility (cf. Chambers and Kalff, 1987; Ali *et al.*, 1995; Robach *et al.*, 1996; Baattrup-Pedersen and Riis, 1999). However, there is some evidence of the potential for competition even if direct experimental evidence is limited. The characterisation of interspecific versus intraspecific effects in submerged macrophyte communities remains neglected (McCreary, 1991); possibly due to the problems of excluding confounding factors.

Competition experiments in artificial recirculating streams indicated that, under increased phosphorus loading, *Potamogeton pectinatus* is a more competitive species than *Ranunculus penicillatus* subsp. *pseudofluitans* (Spink *et al.*, 1993). In one of the few studies looking at competition for sediment resources, *Hydrilla verticillata* and *Vallisneria americana* were grown together at various densities in tanks with sediments of two levels of fertility (Van *et al.*, 1999). *Hydrilla* was found to respond to increased nutrients to a greater degree than *Vallisneria*. However, the competitive outcome between the two species depended on the sediment fertility level. *Vallisneria* was a better competitor when nutrients were limited and *Hydrilla* was better when nutrients were elevated.

Much of the published work indicates a limited role for competition in structuring macrophyte communities (McCreary, 1991; Wilson and Keddy, 1991). However, there have been numerous observations suggesting species interactions in natural situations. A cyclic relationship between *Ranunculus* spp. and *Rorippa nasturtium-aquaticum* agg. has been described by Dawson *et al.* (1978) in which the *Ranunculus* species colonises coarse substrates in moderate to high water velocities causing siltation to occur. This increase in fine sediments combined with a decrease in flow during late summer enables *Rorippa nasturtium-aquaticum* plants to invade the *Ranunculus* spp. beds and reach maximal biomass in late summer, high discharges during autumn and winter wash out the *Rorippa nasturtium-aquaticum*, allowing the cycle to begin again in the following spring. This observed invasion of *Ranunculus* sp. beds highlights the differing requirements of the two species for flow and sediment variables and suggests a competitive advantage for each of the species under its favoured conditions. These different physical requirements are combined with what may be considered as temporal partitioning to allow both species to exist within the same habitat (Dawson *et al.*, 1978).

There are few examples of competition from lotic environments, yet the highly heterogeneous nature of most streams suggests great potential for habitat partitioning which is interpreted as evidence of potential competitive interactions between species. Measurements of abiotic characteristics and niche overlap have shown coexistence of species in riverine habitats both with and without habitat partitioning, and indicated that there was some degree of *interspecific mutual protection* with stands protecting macrophytes growing within them from scouring (French and Chambers, 1996). This concept was further investigated with *in situ* growth experiments which indicated that *Elodea* plants grew better within patches of plants than outside of patches (French and Chambers, 1996). The benefit of mutual protection from neighbouring plants within a stand has also been investigated in *Callitriche cophocarpa* stands, with the conclusion that patches may reduce physical stress and increase nutrient supply through promoting deposition of material (Sand-Jensen and Madsen, 1992).

There is evidently great potential for competition between macrophytes for sediment resources in rivers but there is little evidence that this potential is realised. The high degree of spatial heterogeneity in flowing water environments may allow habitat partitioning and coexistence as investigated by French and Chambers (1996). However, it is also possible that the influence of other factors, particularly spates and periods of low flows, may suppress growth-limiting competitive interactions to certain times of the year.

1.3.3 The influence of macrophyte growth on sediment characteristics

The growth of macrophytes within lowland streams has an effect upon flow movement and ecosystem functioning. Abundant vegetation growth within the channel can impede water flow (cf. Dawson, 1978) and at a smaller scale flow velocity is markedly reduced within dense plant stands (Sand-Jensen and Mebus, 1996). This velocity reduction results in the deposition of fine organic and inorganic particles within plant stands (Sand-Jensen *et al.*, 1989). The quantity of material retained varies with the morphology of the plant species (Sand-Jensen, 1998) and the nutrients associated with this material may be significant to overall stream nutrient dynamics. For example, in Danish streams the nitrogen content of sediments accumulated in *Callitriche cophocarpa* and *Sparganium erectum* stands was 4-5 times higher than the levels in the plants themselves and phosphorus contents were 35 times higher in the sediment of *Callitriche cophocarpa* stands relative to the concentrations in the plant tissue (Sand-Jensen, 1997).

This retention of material is temporary and Sand-Jensen (1998) concluded that macrophytes were more important for sediment stabilisation, through the binding effects of roots, than nutrient retention in macrophyte-dominated streams. However, submerged macrophytes evidently play a key role in the structure and functioning of lowland stream ecosystems and have been described as *biological engineers* in these habitats (Sand-Jensen, 1997). The impact of macrophytes upon flow velocity and sediment accumulation is largely a result of the tendency of submerged, rooted species to grow in distinct patches due to the dominance of vegetative spread over sexual reproduction in such communities. This has the effect of increasing habitat heterogeneity.

Macrophytes are also able to alter the chemistry of the sediment in which they are rooted. Oxygen translocation to the roots of plants has the effect of oxidising the immediate sediment environment, and this may limit phosphorus availability (Moore *et al.*, 1994; Steinberg and Coonrod, 1994; Wigand *et al.*, 1997). This effect on redox potential has been observed to differ between species (possibly due to root physiology and canopy structure) and is dampened in fertile sediments due to

high levels of reductants and high respiratory demands (Wigand *et al.*, 1997). The action of macrophyte roots may also result in phosphorus release, at least in marine environments. For example, *Zostera* sp. growing in carbonate sands was observed to dissolve the carbonate matrix of sediments (possibly through root exudates) with a resulting release of calcium-bound phosphorus (Jensen *et al.*, 1998). This could occur in carbonate-rich sediments of lowland chalk streams. Other effects include lower total alkalinity and pH in vegetated sediments relative to bare sediments (Moore *et al.*, 1994). Furthermore, macrophytes in wetlands have been shown to provide suitable redox conditions for denitrifying bacteria, and a supplementary source of carbon for these organisms and macrophyte detritus provides a nitrate-nitrogen source for denitrification directly from particulate material (Howard-Williams, 1985).

1.3.4 Macrophytes and nutrient dynamics in streams

In shallow, low-energy streams where macrophytes are able to grow abundantly, plants will greatly influence the functioning of the ecosystem, at least at a reach-scale (Marshall and Westlake, 1978; Sand-Jensen, 1997); Figure 1.1 presents a conceptual framework for this influence. The ability of many species to obtain nutrients from both the sediment and water (Section 1.3.1) gives macrophytes a unique position in the ecosystem as a link between sediment and water column. In fact, there is evidence of macrophytes playing a role in the cycling of heavy metals from sediments to the overlying water (Agami and Waisel, 1986) and macrophytes may obtain nitrogen and phosphorus from the sediment then release these elements to the water; this release is most likely during senescence and decay as losses from healthy tissue during laboratory experiments are commonly small (cf. Barko and Smart, 1981). Macrophytes may also function as a source for nutrients by trapping fine organic and inorganic particles, enhancing mineralisation of organic matter through oxidation of the sediments and altering the localised environment enabling phosphorus release through reducing conditions and increased pH and temperature. A comparison of phosphorus release in planted and unplanted areas suggested some of these mechanisms may be operating as total phosphorus release was significantly higher in planted beds, though this was not as marked for SRP (Stephen *et al.*, 1997).

Macrophyte uptake of phosphorus may be rapid, as demonstrated by lake enclosure experiments with *Potamogeton pectinatus* (Howard-Williams, 1981). Agami *et al.* (1990) recorded phosphorus storage in macrophytes of a stream system at a level of 3-43 kg P ha⁻¹. However, the authors concluded that the macrophytes could not function as sinks as the storage was only transitional. Similarly, macrophytes in six Florida lakes were estimated to contain 20-96% of water column phosphorus (Canfield *et al.*, 1983). Even macrophytes growing along the stream margins may have a significant impact upon nutrient processes. For example, watercress plants growing in the margins of a New Zealand stream were shown to accumulate 1.14g N m⁻² d⁻¹, all of the nitrate lost from the stream could be accounted for by this plant uptake (Howard-Williams *et al.*, 1982).

The high levels of biomass that may be attained in lowland chalk streams indicate huge potential for macrophyte uptake of nutrients and subsequent release within these systems; in a study of *Ranunculus penicillatus* var. *calcareus* production, seasonal maximum biomass of the macrophyte in the Bere Stream, Dorset, was 380g dry weight m⁻² (Dawson, 1976). Additionally, internal cycling of phosphorus within plants to shoots or to roots and rhizomes for storage may be significant, accounting for half the annual flux of nitrogen and phosphorus within plants (Howard-Williams, 1985).

Macrophytes in freshwater systems may have an influence on nutrient dynamics beyond simple uptake and release of nutrients. For example, macrophytes provide a substrate for epiphytes, which may take up large quantities of nutrients, and bacteria involved in the nitrogen cycle. Macrophytes may also enable non-rooted organisms to use sediment nutrients - epiphytes growing on *Myriophyllum spicatum* were shown to obtain all of their cobalt and manganese from the sediments via the host plant (Jackson *et al.*, 1994).

The interaction between macrophytes, phytoplankton and nutrients in lakes has been widely investigated with a view to reversing the effects of eutrophication (Phillips *et al.*, 1978; Moss *et al.*, 1986; Granéli and Solander, 1988; Balls *et al.*, 1989). However, it is apparent that the interactions are complex and measures such as reducing the nutrient load, removal of enriched sediment (Pitt *et al.*, 1997) and harvesting macrophytes to reduce nutrients locked in biomass have had limited success. The dominant role of flow and inorganic sediments (Harper, 1992) and the influence of macrophytes upon flow and sediment processes within shallow macrophyte-dominated streams is likely to further complicate these relationships.

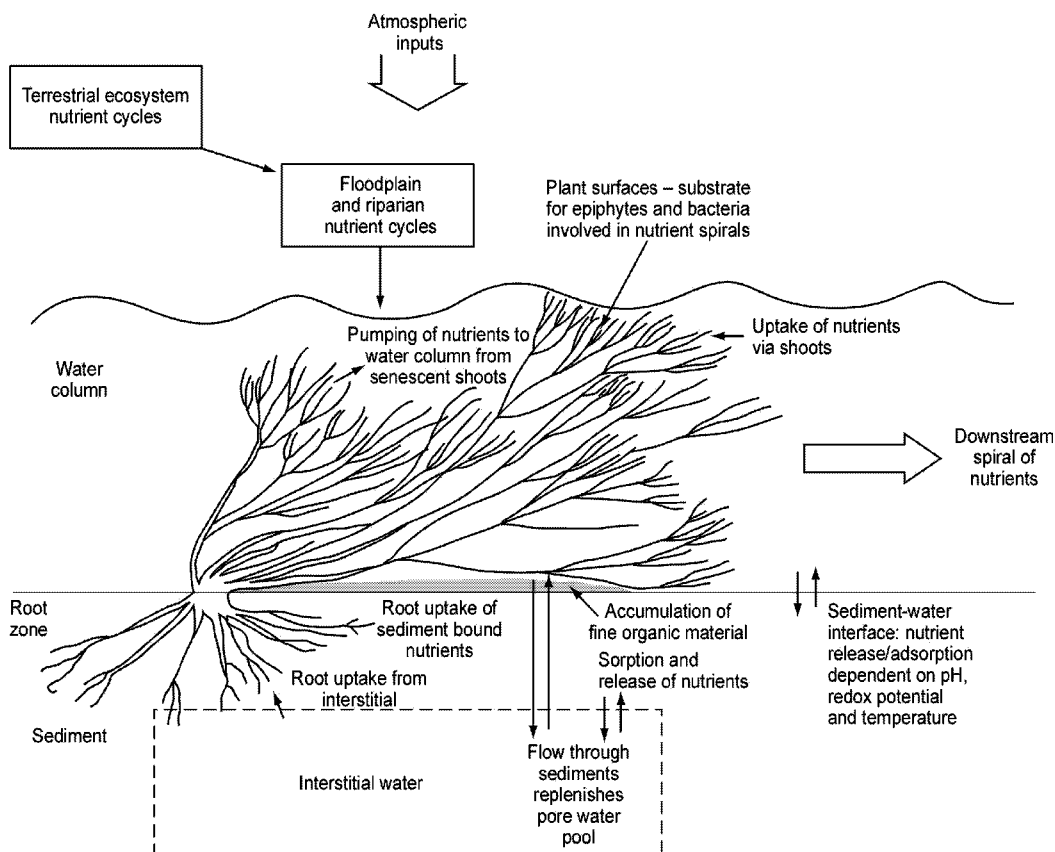


Figure 1.1 Conceptual model showing the role of macrophytes in nutrient dynamics in flowing-water systems

1.4 Research Aims and Objectives

Current understanding of nutrient cycles and processes within rivers is limited and much of the understanding of nitrogen and phosphorus dynamics in freshwater sediments has been established from studies in lakes. The presence of flow within a water body will have a considerable influence on the physical, chemical and biological processes taking place and the transfer of understanding from lakes to rivers is difficult. There have been few studies on the dynamics of nutrients within rivers sediments and there is limited information on the concentrations of nutrients within sediments as, until now, emphasis has been upon water column concentrations. It is therefore important to ascertain levels of nitrogen and phosphorus within lowland river sediments and to understand the processes regulating these concentrations.

Sediment has frequently been considered as one of the key environmental factors controlling macrophyte distribution and growth. Macrophytes have been shown to respond to both the physical structure and the chemistry of the sediment. However, there is a need to quantify the response of the plants to the nature of riverbed sediments. The future application of macrophytes as tools for the biological assessment of eutrophication depends upon the identification of the sediment preferences of different macrophyte species.

The overall aim of the research described herein was to investigate the characteristics of sediments supporting submerged rooted macrophyte species in lowland British rivers. Additionally, in recognition of the limited work on sediment nutrient concentrations in UK rivers, it was considered important to ascertain actual concentrations of nitrogen and phosphorus within riverbed sediments as well as the spatial variability of these concentrations. The research aims to extend and complement work undertaken during the development of macrophyte-based biological assessment methods, such as the MTR, which have so far focused on macrophyte responses to water chemistry.

Specific objectives of the research were -

To determine the range of nutrient concentrations (phosphorus and nitrogen) of vegetated and unvegetated sediments in a sample of lowland British rivers.

To consider the spatial variability of vegetated and unvegetated sediments within river reaches and across this sample of lowland rivers.

To identify the physical and chemical characteristics of sediments associated with particular submerged, rooted macrophyte species.

To consider the role of other environmental factors in mediating sediment-macrophyte relationships.

2. METHODS

Full details of the methodology employed during this research are given in Clarke (2000). A brief outline of the sampling rationale and analytical techniques employed is presented here.

2.1 Sampling Details

The characteristics of sediments of both vegetated and unvegetated areas of the riverbed were investigated at sites in 17 lowland rivers (Table 2.1, Figure 2.1). These 17 river sites were selected from the MTR database (see Dawson, *et al.*, 1999a) on the basis of accessibility, the presence of at least four submerged, rooted macrophyte species, and the availability of water quality data. Sites not included in the MTR database were also considered providing they met these criteria. Sites were located at existing MTR (upstream) sites where possible (Table 2.1). Twenty sediment samples were collected from each 100m site using a corer of similar construction to that described by Maitland (1969). Samples were located randomly within stands of submerged macrophyte species; these vegetated sediment samples were collected from underneath at least four macrophyte species (with a least one replicate from a different stand per species from each stream). Two of the twenty samples at each site were collected from bare, unvegetated areas of the riverbed for reference purposes (except at the Whilton Branch where four bare samples were taken). Details of the sediment samples are given in Table 2.2. Information on the physical characteristics of the site was also obtained in the field (channel geometry, degree of shading) and from archive and map sources (landuse, flow regime and water quality). At each site a macrophyte survey was undertaken according to the MTR methodology (Holmes *et al.*, 1999) to provide information on the plant community present.

2.2 Sediment Analysis

Sediment samples were dried overnight (110°C) and a sample (~ 30g) was taken for organic matter determination by ignition (450°C, overnight) according to the method of Rowell (1993). The remaining sample was subsampled for particle size analysis and chemical analysis. Particle size analysis was performed on material less than 4mm by a combination of dry and wet sieving (see Gee and Bauder, 1986); percentage silt/clay (<63µm) was determined for each sediment sample. Sediment for chemical analysis was prepared by removing the material greater than 2mm, remaining material was ground to pass through a 250µm sieve. This ground material was then analysed for total phosphorus by sulphuric acid digestion and inorganic phosphorus by ignition (method described by Andersen, 1976); orthophosphate in extracts was determined by the method of Murphy and Riley (1962). Total nitrogen and organic carbon contents of the ground material were determined by combustion gas chromatography according to the method of King *et al.* (1998).

2.3 Water Quality and Flow Data

Water quality data for the sites were obtained from the appropriate Environment Agency regions. For sites that were not MTR monitoring sites the nearest Agency water quality monitoring site was selected; these were all within 6km of the sediment sampling site and there were no tributaries or major point source inputs between the two sites. Yearly means (based on monthly means for January–December in the year of sediment sampling) were calculated for pH, orthophosphate and inorganic nitrogen species. Figure 2.2 shows mean values and standard errors for these water quality parameters.

Archive flow data were obtained from the National River Flow Archive (Institute of Hydrology, 1999). Where the sediment sampling sites do not correspond to flow gauging stations, reference was made to the nearest gauging station with regard to the influence of any tributaries of other significant flow inputs. Table 2.3 shows the flow parameters that were calculated for each of the 17 sites.

2.4 Statistical Analysis

All statistical analyses described within this report were performed using SPSS Version 8.0 with the exception of the multivariate analyses described below.

Principal components analysis (PCA) was applied to 26 environmental variables which were site means for sediment characteristics, water quality parameters, flow parameters and habitat measurements. Only three flow parameters were included ($\text{mean}^3 \text{ year}$, $\text{CoV}^3 \text{ year}$, BFI) as there was found to be considerable inter-correlation between all flow variables. All data (except mean water column pH) were normalised through log transformation ($\log(x + 1)$) prior to analysis, as large values for some variables were shown to have excess influence upon the analysis (cf. ter Braak and Smilauer, 1998). Centring and standardisation were applied as recommended for the analysis of variables measured in different units (Jongman *et al.*, 1995).

The relationship between these environmental variables and the species composition of the sites was investigated through canonical ordination. Ordination was performed on species abundance data recorded on a nine point scale (74 species, 330 occurrences) and 26 environmental variables (all log transformed ($\log x + 1$), except water column pH) for each of the sites. In acknowledgement of the taxonomic difficulty of the *Callitriche* genus, *C. obtusangula*, *C. platycarpa*, *C. stagnalis* and those *Callitriche* specimens that could not be assigned to species, were combined under the heading *Callitriche* spp. Twenty three species occurred at only one site (less than 6% of samples) and were considered rare in the dataset and excluded from all ordination analyses.

To select the appropriate model for canonical ordination, a detrended correspondence analysis (DCA) was performed on the species data. The DCA indicated that gradient lengths were less than 3 standard deviations, consequently canonical ordination proceeded using linear methods - redundancy analysis (RDA) (Jongman *et al.*, 1995).

An RDA with forward-selection was performed to reduce the number of environmental variables and to choose only those that best explain the variation in species data. Monte Carlo permutation tests were used (999 unrestricted permutations) to determine whether selected environmental variables were statistically significant in explaining the variation in species data.

Multivariate relationships between plant species and individual sediment samples were investigated through multiple discriminant analysis (MDA). Discriminant analysis is a statistical technique that can be employed to investigate differences between groups of objects. MDA is used to predict group membership from a set of variables and attempts to delineate and minimise within-group variance and maximise between-group variance (Klecka, 1980). The method involves deriving a discriminant function representing the linear combination of the independent variables that discriminate most effectively between two or more *a priori* defined groups (Hair *et al.*, 1998).

MDA was used to investigate whether there are groups of macrophytes that differ from one another in terms of the sediment that they grow upon. The aim was to distinguish groups of plants on the basis of the physical and chemical sediment variables. With the aim of determining whether macrophytes could be distinguished by sediment variables on a taxonomic basis *a priori* groups were established by species. Only species represented by ten or more samples from the 17 rivers were included, resulting in ten species groups: *Apium* spp. *Callitriche* spp, *Elodea canadensis*, *Elodea nuttallii*, *Myriophyllum spicatum*, *Nuphar lutea*, *Potamogeton pectinatus*, *Ranunculus penicillatus* subsp. *pseudofluitans*, *Sparganium emersum*, and *Sparganium erectum*. Additionally, unvegetated samples were included as an eleventh group, to determine whether there was a particular sediment type that did not support macrophytes. Group sizes ranged from 10 (*Elodea canadensis* and *Sparganium erectum*) to 84 (*Ranunculus penicillatus* subsp. *pseudofluitans*). The 294 individual sediment samples that remained once unrepresentative samples (less than 10 samples per species) had been discarded were entered into the MDA as samples. For each sample, the species from underneath which it was taken was indicated by a presence record for the species group. The values for the six sediment variables (total phosphorus, inorganic phosphorus, total nitrogen, organic carbon, percent silt-clay and organic matter) for each of the 294 samples were log-transformed ($\log(x+1)$) and entered as environmental data upon which the linear discriminant functions were to be based.

A forward-selection MDA was performed to determine which of the six sediment samples were statistically significant ($p < 0.05$) in linear combinations best discriminating the eleven groups. Significance was determined by Monte Carlo permutation tests (999 unrestricted permutations).

All multivariate analyses (PCA, RDA and MDA) were performed in CANOCO Version 4.0.

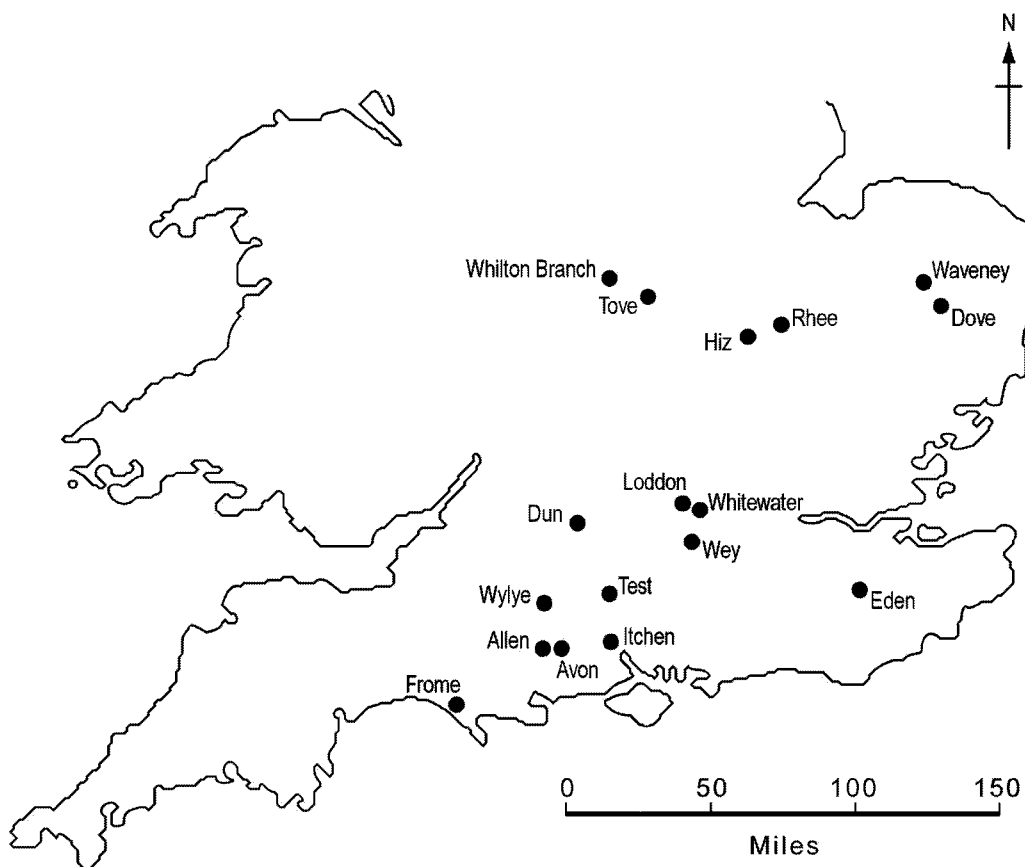


Figure 2.1 Map showing the location of the 17 river sites studied

Table 2.1 Details of sites surveyed and sampled

River	Abbreviation	MTR Site Name	MTR Site No. 1	NGR (Top)²	Solid Geology³	Environment Region	Agency
Allen	ALL	High Hall Farm	-	SU 006 025	Chalk/Sand/Gravels		SW
Avon	AVO	u/s Ringwood	6039	SU 149 036	Chalk and Inter-lava beds		SW
Dove	DOV	u/s Eye	5016	TM 150 737	Crag and Clay		AN
Dun	DUN	Hungerford	-	SU 321 685	Chalk		TH
Eden	EDE	Vanguard Way	-	TQ 418 448	Clay		SO
Frome	FRO	u/s Dorchester	6047	SY 705 904	Chalk		SW
Hiz	HIZ	Arlesey	-	TL 186 355	Chalk and Greensand		AN
Itchen	ITC	u/s Chickenhall	8010	SU 468 180	Chalk and Inter-lava beds		SO
Loddon	LOD	Keeper's Cottage	7040	SU 686 553	Clay		TH
Rhee	RHE	Harston Bridge	5010	TL 417 512	Chalk		AN
Test	TES	u/s Andover	8017	SU 383 393	Chalk		SO
Tove	TOV	u/s Towcester	5112	SP 710 487	Chalk overlain with Clay		AN
Waveney	WAV	u/s Diss	5079	TM 109 794	Chalk overlain with Clay		AN
Wey	WEY	Haw Bridge	7073	SU 745 414	Chalk		TH
Whilton Branch	WHI	u/s Whilton	5122	SP 624 649	Clay		AN
Whitewater	WWA	Lodge Farm	-	SU 733 524	Chalk		TH
Wylfe	WYL	South Newton	-	SU 086 343	Chalk		SO

¹where the site corresponds directly with a site included in the Environment Agency MTR database the MTR site number and name are retained.

²National Grid Reference from UK Ordnance Survey for upstream end of 100m site.

³Solid geology determined from National River Flow Archive (Institute of Hydrology, 1999)

Table 2.2 Distribution of sediment samples amongst macrophyte species

Macrophyte Species	No. of Sediment Samples	No. of Sites Represented
Unvegetated	36	17
<i>Apium nodiflorum</i>	12	4
<i>Butomus umbellatus</i>	2	1
<i>Callitriche</i> spp.	48	14
<i>Chara vulgaris</i>	2	1
<i>Elodea canadensis</i>	10	4
<i>Elodea nuttallii</i>	22	5
<i>Myriophyllum spicatum</i>	16	5
<i>Nuphar lutea</i>	12	4
<i>Oenanthe fluviatilis</i>	2	1
<i>Potamogeton crispus</i>	6	3
<i>Potamogeton natans</i>	6	2
<i>Potamogeton pectinatus</i>	16	5
<i>Potamogeton perfoliatus</i>	6	2
<i>Ranunculus penicillatus</i> subsp. <i>pseudofluitans</i>	84	12
<i>Rorippa nasturtium-aquaticum</i> agg.	2	1
<i>Sagittaria sagittifolia</i>	6	2
<i>Schoenoplectus lacustris</i>	4	2
<i>Sparganium emersum</i>	28	7
<i>Sparganium erectum</i>	10	4
<i>Veronica</i> spp.	4	1
<i>Zannichellia palustris</i>	6	3

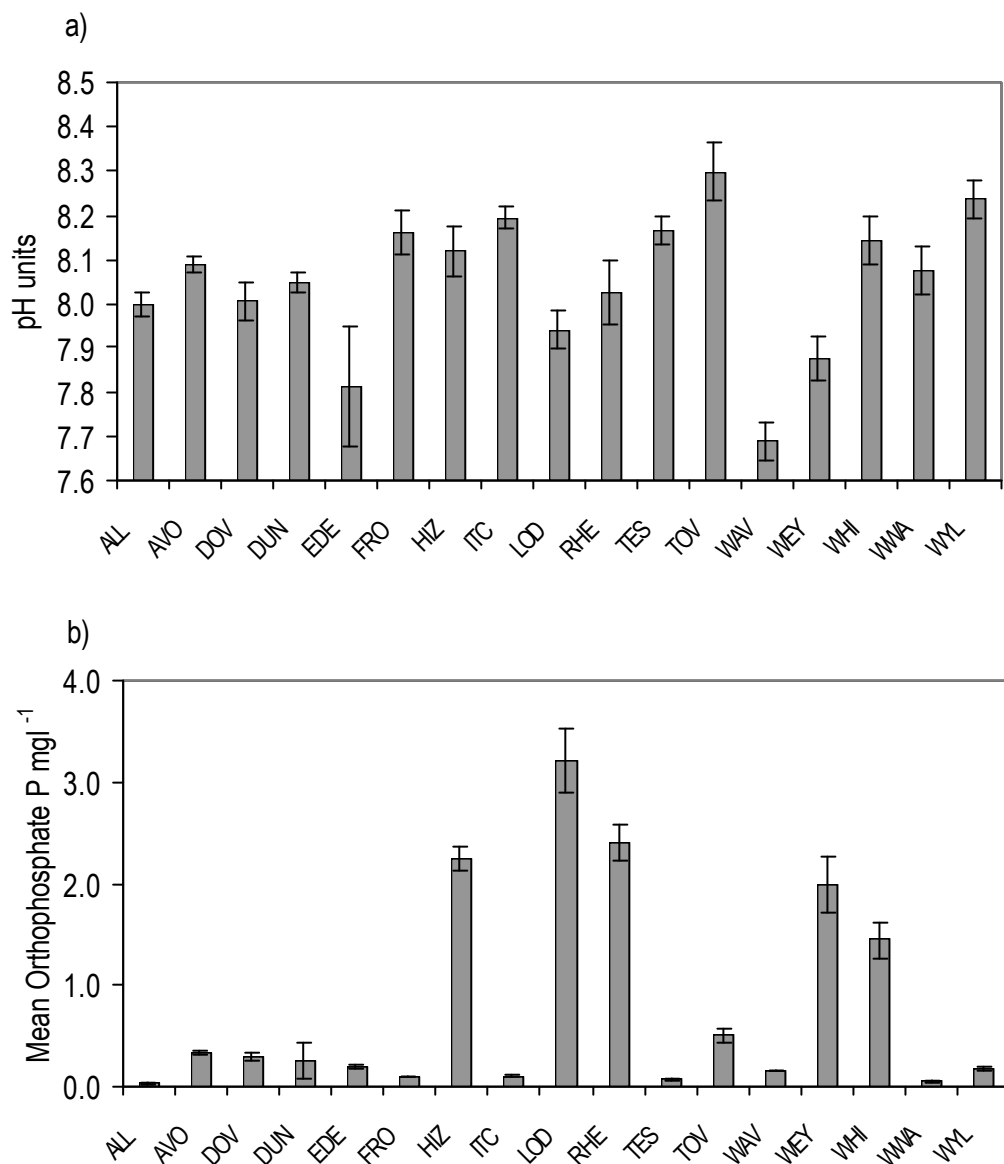


Figure 2.2 Mean values and standard errors for water chemistry parameters for each of the 17 rivers sampled. Means calculated from monthly mean values for the year of sediment sampling. (Source of data: Environment Agency)

a) pH units b) Orthophosphate-P mg l⁻¹ c) TON mg l⁻¹ d) NH₃-N mg l⁻¹

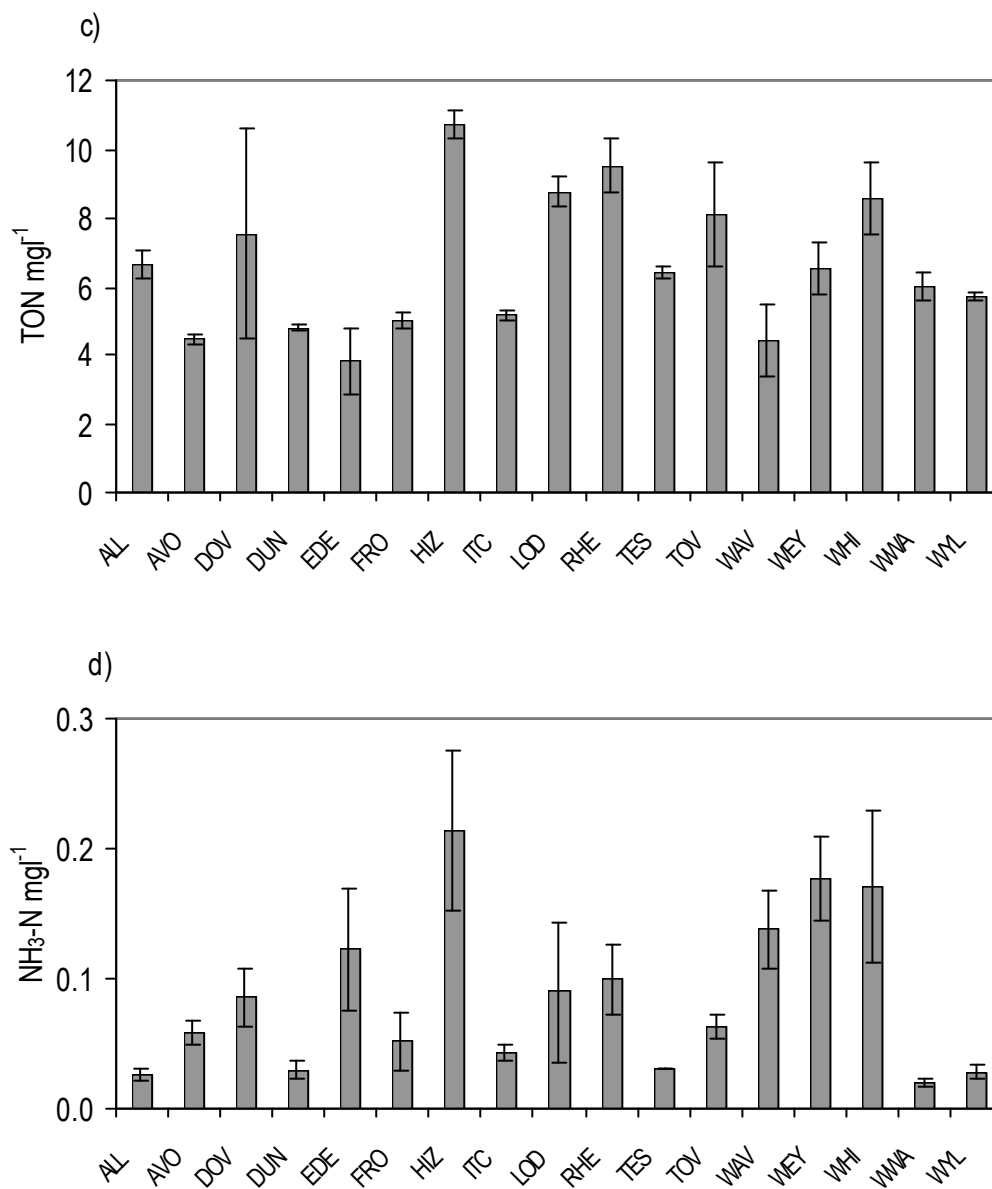


Figure 2.2 continued. Mean values and standard errors for water chemistry parameters for each of the 17 rivers sampled. Means calculated from monthly mean values for the year of sediment sampling. (Source of data: Environment Agency)

a) pH units b) Orthophosphate-P mg l⁻¹ c) TON mg l⁻¹ d) NH₃-N mg l⁻¹

**Table 2.3 Flow parameters selected from National River Flow Archive
(Institute of Hydrology, 1999)**

Parameter	Description
Mean ^{day*}	- the daily flow for the day on which the river was sampled,
Mean ^{1 year}	- the mean flow for the year in which the river was sampled calculated from the mean daily flows. The standard deviation is given.
Mean ^{3 year}	- the mean flow for the years 1996-98 inclusive, covering the period of sampling. Calculated from the mean daily flows for the period, standard deviation was also calculated
Mean ^{archive}	– the mean flow for a gauging station as given in the National River Flow Archive (Institute of Hydrology, 1999).
Q ₉₅	- the flow exceeded 95% of the time at the gauging station as given in the National River Flow Archive (Institute of Hydrology, 1999).
Base Flow Index (BFI)	– a catchment characteristic which is the “ratio of the smoothed minimum daily flow to the mean daily flow of the total recorded hydrograph” (Shaw, 1994, pg. 326), it is an indication of the proportion of the runoff that is derived from natural storage within the catchment. It is quoted in the National River Flow Archive (Institute of Hydrology, 1999).
CoV ^{3 year}	- the coefficient of variation of the mean ^{3 year} parameter

* Some sites have no “Mean^{day}” values.

Note: Some daily flows are missing. Therefore calculated parameters are based on differing numbers of observations.

3. RESULTS

3.1 Sediment Characteristics

3.1.1 Total phosphorus (TP)

The range of total phosphorus concentrations measured in sediment samples from the 17 rivers was large (35 to 2660µg/g). The mean value for the 17 sites overall was 944µg/g P whilst mean concentrations for individual rivers ranged from 154µg/g P (Avon) to 2247µg/g P (Wey).

Table 3.1 Total phosphorus concentrations reported in the literature for various sediment types

Authors	Sediments	TP µg/g
Williams <i>et al.</i> (1976)	Lake Erie	188-2863
Hieltjes and Lijklema (1980)	Lake Brielle	746-4158
Nürnberg (1988)	Seven lakes (N. America)	1190–3060
Nürnberg (1988)	41 lake samples (literature)	500-10300
Moutin <i>et al.</i> (1993)	Coastal lagoon (France)	617 ⁺ / 34 (mean)
Svendsen <i>et al.</i> (1993)	Gjern and Gelbæk rivers (Denmark)	460-682
Rose (1995)	Welland (England) and Morava (Czech Republic) rivers	168–6158
Baldwin (1996)	Various lakes (Australia)	300-1600
Fabre <i>et al.</i> (1996)	River Garonne	226-923
Pitt <i>et al.</i> (1997)	Norfolk Broads	1020–2100
Sfriso and Marcomini (1999)	Venice lagoons – within macroalgae and macrophyte dominated areas	380 (mean <i>Ulva</i>) 453 (mean <i>Zostera</i>)
This study	17 English, lowland rivers	35-2660

The total phosphorus values recorded for sediments of these English lowland rivers are of the same order of magnitude as those of other studies of sediment nutrient status (Table 3.1). Figure 3.1a displays the summary statistics for total phosphorus by river. Different rivers are clearly separated on the basis of the total phosphorus contents of their sediments, suggesting a continuum within the 17 rivers from those with relatively low sediment total phosphorus concentrations through to those with high concentrations. There are a number of rivers with well-defined sediment total phosphorus concentrations with little variability within the reach. These include rivers with relatively low total phosphorus concentrations (Allen, Avon, Whitewater), those with moderate concentrations (Dun, Wylye), and those with relatively high total phosphorus concentrations (Eden, Rhee, Tove, Whilton). The Wey is distinct as a river with sediments with much higher concentrations of total phosphorus. However, there are rivers which have a wide range of sediment total phosphorus concentrations (Loddon, Waveney). It is possible to distinguish three groups of rivers on the basis of the total phosphorus concentrations of the majority of sediment samples: - sediments < 500µg/g P (Allen, Avon, Frome, Itchen, Whitewater); 500 – 1500 µg/g P (Dove, Dun, Hiz, Loddon, Test, Tove,

Whilton, Wylfe); > 1500 µg/g P (Wey). Figure 3.1a indicates that the Avon and Waveney have the most variable concentrations of total phosphorus.

3.1.2 Inorganic phosphorus (IP)

Sediment inorganic phosphorus concentrations ranged from 6µg/g P to 1209µg/g P with a mean value of 226µg/g P for the 17 rivers overall. In agreement with sediment total phosphorus concentrations the highest (750µg/g P) and lowest (39µg/g P) inorganic phosphorus concentrations in individual rivers also occurred in the Wey and Avon, respectively. Figure 3.1b displays the mean, median and range for sediment total phosphorus concentrations in each of the 17 rivers.

Despite the obvious relationship between total and inorganic phosphorus, the rivers are less distinct on the basis of inorganic phosphorus concentrations than total phosphorus concentrations. Differences between total and inorganic phosphorus concentrations are evident for the Tove and Wey samples; the Tove has relatively high total phosphorus sediments with little variability and relatively low inorganic phosphorus concentrations with considerable variability. The Wey has the highest total phosphorus concentrations with relatively little variability yet a wide range of sediment inorganic phosphorus concentrations. Inorganic phosphorus concentrations, in seven of the rivers (Allen, Avon, Dun, Frome, Itchen, Whitewater and Wylfe) display small ranges but variation may be high due to the low mean values of some of these rivers. Coefficients of variation for inorganic phosphorus concentrations are over 50% for the Eden, Frome, Test, Tove, Waveney but less than 3% for the Dun.

3.1.3 Total nitrogen (TN)

Sediment total nitrogen contents ranged from below the limits of detection to 0.84% and the mean content for the 17 rivers overall was 0.12%. The highest mean value of total nitrogen for an individual river was 0.52% (Waveney) and the lowest 0.02% (Eden). Figure 3.2a indicates that, whilst most sediment samples (excluding those from the Waveney) had total nitrogen contents of less than 0.5%, variability within rivers was high.

3.1.4 Organic carbon (OC)

Sediment organic carbon contents ranged from 0.20% to 13.96% in the 17 rivers, with an overall mean organic carbon content of 2.06%. In individual rivers mean % organic carbon contents ranged from 0.60% (Eden) to 9.07% (Waveney). Figure 3.2b displays sediment organic carbon contents for individual rivers and shows a similar pattern to the plot of total nitrogen contents (Figure 3.2a), suggesting an association between the two elements (see Section 3.2).

3.1.5 Organic matter (OM)

Across the 17 rivers, organic matter contents ranged by two orders of magnitude from 0.52% to 52%, with a mean content of 5.64%. The lowest mean organic matter content for an individual river was 2% in the Hiz and the highest was 21% for the Waveney. Most samples had organic matter contents of less than 10%, however, some samples had contents of over 30%. Sediment organic matter contents for individual rivers are shown in Figure 3.3a.

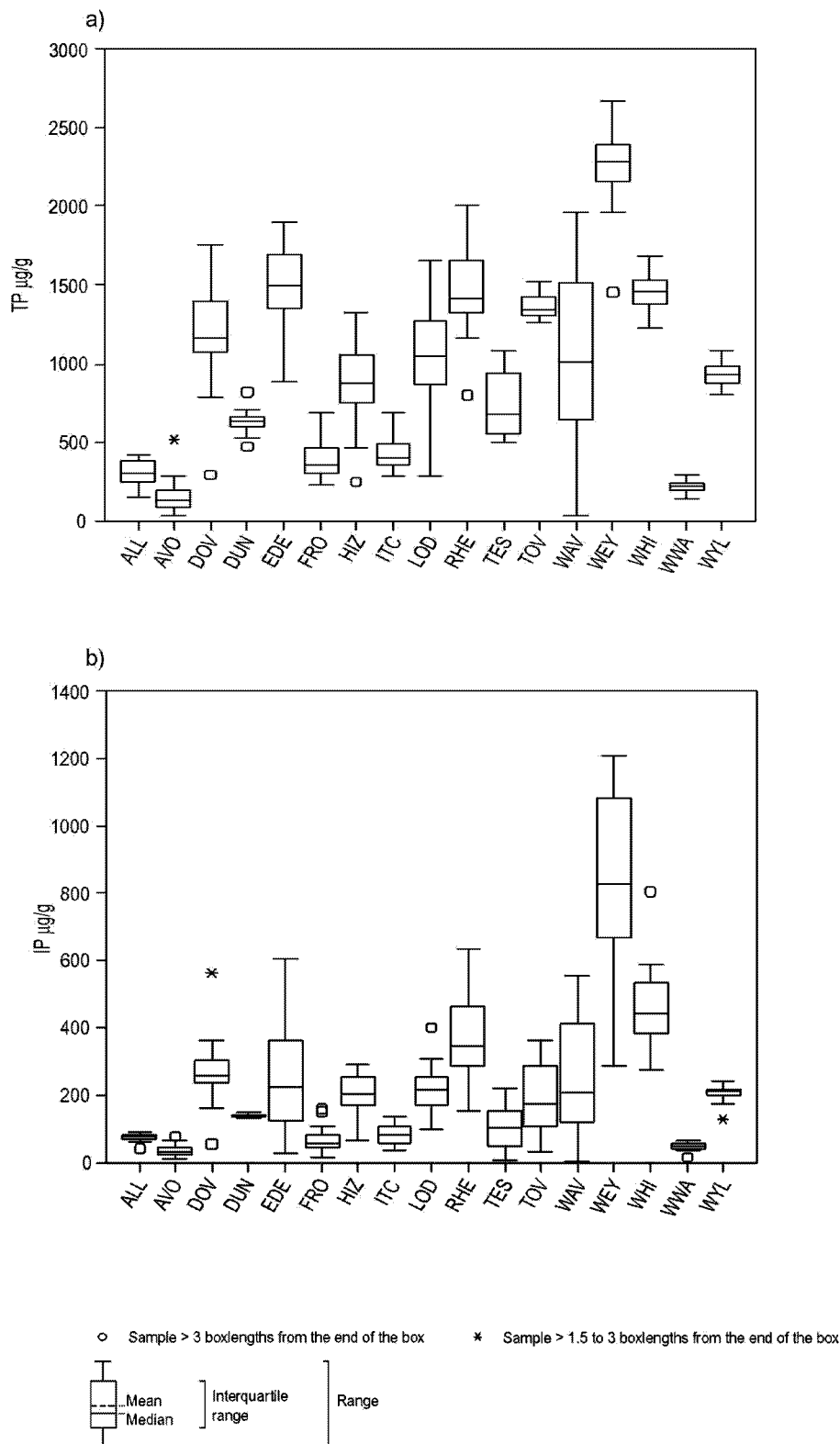


Figure 3.1 Boxplots of sediment characteristics by river

a) Sediment total phosphorus ($\mu\text{g/g}$)

b) Sediment inorganic phosphorus ($\mu\text{g/g}$)

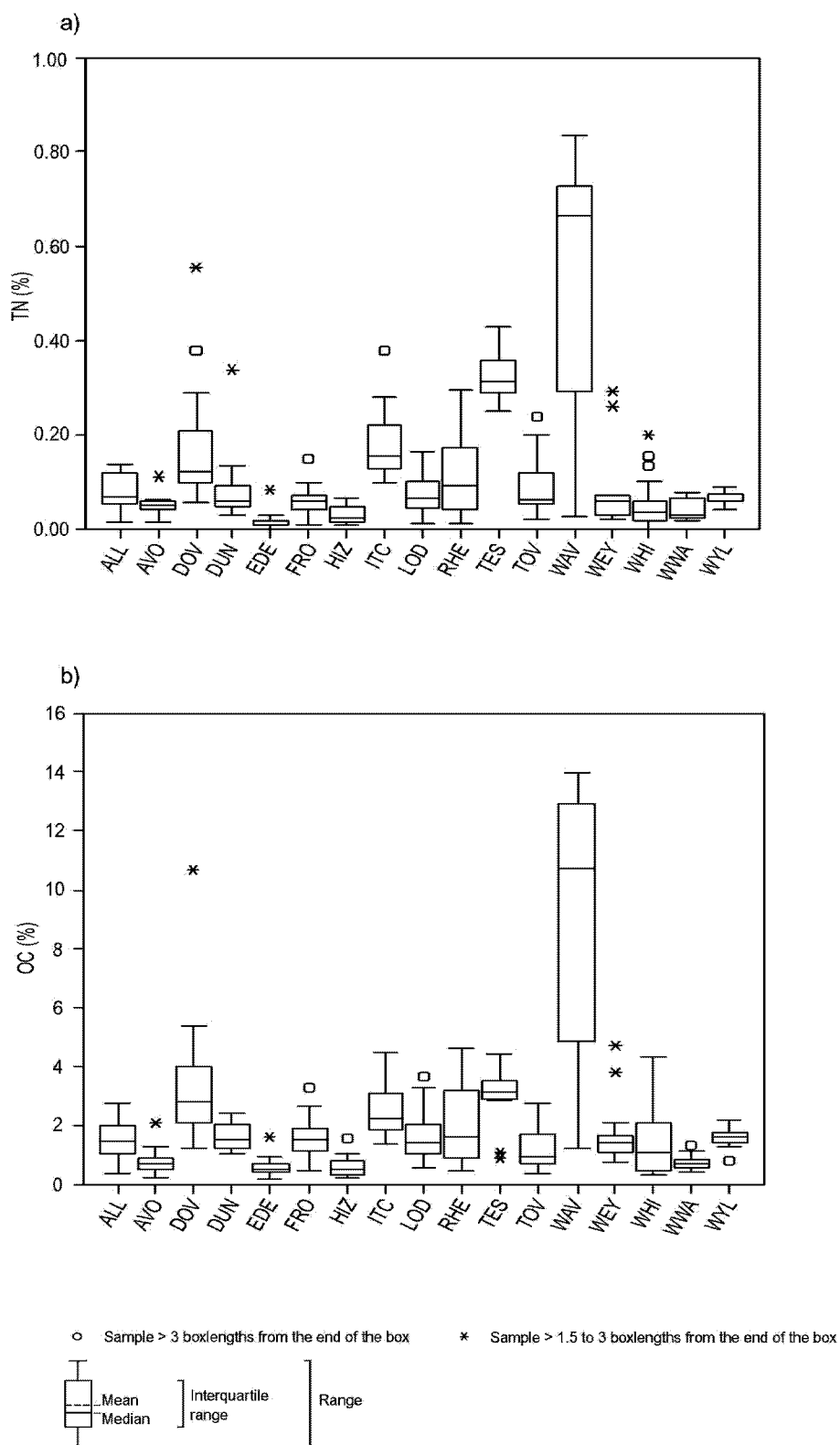


Figure 3.2 Boxplots of sediment characteristics by river

- a) Sediment total nitrogen (%)
b) Sediment organic carbon (%)

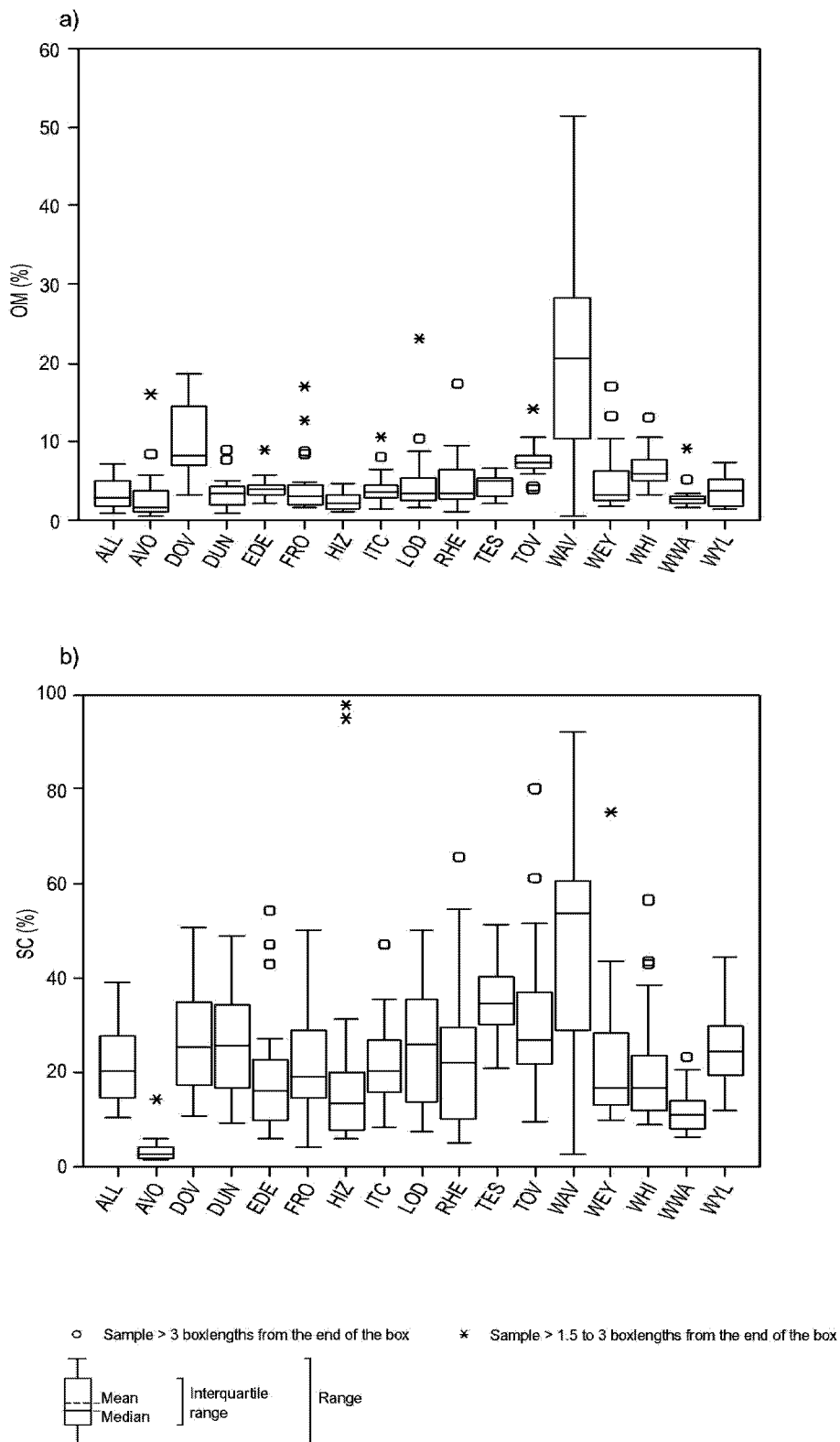


Figure 3.3 Boxplots of sediment characteristics by river

- a) Sediment organic matter (%)
b) Sediment percent silt-clay (%)

3.1.6 Percent silt-clay (SC)

The proportion of the sediment (<4mm) that was silt or clay (<63µm) ranged from 1.42% to 98% across all rivers with an overall mean of 24%, reflecting the heterogeneous nature of river sediments. In individual rivers mean percent silt-clay varied from 4% in the Avon to 45% in the Waveney. All rivers except the Avon had a fairly wide range of percent silt/clay contents (Figure 3.3b). Material of silt/clay sizes generally constituted between 10 and 40% of the sediment although the Avon had coarser sediments than this and the Waveney had considerably finer sediments. The Avon had a mean silt-clay proportion of 4% with a maximum of just 14% indicating very sandy sediments.

3.1.7 Sediment variability between rivers - ANOVA testing

A series of one-way ANOVA tests (Model II) indicated that, on the basis of all six sediment parameters (using log (x+1) transformation of organic matter), between-river variability was greater than within-river variability and therefore the mean values for each parameter in each river were different ($P < 0.001$).

3.1.8 Sediment variability and sampling effort

There are a number of statistical formulas that can be used to calculate the number of samples required for random sampling with a given level of error. One such calculation is -

$$n = (1.96\sigma)^2 / \epsilon^2$$

where:

n = number of samples

σ = standard deviation expressed as % of mean

ϵ = level of error in %

(Hunt and Wilson, 1986)

This formula was used to calculate the number of samples that would be required to sample the sediments of the 17 rivers of this study, with a sampling error of 10%, for the determination of reach values of the six sediment variables – total phosphorus, inorganic phosphorus, total nitrogen, organic carbon, organic matter and percent silt-clay (Table 3.2).

Table 3.2 Numbers of samples required per 100m to sample each of the 17 rivers with 10% error

River	TP	IP	TN	OC	OM	SC
Allen	22	10	96	60	128	62
Avon	183	69	52	105	507	255
Dove	25	46	183	142	102	66
Dun	5	<1	289	31	119	67
Eden	11	169	426	109	48	186
Frome	53	117	105	67	327	119
Hiz	33	34	124	107	70	576
Itchen	25	56	55	42	105	83
Loddon	33	42	132	99	365	98
Rhee	15	45	230	156	232	185
Test	29	137	10	43	40	22
Tove	1	100	164	140	33	106
Waveney	113	193	105	94	179	103
Wey	5	38	385	133	254	174
Whilton	2	23	388	238	52	158
Whitewater	12	17	104	36	119	56
Wylye	3	5	20	14	93	44

3.2 Associations Between Sediment Parameters

Table 3.3 shows correlation coefficients for sediment parameters across all sediment samples in the 17 rivers and Figure 3.4 is a matrix of scatterplots showing the nature of relationships between variables. Table 3.4 shows the results of regression analyses applied to these relationships.

Table 3.3 Pearson's product moment correlation coefficients for sediment parameters across all rivers (n = 340)

	TP	IP	TN	OC	OM	SC
TP	1					
IP	0.858*	1				
TN	0.047	- 0.038	1			
OC	0.089	0.023	0.941*	1		
OM	0.184*	0.090	0.725*	0.820*	1	
SC	0.179*	0.021	0.590*	0.576*	0.574*	1

* correlation is significant at 0.01 level (two tailed)

There was a significant and strong correlation between the two phosphorus measurements (Table 3.3) although the relationship between the two variables was not linear (Figure 3.4). Curve-fitting using SPSS indicated that the relationship was well modelled by a cubic equation (Table 3.4). Figure 3.4 suggests that there is an almost linear relationship between the two parameters at total phosphorus concentrations below approximately 1500 µg/g P. Sediments with total phosphorus

concentrations greater than this have higher inorganic phosphorus concentrations than would be predicted by a linear relationship. Many of the samples with total phosphorus concentrations greater than 2000 µg/g P (causing the cubic relationship) are from the Wey. In the absence of further samples with total phosphorus concentrations of this magnitude it is difficult to ascertain whether there is a genuine departure from the linear relationship or whether the Wey is a site with distinct sediment nutrient concentrations. There were only weak correlations between phosphorus concentrations (total and inorganic) and the other sediment characteristics.

Plots of total nitrogen and organic carbon by river (Figures 3.2a and 3.2b) were very similar and Table 3.3 indicates that there is a strong and significant association ($r=0.941$) between the two variables. This is consistent with the findings of Martinova (1993), who discovered correlation coefficients of $r=0.9-0.95$, for associations between total nitrogen and organic carbon in the sediments of 176 Russian lakes. Figure 3.4 shows a linear relationship between the two parameters but, as most samples have both low total nitrogen and organic carbon, a few samples with high total nitrogen and organic carbon have a strong influence on the regression ($R^2=0.885$, Table 3.4). These samples are almost exclusively from the River Waveney. The River Test samples also appear distinct on the plot, having a similar linear relationship to the regression model but possessing lower organic carbon contents than would be predicted. To investigate whether the Waveney and Test samples were unduly influencing the regression model, and to further investigate the relationship, all samples with total nitrogen contents greater than 0.20% were deleted and the regression analysis undertaken again (not shown). However, no improvements on the original model were found ($R^2=0.716$).

The correlation between total nitrogen and organic matter is significant and strong ($r=0.725$). The plot of these two parameters indicates there is considerable scatter with most samples having low total nitrogen and organic matter (Figure 3.4). A regression analysis gave an adjusted R^2 value of 0.525 reflecting this degree of scatter. The River Waveney is again distinct in the scatter-plot having a range of organic matter contents (much higher than any other river) but with relatively constant total nitrogen contents between 0.6% and 0.9%.

Table 3.3 indicates that there was a significant correlation ($r=0.590$) between total nitrogen and percent silt-clay. Figure 3.4 displays the nature of this relationship and the regression gave an adjusted R^2 of 0.346 (Table 3.4). There is a wide scatter of points with samples from certain rivers appearing distinct. The River Waveney sediment samples are of a fine particle size and have high total nitrogen contents. In contrast, the Avon samples are coarse and have low total nitrogen contents. Between these two rivers, the Eden has a range of percent silt-clay contents but low total nitrogen contents throughout. Additionally, there are two Hiz samples with very high percent silt-clay content but very low total nitrogen contents.

Organic carbon and organic matter are more strongly correlated ($r=0.820$) than total nitrogen and organic matter (Table 3.3). Figure 3.4 depicts a similar relationship between organic carbon and organic matter to that of total nitrogen and organic matter with many samples having both low organic carbon and low organic matter and the Waveney having much higher organic matter and organic carbon contents. The regression analysis gave an adjusted R^2 value of 0.671 (Table 3.4) but when samples with 10% organic matter or less were plotted alone there was a great deal of scatter. This second regression (not shown) gave an adjusted R^2 value of just 0.133.

The correlation between organic carbon and percent silt-clay ($r=0.576$) and the regression (adjusted $R^2=0.330$) (Tables 3.3 and 3.4, respectively) reflect the considerable degree of scatter in the

relationships between these two sediment variables. As with the total nitrogen–percent silt-clay plot (Figure 3.4) there are coarse sediments that seem to form a relationship with organic carbon, for example, the Allen and Avon samples.

The association between organic matter and percent silt-clay is significant and moderately strong ($r=0.574$). The relationship is strongest at percent silt-clay contents of less than about 30%. The linear regression model gave an adjusted R^2 value of just 0.327 reflecting the scatter of samples particularly in sediments finer than approximately 30% percent silt-clay. Again, the organic matter content and percent silt-clay seem to be related in the finest sediments and the relationship is less clear for the coarsest sediments.

Table 3.4 Adjusted R^2 values for least squares linear regression analyses

	TP	IP	TN	OC	OM	SC
TP						
IP	0.840*					
TN	-	-				
OC	-	-	0.885			
OM	-	-	0.525	0.820		
SC	-	-	0.346	0.330	0.327	

- the correlation coefficient indicated a weak association and regression analysis was not performed

* non-linear curve fitted, modelled by a cubic equation

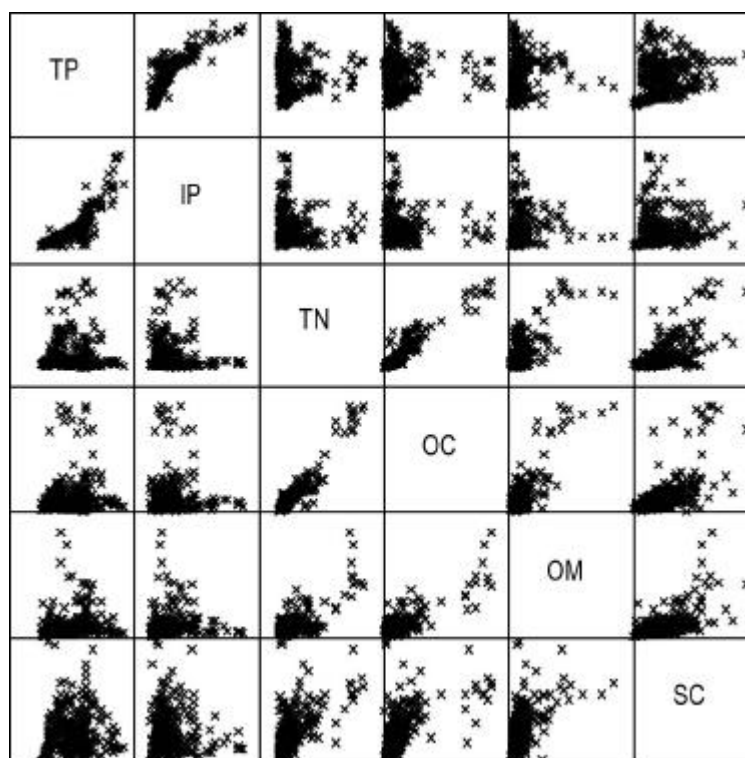


Figure 3.4 Scatterplot matrix showing relationships between sediment characteristics

3.3 Relationships Between Water Chemistry and Sediment Parameters

The relationships between mean values for sediment variables at each river site and yearly mean water chemistry parameters were investigated by calculating Pearson's product moment correlation coefficients (Table 3.5). Figure 3.5 shows scatterplots for significant relationships.

Table 3.5 Pearson's product moment correlation coefficients for mean sediment variables and mean water chemistry variables (n=17)

	pH	TON	Ammonia	Orthophosphate
TP	- 0.321	0.330	0.663**	0.507*
IP	- 0.347	0.270	0.682**	0.517*
TN	- 0.369	- 0.226	0.003	- 0.281
OC	- 0.506*	- 0.236	0.116	- 0.223
OM	- 0.507*	- 0.144	0.265	- 0.154
SC	- 0.226	0.042	0.107	- 0.065

** Significant at the 0.01 level (two tailed)

* Significant at the 0.05 level (two tailed)

Table 3.5 indicates that only six associations were significant; these were between the two sediment phosphorus forms and water column ammonia and orthophosphate and between water column pH and organic carbon and organic matter.

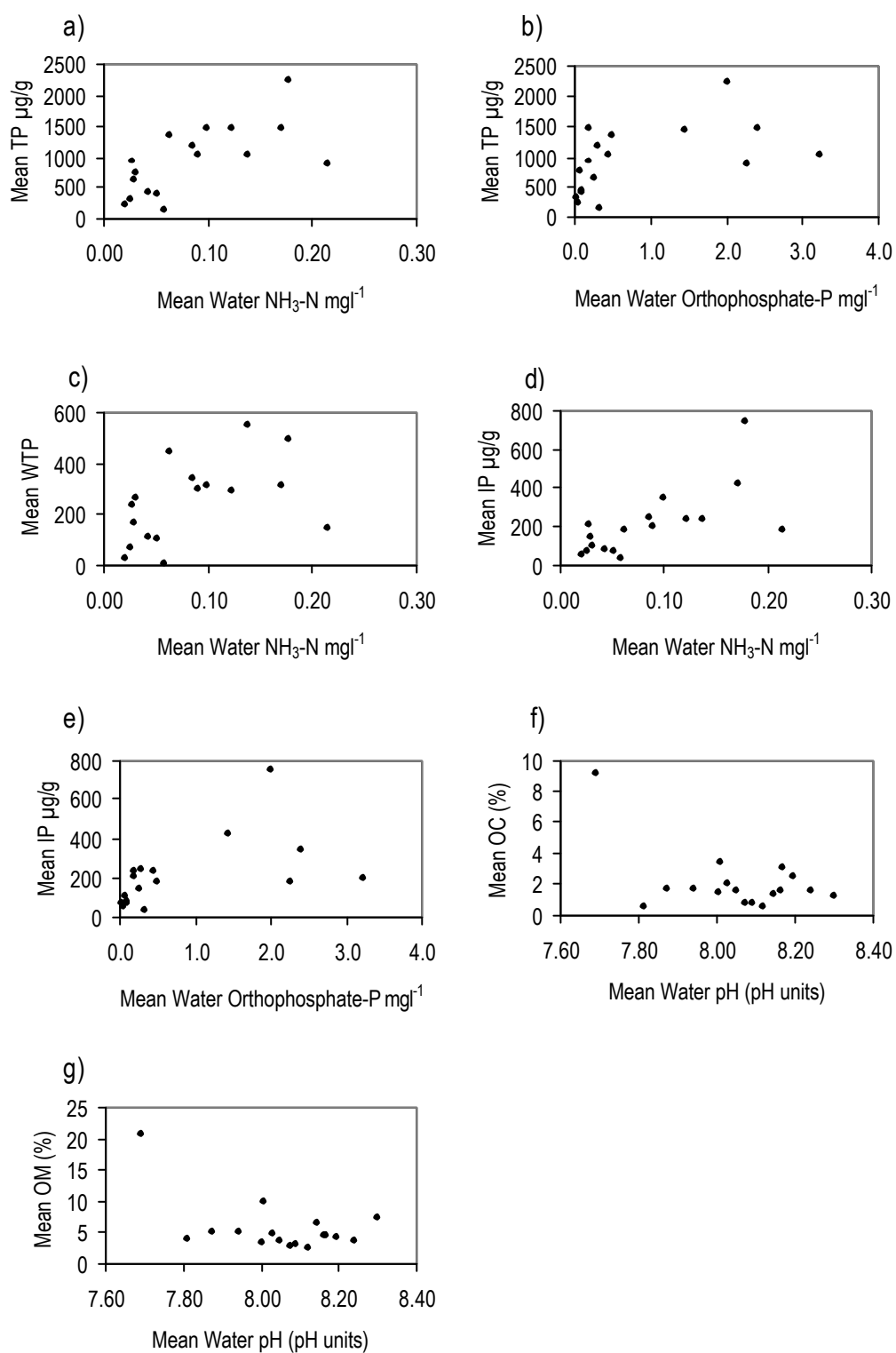


Figure 3.5 Scatterplots showing the relationships between mean values for sediment parameters (n=17) and selected water chemistry parameters (n=12, monthly mean for year of sampling).

3.4 Principal Components Analysis of the Characteristics of the Habitat, Water and Sediment

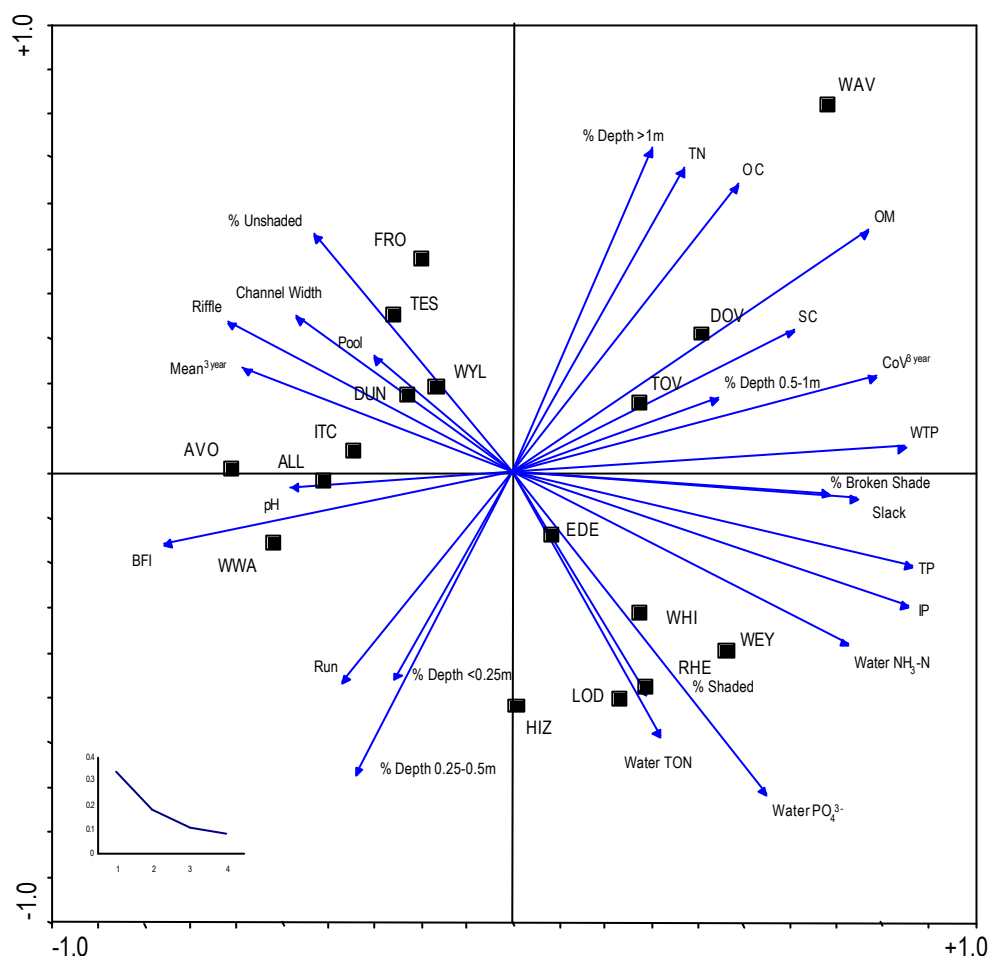


Figure 3.6 PCA Biplot of log transformed environmental variables. The scaling of the ordination scores is focused on inter-environmental variable correlations and the environmental data are centred and standardised. The first two axes of the ordination explain 33.9% and 18.4%, respectively. The inset shows the eigenvalues for the four axes derived. Environmental variables are shown as arrows and sites as squares. Abbreviations are those used throughout the report.

Figure 3.6 shows the first two axes of the PCA which explained 33.9% and 18.4% of the variation in the environmental data. Figure 3.6 indicates that many variables are correlated with one another and thus, the importance of some variables may be underestimated. The first axis appears to represent a gradient of increasing sediment phosphorus concentrations and increasing flow variability. There is a continuum from base-rich, stable-flow chalk streams on the left of the ordination plot (Figure 3.6) through to streams with finer, more nutrient-rich sediments and flashy regimes on the right of the plot. The highest scores on the first axis are those for weighted sediment total phosphorus (a product of total phosphorus content and percent silt-clay), % slack, flow variability and BFI (negative). The second axis would appear to relate to channel depth with shallow streams at the bottom of the plot. The second axis also reflects a gradient of sediment nitrogen and carbon content, which are correlated with one another as indicated in Section 3.2. There is also an apparent shade gradient although this seems to be correlated with water column concentrations of orthophosphate and total oxidised nitrogen. The ordination plot shows a grouping of chalk streams, characteristically wide and unshaded, on the left (Avon, Allen, Dun, Frome, Itchen, Test, Whitewater, Wylfe,) a group of streams with chalk geology overlain with clay (Loddon, Rhee, Wey, Whilton) where shade seems to be important and a group with fine organic rich sediments (Dove, Tove, Waveney). The PCA further highlights the correlations investigated above between sediment organic matter content and nitrogen and carbon contents.

3.5 Macrophyte Species and River Sediment Characteristics

Figures 3.7–3.9 display the characteristics of sediments underlying the sampled macrophyte species.

Figures 3.7a and 3.7b display the total phosphorus and inorganic phosphorus contents of sediments underlying the various species. Figure 3.7a shows that there is some separation of species on the basis of the phosphorus concentration of the sediments in which they are rooted. Samples from bare sediments cover a wide range of total phosphorus concentrations reflecting the representation of all 17 sites. However, *Callitriche* spp. and *Elodea nuttallii* are both found on a wide range of sediments with respect to total phosphorus. A number of species seem to be associated with high total phosphorus concentrations ($>1000\mu\text{g/g P}$): *Nuphar lutea*, *Potamogeton natans*, *Sagittaria sagittifolia*, *Sparganium emersum* and *Sparganium erectum*. Other species such as *Myriophyllum spicatum* and *Potamogeton perfoliatus* are associated with total phosphorus concentrations of less than $500\mu\text{g/g P}$, although *Myriophyllum spicatum* was also recorded on sediment in the River Waveney with total phosphorus concentrations of over $1500\mu\text{g/g P}$.

Figure 3.7b indicates that species are less distinct with respect to the inorganic phosphorus concentrations of the sediments in which they are rooted than the total phosphorus concentrations. Figure 3.7b does, however, show a marked difference in the range of inorganic phosphorus concentrations in sediments underlying *Elodea nuttallii* relative to other species. A difference between the two *Elodea* species is clear, with *Elodea nuttallii* being associated with slightly higher inorganic phosphorus concentrations and a wider range of inorganic phosphorus concentrations than *Elodea canadensis*.

Figure 3.8a displays the total nitrogen contents of sediments in which the various species are rooted. *Elodea nuttallii*, *Myriophyllum spicatum*, *Potamogeton crispus*, *P. pectinatus*, *P. perfoliatus* and *Zannichellia palustris* are all associated with low and limited ranges of total nitrogen contents if outlying values are excluded. In contrast *Potamogeton natans* and *Sagittaria sagittifolia* are both

found across a relatively wide range of sediment total nitrogen contents. However, mean and median contents of total nitrogen are less than 0.4% for all species with a representative number of samples ($n > 6$). *Ranunculus penicillatus* subsp. *pseudofluitans* and *Sparganium emersum* are both found on sediments with similar low-medium mean total nitrogen contents and ranges.

Figure 3.8b shows the organic carbon contents for the river sediments by species. This plot again reflects the relationship between organic carbon and total nitrogen with an almost identical pattern to Figure 3.8a. Figure 3.9a shows that many of the species in the 17 rivers of this study are growing on sediments with organic matter contents of less than 10% if outlying samples are excluded. The species associated with sediments that have a wide range of organic matter contents (for example, *Potamogeton natans*) are also the species with sediments with high total nitrogen and organic carbon ranges further highlighting the relationship between these three variables.

Figure 3.9b shows that, in this study there are species associated with a wide range of sediment types, for example, *Callitriche* spp., *Potamogeton natans*, *Sparganium emersum* and *Sparganium erectum*. However, *Elodea nuttalli*, *Myriophyllum spicatum*, *Potamogeton crispus*, *Potamogeton perfoliatus* and *Zannichellia palustris* are all associated with samples which are mostly less than 20% silt-clay.

3.5.1 Differences between vegetated and unvegetated Sediments

The characteristics of unvegetated reference samples are shown in Figures 3.7 – 3.9. A series of two-sample Student's *t* tests were performed to investigate the difference between mean values of sediment characteristics for vegetated and unvegetated sediments (Table 3.6). Table 3.6 indicates that vegetated and unvegetated sediment samples were not statistically different on the basis of the six sediment characteristics, and confirms the observations of the boxplots.

Table 3.6 Results of two-sample Student's *t* test used to test the difference in means of vegetated (n=304) and unvegetated (n=36) samples

	TP	IP	TN	OC	OM	SC
p value (two-tailed)	0.482	0.614	0.385	0.501	0.326	0.302

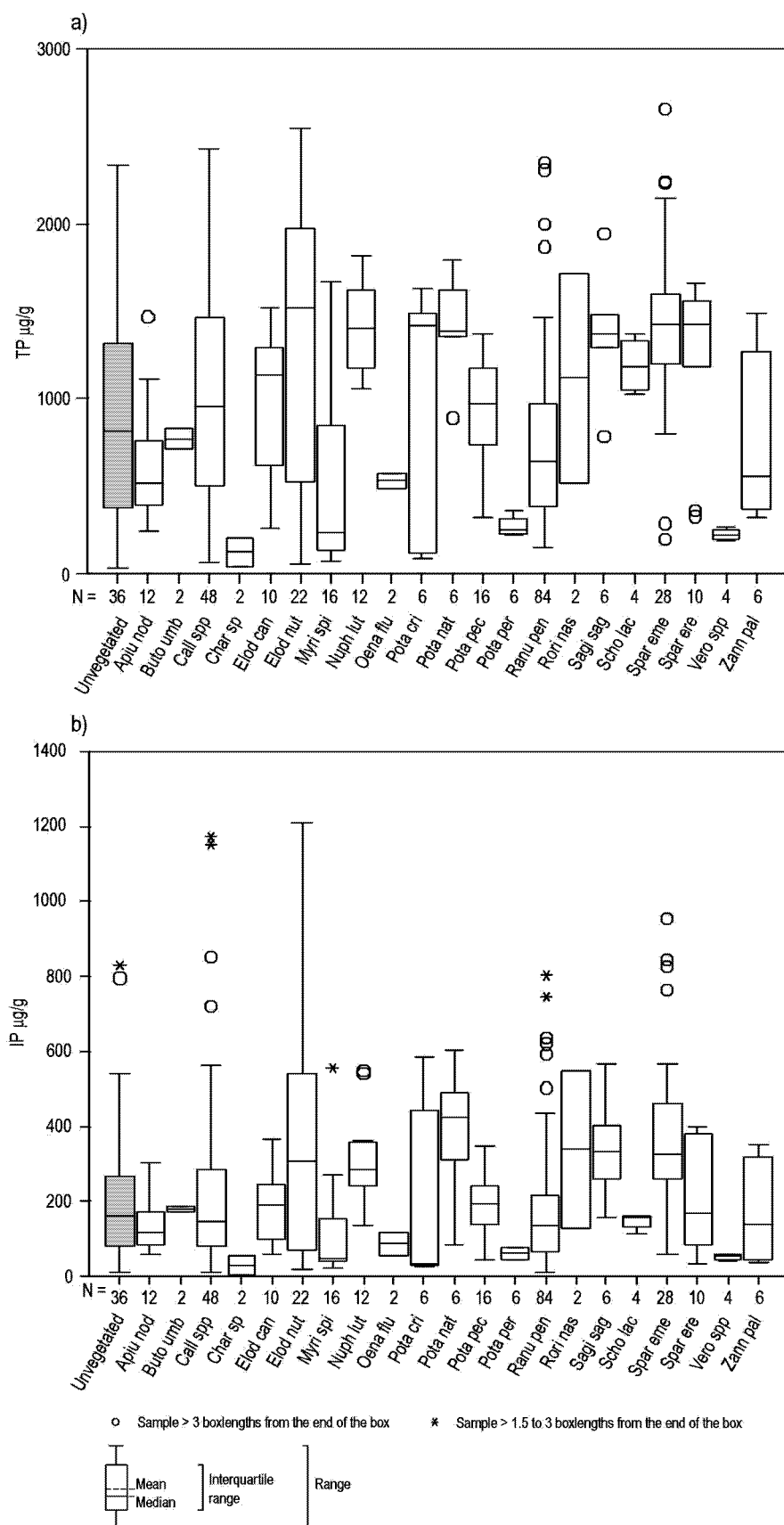


Figure 3.7 Boxplots of sediment characteristics by macrophyte species

a) Sediment total phosphorus

b) Sediment inorganic phosphorus

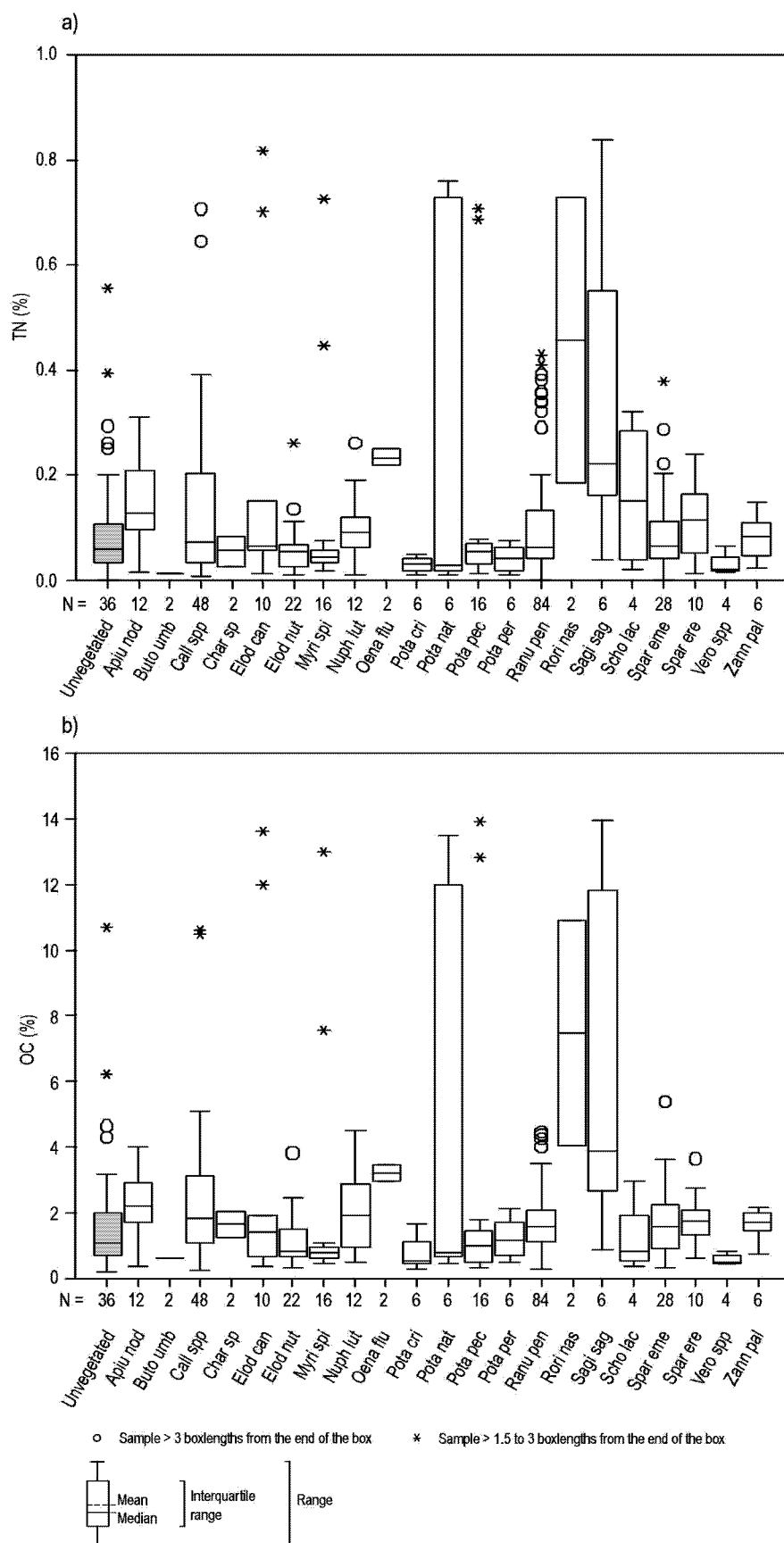


Figure 3.8 Boxplots of sediment characteristics by macrophyte species
a) Sediment total nitrogen
b) Sediment organic carbon

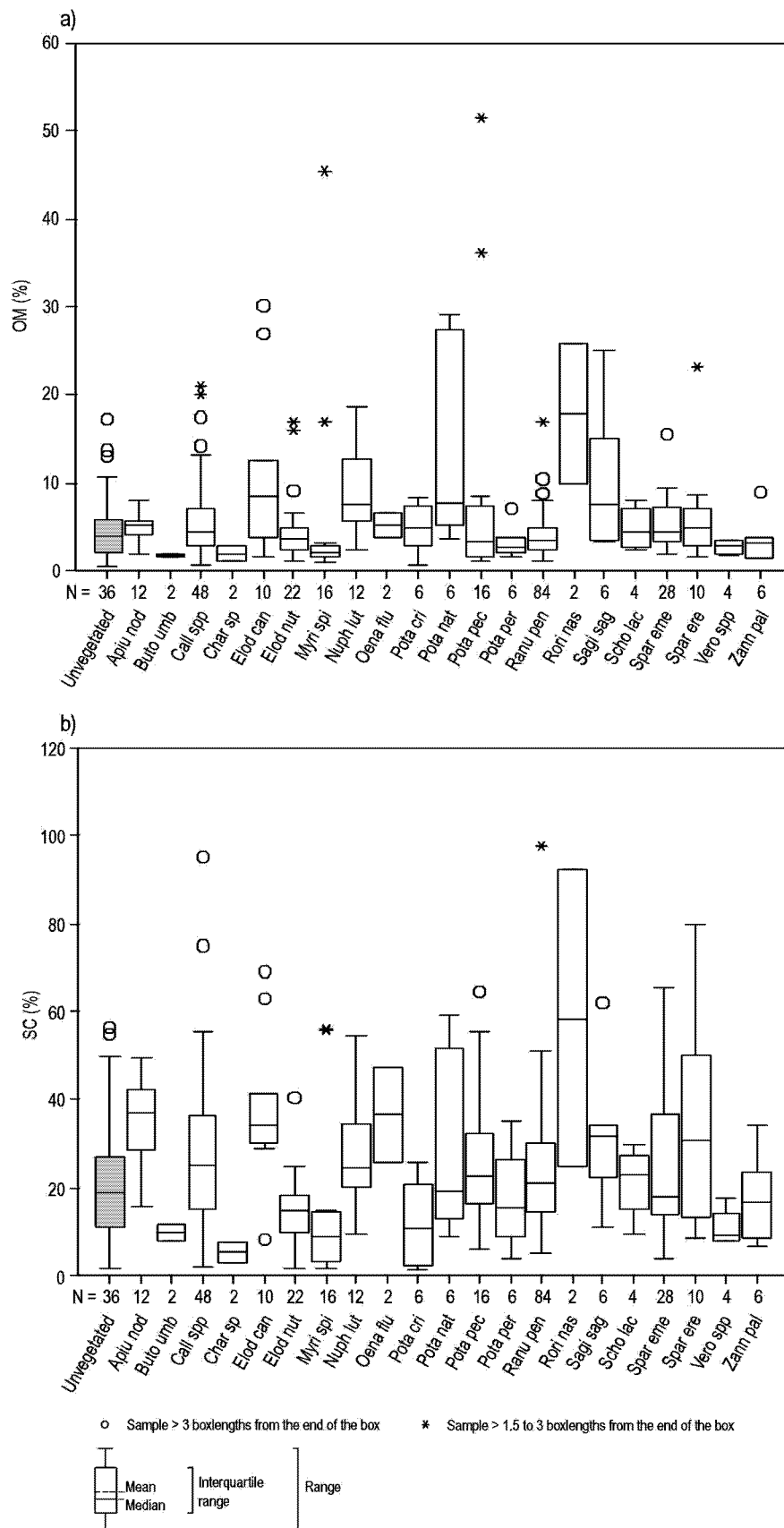


Figure 3.9 Boxplots of sediment characteristics by macrophyte species

a) Sediment organic matter

b) Sediment percent silt-clay

3.5.2 Multiple discriminant analysis

The forward selection MDA showed that total phosphorus ($p=0.001$), percent silt-clay ($p=0.001$) and organic matter ($p=0.010$) were statistically significant in linear combinations best discriminating the 11 groups. A second MDA was performed with these three significant variables only, four discriminant functions were derived in total but the final function was unconstrained. Both the first function and all four functions together were significant ($p<0.05$, Monte Carlo tests, 999 unrestricted permutations). The eigenvalues given by CANOCO are atypical for an MDA and are best reported as:

$$\theta = \lambda / (1-\lambda)$$

where: λ is the eigenvalue given by CANOCO

(ter Braak and Smilauer, 1998, p. 297)

The three MDA eigenvalues (θ) were 0.256, 0.208 and 0.058, the fourth eigenvalue was 1.000. Figure 3.10 is a biplot of the MDA based on species groups and shows the three sediment variables and the tolerances of the ten groups. The tolerances represent the within-group variation. The discriminant functions cumulatively explain between 0.25% (*Potamogeton pectinatus*) and 10.82% (*Myriophyllum spicatum*) of the within-group variance for each individual group.

The biplot (Figure 3.10) shows that there is considerable overlap between the tolerances of the groups, indicating that the discriminant function separates the groups of species poorly. This is confirmed by the low amount of variance in species data explained by the first two discriminant functions (2.0% and 1.8%). Only the *Myriophyllum spicatum* group and the *Elodea nuttallii* group have a significant area which does not overlap with any other group. However, this is largely a result of the large tolerance values for these two groups. The MDA biplot indicates that the unvegetated sediments are not different to those that support macrophytes, with respect to the parameters considered. The biplot shows that neither of the first and second discriminant functions closely reflect the three environmental variables included in the analysis.

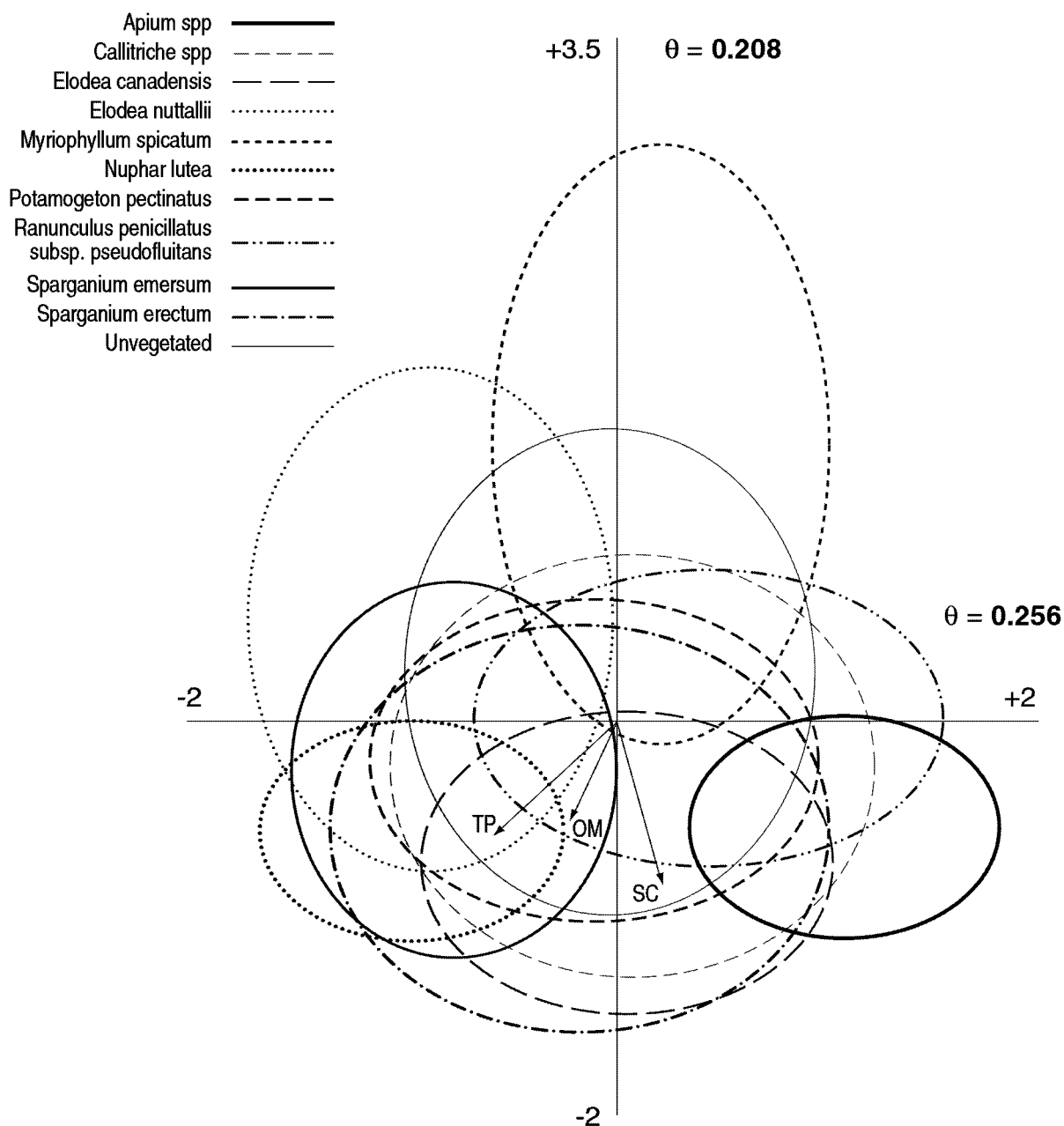


Figure 3.10 MDA biplot showing the distribution of macrophytes, classified according to species along the first two discriminant functions. Only species represented by 10 or more sediment samples were included; unvegetated samples were included for comparison. The sediment variables that were significant at separating the species groups are also shown. The influence of sediment variables was determined by forward-selection using Monte-Carlo tests (999 unrestricted permutations). Species groups are displayed by their tolerances around the centroid for each group, thus the centroid for a particular ellipse is located at its centre point.

3.5.3 Canonical ordination of river species data

The forward-selection RDA identified three environmental variables: Base Flow Index (BFI); mean sediment total nitrogen concentrations and the percentage of the channel shaded that significantly ($p < 0.05$) explained the variation in macrophyte species abundance data.

The triplot (Figure 3.11) and ordination results indicate that a considerable amount of variability in species data is explained by Base Flow Index (BFI) and that the importance of sediment nitrogen concentrations may largely be a result of high values of this variable in the River Waveney. Figure 3.11 indicates that Axis 1 represents either a combination of environmental variables or a factor that was not considered during this study. Axis 2 seems to reflect increasing sediment total nitrogen concentrations. The ordination suggests that of the environmental variables studied, sediment total nitrogen and BFI are most important in explaining species composition. The percentage of the channel shaded has less importance but is still statistically significant.

The relationship of a species to the environmental variables is determined by the size of the angle between the environmental variable vector and a vector linking the species point to the origin of the ordination. Species (or sites) close to the centre of the diagram are less correlated with the environmental variables than species whose point lies further from the centre (Jongman *et al.*, 1995). Using these criteria, it is clear that the abundance of *Ranunculus penicillatus* subsp. *pseudofluitans* is positively correlated with BFI. In contrast, species, such as *Sparganium erectum* and *Nuphar lutea*, are negatively associated with BFI. This is intuitive and reflects the presence of *Ranunculus penicillatus* subsp. *pseudofluitans* in chalk streams which have a high BFI.

Conversely, the other two species commonly occur in slower-flowing, deeper habitats, such as clay streams where the BFI is likely to be considerably lower. A number of species are correlated with increasing sediment total nitrogen concentrations; *Phragmites australis*, *Callitriche* spp., *Alopecurus geniculatus* and *Carex riparia*, in particular. However, it seems likely that these correlations reflect the presence of the species in the River Waveney which has particularly high sediment total nitrogen concentrations. Marginal, wetland species such as *Glyceria maxima* and *Lycopus europaeus*, filamentous green algae species and the moss *Amblystegium riparium* are all correlated with the shade gradient. Some species are positioned near the centre of the triplot and therefore they are not well represented by the ordination plot. These species include the two submerged species, *Potamogeton pectinatus* and *Elodea canadensis*. This may reflect the wide range of conditions in which these two species were found in the 17 rivers. Both species were found to have wide tolerances with respect to sediment nutrient concentrations (MDA, Figure 3.10).

The positioning of the sites on the ordination plot highlights the importance of catchment scale factors in determining the macrophyte community composition at a particular site. There is a clear grouping of chalk streams (Allen, Avon, Dun, Hiz, Itchen, Whitewater, Wylfe and possibly the Frome) associated with the BFI gradient. Rivers with a more impermeable geology, Dove, Eden and Tove, are negatively correlated with BFI. The River Waveney and the River Test appear to be more closely correlated with sediment total nitrogen values than this BFI gradient. This may reflect the large quantities of organic material retained within the sediments of plant stands in these two rivers. Finally, the rivers Loddon, Rhee and Wey are associated with the shade gradient, further reinforcing the view that catchment and reach scale characteristics may be of greater importance than sediment fertility in determining macrophyte community composition.

The relationships between the nutrient status of the sediment and the macrophyte communities were considered by including the sediment variables in the RDA as supplementary variables. These supplementary variables are displayed in Figure 3.11. The position of the sediment variables reflects the associations between variables. Sediment total nitrogen and organic carbon are evidently closely correlated and therefore, the inclusion of total nitrogen as a significant variable in the forward selection RDA would cover any variation explained by organic carbon. Figure 3.11 also shows a correlation between percent silt-clay and total nitrogen, that was less obvious in earlier analyses. The sediment phosphorus variables (total phosphorus and inorganic phosphorus) are closely correlated (see Section 3.2) and are opposite the arrow for BFI, reflecting the higher sediment phosphorus concentrations in clay streams relative to base-flow dominated systems. This is a result of the finer sediments present and the typical land-use of the clay catchments studied (mainly intensive arable). WTP (weighted TP) appears as a combination of total phosphorus and percent silt-clay according to the manner in which it was calculated (as the product of the two other values).

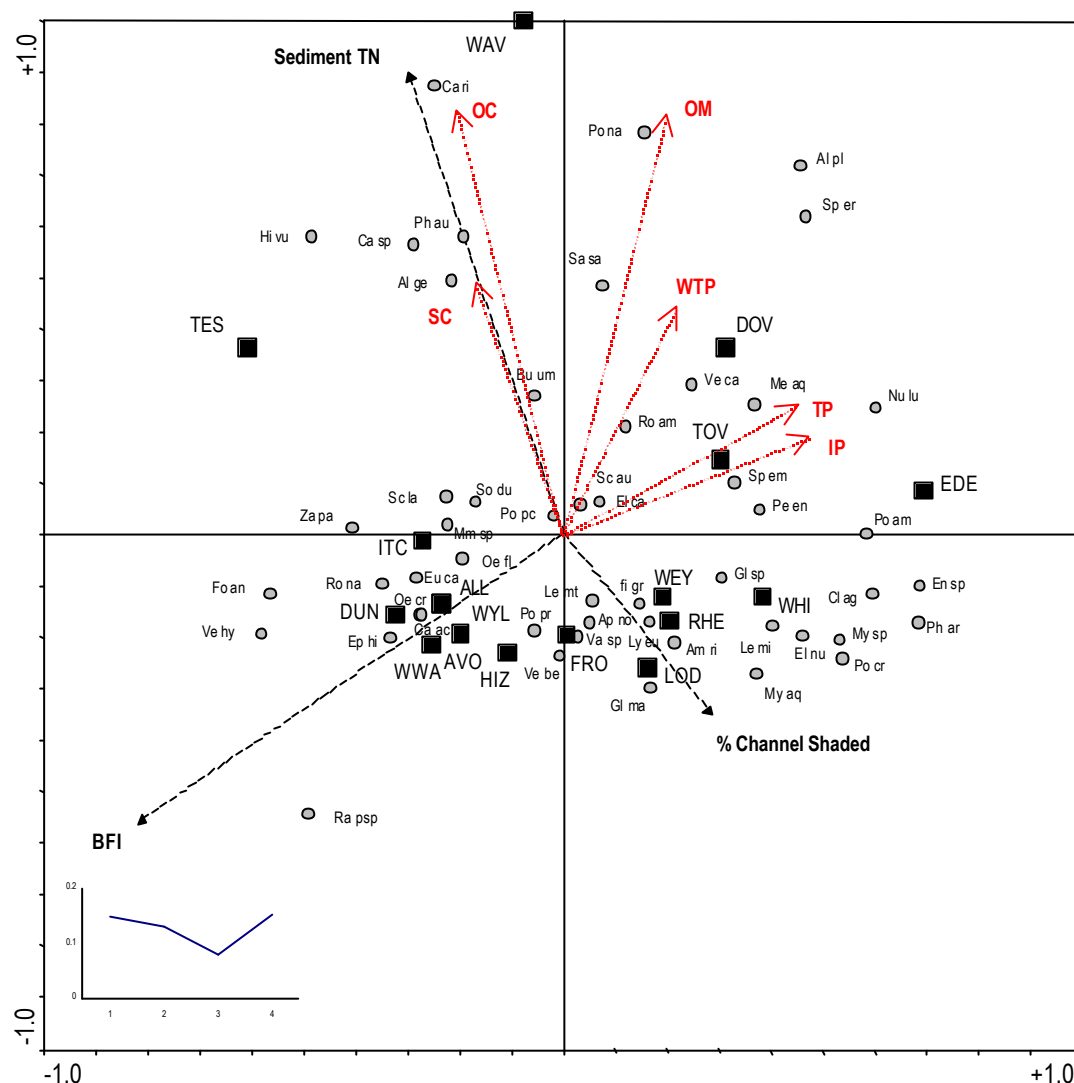


Figure 3.11 RDA triplot showing statistically significant environmental variables (as determined by forward selection) as dashed arrows and sediment variables (non-significant and included as supplementary variables) as dotted arrows. Sites are displayed as squares and species are shown as circles. Scaling is focussed on inter-species correlations and species scores are divided by their standard deviations. The first two ordination axes together explain 27.9% of the variation in species data.

Key : Va sp – *Vaucheria* spp., En sp – *Enteromorpha* spp., Cl ag – *Cladophora* agg. fi gr – filamentous green algae, Pe en – *Pellia endiviifolia*, Am ri – *Amblystegium riparium*, Fo an – *Fontinalis antipyretica*, Ap no – *Apium nodiflorum*, Ca sp – *Callitriche* spp., Ep hi – *Epilobium hirsutum*, Eu ca – *Eupatorium cannabinum*, Hi vu – *Hippuris vulgaris*, Ly eu – *Lycopus europaeus*, Me aq – *Mentha aquatica*, My sp – *Myosotis* spp, My aq – *Myosoton aquaticum*, Mm sp – *Myriophyllum spicatum*, Nu lu – *Nuphar lutea*, Oe cr – *Oenanthe crocata*, Oe fl – *Oenanthe fluviatilis*, Po am – *Polygonum amphibium*, Ra psp – *Ranunculus penicillatus* subsp. *pseudofluitans*, Ro am – *Rorippa amphibia*, Ro na – *Rorippa nasturtium-aquaticum*, Sc au – *Scrophularia auriculata*, So du – *Solanum dulcamara*, Ve be – *Veronica beccabunga*, Ve ca – *Veronica catenata*, Ve hy – *Veronica* hybrid, Al pl – *Alisma plantago-aquatica*, Al ge – *Alopecurus geniculatus*, Bu um – *Butomus umbellatus*, Ca ac – *Carex acutiformis*, Ca ri – *Carex riparia*, El ca – *Elodea canadensis*, El nu – *Elodea nuttallii*, Gl ma – *Glyceria maxima*, Gl sp – *Glyceria* spp, Le mi – *Lemna minor*, Le mt – *Lemna minuta*, Ph ar – *Phalaris arundinacea*, Ph au – *Phragmites australis*, Po cr – *Potamogeton crispus*, Po na – *Potamogeton natans*, Po pc – *Potamogeton pectinatus*, Po pr – *Potamogeton perfoliatus*, Sa sa – *Sagittaria sagittifolia*, Sc la – *Schoenoplectus lacustris*, Sp em – *Sparganium emersum*, Sp er – *Sparganium erectum*, Za pa – *Zannichellia palustris*

4. DISCUSSION

4.1 Sediment Characteristics and Variability

4.1.1 Total phosphorus

The degree of spatial variability in sediment total phosphorus concentrations within an individual river reach will be a consequence of localised sedimentation or erosion and the presence or absence of plant patches which will modify flow and sedimentation (Sand-Jensen and Mebus, 1996; Sand-Jensen, 1998). A high degree of spatial variability in sediment total phosphorus concentrations is common in aquatic systems. Sediments of a subtropical shallow eutrophic lake were found to be highly variable with respect to chemical composition in a spatial dimension, yet temporal variability was minimal (Arshad *et al.*, 1988). In the Pembina River, Canada, there were significant differences in exchangeable phosphorus concentrations between sites with different sediment sizes (Chambers *et al.*, 1992).

4.1.2 Inorganic phosphorus

The highest and lowest mean inorganic phosphorus concentrations for the 17 rivers coincided with the highest and lowest mean total phosphorus concentrations. As inorganic phosphorus constitutes a proportion of total phosphorus one would expect a close correlation between sites with high sediment inorganic phosphorus concentrations and high total phosphorus concentrations. However, the proportion of sediment total phosphorus that is organic will vary with the nature of the sediments and the source and form of phosphorus entering the sediments. For example, in *Ulva* sp. and *Zostera* sp. beds of Venetian lagoons the organic fraction of total phosphorus was approximately 23-24% giving an inorganic proportion of 76-77% (Sfriso and Marcomini, 1999). In contrast, a sequential extraction scheme estimated an inorganic fraction in River Garonne sediments of around 47% of total sediment phosphorus (Fabre *et al.*, 1996). The inorganic phosphorus in the river sediments is likely to comprise phosphorus loosely bound to sediment particle surfaces and bound to other elements (Fe, Al and Ca) as minerals. Differences between total and inorganic phosphorus concentrations reflect the variable quantities of organic phosphorus fractions within river sediments (cf. De Groot and Golterman, 1993).

4.1.3 Total nitrogen

It is clear from the total nitrogen contents of the sediments (Figure 3.2a) that nitrogen is a small component of the sediment with the highest concentration measured being 0.84%. Sediment nitrogen concentrations of 31 rivers in north-east England were of this order (mean 0.06%, range <0.001–0.51%) (Garcia-Ruiz *et al.*, 1998). These values are also similar to the mean total nitrogen contents equivalent to 0.143% and 0.082% found in *Ulva* and *Zostera* dominated lagoons, respectively (Sfriso and Marcomini, 1999) and to the range of 0.1% to 4% suggested by Keeney (1973) for surface sediments in sediment-water systems in general. The forms of nitrogen that constitute this total nitrogen within the sediments of the 17 rivers will depend on whether the sediments are oxidised (nitrogen is likely to be in the form of nitrate) or anoxic (ammonia forms dominate) (Forsberg, 1989). However, it is likely that much of the nitrogen present is organic in form (Keeney, 1973).

4.1.4 Organic carbon

Organic carbon constitutes a much larger proportion of riverbed sediments than phosphorus or nitrogen forms and ranged from 0.20% to 13.96% in the 17 rivers. Sediments from two lagoons had organic carbon contents of similar magnitude (0.94% and 0.73%) (Sfriso and Marcomini, 1999). The range of sediment organic carbon contents in Lake Monroe, a subtropical shallow eutrophic lake, were from 0.1% to 18.2% (Arshad *et al.*, 1988). The relative proportions of C, N and P in the sediments will be influenced by the source of the nutrients, much of which will be organically-derived. C, N and P occur in living plant material in relatively consistent ratios; in algal tissue ratios of C:N:P are consistently 106:16:1 (the Redfield ratio, Redfield *et al.*, 1963).

4.1.5 Organic matter

The organic matter content of the river sediments, as determined by ignition, will be dependent on both the retention capacity of the sediment and the rate of microbial degradation. The organic matter content for some of the samples collected during this study is considerably higher than the values recorded for sediments in Lake Kalgaard which were 0.3% -5.1% (Sand-Jensen and Søndergaard, 1979). However, this lake was oligotrophic and may be expected to be less productive than the more nutrient-rich systems considered here. The decomposition of organic matter in aerobic systems has been shown to be almost complete (Goldshalk and Wetzel, 1976). Organic matter is therefore unlikely to accumulate in flowing waters, such as the streams of this study, as dissolved oxygen concentrations are likely to be fairly high. However, within dense plant stands, there is considerable potential for anoxia to persist. The organic material that accumulates within these areas may not be completely decomposed, and organic compounds will steadily increase until the plants die back, and material is either washed out, begins to break down or becomes incorporated into the sediment. This may explain the high organic matter contents of many of the samples that were collected from within plant stands.

4.1.6 Percent silt/clay

Particle size, shape and density are acknowledged to play important roles in determining the chemistry and ecology of sediments (Maher *et al.*, 1999). The percentage of fine material in sediments will determine the surface areas available for the binding of elements, the capacity of the sediment for pore water and organic matter, and the degree of exchange between sediments and water. Consequently, the proportion of the sediments that is silt or clay (<63µm) will have an influence on many other sediment characteristics and sediment processes. The sandy sediments observed in the River Avon would be expected to result in a smaller surface area than finer sediments, and thus less binding capacity (cf. Chambers *et al.*, 1992; Stone and English, 1993). One would therefore expect the elemental composition of the Avon sediments to be lower than for other rivers with finer sediments; Figures 3.1a to 3.2b support this expectation.

4.1.7 Sediment variability and sampling effort

The results of the ANOVA tests (Section 3.1.7) indicate that mean values for each parameter (total and inorganic phosphorus, total nitrogen, organic carbon, organic matter and percent silt/clay) in each river were significantly different. This suggests that even within a relatively small geographical region, and across a fairly narrow range of trophic status, river sediments are highly variable and in-channel variability is secondary to catchment differences (influences such as geology and land-use).

The differences in total phosphorus are likely to be attributable to differences in the presence of humic substances, metals and calcium carbonate which are able to bind phosphorus in the sediment. Differences in phosphorus inputs to the river channel may also be a key factor. Differences in the sediment content of organic matter, organic carbon and total nitrogen are possibly related to the relative importance of allochthonous and autochthonous material reaching the river channel; a direct result of in-channel productivity and catchment land-use. Finally, inter-river differences in the proportion of fine material in the sediments will reflect differences in hydrology, macrophyte production and the associated trapping of fines. The size of sediment particles within plant stands will also differ with the macrophyte species, as different species affect flow and sedimentation patterns differently depending on their morphology (Sand-Jensen, 1998).

Figures 3.1 to 3.3 of sediment parameters suggest that the Waveney is distinct from the other rivers sampled. The sediments of the Waveney are very fine and associated with large amounts of decaying organic matter. This organic matter and the fine sediments may explain the relative high percent organic carbon and total nitrogen concentrations of the sediment. The Waveney was characterised by very high macrophyte cover and biomass at the time of sampling. The dense macrophyte stands will trap organic material, and senescent plant material will be decomposed *in situ* as there is little flow within stands to transport material downstream and out of the reach. Consequently, there is likely to be a great deal of decomposition occurring *in situ* and this will result in high concentrations of organically-derived chemicals such as nitrogen and carbon.

The analysis indicated that all six sediment parameters display a wide range of values across the 17 rivers. This degree of spatial variability in the six sediment characteristics has implications for the number of samples required in future studies of river sediments. It is evident from the estimates given in Table 3.2 that in many lowland rivers an unrealistic number of samples would be required to sample the sediments of a 100m reach with only 10% sampling error. In many rivers over 100 samples would be required per 100m reach and to sample sediment organic matter in the Avon and silt-clay in the Hiz to this specified level of accuracy would require over 500 samples. It is obviously not possible to sample to this degree in most studies due to time and cost constraints and thus a greater margin of error would have to be accepted. Additionally, a well directed sampling rationale designed with the specific aims of the particular project in mind could further reduce the influence and importance of this sampling error.

The analysis of the variability of sediment characteristics both within and between the 17 rivers does not necessarily represent the most appropriate way of investigating such phenomena. The way in which sediment samples were collected was optimised to provide data on the relationships between macrophyte species and sediment characteristics, and this is not completely compatible with providing information on sediment variability. However, the data do give a clear indication of the degree of heterogeneity in the riverbed sediments in both vegetated and unvegetated areas (though chiefly in the former areas) and provide a useful starting point for future investigations of sediment variability.

4.2 Associations Between Sediment Parameters

4.2.1 Relationships between total and inorganic phosphorus

The cubic relationship between total phosphorus and inorganic phosphorus suggests that sediments in these 17 rivers with the highest total phosphorus concentrations are phosphorus-rich because of geologically-derived mineral phosphorus or because of an inorganic phosphate loading. Sediments from Lake Erie also showed a high degree of association ($r=0.98$) between total phosphorus and inorganic phosphorus (determined by a sequential extraction procedure) (Williams *et al.*, 1976). The relative contributions of various phosphorus fractions to total phosphorus in lake and river sediments has been shown to vary considerably, both over spatial and temporal scales (Arshad *et al.*, 1988; Moutin *et al.*, 1988; Stone and English, 1993). This variability will reflect variability in water column phosphorus concentrations, seasonal variation in porewater phosphorus concentrations (Søndergaard, 1990); adsorption-desorption and mineralisation rates, and patterns of deposition and settling of fine particles and organic material. Baldwin (1996) discovered “*at least a partial decoupling between inorganic sediment composition and phosphorus speciation*” determined by a SEDEX sequential extraction procedure, which was attributed to the importance of organic and biogenic forms of phosphorus in the sediment. Similarly, the differences between total and inorganic phosphorus illustrated in Figure 3.4 may reflect the relative contributions of organic phosphorus forms mediated by the specific environmental conditions of the sediments and overlying macrophyte vegetation.

4.2.2 Relationships between phosphorus forms and total nitrogen

The absence of a relationship between nitrogen and phosphorus may reflect their different sources and behaviour in aquatic systems. Nitrogen is dynamic and soluble, and thus sediment concentrations will be highly variable depending on rates of nitrification and denitrification and movement from interstitial water to overlying waters. By contrast, phosphorus tends to be retained in the sediments adsorbed to particle surfaces or associated with metals and calcium carbonate. Thus, there is a tendency for phosphorus to accumulate in the sediments whilst nitrogen concentrations will fluctuate and reflect conditions over shorter temporal scales (cf. Holtan *et al.*, 1988; Heathwaite, 1993).

4.2.3 Relationships between phosphorus forms and organic carbon

Organic carbon will be associated with organic material that reaches the sediment and is decomposed by the action of micro-organisms. By contrast, it is evident that the phosphorus in sediments of the 17 rivers was both inorganic and organic in form (Section 4.1.2). Thus, organic carbon may be related to the organic phosphorus fraction, as strong associations between organic carbon and organic phosphorus were found in Lake Erie sediments (Williams *et al.*, 1976). As specific organic phosphorus fractions were not determined during this study, such relationships were not apparent.

4.2.4 Relationships between phosphorus forms and organic matter content

Rose (1995) also failed to find relationships between sediment organic matter and sediment phosphorus in samples from the River Welland (UK) and Morava (Czech Republic). As outlined above, any relationship between organic matter and organic phosphorus fractions derived from

decaying plant material are likely to be obscured by the proportional dominance of inorganic and other organic phosphorus fractions. However, organic matter may be expected to exert some control over sediment phosphorus concentrations as in a subtropical lake the capacity of the sediment for phosphorus retention was enhanced by organic matter (Arshad *et al.*, 1988). This may be attributable to the presence of iron and aluminium compounds in organic material (Stone and English, 1993). However, according to Hesse (1973), adsorption of phosphorus in sediments may be depressed by the presence of organic matter, although this is likely to depend on the nature and composition (particularly the metal content) of the organic material.

Conversely, high phosphorus levels could lead to increased organic matter production and retention if macrophyte productivity was significantly increased; for example, the retention of organic matter in the Bere stream by *Ranunculus penicillatus* var. *calcareus* stands, observed by Dawson (1981). This link between phosphorus-enhanced productivity and organic matter differs for macrophytes and phytoplankton. Macrophytes need five times less nitrogen and phosphorus per unit biomass production than phytoplankton. Therefore, for a given quantity of nutrients, macrophytes will build up as much as five times the biomass of phytoplankton (Golterman, 1995). Relationships between organic matter and phosphorus, particularly phosphorus release, may depend on the trophic status of the river. In eutrophic lakes in Germany, mineralisation of organic matter seemed to be driving phosphorus release whereas in oligotrophic lakes release of phosphorus was through the mobilisation of iron and manganese bound phosphorus by burial of oxic surface sediments into deeper anoxic zones (Gonsiorczyk *et al.*, 1998).

4.2.5 Relationships between phosphorus forms and percent silt-clay

Many studies have found a relationship between the phosphorus concentration of sediments and the particle size distribution (cf. Stone and English, 1993). Chambers *et al.* (1992) found that exchangeable phosphorus in sediments from the Pembina River, Canada, was highest in fine sediments and markedly lower in sandy sediments. A study of phosphorus dynamics in the River Wey (one of the 17 rivers of this study) also found higher total phosphorus contents in a fine sediment site (House and Denison, 1998). A high clay, silt or Fe(OOH) content in sediments results in a large phosphorus-binding capacity (Golterman, 1995) as particle size is negatively related to specific surface effects (Hesse, 1973). The increased temporal variability of phosphorus concentrations in sandy sediments is likely to be a result of greater sediment porosity (Slomp *et al.*, 1998) and the associated exchange of porewater with overlying waters. In a study of the distribution of phosphorus amongst the silt and clay fractions, Stone and English (1993) found total phosphorus to be most abundant in particles of 2µm and to decrease with increasing grain size. As iron, aluminium and manganese were also most abundant in this size fraction but calcium was fairly constant throughout size ranges, the authors suggested that phosphorus in the smaller fractions was bound to metal oxides.

Table 3.3 reveals no such association in the data presented here. Similarly, total and inorganic phosphorus were only weakly associated with the mean particle size of the silt and clay fractions of sediment from Lake Erie (Williams *et al.*, 1976). However, Figure 3.4 shows that although there is a wide scatter of samples, there are samples of coarse sediments which appear to follow a linear relationship with total phosphorus. It is possible that, in coarse sediments low in phosphorus, the percentage of fine material controls the amount of phosphorus. Where silt and clay contents are

higher, the relative proportion of silt to clay particles in the finest fraction may be important and relationships with phosphorus may not be evident without further separation of the fraction less than 63µm. Equally, higher phosphorus concentrations could overwhelm any relationship with silt-clay. The absence of a relationship may be the result of the method used to determine phosphorus in the sediment samples as phosphorus was only determined for material that had been ground to pass through a 250µm sieve. Additionally, no attempt was made to separate the fractions of less than 63µm, and it was within this smallest fraction that Stone and English (1993) found relationships between phosphorus content and particle size.

4.2.6 Relationships between total nitrogen and organic carbon

The analysis indicated a strong association between these two variables. Both total nitrogen and organic carbon are required by and present in living plant tissue, and total nitrogen and organic carbon in sediments have their origin in decaying organic material. The decomposition of this material through microbial processes is the main control on the turnover of nitrogen and carbon in aquatic systems (Forsberg, 1989). The relationship between total nitrogen and organic carbon is probably mediated by the organic matter content of the sediment, and should result in relationships between the two parameters and organic matter.

4.2.7 Relationships between total nitrogen and organic matter

There was also a strong correlation between total nitrogen and organic matter although the plot (Figure 3.4) indicated considerable scatter in the relationship. This scatter may reflect the dynamic nature of nitrogen and the variable rate of its release from organic matter. A possible explanation for the absence of a linear or logarithmic relationship between total nitrogen and organic matter may be loss of nitrogen from the sediments due to variation in rates of denitrification. The rate of denitrification in rice fields in the Camargue, France, was seen to increase with increasing organic matter content (Minzoni *et al.*, 1988). Similarly, the highest denitrification rates in 30 rivers in north-east England were found in organically-polluted lowland rivers where sediments tended to be covered by decomposing algal or other organic debris (Garcia-Ruiz *et al.*, 1998). Organic material within the sediment may therefore influence total nitrogen contents through both supply of nitrogen via decomposition and through enhancement of denitrification.

4.2.8 Relationships between total nitrogen and percent silt-clay

There was an association between the nitrogen content of sediments and percent silt-clay content; however, there was a wide scatter of points (Figure 3.4) and certain sites appeared distinct, not following the general relationship. Therefore, if there is any general relationship between the particle size of sediments and total nitrogen, it is not universal across the 17 rivers. There have been few studies of the nitrogen content of sediments but, in North Sea continental margin sediments, nitrogen contents were higher in silty sediments than in sandy sediments (Slomp *et al.*, 1998). Possible links between total nitrogen and the particle size of sediments are likely to be controlled by the retention of organic material, sediment porosity and the degree of exchange between interstitial and overlying waters and surface area for bacterial colonisation.

4.2.9 Relationships between organic carbon and organic matter

Relationships between organic carbon and organic matter are expected as organic carbon is often calculated through the determination of organic matter through the loss-on-ignition (LOI) method and subsequent conversion using the Von Bemmelen factor (1.724) which assumes 58% of organic matter is organic carbon (Sutherland, 1998). Figure 3.4 shows that there is no simple relationship between organic carbon and organic matter, and this is probably a result of assumptions inherent to the LOI method and the variable nature of river sediments (Sutherland, 1998). Thus, the use of a LOI method in river sediments of this type is unlikely to give accurate results.

4.2.10 Relationships between organic carbon and percent silt-clay

The relationship between organic carbon and percent silt-clay was similar in form to that between total nitrogen and percent silt-clay (Section 4.2.8), reflecting the association between nitrogen and carbon (Section 4.2.6). Organic carbon content in North Sea continental margin sediments was considerably higher in silty than sandy sediments (Slomp *et al.*, 1998); this is possibly related to the amount of organic matter in finer sediments and the lower porosity of fine sediments aiding the retention of dissolved organic carbon.

4.2.11 Relationships between organic matter and percent silt-clay

The relationship between these two variables possibly reflects the retention capacity of the sediment for organic material. Organic matter increases with increasing particle size because interstitial spaces increase in size and frequency. However, there is likely to be an upper-limit to this relationship as beyond a certain particle size there is an increased likelihood of wash-out of organic matter from the sediments. This upper threshold may explain the breakdown of the relationship beyond approximately 50% silt-clay content in Figure 3.4.

4.2.12 Conclusions on relationships between sediment parameters

The preceding sections indicate that the strongest relationships in sediments of rivers analysed are between the two phosphorus measurements (total phosphorus and inorganic phosphorus); between organic matter and compounds derived from this material (total nitrogen and organic carbon); and between these organic matter variables and the physical structure of the sediment (total nitrogen, organic carbon, organic matter and percent silt-clay). Many of these relationships are intuitive and may be expected, but the analysis has indicated that the nature of the relationships varies with the river and the nature of the sediments (for example, the relationship between total phosphorus and inorganic phosphorus). It is also likely that, as most sediments were sampled from vegetated patches, these relationships will be influenced by the action of plant-mediated processes. In general terms, it seems that sediment nutrient status (phosphorus, nitrogen and carbon) may be determined by the composition of the sediments (organic component and particle size distribution). In turn, the composition of the sediments is likely to be determined by channel and catchment scale processes.

4.3 Relationships Between Water Chemistry and Sediment Parameters

Sediment phosphorus concentrations were significantly correlated with mean water column ammonia concentrations (total phosphorus and inorganic phosphorus) and with mean water column orthophosphate concentrations (total phosphorus and inorganic phosphorus). The positive correlations may simply reflect that the most nutrient rich streams have both high concentrations of water column nutrients and nutrient rich sediments. The correlations between water orthophosphate and sediment total phosphorus and inorganic phosphorus may be the result of a direct causal equilibrium mechanism operating. However, the relationships between ammonia and sediment phosphorus concentrations are unlikely to be direct. Figure 3.5 shows that there is considerable scatter in these relationships.

There were only two other significant correlations between sediment characteristics and water chemistry variables: organic carbon and organic matter were both significantly correlated with water column pH. These correlations may reflect the differences in the clay and chalk streams as pH will describe a gradient from base-rich chalk streams through to more acidic or circumneutral streams on other geological types. Clay streams tend to have finer sediments with greater potential for the retention of organic particles hence the higher organic matter and organic carbon contents (Section 3.1). The absence of significant correlations between mean sediment total nitrogen concentrations and water chemistry variables may be due to the dynamic nature of nitrogen within the sediment and exchange across the sediment-water interface (Keeney, 1973). Additionally, the analysis of correlations between different sediment characteristics (Section 3.2) suggests that a large proportion of total nitrogen in the sediment has its origin in decaying plant material. Thus, water column nitrogen concentrations would have no impact on this proportion of sediment total nitrogen.

Other studies have failed to find significant relationships between water and sediment chemistry (cf. Arshad *et al.*, 1988; Chambers *et al.*, 1992; Rose, 1995) despite the hypothesis, generated from the study of lake systems, that the sediment and water concentrations are in a state of dynamic equilibrium (cf. Holtan *et al.*, 1988). Chambers *et al.* (1992), discussing data collected from the Pembina River, Canada, speculated that, in flowing waters, the gradients in nutrient concentrations across the sediment-water interface would be less predictable and thus, equilibrium may not be achieved. In the Pembina River, although sediment chemistry differed between sites, there was no significant difference between water column nutrient concentrations suggesting sediment chemistry has little impact on the water column. Evidently, the relationship between water column and sediments will be more complex in flowing waters and any equilibrium may only be evident in data collected over a long period or from rivers with limited flow variability. The influence of other factors such as biotic (plant nutrient uptake and release, bioturbation) and abiotic (temperature and redox change, discharge) processes will further confound the complex interaction between sediments and waters across an inherently dynamic interface. General relationships indicating, for example, that eutrophic sites have both nutrient-rich sediments and waters may be derived from data such as that collected during this study. However, the concept of equilibrium between water and sediment chemistry requires further investigation and the situation of nutrient-rich water associated with nutrient-poor sediments or vice versa should be considered, possibly through the use of an experimental approach.

4.4 Principal Components Analysis

The main conclusion to be drawn from the PCA is that there is a clear separation of sites, and indeed rivers, on the basis of large-scale factors, such as geology. The importance of BFI highlights the influence of groundwater, the dominance of which leads to stability of the flow regime; low temperature variability; low variation in water chemistry determinants; low suspended sediment concentrations; and high water clarity (Sear *et al.*, 1999). These are characteristics of chalk streams with a particular character and ecology. A survey of chalk and clay streams, with similar stream power, from Environment Agency River Habitat Survey data indicated that chalk streams had infrequent in-channel sediment storage areas and a lack of fines due to low rates of sediment transport, whereas clay streams had more sediment storage areas (Sear *et al.*, 1999). This may explain the positioning of the chalk streams, to the left of the first PCA axis which is positively correlated with all sediment variables. The survey by Sear *et al.* (1999) also indicated that groundwater-dominated rivers had a particular geomorphology with larger width:depth ratios than clay streams. This wider, shallower cross-sectional form may be expected to reduce channel shading from bank-side vegetation as indicated in the PCA biplot.

4.5 Macrophyte Species and River Sediment Characteristics

4.5.1 Sediment phosphorus and macrophyte tolerances

As outlined in Chapter One many studies have found sediments to be the major source of phosphorus for macrophytes (cf. Barko *et al.*, 1991) and it has been stated that sediments are the major source of nutrients for macrophytes in rivers (Chambers *et al.*, 1989). This suggests that some degree of relationship between sediment phosphorus and macrophyte species may be expected. The view that species have different trophic requirements (Holmes and Newbold, 1984) and respond differently to sediment nutrient supply (Denny, 1972), would suggest that across a number of rivers, there should be some evidence of different species responses to sediment phosphorus. That is, some species will be associated with low concentrations of sediment phosphorus and others will be associated with higher concentrations. Denny (1980) suggested that there would be a continuum of species in aquatic environments from those which depend exclusively on shoot uptake of nutrients through to those which depend on sediment nutrients alone. Therefore, there may be species which do not respond to sediment nutrients and will therefore show no particular preference for sediments of a particular nutrient status.

The species associated with high sediment total phosphorus concentrations (*Nuphar lutea*, *Potamogeton natans*, *Sagittaria sagittifolia*, *Sparganium emersum* and *Sparganium erectum*) are characteristic of silt and clay sediments and sluggish flows. But these sediments would be expected to be the most nutrient-rich, and therefore, it is difficult to distinguish a species effect from a river effect. In contrast *Myriophyllum spicatum* appears to be associated with sediments with relatively low total phosphorus concentrations. *Myriophyllum spicatum* grown in a two-chamber experiment was found to derive most phosphorus from the sediment rather than water (Bole and Allan, 1978), so the species would be expected to respond to different levels of phosphorus in the sediment. In the UK *Myriophyllum spicatum* is characteristically associated with a range of substrates, but is “more frequent over sand and gravel than over fine clay or silt” (Preston and Croft, 1997). As sand and gravel sediments characteristically have lower phosphorus concentrations than silt and clay sediments (Section 4.2.5), *Myriophyllum spicatum* will therefore be expected to

occur on sediments of fairly low phosphorus status even within in eutrophic systems where the species is often found.

Figure 3.7a shows that *Potamogeton pectinatus* is associated with higher mean sediment total phosphorus concentrations than *Ranunculus penicillatus* subsp. *pseudofluitans* which is consistent with the established view that the former species is more tolerant of eutrophication than the latter (see trophic ranking in Holmes, 1995). However, both species are found on a similar range of total phosphorus concentrations, and *P. pectinatus* is not associated with the highest sediment total phosphorus concentrations recorded during this study. This possibly arises because either this study did not sample the species on the most eutrophic sediments or the species shows a greater response to the trophic status of the water column rather than the sediments.

The differences noted between the two *Elodea* species are consistent with the findings of Eugelink (1998) who found that the growth rate of *Elodea nuttallii* was greater than *Elodea canadensis* in phosphorus uptake experiments. The differences were attributed to the fact that *Elodea nuttallii* sourced more of its phosphorus from the sediments and was able to over-winter as prostrate shoots with green leaves. This allowed *Elodea nuttallii* to grow faster earlier in the year and gain a competitive advantage over *Elodea canadensis* which dies back at the onset of cold temperatures and must grow from underground stems when temperatures increase. *Myriophyllum spicatum* and *Potamogeton perfoliatus* were both found on sediments with very low inorganic phosphorus concentrations.

It is difficult to determine the sediment phosphorus requirements of different species on the evidence of Figures 3.7a and 3.7b because: there is considerable overlap between the ranges of species; sample numbers differ for species; and the site effect cannot be excluded completely with only 17 rivers (some species were sampled only in two rivers and both of these rivers may have had sediments with similar phosphorus concentrations). In addition to these sampling effects, there are a number of other reasons why clear relationships between species and sediment phosphorus concentrations are absent.

First, relationships between macrophytes and sediment phosphorus concentrations often indicate a biomass response to phosphorus concentration (cf. Rattray *et al.*, 1991). In one of the few studies of nutrient uptake by macrophytes in flowing waters, biomass and shoot density were consistently greater for plants growing in high nutrient sediments but showed no significant response to water phosphorus or nitrogen levels (Chambers *et al.*, 1989). A study of sediment phosphorus concentrations and macrophyte biomass in two rivers in the UK and Czech republic found a relationship ($R^2=0.796$) (Rose, 1995); this was with only ten data points and so the conclusions must be treated cautiously. Frequently, macrophyte response to sediment fertility is manifest through redistribution of biomass with root:shoot ratio increasing in nutrient-poor sediments (increasing the root surface area and thus improving uptake) (Barko *et al.*, 1991). This response of root:shoot biomass differs between macrophyte species (Barko and Smart, 1981).

Second, is the problem of selecting a representative phosphorus measurement to link to macrophytes. There is an outstanding need for an analytical technique that extracts only the phosphorus available to macrophytes from the sediment. Possible bioavailable fractions are discussed in Chapter Three of Clarke (2000). It is unlikely that either total phosphorus or inorganic phosphorus accurately reflect the phosphorus that is important to macrophytes, and there is no

consistent relationship between total phosphorus and quantity of phosphorus available for uptake (Golterman *et al.*, 1983). Additionally, no attempt has been made to determine interstitial water phosphorus concentrations which may represent an important nutrient source for macrophytes. Agami and Waisel (1986), in a review of the sources of phosphorus for macrophytes, argued that rates of phosphorus uptake by plants would be more a function of phosphorus chemistry and availability and less a result of the characteristics of the absorbing organ. This suggests that differences in phosphorus fractions may be more important to macrophyte communities than the differences in species themselves. Jensen *et al.* (1998) observed dissolution of the carbonate matrix and resultant release of phosphorus within the rhizosphere of *Zostera* beds in Bermuda (see Section 1.2.1). If this phenomenon is widespread, there is the possibility that macrophytes in calcareous streams are able to capitalise on mineral forms of phosphorus that conventional ideas on bioavailability would suggest to be locked within the sediment. This hypothesis remains untested.

Third, it is possible that sediment phosphorus responses are of less importance in the structuring of macrophyte communities than other factors. For example, in highly turbulent flow or where there is a high suspended sediment load plant growth may not respond to nutrient increases as productivity will be suppressed by physical controls (Golterman *et al.*, 1983). Finally, differential responses to sediment phosphorus concentrations suggest that macrophyte species have distinct niches with respect to sediment phosphorus and this would manifest itself through competitive exclusion which Mainstone *et al.* (1993) suggest is the main mechanism for phosphorus impacts on macrophytes. However, such a view does not take account of the complex combination of factors which are responsible for determining macrophyte community structure in lotic waters, and assumes there are competitive interactions between macrophytes in such environments for which there is little evidence (McCreary, 1991). Although, experiments have demonstrated competition for sediment resources between *Hydrilla verticillata* and *Valisneria americana* (Van *et al.*, 1999). There may be no relationship between macrophytes and sediment phosphorus which is strong enough to exclude particular species (either within the range represented by these 17 rivers or in riverine environments in general). Little is known about the influence of nutrients on macrophytes (Golterman, 1995). The high concentrations of phosphorus in interstitial water and sediment suggest that it is unlikely that submerged aquatic macrophytes are limited by phosphorus (Barko *et al.*, 1991).

4.5.2 Sediment nitrogen and macrophyte species

Whether macrophytes obtain nitrogen from the sediments or water column is less certain than for phosphorus, and there is evidence that both root and shoot uptake occur (cf. Agami and Waisel, 1986). In flowing-waters, sediment concentrations of nitrogen and phosphorus producing maximum tissue concentrations in *Potamogeton pectinatus* were 140µg/g N and 400µg/g P (Carr and Chambers, 1998). The lower requirements for sediment nitrogen concentrations were attributed to the plants being able to source nitrogen from both water and sediment (Carr and Chambers, 1998). Similarly, transplant experiments in Lake Taupo and Lake Rotorua, New Zealand, indicated that, although *Myriophyllum triphyllum* and *Lagarosiphon major* plants grew better and had higher tissue concentrations of phosphorus on eutrophic sediments, there were no consistent trends in tissue nitrogen concentrations with the different sediments (Ratray *et al.*, 1991).

The importance of nitrogen for macrophytes has been demonstrated in fertilisation experiments with *Myriophyllum spicatum* (Anderson and Kalff, 1986). Nitrogen, phosphorus and potassium were added to *in situ* enclosures but only nitrogen significantly affected biomass and shoot length, and no

interaction between the three nutrients was statistically significant (Anderson and Kalff, 1986). In this particular situation, natural interstitial water concentrations of nitrogen were very low in spring. Therefore, the addition of nitrogen allowed *Myriophyllum spicatum* plants in fertilised plots to begin growth earlier in the year, promoting earlier flowering and canopy formation (Anderson and Kalff, 1986). The importance of nitrogen was also apparent in experiments where *Elodea nuttallii* was grown in sediments fertilised with combinations of nitrogen, phosphorus and potassium; growth was significantly stimulated by nitrogen, nitrogen and phosphorus and all three nutrients together but no effect was seen with phosphorus and/or potassium additions (Best *et al.*, 1996). Synergistic effects between nutrients have been observed elsewhere. In experiments in which *Myriophyllum spicatum* was grown in sand and sediment, phosphate additions were seen to increase nitrate availability (Best and Mantai, 1978). Different forms of nitrogen are likely to be related to macrophyte community structure and functioning in different ways and to different degrees.

Although plants take up nitrogen as both ammonium and nitrate, ammonium needs no energy for reduction (Agami and Waisel, 1986) and so is the preferred form of nitrogen for plant uptake. As ammonium is usually present in higher concentrations in the sediment than in the water, Barko *et al.* (1991) concluded that sediments were the principal source of nitrogen for macrophytes. However, Barko *et al.* (1991) conceded that this may not apply to enriched riverine systems. There is also evidence that nitrogen may be depleted from the sediments more rapidly than phosphorus, as pools of ammonium in the sediment interstitial water appear to be buffered by smaller exchangeable pools than those for phosphorus (Barko *et al.*, 1991). Thus, nitrogen may be the limiting nutrient rather than phosphorus and many submerged macrophyte communities. Possible depletion of nitrogen, phosphorus and potassium in sediments was investigated by growing *Hydrilla verticillata* plants on sediments that had been previously planted and those that had not (Barko *et al.*, 1988). *Hydrilla verticillata* biomass was reduced to a third on sediments that had previously supported plants and nutrient uptake was reduced to 26% (N), 26% (P), and 38% (K) of uptake on sediments that had not been planted. Furthermore, two growth periods resulted in sediment concentrations of nitrogen and phosphorus being reduced by 95% and 36%, respectively, but exchangeable potassium concentrations being increased by 32% (Barko *et al.*, 1988).

Differences in the ability of species to assimilate nitrogen species, as well as a possible toxic effect of high ammonium concentrations, have been recorded. Dendène *et al.* (1993) found that three *Elodea* species were affected by high concentrations of ammonium in the water column; whereas the net photosynthesis of *Elodea nuttallii* was stimulated, that of *Elodea canadensis* was inhibited whilst the net photosynthesis of *Elodea ernstiae* was unaffected. Other experiments with *Elodea nuttalli* and *Elodea canadensis* at different water nitrogen concentrations indicated that both species preferentially took up ammonium over nitrate and were negatively affected by nitrogen concentrations greater than 4mg l⁻¹ (Ozimek *et al.*, 1993). However, the relative growth rate of *Elodea nuttallii* was consistently greater than that of *Elodea canadensis* (Ozimek *et al.*, 1993). The differences between the two species may be attributable to the lesser competitive ability of *Elodea canadensis* (Robach *et al.*, 1995). Schuurkes *et al.* (1986) demonstrated that species characteristic of nitrogen-poor soft waters took most of their nitrogen as nitrate (63–73%) via their roots (83% of uptake), in contrast species growing in nitrogen-enriched acid waters took mainly ammonium (85–90% uptake), with shoots (71–82%) as the major uptake site.

The reciprocal relationship between macrophytes and sediments means that macrophytes are themselves able to alter the nitrogen chemistry of sediments and the water column. Macrophytes are

able to take up large quantities of nitrogen and influence denitrification by providing a continuous supply of organic matter, increasing the wet surface area for biofilms and trapping organic sediment (Faafeng and Roseth, 1993). In sediments, nitrification may occur in the rhizosphere through the transport of oxygen to roots but, in anoxic sediments, ammonification is likely to be the dominant process (Agami and Waisel, 1986). The effect of macrophytes upon the nitrogen concentrations of sediment will therefore be related to the chemistry of the sediment and the supply of organic material to the sediments.

4.5.3 Sediment organic carbon and macrophyte species

There is little evidence of the importance of organic carbon in structuring macrophyte communities. In marine lagoons, *Zostera* biomass was significantly correlated with organic carbon in surface sediments (Sfriso and Marcomini, 1999). However, in marine systems, carbon limitation is more likely than in calcareous running freshwaters of the type sampled in this study. Vadstrup and Madsen (1995) investigated the role of inorganic carbon nutrition with *in situ* enrichment experiments, adding CO₂ and HCO₃⁻ to *Elodea canadensis* and *Callitriche cophocarpa*, but found light to be the ultimate control on plant growth. Vascular plants are able to source carbon through roots (Sfriso and Marcomini, 1999) although the actual site of uptake will depend on species (Agami and Waisel, 1986). The samples collected from the 17 rivers of this study provide no evidence to suggest that macrophyte species are responding differently to organic carbon contents.

4.5.4 Sediment organic matter and macrophyte species

The relationship between macrophytes and organic matter is complicated because the plants will increase the organic matter content of the sediments through decay and trapping of organic particles; and the ability of species to build up deposits of organic matter at their base will depend on the shoot morphology and stand type (Sand-Jensen, 1998). Additionally, temporal variability will confound patterns between species and organic matter as some species reach maximal biomass earlier in the year and thus plant material is returned to the sediment at varying rates and times.

The accumulation of organic matter within plant stands may ultimately limit plant growth as organic matter has been demonstrated to have an inhibitory effect, particularly in submerged species which are unable to oxidise the rhizosphere (Agami and Waisel, 1986). Barko and Smart (1983) grew three emergent and three submerged macrophytes on sediment with added labile and refractory organic matter. The organic matter caused changes in the interstitial water chemistry reducing dissolved organic carbon, conductivity, manganese, iron and phosphate and reduced growth of the macrophytes. Consistent with the view of Agami and Waisel (1986), inhibition was greatest for submerged plants and was associated with high concentrations of soluble organic compounds in the interstitial water. The type and state of the organic matter was important with aged *Myriophyllum* sp. material (labile) actually increasing growth and refractory material having the greatest inhibitory effect (Barko and Smart, 1983).

The effect of organic matter is manifest through two possible mechanisms. First, macrophyte nutrition on highly organic sediments may be affected by the presence of phytotoxins; and, secondly, as organic matter content is intrinsically related to sediment density, nutrient uptake by macrophytes is hindered on low density organic sediments due to the long distances over which nutrients must diffuse (Barko *et al.*, 1991). It is unknown whether these organic matter effects are evident in nature as

there are a large number of species with a wide range of organic matter tolerances (Anderson and Kalff, 1988).

Without knowledge of the composition of the organic matter displayed in Figure 3.9a it is difficult to conclude whether any of the sediments have the potential to inhibit macrophyte growth. Contents are less than the 20–30% organic matter shown by Wertz and Weisner (1997) to give maximal *Potamogeton pectinatus* biomass, but many are greater than the 5% content that inhibited growth in *Hydrilla verticillata*, *Myriophyllum spicatum* and *Elodea canadensis* in Barko and Smart's (1983) study. The type of organic matter in the sediments will depend on small-scale retention within plant stands through to catchment-scale processes regulating terrestrial inputs. In-stream retention of organic material by macrophyte beds may be significant (Sand-Jensen, 1998) and may explain higher denitrification rates of vegetated sediments compared with bare sediments (Christensen and Sørensen, 1988 quoted in Sand-Jensen, 1997). Retention of material closes the nutrient cycle, making nutrients available again for macrophyte growth. The rate at which these nutrients become available again depends on the origin of the organic material. Nutrients from phytoplankton will be remineralised within days, however most macrophytes die-back during the autumn and so their material mixes with the sediment where remineralisation may take months or years (Golterman, 1995).

4.5.5 Sediment silt–clay content and macrophyte species

The physical structure of the sediments will influence nutrient availability and the ability of plants to root within the sediments. The interaction between flows of river water and sediment composition is complex and has the result that macrophytes appear to respond to both flow and sediment particle size. Species associated with finer sediments include species that grow as dense stands and thus, may accumulate large quantities of fine material (*Apium nodiflorum*, *Potamogeton pectinatus* and *Ranunculus penicillatus* subsp. *pseudofluitans*) and deeper-rooted species of sluggish channels (*Nuphar lutea*, *Sagittaria sagittifolia* and *Sparganium* spp). This is consistent with the established view that coarse sediments support genera with tough stems, roots and adventitious roots (for example, *Ranunculus* spp. and *Myriophyllum spicatum*) and finer sediments support more fragile stoloniferous plants, for example, *Callitriche* spp. and plants with buried rhizomes such as some *Potamogeton* spp. and submerged *Sparganium* spp. (Hynes, 1970). However, even in rivers with coarser sediments, silt and clay contents may be high within plant stands due to deposition through flow reduction and trapping of fine particles (cf. Petticrew and Kalff, 1992; Sand-Jensen and Mebus, 1996).

The effect of sediment particle size on macrophytes is both direct, affecting rooting and anchoring ability, and indirect as finer sediments are generally more fertile. However, once rooted, plants are able to modify the sediment and flow environment and, therefore, it is possible that the effect of sediment particle size is only important in allowing the colonisation and establishment of plants. Early experiments (see Hutchinson, 1975) compared the growth of macrophytes on sand and mud, but it is likely that differences in growth rate were a consequence of nutrient supply rather than any physical effect of particle size. More recent work has shown that three species grown at various lake depths had higher biomass when grown on sediments than when grown on sediments with 70% and 90% sand (Chambers and Kalff, 1987). However, although *Potamogeton praelongus* was more affected by sediment type than lake depth, *Potamogeton robbinsii* growth was primarily controlled by irradiance (Chambers and Kalff, 1987). Similarly, total macrophyte biomass was significantly

different among sediment classes in ten Canadian lakes with organic sediments supporting significantly more biomass than gravel sediments, and silt sediments supporting more biomass than sand sediments (Anderson and Kalff, 1988). In contrast, Wertz and Weisner (1997) found no significant difference between the average plant growth of either *Myriophyllum spicatum* or *Potamogeton pectinatus* grown on sandy and non-sandy sediments. Owing to the influence of macrophytes upon sedimentation of fine material and the intrinsic link between sediment chemistry and particle size, it is difficult to ascribe species preferences for a particular sediment type on the basis of physical structure alone.

4.5.6 Differences between vegetated and unvegetated sediments

At each of the sites sampled in this study, two sediment samples were taken (except in the Whilton where four samples were taken) from bare, unvegetated sediments. Figures 3.7-3.9 suggest that there were no obvious differences between these unvegetated sediments and the other samples from within macrophyte stands. In terms of all six sediment variables, the unvegetated sediments cover almost the whole range of values in the dataset. These results do not support the findings of research that has found that macrophytes are able to significantly alter the sediment environment, as described in Section 1.3.3 (cf. Sand-Jensen *et al.*, 1989; Petticrew and Kalff, 1992; Moore *et al.*, 1994; Wigand *et al.*, 1997; Sand-Jensen, 1998).

The data from the 17 rivers in the present study do not indicate any apparent differences between vegetated and unvegetated sediments. However, this may be a function of the high degree of sediment heterogeneity evident at the sites and that bare sediments were collected on a random basis. Additionally the small number of samples from unvegetated sediments is unlikely to be representative of the bare area of the river bed as a whole. A comparison of vegetated and unvegetated sediments is required with equal numbers of vegetated and unvegetated samples collected in a number of streams.

4.6 MDA: Statistical Testing of Macrophyte Preferences

The MDA of macrophyte and sediment data indicated that there is considerable overlap between the different species in terms of the sediments within which they are rooted. Although, *Myriophyllum spicatum* does appear distinct in the biplot all other species seem to be growing on similar sediment types. The MDA highlights the complex interactions that occur between macrophytes and sediment as discussed in the preceding Section 4.5.

4.7 RDA: Canonical Ordination of Species Data

The RDA provided little information on the role of sediment nutrients in determining macrophyte communities within the 17 rivers. However, the RDA indicates that catchment scale factors such as geology (BFI) may be more important in determining macrophyte community composition than the trophic status of water or sediment. This may reflect the limited trophic range of the 17 rivers which may all be considered meso-eutrophic.

Often, the numerous factors affecting riverine macrophyte communities lead to ordination analyses that either reflect weak gradients with respect to the environmental variables of interest, or else highlight very general gradients such as the effect of stream type and geology in the RDA presented here (cf. Carbiener *et al.*, 1990; Grasmück *et al.*, 1995; Haury, 1996; Robach *et al.*, 1996; Spink

et al., 1997). For example, in a DCA of 23 sites on the River Welland, UK, Demars and Harper (1998) derived an axis related to water course size and a second axis with no obvious gradient, leading to the conclusion that the over-riding factor affecting macrophyte species distributions within the catchment was the stream size. Demars and Harper (1998) suggested that stream size reflected other environmental factors, of direct importance, such as immediate landuse, riparian disturbance by cattle and shade. The nature of ordination techniques in reflecting all gradients of variation within macrophyte communities may therefore lead to certain factors obscuring the gradients of interest.

4.8 Sediment Nutrients as a Control on Macrophyte Communities

The results presented in this report have clearly indicated that factors other than sediment nutrient concentrations or sediment physical structure have a role in determining species distribution. Clear relationships between particular sediment conditions and the distribution of individual species may not be apparent for a number of reasons discussed below. These issues must be addressed if sediment-macrophyte relationships are to be successfully incorporated into macrophyte-based biological assessment schemes.

Possible reasons for the absence of clear relationships between sediment nutrient concentrations and macrophyte species preferences are considered further below but may be summarised as follows:

- sediment nutrient concentrations have no influence over macrophyte species distribution and/or survival;
- relationships are evident only at particular spatial or temporal scales;
- macrophytes respond to sediments in a general way and there are no clear differences between species;
- macrophytes are able to modify the sediment habitat to provide more favourable conditions;
- the influence of sediment may be secondary to other factors or mediated through the influence of other factors.

4.8.1 Spatial and temporal variability

Many of the species for which data have been collected are associated with a range of sediment nutrient concentrations (Section 4.5). The absence of clear relationships between particular species and the phosphorus and nitrogen concentrations of sediments may be a result of the spatial or temporal scales considered in this study. Alternatively, many macrophyte species may be constrained to particular sediments irrespective of the level of nutrients. For example, many species are restricted by water depth or flow velocity.

The rivers included in the sampling programme are from a limited geographical region and, as most are chalk or have a large chalk component to their geology, the rivers are likely to have similar catchments, channel geomorphology and macrophyte communities. The role of sediments may be most significant in the middle reaches of rivers or in medium-sized streams, as in spatey, upstream-reaches, sediments are coarse and bryophytes dominate the macrophyte community whereas in deep, sluggish, downstream-reaches macrophytes are limited to the margins and shallows. Thus, there are good reasons for concentrating efforts in the medium-sized lowland chalk and clay streams which support relatively diverse macrophyte communities.

The water chemistry data obtained from the Environment Agency indicate that the 17 rivers are reasonably similar in terms of trophic status. This is supported by the MTR values recorded for the sites at time of sampling, with all sites falling within the range 27 (Tove) to 42 (Allen and Whitewater). The trophic ranks of many of the species recorded were also broadly similar, with most species encountered having ranks of less than 5. Without a large dataset covering a range of conditions from oligotrophic through to hypertrophic, a turnover of species along a gradient of trophicity may not be apparent. The rivers studied may be considered mesotrophic to eutrophic and thus phosphorus and nitrogen are likely to be available in concentrations high enough to prevent nutrient limitation. However, during certain periods of the year, macrophytes may experience limitation of one or both of these nutrients due to localised resource depletion or the growth of other primary producers. Equally, there is no evidence that phosphorus and nitrogen are present in quantities that would be toxic to any macrophyte species. Thus, the exclusion of any species due to the trophic status of the rivers would have to be the result of competitive exclusion of which there is limited evidence (cf. McCreary, 1991; Wilson and Keddy, 1991). Competition between algae and macrophytes is a potential result of increased nutrient concentrations but this is most likely to be a shading effect rather than direct competition for nutrients.

Within the range of streams sampled, there are a range of sediment total phosphorus concentrations, from less than 100 µg/g to over 2500 µg/g P. It is particularly difficult to assess whether this range of sediment phosphorus concentrations is sufficient to highlight a species turnover and differential preferences, as little is known of the relative contributions of water and sediment-derived nutrients and the fractions of sediment nutrients that are important to macrophytes. Furthermore, it seems likely that, given the high degree of sediment heterogeneity at many sites, macrophyte-sediment relationships will be very localised with macrophyte survival or biomass being related to sediment patches. Data have been collected and analysed over a 100m reach where it is likely that other factors such as land-use, disturbance and shading are more important than trophic status (cf. Demars and Harper, 1998). The results of the RDA of macrophyte communities indicate that this may be the case, with BFI and shade emerging as variables which significantly explain the variation in species distributions. The role of small scale sediment microsites and patchiness in stream ecosystems is considered further in Section 4.8.3.

Alternatively, investigations of sediment-macrophyte relationships may need to consider a range of temporal scales. The survey approach has resulted in a time-integrated dataset on the response of macrophytes to sediment conditions as sites were only visited once. However, it is possible that clearer relationships between sediments and macrophytes might be evident with measurements over a longer period. For example, macrophyte biomass may be related to sediment nutrient availability over the growing season, or high sediment phosphorus concentrations may cause a shift in community composition over several years. The nature of phosphorus in sediments suggests that longer-term responses are more likely as phosphorus is sequestered in the sediment and released gradually to the water column (Agami and Waisel, 1986). Therefore, the sediments might buffer the effect of short-term fluctuations in water-column nutrients on macrophytes. The long term response of macrophytes to nutrient status has been noted elsewhere. Robach *et al.* (1995) found that the macrophyte vegetation of the Rhine floodplain was better related to three year mean values of water nutrient concentrations than monthly values, suggesting that the vegetation was integrating annual variation in water quality.

Current understanding of macrophyte response to nutrient loading is limited and thus the response of a particular species to particular sediment conditions is difficult to predict. Experiments in enclosures have shown that, where they remain in eutrophic lakes, submerged macrophytes are able to strongly buffer the effects of increased nutrient loading possibly through functioning as a sink for phosphorus and nitrogen (Balls *et al.*, 1989). The response of macrophytes to elevated sediment concentrations of nutrients might not therefore be evident. Furthermore, species with different morphological structures and life history strategies may respond differently, especially as there is evidence that emergents and submerged species will act differently as sources and sinks (Granéli and Solander, 1988). Equally, the role of sediments themselves as a potential sink and source of phosphorus (cf. Stephen *et al.*, 1997) may moderate the effect of nutrients on macrophytes. There is also the possibility that macrophyte species are chiefly controlled by other factors (see Section 4.8.4) and that many species are cosmopolitan in their tolerances to sediment nutrients.

It is possible that the influence of sediment upon macrophytes may be due to a sediment component or characteristic that was not measured in this study. First, macrophytes may be restricted to sediments of a particular physical structure, for example, species with a particular root character can only anchor in particular sediments (Haslam, 1978). There is likely to be an interdependent effect between sediment particle size and sediment nutrient concentration as fine sediments are more likely to be more fertile due to greater porewater retention and binding capacity (Golterman, 1995). It is difficult to isolate the influence of sediment particle size and the ability of species to anchor within sediments from sediment fertility, and any attempt to do so would result in the modelling of situations rarely encountered in natural systems.

Second, there is considerable circumstantial evidence to suggest that potassium within the sediment may have a direct or indirect effect on plant growth. For example, a study of macrophyte biomass in ten temperate lakes in Canada indicated that exchangeable potassium in the sediment was the only sediment variable significantly related to total macrophyte biomass, from a number of variables which comprised exchangeable sediment nitrogen, phosphorus and potassium; sediment organic matter content; sediment water content; and sediment type, including, organic, gravel, sand and silt (Anderson and Kalff, 1988). However, the link did not appear to be direct, as fertilisation experiments indicated that the macrophytes were limited by nitrogen rather than potassium. In laboratory experiments, in which four macrophyte species were grown in chambers with water and sediment separated, Barko and Smart (1981) also found that whilst plant tissue concentrations of nitrogen and phosphorus either increased or stayed the same during the study period, potassium concentrations decreased significantly suggesting potassium limitation.

It is postulated that, as both ammonium ions and potassium ions have a similar charge and nearly identical atomic radii, there may be competition between the ions for exchange sites on macrophyte root surfaces (Barko and Smart, 1981). As potassium ions are generally derived from the weathering of rocks and ammonium ions from the breakdown of organic matter, the supply of the former will vary little throughout the year but ammonium will be limited during the growing season (Anderson and Kalff, 1988). In experiments with *Hydrilla verticillata*, Barko *et al.* (1988) have also shown that when nitrogen is limiting, potassium may be obtained from the water column and translocated to the roots to be exchanged at the root surfaces for ammonium ions. It is possible that sediment

potassium concentrations could be moderating and obscuring the influence of other sediment parameters on the macrophytes of the 17 rivers.

4.8.2 Relationships at the species level

The results from the 17 rivers suggest that few species are restricted to a particular range of sediment phosphorus or nitrogen concentrations, and most species seem to be able to grow throughout the range of concentrations encountered. It is possible that many species are cosmopolitan and show no preference for sediments of a particular fertility. For example, *Potamogeton pectinatus* is known to be tolerant of a wide range of ion concentrations (Van Wijk, 1989a), and although it is generally associated with enriched waters the species has been demonstrated to grow in low nutrient situations (cf. Van Wijk, 1989b). Similarly, the growth of *Ranunculus* spp. has been shown to be unaffected by sediment particle size (Spink, 1992). The evaluation of the MTR undertaken by Dawson *et al.* (1999b) also found that many species were cosmopolitan with respect to water column concentrations of phosphate and nitrate. As many macrophytes are ubiquitous, for example, *Sparganium emersum* (Grasmück *et al.*, 1995), it seems that many species have a wide ecological amplitude (Carbiener *et al.*, 1990; Papastergiadou and Babalonas, 1993). Furthermore, it has been suggested that the biochemical and morphological similarities between aquatic angiosperms will result in similar nutrient optima between species (Gerloff and Krombholz, 1966; Duarte, 1992).

It is possible that relationships between macrophytes and sediments are not evident if plants are grouped taxonomically, as different species may have similar morphologies and nutrient requirements. Work relating macrophyte functional attributes to trophic status (cf. Ali *et al.*, 1999) may be able to address how morphology and life strategy relate to sediment nutrients. It is equally possible that preferences to nutrient status are general and expressed at the community rather than individual species level (cf. Carbiener *et al.*, 1990) which may explain the relative success of the MTR scheme, which relies on community level comparisons, and why, within the scheme no one species was related to phosphate or nitrate concentrations strongly enough to merit its use as a key species (Dawson *et al.*, 1999b). Individual species tolerances in aquatic macrophytes are further distorted by the high degree of plasticity exhibited by many species (cf. Idestam-Almquist and Kautsky, 1995). For example, many species show increased root:shoot biomass ratios in nutrient poor sediments (cf. Best and Mantai, 1978; Idestam-Almquist and Kautsky, 1995) and *Myriophyllum spicatum* plants have been observed to undergo phenotypical changes to give a more competitive ruderal strategy (Kautsky, 1988). Therefore, there is the possibility that particular phenotypes and genotypes will display clear sediment preferences but species will not.

4.8.3 The reciprocal relationship between macrophytes and sediment

Flow velocity is reduced within plant patches (Sand-Jensen and Mebus, 1996; Sand-Jensen and Pedersen, 1999) and therefore, macrophytes influence the sedimentation and erosion of inorganic and organic particles in and around patches (Sand-Jensen, 1997). The effect of plant stands on flow velocity has been demonstrated to be dependent on plant morphology (Sand-Jensen and Mebus, 1996). Attribute groups such as those proposed by Willby *et al.*, (2000) may therefore, be a good way to study the effect of macrophytes on sediments.

The enrichment of sediments by macrophytes through the trapping of nutrient-rich particles has the potential to alleviate nutrient limitation of plant growth (Sand-Jensen, 1997) and may explain why many of the species studied are found across such a wide range of sediment types. Macrophytes have also been shown to have an effect on the chemistry of sediments through oxidation of the root zone (Moore *et al.*, 1994; Steinberg and Coonrod, 1994; Wigand *et al.*, 1997). This has been shown to lead to a mosaic of aerobic areas and anaerobic areas within macrophyte beds (Howard-Williams *et al.*, 1982). The reciprocal relationship between macrophytes and sediments has led Barko *et al.* (1991) to suggest that the physical and chemical properties of sediment are as much a product of macrophyte growth as they are controls of growth. Thus, plants have the ability to modify the immediate sediment environment to improve the conditions for growth.

Given the influence of macrophytes on sediment structure and chemistry, it is possible that sediment nutrient status does not exert a direct control on macrophyte presence-absence or biomass. The sediment conditions encountered in the 17 rivers possibly reflect a range of sediments from those that are not influenced by plant growth through to those which are entirely the product of plant growth; such as the thick deposits of fine organic material that may accumulate within dense plant stands, even in fairly fast-flowing streams where the unvegetated sediments are coarse and eroded.

Sediment–plant relationships may operate at the patch scale *sensu* Sand-Jensen and Madsen (1992) and only be apparent at the reach scale in a very general manner. Patches have been shown to be of great importance to the survival of some macrophyte species, for example, *Callitriche cophocarpa* (Sand-Jensen and Madsen, 1992). Patches are able to reduce physical stress and increase nutrient supply through the mechanisms described above (Sand-Jensen and Madsen, 1992) and may be considered as evidence of interspecific mutual protection (French and Chambers, 1996). Within patches, ramet extension (the growth of individual plants) allows plants to capitalise on nearby microsite nutrient pools (McCreary, 1991) and so vegetative spread is very common in submerged macrophyte populations. There is evidence that temporary unstable silt may be a very important nutrient source where the stable substrate is poor in nutrients. This temporary nutrient source may be in the form of firm hummocks or as silty water trapped between plant shoots, and may allow intermittent good uptake (Haslam, 1978). The presence or absence of a plant will therefore be determined by whether or not a vegetative propagule reaches a suitable site and whether or not the plant is able to persist long enough to establish a patch. Once a patch is established, the plant is able to modify the environment to such an extent that sediment nutrient concentrations have only limited control over plant growth. This view places greater emphasis on the role of stochastic events such as plant dispersal and disturbance events than ecological controls such as resource competition and biotic interactions in the structuring of riverine submerged macrophyte communities.

4.8.4 The role of flow and disturbance events

If, as suggested, macrophytes are able to modify the sediment to the extent that initial sediment nutrient concentrations are not a significant controlling factor then it follows that factors other than sediment nutrient status will be important in determining macrophyte distribution. The RDA of the macrophyte communities of the 17 sites (Section 3.5.3), supports this conclusion. A number of authors have found that other environmental factors, such as flow velocity, catchment land-use, water hardness and conductivity, and shade, may be more important than sediment fertility (Anderson and

Kalff, 1986) and water trophic status (Grasmück *et al.*, 1995; Spink *et al.*, 1997; Demars and Harper, 1998).

Macrophyte ecology has largely ignored the role of temporal events such as spates and droughts in structuring riverine communities, although a number of studies have considered that the role of flow, whether large-scale (reach-wide discharge and annual spates) (Barrat-Segretain and Amoros, 1996) or small-scale (instream variability) (Chambers *et al.*, 1991), may have an important role in determining community structure. By comparison, the effects of short-term changes in flow characteristics have long been a feature in studies of stream invertebrate ecology. Assuming flow to be a major determining factor, and that sediment fertility is not the primary control in most situations due to the ability of macrophytes to alter the sediment both at the surface and at depth, the most important function of roots in many submerged species may be as anchorage. This view is in agreement with the observation that many species of fast-flowing habitats, (for example, Batrachian *Ranunculus* species) have shallow roots which curl around large sediment particles but do not penetrate deeply into the sediment to obtain nutrients. Evidence that both macrophyte roots and shoots are able to obtain nutrients (Agami and Waisel, 1986), and that phosphorus translocation in two *Elodea* species was greater from shoot to root than from root to shoot (Eugelink, 1998), suggests that nutrient acquisition by roots may be a secondary function in some species and situations. Therefore, the importance of sediment nutrients to macrophytes will be dependent upon both species or morphological type and the environment both in terms of trophic status and flow. This is in agreement with Denny's (1980) concept of a continuum of species with increasing dependence on sediment nutrients. Other factors such as shade, competition (both with other macrophytes and epiphytic algae), herbivory, water pollution (other than eutrophication) and management are likely be important on an individual site basis.

5. CONCLUSIONS

The key findings of the research are summarised here. Those findings which are considered particularly noteworthy are indicated by bold-type.

- All 17 rivers had broadly similar water chemistry and may be considered mesotrophic to eutrophic.
- **Sediments varied considerably both within and between the 17 sites. The rivers were most distinct in terms of sediment phosphorus concentrations whereas sediment organic carbon and total nitrogen contents were fairly similar for all rivers with the exception of a number of particularly organic-rich sediments.**
- Total phosphorus concentrations in the rivers were of a similar order of magnitude to levels quoted in the literature for a variety of freshwater (and marine) sediments, although the river sediments tended to have lower concentrations reflecting the more depositional nature of standing waters.
- The silt-clay content of sediments was generally between 10% and 40% of the fraction less than 2mm.
- **Despite the high degree of sediment heterogeneity within reaches, between-river variability was significantly greater than within-river variability in terms of all six sediment parameters.**
- A number of sediment parameters were correlated with one another, including total and inorganic phosphorus; and total nitrogen, organic carbon and organic matter. However, there were no clear relationships between nutrient concentrations and the silt-clay contents of sediments.
- On the basis of sediment samples collected during this study, the loss on ignition method for estimating organic carbon is not recommended for sediments from running waters.
- **Investigations of the relationships between sediment parameters and water chemistry, flow regime, channel geometry and channel shading, indicated that most differences in sediments could be explained by catchment geology, as determined by the BFI value.**
- Relationships between mean sediment variables and mean water chemistry parameters were complex, and suggested that factors other than nutrient concentrations in water and sediment may be of importance in governing the equilibrium of sediment-water concentrations.
- **Species showed broad tolerances to all sediment variables. Some species appeared to be associated with high sediment phosphorus concentrations, but this may be an effect of the stream type in which they were sampled. The percentage of fines in sediments on which species occurred did seem to differ, but the intrinsic link between sediment size and fertility makes interpretation difficult.**
- It is hypothesised that, the influence of macrophytes upon the sediments through enhancing the accumulation of fine material has a significant effect upon stream ecology and may further complicate attempts to determine macrophyte preferences for sediment types.
- **Sediment variables did not appear important in determining the species communities of the 17 rivers. Of the variables supplied in canonical ordination, BFI, sediment concentrations of total nitrogen and the percent of the channel shaded were those which explained most of the variation in species community, again reflecting the importance of geology and reach-scale factors. The significance of total nitrogen concentrations in the ordination is believed to be a result of the influence of high concentrations in sediments collected in the River Waveney.**

- The literature supports the hypothesis that macrophytes can absorb nutrients via both roots and shoots, and also transfer then between these components. There appears to be a continuum of dependence on root versus shoot uptake, with evidence that the anchoring function of roots may be more importance than their capacity for nutrient uptake in some of the species studied here.
- Given this continuum of species and interspecific differences in macrophyte response to sediment, it is important that observations of particular species are not extrapolated to submerged macrophytes in general.

6. RECOMMENDATIONS

The research described within this report highlights a number of areas where current understanding is limited and further research is required. Recommendations arising from the research are considered here; these relate to future research needs (Section 6.1), protocols for monitoring ecological integrity in running waters (Section 6.2) and river management policy (Section 6.3). These recommendations must be addressed before the use of macrophytes in biological assessment can be fully realised.

6.1 Future Research Needs

A review of current literature and the findings of the research indicate that there is a need to understand processes of ecosystem function in macrophyte-dominated lowland streams and more generally to better understand nutrient dynamics in running waters. In addition there is a need for macrophyte-focused research in recognition of the functional and structural importance of these organisms, particularly in lowland rivers of the type sampled during this study. Recommendations for future research effort include:

- Sediment variability (spatial and temporal) must be investigated across a wider range of river types to determine the generality of relationships and patterns identified during this research.
- Process-based studies of sediment, flow and nutrient dynamics are required in streams with abundant macrophyte growth. These studies should consider temporal variability as this research has indicated that spatial variability within such systems may be high; given the seasonal nature of macrophyte growth some temporal variation may be expected. It is suggested that this includes work at the scale of the plant patch as it is evident that the development of patches may cause the accumulation of large quantities of potentially nutrient-rich fine material.
- Monitoring and modelling approaches should be applied to understanding nutrient dynamics within running waters. It is important that changes to nutrient forms within the water column are understood and that the equilibrium between sediments and water is investigated under the influence of flow, numerical modelling approaches are likely to be most appropriate due to the logistical problems associated with establishing experimental equipment in natural systems.
- Plant-mediated sediment and nutrient processes must be related to larger scale hydrological and geomorphological processes to identify catchment controls on instream functioning.
- It must be recognised that current paradigms of nutrient cycling, based as they are upon work in standing waters, are not applicable to running waters which have: a clear unidirectional flux of energy and material; greater sediment surface area to water volume ratio; coarser, more mineral sediments; and greater hydrologic connectivity with terrestrial and semi-aquatic systems than standing water systems.
- The importance of sediment nutrients to macrophytes must be further investigated with particular attention to species differences and the sediment fractions of nitrogen and phosphorus that are significant. Additionally, the role, both direct and indirect, of sediment potassium concentrations should be further investigated. The use of manipulative experimental *in situ* approaches is recommended for this purpose.
- Greater effort must be directed at understanding the mechanisms controlling macrophyte community structure and function. In particular, the way in which eutrophication may affect macrophyte communities in open running water systems needs further research; there is little evidence of competition in macrophyte communities (either between species or between

macrophytes and epiphytes) yet this is often cited as the mechanism by which macrophytes are affected by nutrient enrichment.

6.2 Monitoring Ecological Integrity

The research indicates that both sediments and macrophytes are potentially important components of the nutrient cycle in lowland rivers, thus there are implications arising from this work for the monitoring of water quality and ecological integrity by the Environment Agency:

- The high concentrations of nutrients within the sediments of the 17 lowland rivers means it is important to consider sediments when assessing the trophic status of these systems. It is recommended that the collection and analysis of sediment samples be incorporated more extensively into existing Agency monitoring schemes, if only to provide a dataset that allows spatial and temporal variability of sediment nutrient concentrations in rivers to be assessed.
- The high degree of variability in nutrient concentrations measured both within and among rivers in this study suggests that a number of sediment samples are required to characterise a particular river reach. It is recommended that at least five samples are taken from each 100m reach and that these are collected in a stratified manner from distinct areas of the reach. Samples could be located by reference to visually identifiable habitats, such as those proposed by Harper *et al.* (1996). Sampling effort should be reviewed once there is sufficient data to better determine spatial and temporal variability.
- The research has also identified methodological needs for river sediment sampling and analysis. Other methods for collecting sediments should be investigated such as freeze-coring to ascertain whether this method unduly influences subsequent chemical analyses. Additionally, analytical methods for determining nitrogen and phosphorus in river sediments need further development, in particular methods that sequentially extract different nutrient fractions should be considered. The Agency should adopt a standardised method for determining nitrogen and phosphorus in river sediments and this should be selected with consideration to: the ecological significance of the determined fractions, reproducibility and cost-effectiveness.
- Nutrient concentrations within plant tissue have been shown to be considerably higher than those in the sediment (see Clarke, 2000); thus at particular times of year the nutrients within plant tissue will represent an important component of the nutrient budget for a reach. It is recommended that during summer months when macrophyte biomass is greatest any attempt to quantify the trophic status of a river reach considers this nutrient store, this approach has been advocated by Canfield *et al.* (1983) for lakes with abundant macrophyte growth.

6.3 River Management Policy

Finally, the research has implications for areas of river management that are of concern to the Environment Agency:

- Macrophytes have considerable potential as tools for biological assessment of river trophic status but development is dependent on improvements in our understanding of the role of macrophytes in running water nutrient dynamics and the affect of nutrient enrichment upon macrophyte communities (see above).
- Any activity which influences either macrophyte biomass (cutting) or sediment dynamics (dredging) will impact upon both ecological integrity and nutrient dynamics. Thus, it is

important to consider the likely influence of these activities when determining management policy.

- Attempts at river restoration in lowland streams must consider the role of macrophytes in ecosystem function. Geomorphologically-led channel designs should consider the potential influence of macrophyte growth on sediment processes and nutrient dynamics.

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List of Abbreviations

Rivers		Sediment Variables	
ALL	Allen	TP	Total phosphorus
AVO	Avon	IP	Inorganic phosphorus
DOV	Dove	TN	Total nitrogen
DUN	Dun	OC	Organic carbon
EDE	Eden	OM	Organic matter
FRO	Frome	SC	Silt-clay
HIZ	Hiz	WTP	Weighted TP (TP x SC)
ITC	Itchen		
LOD	Loddon	Other	
RHE	Rhee	MTR	Mean Trophic Rank
TES	Test	TDI	Trophic Diatom Index
TOV	Tove	SRP	Soluble reactive phosphorus
WAV	Waveney	TON	Total oxidised nitrogen
WEY	Wey		
WHI	Whilton Branch		
WWA	Whitewater		
WYL	Wylfe		