The influence of variations in reedswamp structure and extent upon macroinvertebrates and associated ecological processes within the littoral zone of lakes

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Abstract

Reedswamps are a key feature of the shallows of many lakes, influencing biodiversity and functioning, but are in decline in lakes throughout Europe for reasons that are unclear. Metadata analysis of data extending over 100 years suggested that multiple stressors were implicated in reedbed decline within Windermere (UK), and that the influences of individual stressors should be investigated by comparing genetic diversity and environmental factors across lakes within the same catchment or region. Furthermore, the consequences of changes in reedswamp structure and coverage for whole lake functioning is an important gap in knowledge for Windermere and many other lakes. Macroinvertebrate data from two lakes in the Windermere catchment were used to investigate the influence of reedswamp habitat upon biodiversity, and key ecological processes such as decomposition.

A semi-quantitative survey highlighted the importance of reedswamp size, shape, and structure in determining the ways in which macroinvertebrates influence lake functioning. Collection of macroinvertebrates from a wide range of niches along vertical and horizontal axes using a hand-net was a unique approach, and provided novel insights into key ecological processes. For example, seasonal influences were modified by structural heterogeneity, and position within reedswamps. This was supported by the findings of a field-based litter bag experiment; differences in macroinvertebrate seasonal dynamics were associated with differences in litter structure from two species of reed. Furthermore, there were interspecific differences in seasonal patterns of litter deposition. Both macroinvertebrate methods were efficient and effective, and should form the basis of a standardised sampling protocol for the shallows of lakes. This body of research on local variations (~8 m) demonstrates the need for a detailed understanding of how structural heterogeneity influences whole lake functioning. This should include comprehensive food webs that include vertebrates, macroinvertebrates, macrophytes, algae, and microbes for reedswamp and other key habitats.

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Abbreviations

A	Total abundance
Ab	Absorber
Adonis	Analysis of variance using distance matrices
AFDM	Ash free dry mass
ANCOVA	Analysis of covariance
ANOVA	Analysis of variance
Anosim	Analysis of similarity
AOD	Above ordnance datum
B	Borrans reedswamp
B1e	Edge of transect 1 across Borrans reedswamp
B1m	Middle of transect 1 across Borrans reedswamp
BO	Borrans ‘open’ stony-littoral site
BC	Bray Curtis dissimilarity Index
BNE	Borrans reedswamp northeast corner
BOD	Biochemical oxygen demand
BSW	Borrans reedswamp southwest corner
CA	Canonical analysis
Chl *a*	Chlorophyll *a*
CO_2	Carbon dioxide
CPOM	Coarse particulate organic matter
D	Simpson’s index
De	Deposit-feeder
DEFRA	Department for Environment, Food and Rural Affairs
df	Degrees freedom

DM	Dry Mass
e	Edge
EA	The Environment Agency
F	Filter-feeder
FBA	The Freshwater Biological Association
FCA	Fuzzy Correspondence Analysis
FFG	Functional Feeding Groups
FPOM	Fine particulate organic matter
H	Shannon Index
H^+	Hydrogen ion
Ha	Hectares
HSD	Honest Significant Difference
IPCC	Intergovernmental Panel on Climate Change
k	Mass loss rate
LDNPA	Lake District National Park Authority
m	Middle
NMDS	Non-metric multidimensional scaling
NVZ	Nitrate Vulnerable Zone
O	Open stony-littoral
Pa	Parasite
PAH	Petroleum-derived Aromatic Hydrocarbons
PAR	Photosynthetically active radiation
PCA	Principal components analysis
PERMANOVA	Multivariate permutational analysis of variance
Pi	Piercer
Pr	Predator
RIVPACS	River Invertebrate Prediction and Classification System
RM-ANOVA	Repeated measures analysis of variance

RSPB	Royal Society for the Protection of Birds
Rs	Reedswamp
RW-N	Northern shore of Rydal Water
RW-S	Southern shore Rydal Water
S	Taxon richness
SA	Surface area
Sc	Scraper
SCRT	South Cumbria Rivers Trust
Sh	Shredders
Ss	Swan Stone reedswamp
STW	Sewage treatment works
TP	Total phosphorus
T_{50}	Half-life
WFD	Water Framework Directive
Wi	Windermere
Wm	White Moss
Wm2e	Edge of transect 2 across White Moss reedswamp
Wm2l	Landward side of transect 2 across White Moss reedswamp
Wm2m	Middle of transect 2 across White Moss reedswamp
WMO	World Meteorological Organisation

CHAPTER 1 Introduction and Rationale

Natural lakes are key features of many European landscapes, and are of great cultural, economic, and ecological importance. Lakes provide a broad range of ecosystem services, and are a major economic resource for many countries (Schmieder, 2004). Wetland habitat (*e.g.,* wet woodland, willow carr, fen, and reedswamp) associated with the shoreline is particularly important, making a significant contribution to Europe's biodiversity, and underpinning processes that influence the whole lake (Good *et al.*, 1978; Christensen *et al.*, 1996; Maltby, 2009; Keddy, 2010). In common with other wetlands the transitional zone around lakes represents the natural transition from the terrestrial to the aquatic environment (the land-water ecotone). Any disturbance or loss of continuity within the ecotone of lakes can have serious consequences for biodiversity, whole lake functioning and the provision of ecosystem services (Ostendorp *et al.*, 1995). One of the key functions of the land-water ecotone is to buffer the aquatic environment from adverse changes originating in the terrestrial environment, such as diffuse and point source nutrient enrichment (Lake *et al.*, 2000; Ferrati *et al.*, 2005; Keddy, 2010). Consequently, sustainable use of lakes is dependent upon the condition of the land-water ecotone. However, due to the position of the ecotone within lakes it is vulnerable to a range of anthropogenic (*e.g.,* shoreline development), and natural (*e.g.,* hydro-meteorological changes) stressors (Ostendorp, 2004).

Land-water ecotones are typically characterised by progressive spatial changes in plant communities and hydrological conditions (Hejny and Husak, 1978; Ferrati *et al.*, 2005). Plant communities enhance stability of lake margins, and provide habitat for wildlife (Tscharntke, 1992). The common reed, *Phragmites australis* (Cav.) Trin. is a principal component of lacustrine land-water ecotones throughout Europe (Sahuquillo *et al.*, 2008). *Phragmites* reedbeds typically extend across ecotones, and can be subdivided into different habitat types. For example, permanently wetted sections of reedbeds are referred to throughout this thesis as reedswamp (*sensu* Gilman, 1994; Rodwell, 1995). Reedswamp provides an aquatic environment that is structurally and functionally distinct from other habitat types within the littoral zone (Polunin, 1984; Schreiber and Brauns, 2010). Within Europe, *Phragmites* reedswamp is more highly valued for its contribution to key functions (*e.g.,* influencing trophic interactions), and biodiversity at the whole lake scale compared to other common reedswamp forming emergent macrophytes such as *Typha angustifolia* (Ostendorp, 1993). Due to clear morphological differences throughout their life histories, *Phragmites* and *Typha* are easily distinguished within reedswamp habitat (Figure 1.1). Consequently, a decline in *Phragmites* dominated wetlands throughout Europe over recent decades has been obvious and has caused concern (van der Putten, 1994; Brix, 1999a). This contrasts with the situation in many other parts of the world (including the USA and Australia), where the expansion of invasive non-native subspecies of *Phragmites* has had a negative effect upon wetland function and biodiversity by displacing native species of *Typha* (Chambers *et al.*, 1999).

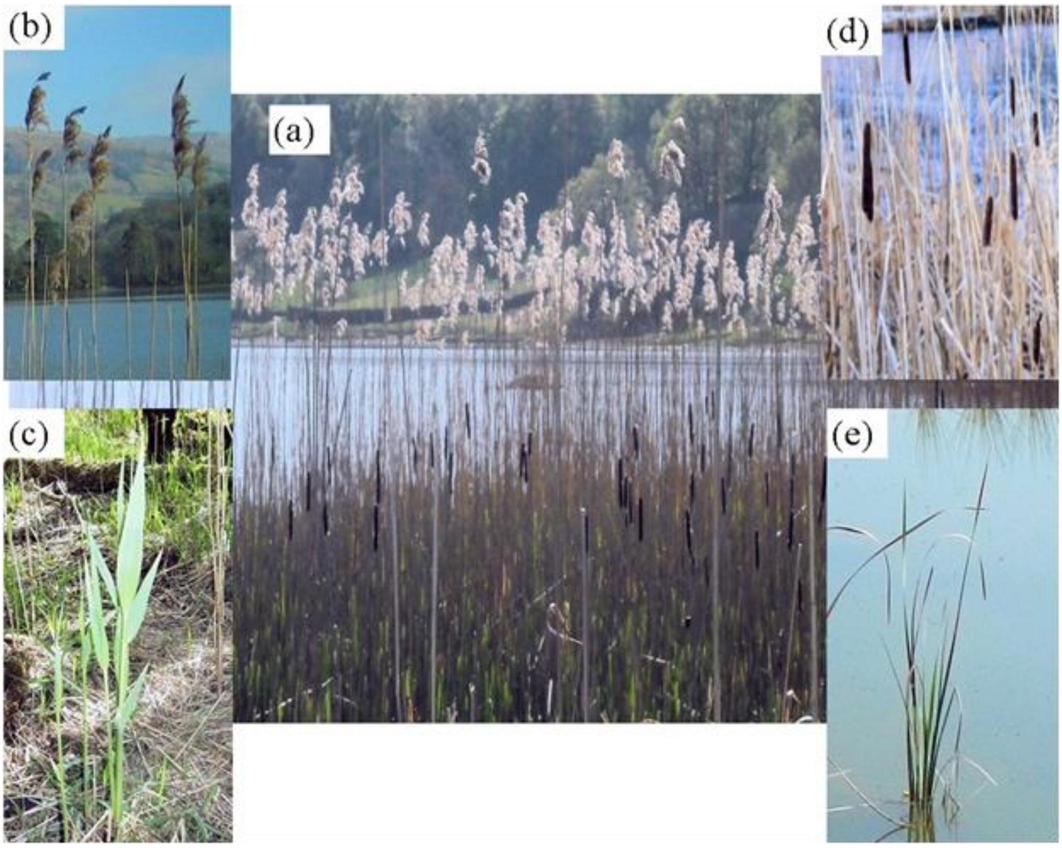


Figure 1.1 These photographs highlight key differences in morphology between two common reedswamp forming plants located within the Windermere catchment, UK. (Photographs a-e: [a] *Phragmites australis and Typha angustifolia* reedswamp, [b] *Phragmites* seed heads, [c] young shoots of *Phragmites*, [d] seed heads of *Typha*, and [e] young *Typha* shoot)

Phragmites is a cosmopolitan species and is widespread within temperate zones across both hemispheres under a range of different environmental conditions (Clevering *et al.*, 2001; Haslam, 2010). Consequently it has been the focus of a great deal of academic attention. However, until the Eureed project (1993–1998), coordinated and comprehensive research into the functions and sustainable use of reedbeds across large geographic areas (*e.g.,* Europe) was lacking. Eureed was a response to widespread losses of

Phragmites wetland habitats across Europe. It was a strategic research programme which focused upon: (1) reedbed ecotone functioning, (2) reed die-back syndrome and the development of diagnostic tools, (3) the role of genetic diversity and phenotypic variation in reedbed resilience, and (4) the provision of management advice for the sustainable use of *Phragmites* dominated wetlands (Brix, 1999a). The Eureed project demonstrated that the response of *Phragmites* to individual environmental factors is highly variable due to the high genetic diversity and phenotypic variation of this species. Consequently investigation of the *Phragmites*-ecosystem interaction within the natural environment is challenging, because of the high variety of different combinations of hydro-meteorological, physicochemical, and ecological variables that occur in natural environments throughout Europe. In addition, investigating *Phragmites* persistence (*e.g.,* reed die-back) within the natural environment is time consuming, expensive, and requires a high level of technical expertise (Brix, 1999a).

Coordinated research into reedswamp ecology is lacking, consequently little is known regarding the contribution of internal biotic interactions to reedswamp functioning. Within aquatic habitats, biological processes (*e.g.*, primary production, grazing, and decomposition) control whole lake ecosystem functioning (Kuehn and Suberkropp, 1998; Covich *et al.*, 1999). For example, macroinvertebrate consumers have a strong influence upon the translocation and cycling of carbon and nutrients by acting as the vital link between primary production and many vertebrate consumers (Murkin and Wrubleski, 1988). As a result, the interaction between macroinvertebrates and reedswamps has the potential to drive nutrient dynamics and energy flux within lakes (Good *et al.*, 1978; Maltby, 2009). Published studies have demonstrated that macroinvertebrate assemblages are sensitive to structural differences (including reedswamp habitat) throughout the littoral zone (White and Irvine, 2003; Schreiber and Brauns, 2010). However, the functional significance of spatial variations in macroinvertebrate assemblages within the littoral zone of lakes has received little attention. In particular, the influence of differences in reedswamp; shape, size, and structure upon the contribution of macroinvertebrates to key processes is unknown.

Investigations into the consequences of structural changes in the littoral zone for aquatic communities are lacking for the majority of lakes, including those that have been studied in great detail. For example, Windermere is the largest lake in England (Pickering 2001), and has been the focus of a great deal of multidisciplinary limnological research over the last century. Historical archival records (*e.g.,* changes in human activities) in conjunction with long-term physicochemical, ecological, paleontological, and meteorological data have provided valuable insights into ecosystem functioning (George *et al.*, 2004; Thackeray *et al.*, 2008; M^{c}Gowan *et al.*, 2011; Elliott, 2012). Consequently, Windermere provides a valuable model for the ways in which multiple stressors influence the ecosystem functioning of lakes (M^{c}Gowan *et al.*, 2011). While the focus has been upon the pelagic zone, there have been a number of valuable investigations into key aspects of littoral zone functioning (Godward, 1937; Macan, 1970b; Macan, 1970a; Winfield, 2004). However, the Windermere model would benefit from information that places historic changes within the littoral zone into a contemporary context.

Prior to this thesis, investigation of the macroinvertebrate-reedswamp interaction within Windermere was limited to Moon (1936) who studied an individual reedswamp. In addition, the only comprehensive investigation of littoral macroinvertebrates throughout Windermere was by Macan and Maudsley (1969). Contemporary data on macroinvertebrate assemblages throughout the littoral zone of the Windermere catchment collected during this thesis are intended to provide an insight into the consequences of reedswamp habitat decline. This was facilitated by maps that illustrate long-term changes in reedswamp distribution within Windermere (Alvarez-Codesal, 2012). In addition, analysis of trends in multiple stressors for reedswamp habitat gives an indication of the future structure and function of the littoral zone of Windermere.

1.1 Aims/objectives and thesis structure

The overall aim of this thesis is to examine historic and contemporary changes in reedswamp wetland and the consequences for aquatic macroinvertebrate communities within Windermere. There are five main thesis aims/objectives: (1) to identify key reasons for reedswamp loss within Windermere, (2) to assess the contribution of reedswamp habitat to macroinvertebrate biodiversity within lakes, (3) to assess the potential of multiple traits as a tool for inferring the influence of reedswamp habitat upon the processing of organic matter by macroinvertebrates, (4) to investigate the ecological significance of interspecific differences in reed leaf-litter, and (5) to develop a new conceptual outline for investigating spatiotemporal variations in macroinvertebrate assemblages within the littoral zone of other lakes. The ways in which the contents of individual chapters combine to address these objectives are illustrated by Figure 1.2.

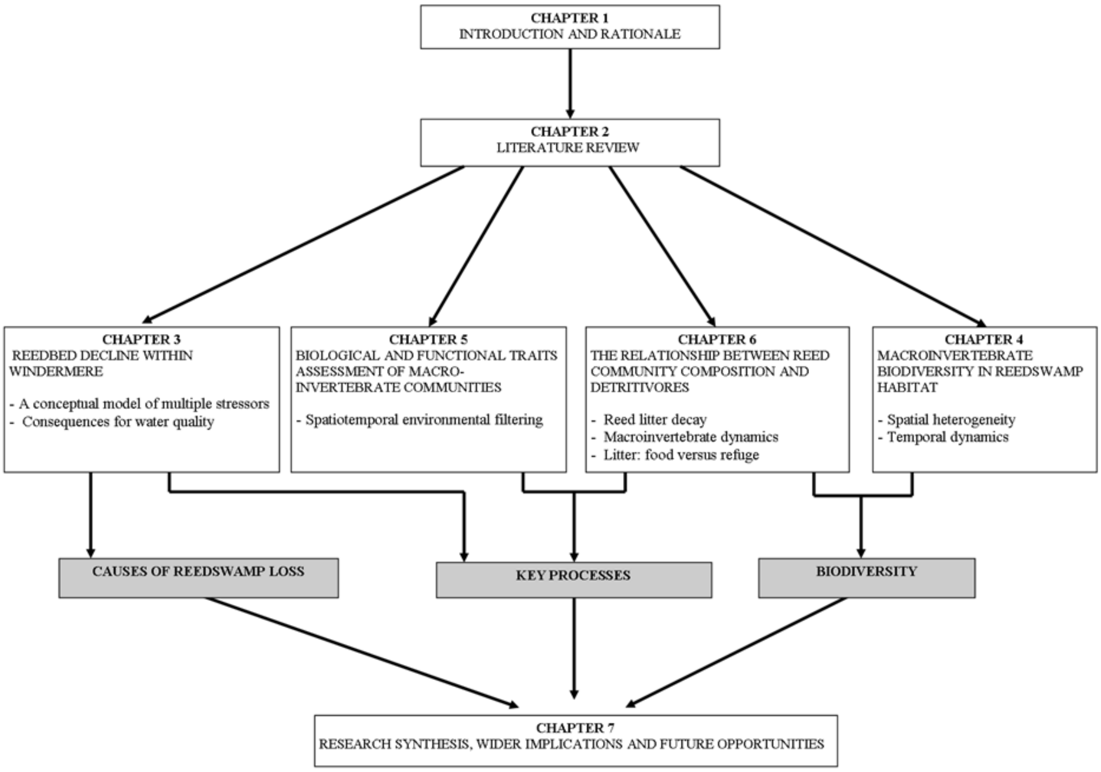


Figure 1.2 This diagram provides an overview of the thesis structure; arrows show how chapters combine to investigate the thesis themes (shaded boxes).

CHAPTER 2 Macroinvertebrates and ecosystem functioning in lake littoral reedswamps: a review

2.1 Chapter Introduction

Current understanding of the contribution of reedswamps and their macroinvertebrate assemblages to important ecological processes within lakes is reviewed. Furthermore, possible consequences of changes in the dominance of reedswamps within the littoral zones are discussed. Future research in this area is facilitated by the identification of key research questions and by reviewing published survey methods.

2.1.1 Introduction

Littoral zones are intimately connected with open water environments, but their high abiotic and biotic heterogeneity (spatial and temporal), along with practical difficulties of field research, has deterred many workers from their study (White and Irvine, 2003; Schreiber and Brauns, 2010). This causes problems because existing models of whole lake functioning need to be enhanced by incorporating a more complete understanding of the contributions of littoral zone processes. Compared with the adjacent open water and shore zones, littoral zones can make significant contributions to the functioning of whole lakes (Strayer and Likens, 1986; Wetzel, 1990; Vadeboncoeur *et al.*, 2002). Littoral zones typically possess a rich, diverse and highly productive benthos (Pieczyńska, 1972; Cole, 1983; Bikowski and Kobak, 2007). However, they are also relatively susceptible to change, which is important as the majority of notable anthropogenic impacts upon whole lake functioning (*e.g.,* wave-washing from boats, changes in water level, shoreline development, and invasive species) originate within the littoral zone (Brodin and Gransberg, 1993; Palomäki and Koskenniemi, 1993; Johnson, 1995; Brauns *et al.*, 2007b; Aroviita and Hämäläinen, 2008; Gabel *et al.*, 2008; Tolonen and Hamalainen, 2010).

Reedswamps within lakes are important littoral zone habitats because they provide refuge and food for a variety of organisms, including macroinvertebrates, fish, amphibians, birds and mammals that also interact with adjacent terrestrial and profundal habitats (Sahuquillo *et al.*, 2008); hence, reedswamps tend to have higher biodiversity than neighbouring terrestrial and aquatic habitats (Pieczyńska, 1972; Bikowski and Kobak, 2007). The management of these sites is usually based on the conservation value of their plants, birds or terrestrial invertebrate species or assemblages (Ditlhogo *et al.*, 1992) rather than aquatic macroinvertebrates. This is an oversight because the role of benthic and epiphytic macroinvertebrates in the transfer of reedbed energy and matter to higher trophic levels is thought to be particularly important as they are central components of food chains and contribute significantly to the energy budget of the whole lake (Strayer and Likens, 1986; James *et al.*, 1998; Vadeboncoeur *et al.*, 2002). Key functions of macroinvertebrates in reedswamps are as follows: (1) the recycling of both terrestrial and aquatic organic matter (Cummins, 1974); (2) control of periphyton and possibly other producers biomass (James *et al.*, 1998); and (3) acting as a major food source for fish and bird populations (Vander Zanden and Vadeboncoeur, 2002).

2.2 Wetland structure and functioning

Natural wetlands are transitional ecosystems (ecotones) that link aquatic (saline or freshwater) and terrestrial systems and can be permanently or temporarily flooded (Ferrati *et al.*, 2005; Keddy, 2010). Natural wetlands (*e.g.,* bogs, wet woodlands, fens, and reedswamps) are one of the most productive ecosystems in the world, providing humans with many benefits and services (Costanza *et al.*, 1997; Engelhardt and Ritchie, 2001; Hansen *et al.*, 2007; Maltby, 2009; Keddy, 2010; Acreman *et al.*, 2011). Ecosystem services provided by wetlands include the provision of: goods (*e.g.,* building materials, fuel, medicines, and food), flood defence, potable water supply, waste treatment, habitat for wildlife, climate regulation, agricultural services, and culture and amenity (Christensen *et al.*, 1996; Maltby, 2009; Keddy, 2010; May and Spears, 2012). Contributions to biogeochemical processes (*e.g.,* water, carbon and nitrogen cycles) are particularly significant (Birkett *et al.*, 1996; May *et al.*, 2010). On a global scale, even a small reduction in wetland coverage may result in a significant loss of services (Birkett *et al.*, 1996; Zedler and Kercher, 2005). Since the early 20th century, half of the world's wetlands have been lost (Mitsch and Gosselink, 2007); thus there has already been a significant loss of ecosystem services on a global scale (Zedler and Kercher, 2005).

The term 'wetland' encapsulates a large variety of habitat types, which have a number of key characteristics in common (Finlayson and van der Valk, 1995). Estimates of the contribution of different types of wetlands (*e.g*., bogs, fens, and reedswamps) to global ecosystem services are lacking. Such estimates require the application of a suitable universal classification scheme. A number of classification systems have used the key features of wetlands (*e.g*., associated flora, fauna, and hydrological regime) to place them into broad categories (Gopal *et al.*, 1990; Keddy, 2010). Allocating wetlands to universal categories enables the exchange of knowledge on a global scale to inform broad management decisions (Cowardin and Golet, 1995; Hughes, 1995; Zoltai and Vitt, 1995). However, the diverse nature of wetlands means that it is unlikely that any single classification system could provide accurate ecological information for all wetland types (Cowardin and Golet, 1995). This highlights the need for studies of wetlands to include detailed and holistic descriptions of habitat features (*e.g*., seasonal changes in associated taxa and hydrology) and functional process dynamics.

Wetland macro functionality is influenced strongly by internal ecological structures (*e.g.,* macrophytes) and processes (*e.g.,* nitrogen cycling). In this review, the term ‘macro functionality’ is used to refer to the capability of an individual wetland to support key ecosystem functions. Whereas the term ‘macro functioning’ refers to the ways in which individual wetlands contribute to ecosystem functions. The dynamics and processes of a wetland ecosystem are dictated by the ecological functions of the species within it, and vice-versa (Marcot and Vander Heyden, 2001). The ecological processes that support wetland functions can be placed into three broad categories: (1) biological processes (mainly primary production and decomposition); (2) chemical processes (mainly nutrient dynamics); and (3) physical processes (predominately hydrology and energy flux)(Good *et al.*, 1978; Christensen *et al.*, 1996; Maltby, 2009; Keddy, 2010). Hence, the complex interactions of ecological processes within a wetland determine its dominant functions and dictate the ecosystem services provided by both it and the surrounding terrestrial and aquatic habitats. For example, the functioning of fringing lacustrine wetlands (*e.g.,* wet woodlands and marsh) can have a strong influence upon the ecosystem services provided by the whole lake (Ostendorp, 1993; Weller *et al.*, 1996; Carpenter and Cottingham, 1997; Schmieder, 2004).

The shore and littoral zones of lakes have much in common (*e.g.,* processes, functions, and services) with other types of wetland, however, they also dissipate wave energy (Strayer and Findlay, 2010). Lake shore ecotones (areas immediately above and below the mean water line) are commonly described as 'marsh' dominated wetlands (Ostendorp, 2004). 'Marsh' wetlands are shallow and typically dominated by emergent plants (*e.g., Phragmites australis* (Cav.) Trin. and *Typha angustifolia* (L.)) which are rooted in hydric soils (Keddy, 2010). Emergent vegetation may extend from the shore further into the lake (*i.e.,* the littoral zone) (Ostendorp, 2004). Areas of marsh located upon the shore that are not permanently inundated (*i.e.,* mean summer water table is at or below the substratum) are commonly referred to as 'fen' (Wheeler, 1978; Boorman and Fuller, 1981).

Within the littoral zone permanently inundated marsh communities dominated by the common reed (*Phragmites*) are commonly referred to as 'reedswamp' (Gilman, 1994; Rodwell, 1995), even though the term 'swamp' is often used to describe a different type of wetland. In this review, the term 'reedswamp' is used to refer to permanently inundated reedbeds located within the littoral zone. As water deepens, emergent plants are replaced by submerged plants (*i.e.,* 'reedswamp' marsh is succeeded by 'shallow water' wetland) (Keddy, 2010).

'Shallow water' wetland communities are found at depths in excess of 25 cm and dominated by truly aquatic macrophytes (*e.g.,* the submerged macrophyte *Elodea canadensis* Michx.). Hence, stands of reeds located around shore zones appear as narrow strips and when the circumference of a lake is dominated by reeds, a reed belt or fringe is produced. Other common littoral zone habitats include: coarse woody debris (CWD), tree roots, sand, and stones (White and Irvine, 2003; Gabel *et al.*, 2008; Schreiber and Brauns, 2010). The littoral zone ends at the point where the water is too deep for submerged plants to grow (Ostendorp, 2004).

The term 'reed' is commonly used to refer to *Phragmites* spp. (Ditlhogo *et al.*, 1992; Varga, 2001; Okun and Mehner, 2005; Sahuquillo *et al.*, 2008; Sychra *et al.*, 2010; Schreiber and Brauns, 2010; RSPB, 2011). *Phragmites* is a robust deciduous reed with tall annual cane-like shoots and an extensive perennial rhizome system (Haslam, 1972; Brix, 1999b). Taxonomy of the *Phragmites* genus is highly complex and lacks consensus; however, from a European perspective *P. australis, sensu lato* can be considered to be the only species (Haslam, 2010). The high phenotypic variation observed in the morphological and life history traits of *Phragmites* has been attributed to variations in chromosome numbers, clonal diversity, and plasticity of clones (Clevering and Lissner, 1999). Phenotypic plasticity occurs when a single genotype responds to the environment by producing at least one alternative form (West-Eberhard, 1989), for example, the response of *Phragmite*s to changes in water depth. Vretare *et al*. (2001) observed that in deep water (70–75 cm) shoots were fewer but taller, with the net effect of more resources being allocated to the shoots than the rhizomes. As a result, deep water reeds have relatively low growth and dispersal rates and are susceptible to being uprooted (Vretare *et al.*, 2001).

High phenotypic plasticity combined with effective vegetative reproduction allows *Phragmites* to spread relatively quickly and to colonise a wider range of niches within still waters compared to many other emergent species (*e.g., T. angustifolia*) (Haslam, 1971b). Consequently, *Phragmites* is common in many shallow lakes and the dominant type of vegetation of the littoral zone of lakes (Sahuquillo *et al.*, 2008), occurring as large mono-cultures or as stands of mixed species in natural habitats (Hocking *et al.*, 1983). In North America and Australia the rapid expansion of non-native exotic genotypes means that *Phragmites* is regarded as an invasive weed (Tscharntke, 1999; Saltonstall, 2002). However, within Europe, *Phragmites* habitat (including reedswamp) is in decline (Ostendorp, 1989). Concern regarding changes in reedbed dominance (mostly *Phragmites*) has prompted extensive research programmes across the globe. For example, several high profile European Union projects (*e.g.,* 'Eureed' and 'Bringing Reeds to Life') have investigated the biogeochemistry and ecology of *Phragmites* stands (van der Putten, 1994; Brix, 1999b).

Until recently, the ecological assessment of lakes typically focused upon the analysis of water chemistry and phytoplankton within the open water (pelagic) zone (White and Irvine, 2003). The success of approaches developed for assessing running water habitats over past decades have had a strong influence upon the ways in which lakes are now being investigated. Within running waters, functional and biological trait approaches based mainly upon fish or macroinvertebrate data are well established (Poff, 1997; Dolédec *et al.*, 1999; Tachet *et al.*, 2000; Lamouroux *et al.*, 2004; Poff *et al.*, 2006). Compared to running waters, there are relatively few examples of this is approach being applied to still waters.

The majority of functional studies of lakes and ponds have focused on macroinvertebrate traits (Mason and Bryant, 1975b; Dvořák, 1996; Tolonen *et al.*, 2003; Johnson *et al.*, 2004; Heino, 2008; Bazzanti *et al.*, 2009). One of the earliest accounts of macroinvertebrates traits within still water littoral habitats was by Moon (1936). Moon (1936) found that functional traits of aquatic macroinvertebrate species explained the distribution of such species across structurally distinct habitats (including reedswamp) within the littoral zone of Windermere (UK). Mason and Bryant (1975b) pioneered the use of macroinvertebrate traits in the investigation of ecosystem functioning. Specifically Mason and Bryant (1975b) investigates the influence of reedswamp habitat on the functioning of a lake ecosystem. A key aspect of reedswamp macro functionality observed was the role of different species of macroinvertebrate in the breakdown of reed litter and the consequential nutrient and carbon cycling within the whole lake.

2.2.1 Reedswamp structure and functioning

Any permanently inundated wetland area dominated by tall (~1–8 m) grasses with stems that are either leaf-like or tubular with flat leaves can be described as reedswamp (Haslam, 2010). Gorham (1953) used the term to describe areas of emergent vegetation on the fringes of Windermere (UK). The emergent macrophytes *Phragmites australis* (Cav.) Trin., *Typha latifolia* (L.), *Typha angustifolia* (L.), *Schoenoplectus lacustris* (L.) and *Equisetum limosum* (L.) dominated these reedbeds. Within the littoral zone of a single lake there can be significant variation in reedswamp structure that can be characterised by differences in substratum and reed structure (Figure 2.1). Prefixing the term swamp with generic names such as *Typha* or *Phragmites* adds biological information to a broad category of habitat. In addition, Wheeler and Proctor (2000) advised that this also may avoid confusion, particularly with workers from the USA where the term ‘swamp’ may have a different meaning. For example, Keddy (2010) defined swamp as a tree dominated wetland with soil (not peat) saturated with water. In contrast, Gorham (1953) described the substrate of reedswamp along the shore of lakes as inorganic to peaty.

Reed dominated wetlands are both sinks and sources of greenhouse gases; the plants assimilate CO_2, while the sediments release methane to the atmosphere through decomposition. However, the net effect on global climate is yet to be understood (Asaeda and Karunaratne, 2000). Most of the primary production in littoral habitats can be attributed to reedswamp forming species such as *Phragmites* and *T. angustifolia* (Kuehn and Suberkropp, 1998). Detailed comparative studies of primary productivity between different lacustrine littoral habitats (*e.g.,* reedswamp versus submerged macrophyte beds) are lacking. This is an important gap in our knowledge of lake functioning given the different ways in which habitats influence primary

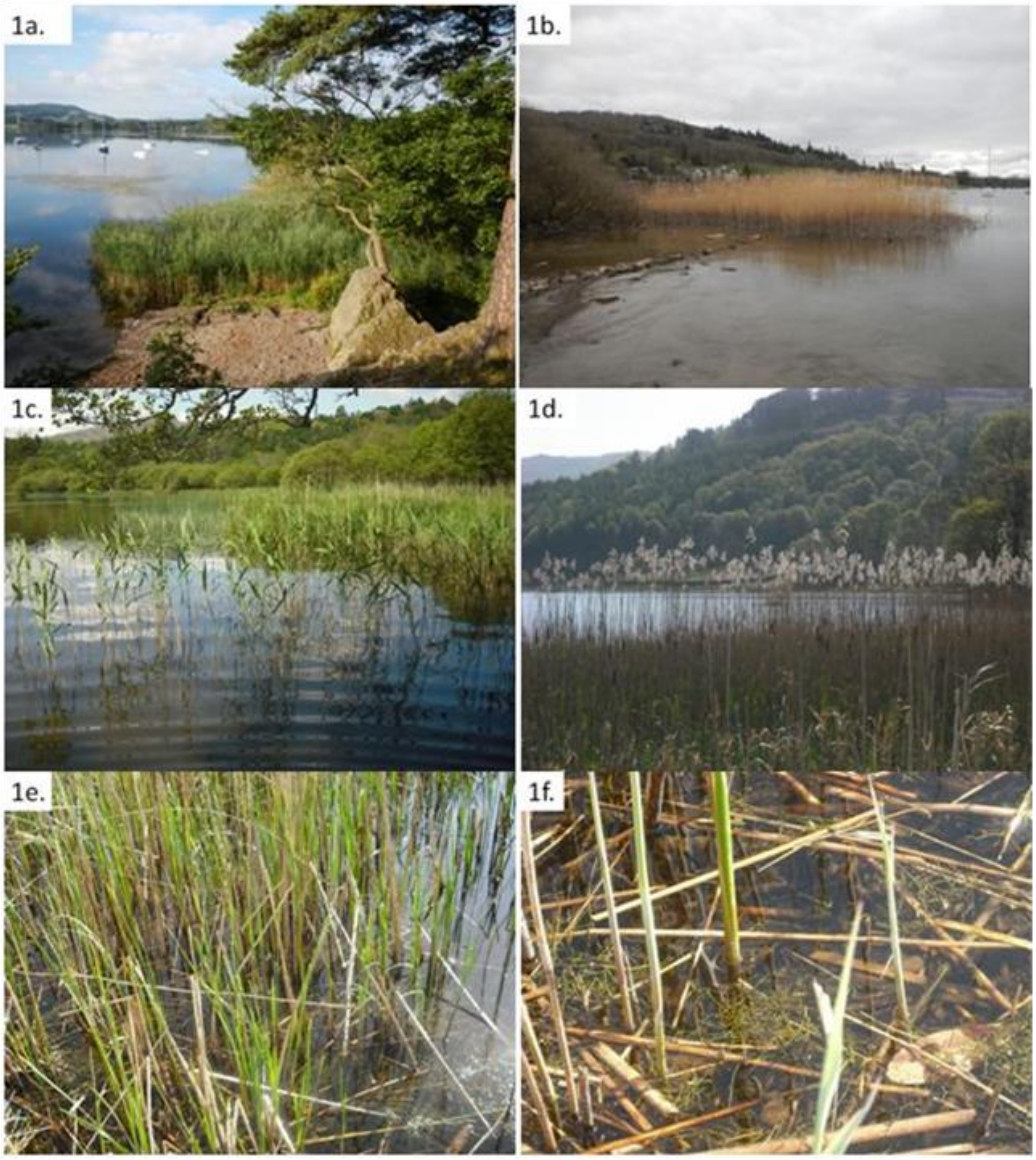


Figure 2.1 Photographs of a variety of different reedswamp habitats located within the Windermere catchment, UK. (a) *Phragmites* reedswamp (the wetted area of reedbed) growing from a consolidated bed of cobbles, (b) *Phragmites* reedswamp growing from a stable bed of stones with a thick layer of overlaying silt, (c) small patch of *Phragmites* reedswamp growing from a very silty and soft sinking bed, (d) mixed (*T. angustifolia* and *Phragmites*) reedswamp growing in a silty and soft sinking area, (e) a patch of *T. angustifolia* that is part of an extensive mixed swamp (*T. angustifolia* and *Phragmites*) growing from a deep and soft sinking substratum dominated by silt and well rotted reed detritus, and (f) the reed detritus dominated substratum of a mixed reedswamp.

productivity. For example, epiphytic algal productivity per unit of macrophyte surface area is significantly lower for emergent macrophytes compared to submerged macrophytes (Allen, 1971; Kajak *et al*., 1972).

At the end of the growing season reeds die-back, leaving behind stands of dead shoots which may persist for a couple of years (Komínková *et al*., 2000). Compared to other macrophytes, reed species vary in their time of death and in their susceptibility to decomposition, for example, *Phragmites* detritus has a much slower decomposition rate than that of submerged plants (Pieczyńska, 1993). In addition, there is significant variation between reed species. For example, Mason and Bryant (1975b) found that within reedswamp habitat, *Phragmites* leaf litter decomposed at faster rate than leaves of *T. angustifolia*. Shed leaves and broken stems fall from the shoots, while wave action transports this reed detritus from deeper parts of the littoral zone to the lake margins (Pieczyńska, 1993). Due to the large volume of deposited reed litter, reedswamps are considered to be predominantly detritus-based ecosystems (Komínková *et al.*, 2000). In addition, reed shoots make an indirect contribution to primary production by providing a vertical substrate for epiphyton (Jones *et al.*, 1994) upon which grazing macroinvertebrates feed (Mason and Bryant, 1975a; Cattaneo, 1983; Lodge, 1985).

Phragmites beds can have a number of important positive impacts upon the lentic environment (Ostendorp, 1993). *Phragmites* stems are less susceptible to fragmentation due to wind and wave action than *Typha* and *Schoenoplectus*, and even dead shoots play a significant role in bank protection. *Phragmites* is more tolerant of inundation than other herbaceous marsh plants and willow, while its ability to ameliorate waste water above ground level is similar to that of other nitrophilic marsh macrophytes, its deep lying roots and rhizomes enable it to purify water deeper in the substratum than other plants (Ostendorp, 1993). *Phragmites* is equally important in the protection of rare species, as many phytophagous species and breeding birds depend exclusively on *Phragmites* compared to other species of emergent macrophyte.

2.2.2 Reasons for reedswamp decline

The decline of *Phragmites* in Europe has been attributed to various factors that are mainly anthropogenic in nature. Some workers include eutrophication as a significant stressor (Čížková-Končalová *et al.*, 1992), whereas others have suggested that eutrophication is conducive to the development of reedbeds (Andersen, 1976). There is also evidence of no ‘general’ relationship between eutrophication and reed die-back in lakes (Ostendorp, 1989). However, significant changes in the life history, physiology, and morphology of *Phragmites* have been associated with excessive levels of nitrogen (Dinka, 1986; Boar *et al.*, 1989; Clevering, 1998). These changes may have contributed to structural instability and the loss of reedbed coverage (Kuhl and Kohl, 1993).

Other factors associated with the decline include: damage by waves or animals (Sukopp and Markstein, 1989), altered water tables (Rea, 1996), fungal disease (Armstrong *et al.*, 1996a), phytotoxins released from sediments (Kovács *et al.*, 1989), and human shore-line development

(Brauns *et al.*, 2007b). A lack of genetic diversity may be responsible for susceptibility to die-back and/or perpetuating it (Armstrong *et al.*, 1996b). Shorter shoots of *Phragmites* may grow slowly or die when exposed to drought, flood, frost, or high levels of salt and this may lead to displacement by other macrophyte species (Haslam, 1971c). Despite the extensive *Phragmites* literature, no single theory can explain the many incidences of *Phragmites* decline (Ostendorp, 1999). This may be because there is no universal/consistent reason for reed loss. Rather than searching for a single explanation, the focus needs to be on developing both diagnostic and predictive techniques and models.

2.2.3 Consequences of reedswamp decline

Ostendorp *et al*. (1995) suggested that as a consequence of reed decline, a cascade of events could result in a possible decline of the littoral community, consisting of: (1) impacts upon important littoral and bank-side habitats as a consequence of erosion due to loss of bank protection, (2) loss of bird species and changes in fish community structure, and (3) changes in the structure and functioning of the whole lake. To understand the impact of habitat loss, it is necessary to consider the extent (area) and pattern (*e.g.,* small or large fragments) of the loss. The impact of these changes upon the structure and functioning of the community is related to the dependency of species upon the original condition of the habitat.

Habitat fragmentation occurs when a loss of habitat reduces connectivity of that particular habitat (Fahrig, 2003). However, there have been very few investigations into the effects of reedbed fragmentation within the littoral zones of lakes. Tscharntke (1992) described seven different types of fragmentation effect within *Phragmites* reedbeds (*e.g.,* reduction in bed size and various changes in shoot morphology). The responses of populations of moths, midges, flies, aphids, and nesting birds to the different effects of fragmentation have been investigated. For example, Tscharntke (1992) found that thirteen species of nesting bird each had different requirements for habitat size (*e.g.,* species specific minimum areas). Báldi and Kisbenedek (1999) investigated the spatial distribution of breeding passerine birds within reedbeds in Hungary. At the landscape scale there were no detectable differences between the interior of reedbeds and their edges with regard to species diversity. However, analysis at the local scale revealed that individual species varied in density between the interior of reed beds and their outer edge habitat.

Fragmentation and its associated ‘edge effects’ have emerged as critical research areas in conservation ecology (Soulé and Kohm, 1989). Murcia (1995) described the edge effects of fragmentation as the abrupt separation of two adjacent ecosystems that brings about an interaction between the two ecosystems. Little is known about the impact of fragmentation and the associated edge effect upon metapopulations, especially with regard to reedbeds. Tscharntke (1992) concluded that fragment area alone could not explain impact upon reedbed moths, midges, flies and aphids, and birds. The degree of edge within a patch is determined by its shape and size, and thus if a remnant patch continues to shrink the proportion of edge also increases. Baldi (1999) investigated the microclimate and vegetation structure of reedbed edges, concluding that species extinctions from edge effects could not be predicted due to the large degree of variation observed. Given that wetlands are declining at a rate faster than any other habitat worldwide, it is surprising that there is a lack of reedbed edge data (Williams, 1990). Baldi and Kisbenedek (1999) concluded that further examination of the structure and width of edges in reedbed and other habitats may contribute significantly to the management of fragmented landscapes (Báldi and Kisbenedek, 1999). Hence, there is clear need to understand the influence of reedswamp loss and fragmentation upon their aquatic macroinvertebrate assemblages.

2.3 Macroinvertebrate functioning

The wide range of habitat types and food resources within the littoral zone of lakes produces a highly diverse macroinvertebrate fauna (Tolonen and Hamalainen, 2010). Given the importance of macroinvertebrates within the littoral zone, the analysis of their traits over space and time has the potential to identify functionally distinct mesohabitats (structurally distinct patches). Within a single reedswamp, there are likely to be significant differences in macroinvertebrate functioning in both space (vertical and horizontal) and time (Dvořák and Best, 1982; Sipkay *et al.*, 2007; Mancinelli *et al.*, 2007; Sychra *et al.*, 2010). The cumulative effect of localised macroinvertebrate functioning determines their contribution to the macro functioning of the whole reedswamp. It is rare for studies to estimate the macro functioning of macroinvertebrates within reedswamps. The majority of studies have focused on particular functional groups (*e.g.,* macroinvertebrate shredders) at a limited number of specific locations within reedswamps (*e.g.,* detritus overlaying the substratum at the centre of the reedswamp).

Most published studies of macroinvertebrate functionality within lacustrine fringing reedswamps have been located within Europe and these have been limited to a small number of reedswamps, lakes and countries (Figure 2.2). The aims of the majority of investigations that have included descriptions of the aquatic macroinvertebrate assemblages of reedswamps have focussed on investigating spatial differences in macroinvertebrate community structure within the littoral zones of whole lakes rather than on reedswamp functioning. Studies that include relatively large numbers of lakes (>10) have focused on structural rather than functional heterogeneity within the littoral zone (Figure 2.2). In order to place the findings of these studies into a broader context (*e.g.,* macro functionality) it is necessary to consider other functional studies (*e.g.,* studies of macroinvertebrate functioning within reedswamps of saline lagoons). In addition, studies that compare the macroinvertebrate assemblages of reedswamps to other habitats (*e.g.,* CWD) within the littoral zones of lakes can also provide valuable information about macro structure and functionality.

Invertebrate consumers are vital links between primary producers and various predators. They also influence the decomposition rates of organic matter (*e.g.,* reed detritus) and the translocation and cycling of nutrients (Murkin and Wrubleski, 1988). Other important regulatory functions of invertebrate consumers include the regulation (inhibition or facilitation) of rates of succession, transport of materials, and the physical restructuring of ecosystems (Jones *et al.*, 1994). Several studies have demonstrated that interactions between host macrophytes, their epiphyton, and associated macroinvertebrates are closely linked (Papas, 2007). Macroinvertebrates obtain food from their host by feeding directly upon its living material, epiphyton, and/or detritus (Urban, 1975; Kornijów *et al.*, 1990; Bedford, 2004). These close links between macroinvertebrates and macrophytes are enhanced by the provision of refuge and sites for oviposition (Rooke, 1984; Scheffer, 2004). The relationship between macroinvertebrates and littoral zone macrophytes has been widely studied but most of this work has focused upon submerged macrophytes (*e.g., Elodea* species) rather than emergents. However, some studies have focused upon reedswamp forming species *(e.g., Typha* species and *Phragmites*) and their associated macroinvertebrates (Polunin, 1982; Oertli and Lachavanne, 1995; Canedo-Arguelles and Rieradevall, 2009).

2.3.1 Herbivores

The impact of aquatic macroinvertebrate herbivores upon living reed tissue is thought to be minimal (Imhof, 1973; Skuhravy, 1978); however, reeds do provide herbivores within an important food resource. Reeds and their associated epiphyton create habitat that shapes their epiphytic macroinvertebrate community (Canedo-Arguelles and Rieradevall, 2009). For example, Oertli and Lachavanne (1995) studied the colonisation dynamics of macroinvertebrates upon the vertical shoots of *T. latifolia* within a pond in Switzerland. They found that age related changes in reed structure (*e.g.,* shoot morphology and the ratio of live to dead tissue), along with associated changes in epiphyton, had an influence upon their epiphytic macroinvertebrate communities (Oertli and Lachavanne, 1995). Vertical *Phragmites* shoots (living or dead) provide a relatively stable environment for epiphytic diatoms (Grimes *et al.*, 1980) and other components of the epiphyton (*e.g.,* green algae). Epiphytic photo-autotrophs (*e.g.,* diatoms and green algae) are significant contributors of epiphyton productivity and provide macroinvertebrate consumers with optimal nutrition (Mazumdlr *et al.*, 1989; Hann, 1991).

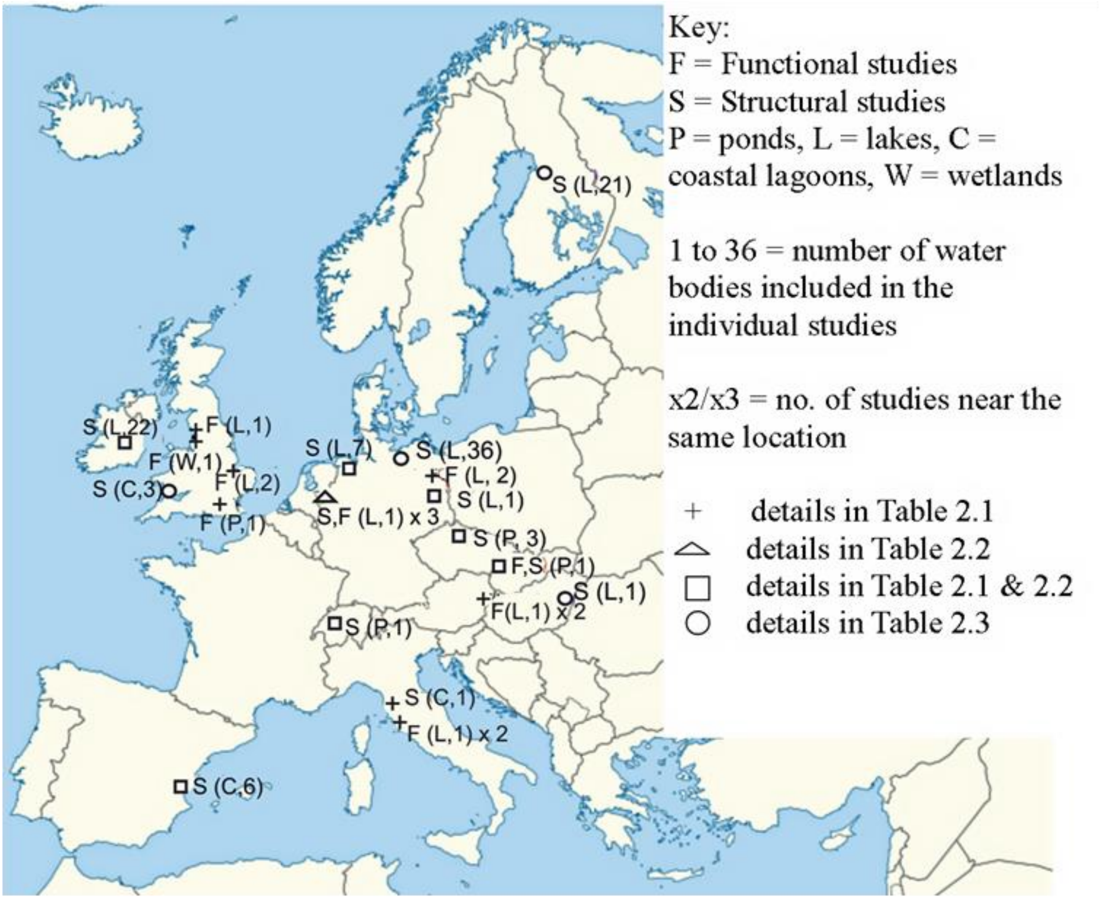


Figure 2.2 Map of Europe illustrating the distribution of key studies that featured descriptions of macroinvertebrate assemblages within reedswamp habitat. Details of these studies are contained within Tables 2.1, 2.2, and 2.3.

Table 2.1 This table summaries studies that focussed upon benthic macroinvertebrate assemblages within reedswamp habitat (*T. ang* = *Typha angustifolia*, *Phrag* = *Phragmites australis,* Oligo = oligotrophic, Meso = mesotrophic, Eu = eutrophic, N/S = Not stated, N/A = Not applicable, and QNT = quantitative)

Research topic	Country	Waterbody type with quantity in brackets	Habitat	Trophic status	Macro-invertebrate groups	Method with sample type in brackets	Reference
Decomposition of reed litter	UK	Artificial Lakes (2)	*T. ang* and *Phrag* swamp	Eu	Diverse	Litter bag (QNT)	Mason and Bryant (1975b)
Decomposition of reed litter	UK	Artificial Pond (1)	*Phrag* swamp	Oligo	Arthropods and Insecta	Litter bag (QNT)	Polunin (1982)
Decomposition of reed litter	Italy	Lake (1)	*Phrag* swamp	Meso	Diverse	Litter bag (QNT)	Sabetta *et al.* (2000)
Decomposition of reed litter	Nether-lands	Lake (1)	*Phrag* swamp	Meso	Gammarids	Litter bag (QNT)	van Dokkum *et al.* (2002)
Decomposition of reed shoot and rhizome detritus	Austria / Hungary	Lake (1)	*Phrag* swamp	Meso	Diverse	Litter bag (QNT)	Varga (2001) (2003)
Decomposition of leaf litter: the influence of flooding upon litter breakdown	UK	Managed Wetland (1)	*Phrag* beds during periods of wetted and dry	N/S	Diverse	Litter bag (QNT)	Bedford and Powell (2005)
Influence of fish predation upon detritivorous macro -invertebrates	Italy	Lake (1)	*Phrag* swamp	Meso	Diverse	Litter bag (QNT)	Mancinelli *et al.* (2002)
Influence of habitat structure upon macro -invertebrate community structure	UK	Lake (1)	Various including *Phrag* swamp and stony substratum.	Oligo	Diverse	Scoop (QNT)	Moon (1936)
Macro -invertebrate assembly in a patchy environment	Italy	Saltern (1)	*Phrag* swamp	N/S	Diverse	Litter bag (QNT)	Bellisario *et al.* (2010)
Reedswamp habitat: a refuge from ship induced waves for benthic fauna	N/A	Wave tank	Various littoral zone habitats including *Phrag* swamp	N/A	5 benthic species	N/A	Gabel *et al.* (2008)
Sample size guidance for macro-invertebrate sampling with lake littoral zones	Germany	Lakes (2)	Various littoral zone including *Phrag* swamp	Oligo – Meso	Diverse	Hand net (QNT)	Schrieber and Brauns (2010)

Table 2.2 This table summarises studies of macroinvertebrates assemblages that were closely associated (attached and free swimming) with reed shoots. (*T. ang* = *Typha angustifolia, T. lat* = *Typha latifolia, Phrag* = *Phragmites australis,* Oligo = oligotrophic, Meso = mesotrophic, Eu = eutrophic, Hyper = Hypertrophic, N/S = Not stated, QNT= quantitative, S-QNT = semi-quantitative, and QLT = qualitative)

Research topic	Country	Waterbody type with quantity in brackets	Habitat	Trophic status	Macro-invertebrate groups	Method with sample type in brackets	Reference
Influence at the mesohabitat scale	Ireland	Lakes (22)	Range of habitats including *Phrag* swamp	Oligo – Eu	Diverse	Hand net (QNT)	White and Irvine (2003)
Distribution of taxa and functional groups along environmental gradients	Czech Republic	Fish Pond (1)	*Phrag* swamp	Hyper	Diverse	Hand net (S-QNT)	Sychra *et al.* (2010)
Distribution of taxa and functional groups along environmental gradients	Spain	Coastal Wetlands (6)	*Phrag Swamp*	Oligo – Hyper	Diverse with focus upon Chironomids	Narrow plastic tube (QNT)	Sahuquillo *et al.* (2008)
Relationship between phytophilous macro-invertebrates and their food resources	Nether-lands	Lake (1)	Various littoral zone habitats including *T. ang* and *Phrag* swamp	Eu	Diverse with focus upon Chironomids .	Hand net (QNT)	Dvorak (1996)
Influence of macrophytes structure upon macro-invertebrates	Nether-lands	Lake (1)	Various macrophytes including *Phrag* and *T. ang*	Eu	Diverse	Hand net + Scuba diving (S-QNT)	Dvorak and Best (1982)
Influence of shoot age upon epiphytic macroinvertebrate communities	Switzer-land	Artificial Pond (1)	*T. lat swamp*	Eu	Diverse	Enclosure device (QNT)	Oertli & Lachavanne (1995)
Influence of shoreline development	Germany	Lakes (7)	Various littoral zone habitats including *Phrag* swamp	Meso– Hyper	Diverse	Hand net (QNT)	Brauns *et al.* (2007b)
The feeding of juvenile fish on macro- and micro-invertebrates within reedswamp habitat	Germany	Lake (1)	*Phrag* swamp and open habitats	Eu	Diverse	Core sampler (QNT) and fish gut contents analysis (QLT)	Okun and Mehner (2005)

Table 2.3 This table summarises studies that used a single (combined) sample method to collect macroinvertebrates from the substratum, reed shoots and associated water column. (*T. ang = Typha angustifolia; Phrag = Phragmites australis*, Oligo = oligotrophic, Eu = eutrophic, Hyper = Hypertrophic, N/S = Not stated, QNT = quantitative, and S-QNT = semi-quantitative)

Research topic	Country	Waterbody type with quantity in brackets	Habitat	Trophic status	Macro-invertebrate groups	Method with sample type in brackets	Reference
The influence of reedswamp structure	North America	Coastal wetland (1)	*Phrag* and *T. ang* swamp	Hyper	Diverse	Throw trap (QNT)	Kulesz *et al.* (2008)
Distribution of taxa and functional groups along environmental gradients	UK	Coastal wetlands (3)	*Phrag* swamp	N/S	Diverse	Hand net (S-QNT)	Arnold and Ormerod (1997)
Distribution of taxa and functional groups along environmental gradients	Finland	Lakes (21)	Range of meso-habitats including *Phrag* swamp	Oligo–Eu	Diverse	Hand net (QNT)	Heino (2000)
Seasonal dynamics	Hungary	Lake (1)	*Phrag* and *T. ang* swamp	Eu	Diverse	Hand net (S-QNT)	Sipkay *et al.* (2007)
Influence of trophic state upon macro-invertebrates	Germany	Lakes (36)	Range of meso-habitats including *Phrag* swamp	Oligo–Hyper	Diverse	Hand net (S-QNT)	Braun *et al.* (2007a)

The changing nature of epiphytic food resources has a strong influence on the structure of phytophilous macroinvertebrate communities (Russo, 1988). Seasonal changes in photosynthetically active radiation (PAR) strongly influence epiphytic photo-autotrophs. For example, within a eutrophic lake in Germany the biovolume of the algal epiphytic community associated with *Phragmites* was dominated by diatoms for most of the year (Müller, 1994). However, a number of important seasonal changes were observed: (1) during late spring or early summer (while PAR was at its peak) chlorophytes (green algae) displaced diatoms; (2) during autumn and winter, closely attached diatoms and chlorophytes became dominant; and (3) at other times of the year loosely attached species dominated (Müller, 1994). The shoot age of emergent macrophytes is another seasonal influence upon the epiphyton; for example, it influences the colonisation and subsequent succession of protozoa and algae upon new shoots (Oertli and Lachavanne, 1995). Competition with phytoplankton for nutrients and light (Vannote *et al.*, 1980; Kairesalo, 1984; Meulemans, 1988) influences the biovolume and structure of epiphyton. A decline in epiphyton productivity within a macrophyte stand can increase the importance of phytoplankton as a food resource for phytophilous macroinvertebrates (Dvořák, 1996). An increase in the ratio of phytoplankton (or suspended detritus derived from phytoplankton) to epiphyton may result in changes in the structure and functioning of macroinvertebrate communities, for example, the displacement of grazers by filter-feeders (Dvořák, 1996).

A combination of environmental conditions and selective grazing by macroinvertebrates influences the structure of epiphyton (Summer and McIntire, 1982). Epiphytic macroinvertebrates (*e.g.,* chironomids, oligochaetes, trichopterans and molluscs) may change the community composition of algae within the epiphyton (Hill and Knight, 1987; Lamberti *et al.*, 1995). For example, grazed epilithic diatoms communities are often dominated by low profile and/or small diatoms, due the removal of larger and/or stalked taxa by grazers (Dickman, 1968; Summer and McIntire, 1982). Differences in selective digestion of algae between different macroinvertebrate species can also alter the community structure of the phytobenthos (Peterson, 1987). Within lotic systems the main mechanism for the redistribution of digested (but still viable) diatoms is likely to be downstream drift. However, within lentic reedswamps, the main direction of travel for excreted diatoms is likely to be from the vertical shoots of reeds down to the substratum. Wave action is likely to redistribute any faecal material that is located near the surface of the substratum. Viable diatoms within the faeces (and dead bodies) of epiphytic macroinvertebrates provide a potential food source for the microbial and detritivorous community (Varga, 2001) rather than acting as a food for grazers or filter-feeders.

2.3.2 Detritivores

The ingestion of *Phragmites* detritus by macroinvertebrates is much more prevalent than feeding directly upon the living plant (Imhof, 1973; Skuhravy, 1978). *Phragmites* leaf detritus plays a vital role in supporting the benthic communities of shallow lakes (Sabetta *et al.*, 2000; Mancinelli *et al.*, 2006). For example, Mancinelli *et al*. (2006) used stable isotope analysis to establish that key trophic contributions were made by the ingestion of *Phragmites* leaf litter by crustaceans, gastropods, and dipterans. Hence, the breakdown of detritus by macroinvertebrates forms part of the main pathway for nutrient and carbon cycling of reedswamp macrophyte tissue within the water column (Imhof, 1973; Skuhravy, 1978). However, detritivorous macroinvertebrates generally have low assimilation efficiencies and utilise the microbes associated with detritus rather than the plant material it ingests (Mackay and Kalff, 1973; Cummins, 1973). Hence, it is the decomposer (microbial) community associated with reed litter that supports macroinvertebrate detritivore communities within reedswamps (Polunin, 1982).

When macroinvertebrates feed upon detritus they expose new surfaces suitable for microbial colonisation (Hargrave, 1970; Howe and Suberkropp, 1994). The influence of different macroinvertebrate taxa upon the decay of *Phragmites* litter in the lentic freshwater environment is highly variable (Mason and Bryant, 1975b; Polunin, 1982). Using a combination of laboratory and field experimentations, Polunin (1982) investigated the processes responsible for the decay of *Phragmites* detritus within a freshwater pond in England. Polunin (1982) found the following: (1) decomposition was closely correlated with breakdown by macroinvertebrates; (2) the abilities of macroinvertebrate species to increase leaf litter breakdown was wide ranging; and (3) some invertebrates (*e.g., Limnephilus marmoratus* Curtis) shredded litter, whereas other species (*Bithynia tentaculata* (L.), *Planorbis carinatus* Muller, *Crangonyx pseudogracilis* Bousfield and *Asellus meridianus* Racovitza) influenced breakdown by the removal of veins and fibres. Hence, the rate of decomposition of plant litter is influenced strongly by the structure of macroinvertebrate communities (Mason and Bryant, 1975b; Carpenter and Adams, 1979; Bärlocher, 1990).

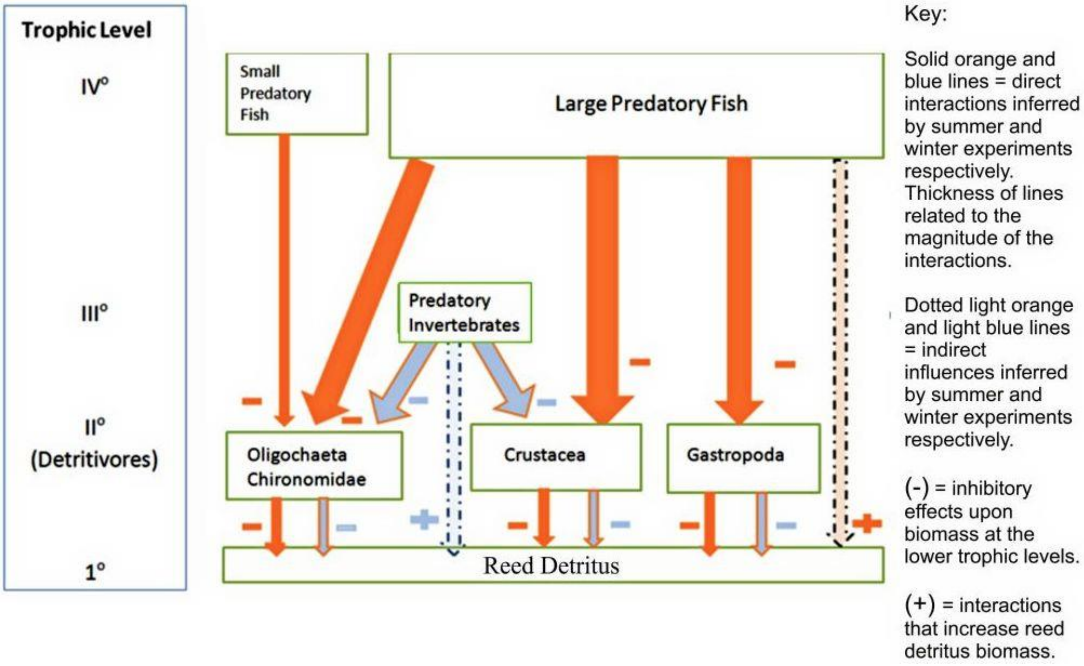
When considering data collected from inundated reed detritus, it is important to distinguish between permanently flooded (reedswamp) and temporarily flooded (fen) habitat. Given the scarcity of published accounts of detritivores within reedswamp, it may be useful to consider data relating to reedbeds that are not permanently wetted. Bedford and Powell (2005) carried out a long-term study into changes in aquatic macroinvertebrate assemblages within *Phragmites* detritus in a reedbed located at Leighton Moss (UK). The reedbed benthos experienced a cycle of dry and wet which was related to seasonal changes in climate and management of water levels. Many of the taxa recorded at this reedbed (fen rather than reedswamp) have also been recorded from within UK reedswamp habitat (Moon, 1936; Mason and Bryant, 1975b; Polunin, 1982). Hence, existing data may be used to increase our understanding of the influence of long-term inundation upon the functionality of detritivorous communities.

2.3.3 Macroinvertebrates - a food resource for predators

The consumption of invertebrates by fish and other predators plays an important role in the cycling and translocation of carbon and nutrients within lakes. Fish excrete nutrients in a dissolved form suitable for uptake by primary producers, and compared to many other aquatic animals, are able to transport nutrients rapidly over wide areas (Vanni, 2002). However, the majority of studies into fish structure and functioning within lakes have concentrated upon pelagic rather than littoral habitats (mainly stands of submerged macrophytes) (Lewin *et al.*, 2004). Structurally complex and dense habitats (*e.g.,* beds of submerged macrophytes, reedswamps, and woody debris) provide refuge for the following: (1) large zooplankton species from pelagic planktivorous fish (Timms and Moss, 1984; Lauridsen and Buenk, 1996; Burks *et al.*, 2001); (2) benthic and epiphytic macroinvertebrates from predators (including fish) (Rooke, 1984; Scheffer, 2004; Papas, 2007); and; (3) juvenile planktivorous fish from visual predators (Bean and Winfield, 1995; Lewin *et al.*, 2004; Pelicice *et al.*, 2008; Teixeira-de Mello *et al.*, 2009; Li *et al.*, 2010). Okun & Mehner (2005) suggest that the main influence of reedswamp habitat upon juvenile fish communities is the provision of food rather than refuge from predation. Unfortunately, studies of the complex relationships between fish and their prey within reedswamps are rare (Lauridsen and Buenk, 1996; Nurminen and Horppila, 2002; Lewin *et al.*, 2004; Okun and Mehner, 2005).

Studies on the feeding behaviour of fish within European reedswamps have focussed on juvenile stages of perch (*Perca fluviatilis* L.) and roach (*Rutilus rutilus* (L.)), the dominant fish species within the littoral zones of many European lakes. Within complex habitats in the littoral zones of lakes, the feeding of juvenile perch and roach can have a strong influence upon the diversity and biomass of benthic macroinvertebrate assemblages (Lewin *et al.*, 2004; Okun and Mehner, 2005). Okun and Mehner (2005) studied the feeding habits and behaviour of roach and perch communities within a shallow, eutrophic, and polymictic lake in Germany. Roach dominated both reedswamp (*Phragmites*) and open water habitats, but during the daytime juveniles of both species demonstrated a preference for reedswamp habitat. The diel movement of juvenile fish into reedswamp during daylight may have been a way of avoiding visual predators, mainly piscivorous birds. As with studies in other complex lentic littoral habitats (Lewin *et al.*, 2004) the diet of roach was dominated by zooplankton, whereas macroinvertebrates were more prevalent in perch diets. Diel fluctuations in dissolved oxygen within dense stands of emergent vegetation during warm periods within the temperate zone have also been shown to be capable of having a strong influence upon the diel migrations of perch (Suthers and Gee, 1986). This may have been due to a direct influence upon the fish or their free swimming macroinvertebrate prey.

Mancinelli *et al.* (2002) investigated the influence of predatory fish (*e.g.,* juvenile perch) upon benthic macroinvertebrate assemblages associated with *Phragmites* leaf litter located in the littoral zone of a volcanic lake (Lake Vico) in central Italy. They tested the hypothesis that detritus based food webs located within stands of *Phragmites* would consist of four trophic levels as follows: (1) predatory fish, (2) predatory invertebrates, (3) detritivorous invertebrates, and (4) detritus. During the summer months, high numbers of predatory fish fed extensively upon detritivorous macroinvertebrates. In comparison, the impact of fish predation on predaceous macroinvertebrate communities during the summer months was minimal. Experimental evidence (including fish exclusion experiments) indicated that there was a fish-induced trophic cascade which had a strong influence upon the processing and fungal conditioning of reed detritus (Mancinelli *et al.*, 2002). Additional studies revealed that during the winter months there was a significant reduction in the number of predatory fish (compared to the summer), and as a result, predatory macroinvertebrates exerted a stronger influence upon their detritivorous prey compared to fish (Mancinelli *et al.*, 2007). Mancinelli *et al*. (2007) concluded that predators (fish in the summer and macroinvertebrates in the winter) exerted top-down control over detrital breakdown within a food web consisting of these three trophic levels: (1) fish (summer months) or invertebrate (winter months) predators; (2) detritivorous invertebrates, and; (3) detritus (Figure 2.3). The generality of these findings remains to be determined for reedswamps in other locations.



Key:

Solid orange and blue lines = direct interactions inferred by summer and winter experiments respectively. Thickness of lines related to the magnitude of the interactions.

Dotted light orange and light blue lines = indirect influences inferred by summer and winter experiments respectively.

(-) = inhibitory effects upon biomass at the lower trophic levels.

(+) = interactions that increase reed detritus biomass.

Figure 2.3 This figure illustrates a conceptual model of how predation may influence the breakdown of reed detritus within a reedswamp in Lake Vico (central Italy) (modified from Mancinelli *et al*. [2007]). It suggests that the relative influence of different categories of predators may shift between the summer and winter months.

2.3.4 The influence of habitat heterogeneity upon macroinvertebrates within reedswamps

Environmental (abiotic) factors such as alkalinity, eutrophication, dissolved oxygen, and water temperature can have direct impacts upon aquatic macroinvertebrate communities (Pieczyńska *et al.*, 1999; Varga, 2001; Mousavi, 2002; Brauns *et al.*, 2007a). They can also act indirectly by influencing habitat features (*e.g.,* composition and structure of macrophyte and epiphyton communities) and processes (*e.g.,* decomposition) upon which macroinvertebrates rely (Canedo-Arguelles and Rieradevall, 2009; Gunn *et al.*, 2012). The physical structure of reedbeds has an influence upon abiotic and biotic (*e.g.,* predator prey dynamics) factors relevant to aquatic macroinvertebrates. Hejny (1971) placed reedbeds into two structural categories, erosion forms associated with steep or exposed shorelines and accumulation forms that are associated with wind-sheltered lagoons. Accumulation reedbed stands tend to be relatively large and dense with associated environmental conditions that include: extensive shading, low dissolved oxygen levels, and increased accumulation of organic matter. Due to the dense and dominant nature of these reed stands within the littoral zone, they tend to restrict macrophyte abundance and diversity (Hejny and Husak, 1978) and fish access (Ritterbusch, 2007). Reed density influences food availability for detritivores by intercepting and retaining organic matter that includes detritus from the host plant, other plants, and animals (Bedford and Powell, 2005). All of these factors influence the horizontal distribution of aquatic macroinvertebrates (Figure 4; Dvořák, 1970; Jayawardana *et al.*, 2006; Sychra *et al.*, 2010).

Some investigations into the influence of habitat structure heterogeneity upon macroinvertebrate communities within the littoral zones of lakes have included comparisons between reedswamp and other types of habitat, for example, coarse woody debris (Moon, 1936; White and Irvine, 2003; Gabel *et al.*, 2008; Schreiber and Brauns, 2010). However, comprehensive descriptions of reedswamp habitat (*e.g.,* shape and size, dominant substratum *etc.*) and the sample locations (*e.g.,* edge or inner swamp) are often lacking. However, some studies have focussed upon structural differences within reedswamps, and demonstrated that macrophyte composition can have a major impact upon the structure and functioning of its macroinvertebrate community. For example, within the reedswamp of a shallow eutrophic lake in the Netherlands, Dvorak (1996) compared the macroinvertebrate assemblages of three structurally distinct macrophytes *Phragmites, T. angustifolia,* and *Nuphar lutea* (L.) Sm. The macroinvertebrate assemblages associated with *T. angustifolia* differed significantly from those associated with *Phragmites* and *N. lutea*. The main difference was that the chironomid *Glyptotendipes viridis* (Macquart) contributed to the majority of the macroinvertebrate biomass associated with *T. angustifolia*. *G. viridis* mined into the tissues of *T. angustifolia*, from which they filtered seston; whereas, the macroinvertebrate assemblages of *Phragmites* and *N. lutea* were dominated by surface dwelling grazers that utilised epiphyton.

Reedswamps are ecotones and as a result there is likely to be corresponding changes in environmental conditions along transects running from shore to deep water. Within the vegetated littoral zones of lentic waterbodies the proximity of open water influences macroinvertebrate assemblages (Dvořák, 1970; Polunin, 1984; Burton *et al.*, 2004; Sychra *et al.*, 2010). Sychra *et al*. (2010) studied sequential changes (shore to open water) in macroinvertebrate assemblages (*e.g.,* taxonomic and functional composition) within the *Phragmites* dominated littoral zone of a lowland fishpond in the Czech Republic. Changes in macroinvertebrate assemblage from shore to open water were related to changes in environmental factors (*e.g.,* oxygen concentration, water depth, pH, shading, reed shoot density, and organic matter). Sychra *et al*. (2010) found that the macroinvertebrate communities of the deeper parts of reedswamps in a lowland fish pond were characterised by functional groups such as free-swimmers, ectoparasites, gather/collectors, and taxa preferring soft and inorganic substrates (Figure 2.4). In contrast, macroinvertebrate communities located closer to the shore were dominated by functional groups such as shredders, grazers, predators, and taxa preferring phytal and particulate organic matter (Figure 2.4). Strong influences upon environmental factors may also originate from the lateral edges of reedswamps (*e.g.,* the deposition of silt and other material by rivers). These multi-directional influences combine to produce mosaics of different internal habitats (Dvořák and Best, 1982; Oertli and Lachavanne, 1995). It is likely that the relative influence of changes along different directional axes varies significantly between different types of reedswamps (*e.g.,* different shapes and sizes, and proximity to rivers) and water-bodies (*e.g.,* ponds versus lakes).

Rather than studying variation within a single stand of reedswamp, Varga (2001) compared the macroinvertebrate assemblages of two separate reedswamps located in a shallow, alkaline lake straddling the Austrian-Hungarian border. Differences between the dominant functional groups of macroinvertebrate assemblages associated with a stand of reedswamp demonstrating vigorous growth and expansion of range were compared to those of a diminishing reedswamp. Isopoda and Gastropoda (shredder, grazer-scraper feeding groups) dominated areas where the reedbeds were declining; in contrast, chironomids belonging to the collector feeding group tended to dominate reedbeds experiencing vigorous growth. In addition to differences in the condition of the *Phragmites* stands at the two sites, there were also important hydrobiological differences that included proximity to the shore, water depth, transparency, and temperature. However, the published hydrological descriptions of the two sites were not sufficient for the terms ‘reedswamp’ and ‘fen’ to be applied. The findings of Varga (2001) and Sychra (2010) need to be corroborated with studies from other systems before they can be considered as a generalisation.

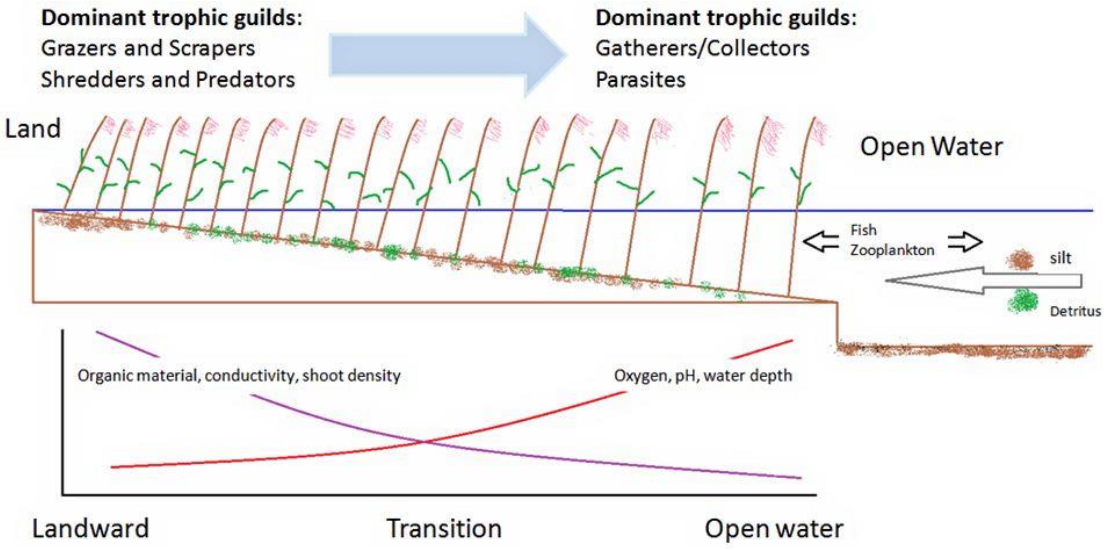


Figure 2.4 This illustration depicts a cross-section of a notional *Phragmites* reedswamp located within the littoral zone of a standing freshwater body (modified from Sychra *et al.* [2010]). The associated graph illustrates changes in environmental factors along a horizontal axis (from land to open water). Representation of spatial variation in environmental factors (*e.g.,* pH) is based upon data from Polunin (1984) and Sychra *et al.* (2010). Spatial variation in dominant macroinvertebrate trophic guilds is based upon data from Sychra *et al.* (2010).

2.4 The need for holistic and standardised survey methods

It is clear from this review that the contribution of aquatic macroinvertebrates to reedswamp macro functioning is not confined to any single type of internal location. For example, there is variation in functionality both vertically (*e.g.,* closely associated with the substratum compared to above it) and horizontally (*e.g.,* position relative to land and the profundal zone). Reedswamp habitat provides many different niches for macroinvertebrates, these niches being distributed across the following: (1) the substratum (often dominated by reed detritus); (2) within or upon macrophyte tissue (including the rhizomes and shoots of reeds); and (3) free water. However, It is rare for studies to integrate (or even collect) information from across the full range of niches within a specified volume of reedswamp. In addition, many studies do not take account of vertical, horizontal, or temporal variation within individual reedswamps. Instead the majority of investigations have focused upon macroinvertebrates assemblages within detritus or attached to reed shoots (rarely both) within a limited number of internal locations (*e.g.,* centre of a reedswamp) during one or two seasons. A wide range of different survey approaches and sample methods have been applied. As a result, there is no consistent guidance for carrying out surveys capable of providing representative data for whole reedswamps. A more holistic and standardised approach would facilitate lake to lake comparisons, and is likely to provide a more realistic understanding of the contribution of invertebrates to reedswamp functioning. In order to devise a survey approach that can be applied universally, it is necessary to appraise all existing sample methods and survey approaches. In the absence of a universal or standard method, the following section will facilitate the selection of an appropriate approach.

2.4.1 A review of sample methods

Jackson (1997) produced a comprehensive critique of the wide range of methods and techniques that have been used to investigate the macroinvertebrates assemblages of macrophytes within the littoral zones of lakes. There are a number of problems with sampling in the littoral zones of lakes, including a lack of harmonised sample methods and minimal guidance on appropriate spatial scales for sampling and/or adequate sample sizes (Schreiber and Brauns, 2010). Even within relatively small and shallow fish ponds, sampling aquatic macroinvertebrates from reedswamps presents a variety of methodological challenges (Kuflikowski, 1970). Access to reedswamps can be restricted and moving within them difficult due to soft sediments, deep water, and dense, resilient, structurally complex vegetation. These factors hinder the rapid deployment of sample devices and may result in the omission of ecologically important taxa (Sychra *et al.*, 2010). Hence, knowledge of how these ecosystems systems function is incomplete.

To sample target organisms effectively it is necessary to understand their relationships with the substrate (*e.g.*, temporally attached to reed stems) and their primary mode of locomotion (*e.g.,* strong swimmers). For example, Sahuquillo *et al.* (2008) and Dvorak (1996) selected methods appropriate for the study of chironomid (larval stages) assemblages attached to *Phragmites* or *Typha* stems within reedswamps. However, this approach is likely to have excluded a number of other important functional groups that interact with sessile chironomids. There are two categories of technique for sampling in wetlands: (1) passive methods (*e.g.,* artificial substrate methods, litter bags and activity traps) and (2) active methods (*e.g.,* pond net sampling and enclosure devices). Three types of device that have been commonly used to collect aquatic macroinvertebrate samples from reedbeds: (1) enclosure devices (*e.g.,* modified Gerking samplers); (2) standard pond nets; and (3) litter bags. Tables 2.1 to 2.3 illustrate the array of contrasting approaches that have been used to investigate macroinvertebrates within a variety of different reedswamp and water-body types. A minority of these investigations have related macroinvertebrate functionality to variations in reedswamp structure in both space (horizontal and vertical) and time (*e.g.,* seasonal changes). The studies listed in Table 2.3 all involved methods designed to collect macroinvertebrates from a variety of different reedswamp niches (the water column and surface, substrate, and reed shoots); these accounted for less than one quarter of the total number of studies listed in tables 2.1 to 2.3.

2.4.1.1 Enclosure methods

Both Sahuquillo *et al.* (2008) and Dvorak (1996) employed quantitative sample methods that utilised ‘enclosure’ devices to sample macroinvertebrates associated with reed-shoots. ’Enclosure’ methods require the cutting of tough aerial reed stems before a sample box or tube can be placed over the tall shoots (Sychra *et al.*, 2010). Some workers (Oertli and Lachavanne, 1995; Sahuquillo *et al.*, 2008; Sychra and Adámek, 2010) cut the aerial shoots of emergent vegetation some time (*e.g.,* 24 hours) before sampling to minimise the impact of disturbing invertebrates attached to the reed shoots. Sahuquillo *et al.* (2008) used narrow plastic tubes based on a design used by Kornijow and Kairesalo (1994) to sample individual shoots whereas Sychra and Adámek (2010) used a modified Gerking box sampler (a metallic box with a built-in cutting device at the base) to enclose and then remove a cluster of shoots within an area of 0.1 m^2. However, the persistent nature of reed shoots means that cutting shoots has the potential to change the physical structure of the reedswamp for a couple of years (Komínková *et al.*, 2000). In addition, making two visits to collect one set of samples has the potential to double the amount of damage and disturbance to this important habitat. Carrying relatively bulky and heavy sample devices (often in addition to sample nets) through reedswamp disturbs and potentially damages reed shoots, the benthos, and reed rhizomes. Disturbance is likely to have an adverse ecological impact (*e.g.,* disturbing nesting birds and the destruction of reed habitat). Some workers (Sahuquillo *et al.*, 2008) have deployed devices from boats at the edge of swamps. This approach protects the inner reedswamp but there is the potential for boats to damage the edge, which may lead to a loss of protection (*e.g.,* from wave washing) for the inner reedswamp.

Enclosure methods are biased towards the capture of macroinvertebrates that are either slow moving or attached to reed shoots including gastropods, chironomids and oligochaetes (Sychra and Adámek, 2010). In contrast, loosely attached and/or strong swimming invertebrates (*e.g.,* adult beetles and water bugs) are more likely to avoid capture (Sahuquillo *et al.*, 2008). Sahuquillo *et al.* (2008) and Sychra and Adámek (2010) investigated the sample bias of enclosure devices by comparing data with that collected by hand net sweep sample techniques. Sychra and Adámek (2010) tested the efficacy of using a Gerking box to sample aquatic macroinvertebrates from a fishpond reedbed. The sole use of the Gerking box was deemed to be adequate for the purpose of quantitative monitoring. However, for a more complete assessment of biodiversity, they recommended additional sampling by sweep net at the same location. This suggests that the use of an enclosure may have been unnecessary. Sampling with a hand net over a known area (not enclosed) may have provided suitably comparable information for both biodiversity and quantitative monitoring. Enclosure devices collect samples with a greater precision than some other methods. It would be beneficial to investigate the requirements for enclosures by determining the necessary level of precision and accuracy required for quantitative sampling. This is important because reliance upon a specialised item of equipment (*e.g.,* a Gerking box) may deter many from adopting a standardised method.

2.4.1.2 Hand nets

Hand nets are commonly used to sample freshwater macroinvertebrates from within a diversity of freshwater habitats. Standardised hand net methods include sweep and kick sample techniques. For example, the invertebrate metrics for the Predictive System for Multimetrics (PSYM) pond assessment method involves a standard three minute hand net kick sample. The PSYM method allows the sample time to be divided equally between the main mesohabitats located within a whole pond (Pond-Action, 2000). In contrast, the River Invertebrate Prediction and Classification System

(RIVPACS) method was originally developed for river sampling and dictates that more time is spent kick/sweep sampling the most dominant habitat within a sample site (Solimini *et al.*, 2006; O'Hare *et al.*, 2007). The current sample method described for sampling the littoral zones of lakes as part of the Water Framework Directive (WFD) is based on the RIVPACS method. It identifies two habitat types that are suitable for sampling: (1) rocky shore without vegetation (which requires kick sampling), and; (2) sites dominated by submerged macrophytes (requiring sweep sampling). Separate methods are described for each of these habitat types but both methods recommend the avoidance of emergent macrophyte habitat (*e.g.,* stands of *Phragmites*) (O'Hare *et al.*, 2007).

The absence of a recognised standard method and a lack of guidance for sampling reedswamp habitat as part of the WFD classification system (and previous legislation), may have contributed to a lack of consistency between the hand net based methods of different investigations (Dvořák and Best, 1982; White and Irvine, 2003; Sipkay *et al.*, 2007; Sychra *et al.*, 2010). For example, Sychra *et al.* (2010) carried out a timed (one minute) sweep of reedswamp that avoided the substratum. In contrast, Sipkay (2007) applied a semi-quantitative method that required ten standardised strokes through the water column and reeds followed by two stokes through the soft mud at the surface of the substratum. Compared to other types of sample device (*e.g.,* enclosure devices) hand nets allow rapid collection of semi-quantitative macroinvertebrate samples that are broadly representative of reedswamp habitat (Sychra *et al.*, 2010). Some workers have collected quantitative macroinvertebrate data by using hand nets to sample over known areas (Dvořák, 1996; White and Irvine, 2003; Brauns *et al.*, 2007b; Schreiber and Brauns, 2010).

2.4.1.3 Litter bags

Litter bags were introduced by Bocock and Gilbert (1957) and have been used extensively in terrestrial, freshwater, estuarine and marine environments for examining breakdown rates of macrophyte litter (Bedford, 2004). Some workers have used litter bags as passive sampling devices to investigate the role of aquatic macroinvertebrate assemblages in the breakdown of *Phragmites* litter within lentic reedbeds (Mason and Bryant, 1975b; Polunin, 1982; Varga, 2001; Bedford, 2005; Mancinelli *et al.*, 2007). For example, Varga (2001) investigated the colonisation by macroinvertebrates of dried *Phragmites* litter in bags of 1 mm mesh (measuring 25×50 cm) within two different *Phragmites* stands in the same lake. The main finding of all these studies was that litter bag macroinvertebrate assemblages are sensitive to changes in hydrology and reedswamp structure.

When interpreting data collected using litter bag techniques, it is important to consider the design of the litter container. The design of a litter bag or cage can have a strong influence upon both the accuracy of litter breakdown rate estimation, and macroinvertebrate assemblages (Anderson and Sedell, 1979; Boulton and Boon, 1991; Bedford, 2004; Loke *et al.*, 2010). For example, Bedford (2004) investigated the influence of three different designs of litter bag upon *Phragmites* litter breakdown within a reedbed at Leighton Moss (UK). Dried *Phragmites* litter was placed into three different litter bag designs, two standard litter bag designs (one with a coarse [5 mm] mesh and the other with a fine mesh [0.5 mm]) and one modified, composite litter bag design (fine mesh on the underside with a coarse mesh upper). Fine mesh only bags are commonly used to exclude macroinvertebrates, so that the role of macroinvertebrates in the breakdown of litter can be assessed. However, over an extended period of time (12 months) the litter within fine bags was colonised by the early stages of macroinvertebrates (*e.g.,* by eggs and first instar larvae of chironomids) (Bedford, 2004). The modified bag was designed so that the coarse mesh upper allowed macroinvertebrates to access the litter, and the fine mesh base retained a higher proportion of material (detritus and macroinvertebrates) during bag retrieval. When the modified bags were retrieved the fine mesh ensured that more fragments of litter and associated macroinvertebrates were retained compared to the coarse mesh bags. This may explain why greater densities of macroinvertebrates were found in the modified bags, compared to the coarse mesh only bags (Bedford, 2004). The retention of more detritus by the modified bag may have given the erroneous impression that breakdown rate was lower than in the coarse bags (Bedford, 2004). Because of the influence of bag or cage design, the suitability of litter bags to collect representative macroinvertebrate data from reedswamp detritus is questionable. However, there may be value in using litter bags to complement active sample techniques (*e.g.,* an *in situ* experiment designed to investigate the preferences of individual macroinvertebrate species for different types of detritus).

2.4.1.4 Activity traps

Within wetlands, passive sampling methods (*e.g.,* using activity traps) are popular methods of sampling aquatic macroinvertebrates. However, the data can be difficult to interpret due to problems converting capture data into meaningful estimates of abundance (Turner and Trexler, 1997). The majority of detailed studies of reedswamp habitats have focused on macroinvertebrates that are closely associated with either detritus or reed shoots. Published accounts of using activity traps (*e.g.,* funnel traps) within reedswamps are rare. The devices most commonly used to sample detritivores and phytophilous macroinvertebrates are hand nets, enclosure devices and litter bags. Compared to activity traps these devices have been less effective in capturing highly motile macroinvertebrates (*e.g.,* diving beetles) from wetland habitat (Jackson, 1997; Turner and Trexler, 1997). For example, reedswamps and other types of dense vegetation restrict the rapid deployment of hand net or enclosure devices. This results in the disturbance of the habitat immediately before the sample device is deployed. In addition, the deployment of the device (enclosure or hand net) may be delayed enough to allow free swimming macroinvertebrates time to escape (Murkin *et al.*, 1983). Consequently, the contribution of free swimming macroinvertebrates to the structure and functioning of macroinvertebrate communities within reedswamp has received less attention than communities of less motile invertebrates (*e.g.,* Chironomidae larvae). The use of activity trap data to supplement data from enclosure devices is likely to produce more complete food webs (*e.g.,* more predators detected) and increase the accuracy of biodiversity estimates.

2.5 Gaps in knowledge and key research questions

The consequences of changes in the global distribution of reedswamp habitat within lake littoral zones (*e.g.,* expanding in the USA and Australia, and receding within Europe) are not fully understood. Even at the local scale (*e.g.,* within individual lakes) there are significant gaps in knowledge. Little is known about how biological processes (mainly primary production and decomposition) determine reedswamp macro functionality. Quantitative or compelling information regarding the role of macroinvertebrates in key processes and the consequences for lake ecology has been limited to a small number of investigations (Andersson *et al.*, 1988; Daldorph and Thomas, 1995; Vaughn and Hakenkamp, 2001; Deines and Grey, 2006). In particular, there is little data regarding the density, biomass, productivity, or the processing rates of macroinvertebrates within reedswamps. Consequently, the cumulative effect of reedswamps and their macroinvertebrate assemblages upon lake processes is unknown. Fundamental research questions relevant to the role of macroinvertebrates in key biological processes in reedswamp functionality include:

(1) What are the cumulative effects of macroinvertebrate assemblages throughout the littoral zone upon biological diversity, functional diversity, and key biological processes within a variety of different lakes types?

(2) What are the consequences of shifts in reedswamp dominance and other key structural changes (*e.g.,* human development) within the littoral zone of lakes? How do these changes impact the contribution of macroinvertebrates assemblages to key processes that underpin whole lake function?

(3) Which physical features (*e.g.,* shape, size, species composition, shoot density, substratum composition) of reedswamps have the strongest influence upon the ways in which macroinvertebrates contribute to reedswamp processes?

(4) Do reedswamps have a significant influence upon the seasonal dynamics of processes driven by macroinvertebrates?

2.6 Summary

There is a clear need for a greater understanding of the ways in which macroinvertebrate assemblages interact with different aspects of reedswamp habitat. A standardised sample methodology would be beneficial as it would facilitate comparisons between different reedswamp and lake types. Chapters 4 to 7 investigate the main ways in which reedswamp habitat influences macroinvertebrate biodiversity and functional traits, and makes recommendations for a standardised survey approach.

CHAPTER 3 Long-term changes in reedbed extent and a comparison with physical and chemical variables

3.1 Chapter Introduction

Chapter 2 focused on the environmental consequences of reedbed loss within lakes throughout the world. This chapter identifies past and present risk factors associated with a major loss of reedbed habitat within Windermere with a meta-analysis of long-term trends in environmental data and reed cover. The possible impacts of reedbed loss upon water quality are also investigated.

3.1.1 Introduction

The persistence of reedbed habitat within wetlands is dependent on the capacity of reeds to adapt to dynamic environmental conditions and expand into new habitats. The common reed, *Phragmites australis* (Cav.) Trin. is a global species and has colonised a broad range of habitat types across diverse climatic and physicochemical environments (Haslam, 2010). Even at the scale of the individual reedbed, phenotypic variation in morphological and physiological responses allow *Phragmites* reedbeds to extend across strong hydrological, chemical, and physical disturbance gradients (Clevering and Lissner, 1999; Vretare *et al.*, 2001). Despite this inherent plasticity, widespread losses of *Phragmites* have occurred throughout Europe (van der Putten, 1997; Clevering, 1998; Brix, 1999b). Because interactions between reeds and environmental conditions are highly variable and complex, the underlying reasons for reedbed decline are poorly understood (Armstrong *et al.*, 1996b).

Reedbed conservation requires an understanding of the ways in which reeds respond to natural and anthropogenic environmental changes across a range of temporal and spatial scales (Marks *et al.*, 1994). The natural process of succession by scrub has accounted for reedbed recession and losses across a broad range of habitat types (Keddy, 2010; RSPB, 2011). In addition, extreme hydrological events can result in catastrophic and irreversible losses. As a result the ability of reeds to colonise new areas is of vital importance. There are two natural processes by which reeds expand their ranges, vegetative spreading and setting seed (Hubbard, 1982). Both vegetative material (rhizomes) and viable seeds require nutrient rich soil, open habitat and appropriate amounts of water (Haslam, 1971a). Vegetative spreading is restricted where there is little opportunity for individual reedbeds to expand into adjacent spaces (RSPB, 2011). For example, proximity to deep water at lacustrine sites, and nature reserves surrounded by non-wetland habitat (*e.g.,* improved grassland and urban areas). Spreading by seed has the potential to bypass adjacent habitats. Unfortunately, there is a lack of suitable sites for creation of new reedbed habitat throughout most of Europe (Amezaga *et al.*, 2002). In addition, reproduction by seed within specific geographic regions (*e.g.,* northwest England) can vary between different populations (M^{c}Kee and Richards, 1996).

Reed die-back syndrome and retarded growth are prevalent throughout Europe. Key physiological changes associated with reed pathology are disturbances in mineral transport, photosynthesis, respiration, water uptake, and vital metabolic processes, such as sugar storage (Armstrong *et al.*, 1996b). Risk factors for these adverse changes include the following: (1) parasitic attack (insects and fungi); (2) mechanical damage; (3) increased water temperature; (4) elevated or static water tables; (5) increases in salinity, and alkalinity; (6) excessive organic matter loading; and (7) eutrophication (Sukopp and Markstein, 1989; Armstrong *et al.*, 1996a; Rea, 1996; Tscharntke, 1999; Zhang and Deng, 2012). Within individual ecosystems, it has been difficult to quantify the relative influences of these different risk factors (Brix, 1999a). While most risk factors have direct influences on reed physiology, there are also a number of indirect mechanisms. Excessive accumulations of organic material (*e.g.,* reed detritus, sewage sludge, and eutrophic deposition) result in anoxic conditions that stimulate production of organic acids and sulphides (also associated with acid rain and brackish water). These substances act as phytotoxins by inducing blockages that impede respiratory and/or vascular systems. The resultant rhizome death and premature shoot senescence then contributes further to anoxic conditions, thus perpetuating the pathology (Armstrong *et al.*, 1996b).

Throughout Europe there are concerns regarding the adverse impact of reedbed decline for biodiversity and ecosystem functioning (Ostendorp, 1999). Natural reedbeds (*e.g.,* lacustrine reedswamps) provide habitat for wildlife and have a positive influence on water quality by acting as buffer zones (Correll, 1996; Johnston *et al.*, 1996; Hoffmann *et al.*, 2009). Buffers created by macrophytes intercept and retain organic material and nutrients in both dissolved and particulate forms (Johnston *et al.*, 1996). Retention of nutrients is only temporary, and there are clear seasonal variations in both uptake and release. Nitrogen and phosphate-phosphorus are incorporated into the tissues of reeds during their vegetative period, and later released into the water via leaching from living and dead tissues (Klopatek, 1977; Ho, 1980; Keddy, 2010). Nutrients are also bound with organic matter that is trapped within reedbed sediments created by bank erosion, agricultural runoff, and sedimentation of internal organic loads (*e.g.,* dead plankton). The liberation of bound-nitrogen from reedbeds is largely due to the microbial process of denitrification, which culminates in the formation of nitrogen gas (Bowden, 1987; Groffman, 1994). The binding of phosphate-phosphorus to organic particles and its subsequent release is determined by chemical processes related to nitrate levels, temperature, oxygen availability and pH (Jensen and Andersen, 1992). Unfortunately, case studies of changes in lake nutrient dynamics within lakes before and after reedbed decline are lacking.

Key threats to reedbed sustainability are prevalent at many UK lakes (Bennion and Simpson, 2011; M^{c}Goff *et al.*, 2013). Consequently, important ecosystem services provided by reedbed fringed lakes in the UK are at risk. Within the English Lake District (Cumbria, UK) lakes provide vital potable water supplies for a large a geographic region that includes major conurbations. In addition, they make important contributions to biodiversity and fish stocks and underpin local economies by providing culture and amenity (Pickering, 2001). Hence, there is a clear need to educate policy makers, managers, academia, and the general public of the importance of reedbeds within specific UK lakes (*e.g.,* Windermere). This would be facilitated by estimating and predicting the consequences of reedbed loss at individual lakes, and identifying the key risk factors associated with their loss (Ostendorp *et al.*, 1995).

3.2 Aim and hypotheses

The overall aim of this study was to identify potential causes for reedswamp decline within Windermere over the last 90 years by using meta-analysis of existing physicochemical datasets and Ordnance Survey maps. Three hypotheses were tested. The first hypothesis (H_1) asserts that Windermere's reedbeds are vulnerable to multiple stressors, like the majority of freshwater ecosystems (Ormerod *et al.*, 2010). The main physical drivers for reedbed loss within Windermere are shoreline development and elevated lake level (*sensu* Brix, 1999a; Pickering, 2001). The second hypothesis (H_2) asserts that contemporary and historic chemical conditions within Windermere are consistent with those associated with chemically induced reed die-back syndrome. The main chemical drivers of reed die-back syndrome within freshwaters are increased levels of nutrients, and alkalinity (Kuhl and Kohl, 1993; Armstrong *et al.*, 1996b). The third and final hypothesis (H_3) asserts that continued reedbed loss due to physical factors causes an adverse shift in chemical conditions within the sediments sufficient to trigger self-perpetuating reed die-back syndrome. For example, failure of reedbed roots to oxygenate the sediments during the summer months diminishes the inhibition of phytotoxin release (Armstrong *et al.*, 1996b).

3.3 Study area

Windermere was formed during the latter stages of the last glacial period ~14000–15000 years ago and is the largest natural lake in England, UK (Pearsall and Pennington, 1947). The underlying geology of the catchment is distinct, with volcanic rock in the north separated from Silurian shale in the south by a thin band of the Dent Group (formerly called the 'Coniston Limestone') (Pickering, 2001). Various streams and rivers enter the lake; the largest single flow into the lake is located on the northern shore and formed by the confluence of the rivers Rothay and Brathay. The lake drains directly into the River Leven which is located on its southern shore. Windermere is divided into two deep basins by a strip of relatively shallow water (average depth 10m) at a narrowing of the lake. This constriction impedes water flow from the north to the south (Reynolds and Irish, 2000). Consequently the shape, size, hydrology, and water quality characteristics of the two basins are distinct (Figure 3.1, Table 3.1).

Windermere and its mountainous catchment area underpin the local economy by providing recreation and leisure for tourists (Bell, 2000; Pickering, 2001). Since the late nineteenth century there has been a large increase in permanent residents and tourists within the catchment (M^{c}Gowan *et al.*, 2011; Elliott, 2012). Popular activities include pleasure cruises, mooring and launching of boats, swimming, angling, and walking. Improvements in local and national infrastructure (*e.g.,* roads, local

Table 3.1 The key functional characteristics of Windermere were described by using key morphological, hydrological, and water quality variables. Data was collated from Maberly *et al.* (2011), Ramsbottom (1976), Reynolds and Irish (2000), Talling (1999), and M^{c}Gowan *et al*. (2011). (* = excluding North Basin area, ø = mean winter values [for 1970–2007], ‡ = mean winter values [for 1946–2007], and ¥ = mean winter values [for 1964–2009], values in brackets relate to mean 2010 values)

Basin	Decimal Degrees	Volume ($m^3 \times 10^6$)	Surface Area (km^2)	Mean depth (m)	Catchment Area (km^2)	Residence Time (days)	Trophic status (2010)	TP ^{ø} (µg/L)	$NO^{-3‡}$ (µg/L)	Chl *a* $^{¥}$ (µg/L)
North	54.387322N 2.940830W	201.8	8.05	25.1	187	180	Mesotrophic	13.4 (11.2)	411.3 (380)	5.6 (12.3)
South	54.306328N 2.954348W	112.7	6.72	16.8	63*	100	Meso–Eutrophic	25.6 (12.6)	425.5 (388)	8.5 (6.1)
Whole Lake		314.5	14.76	-	250	280	-	-	-	-

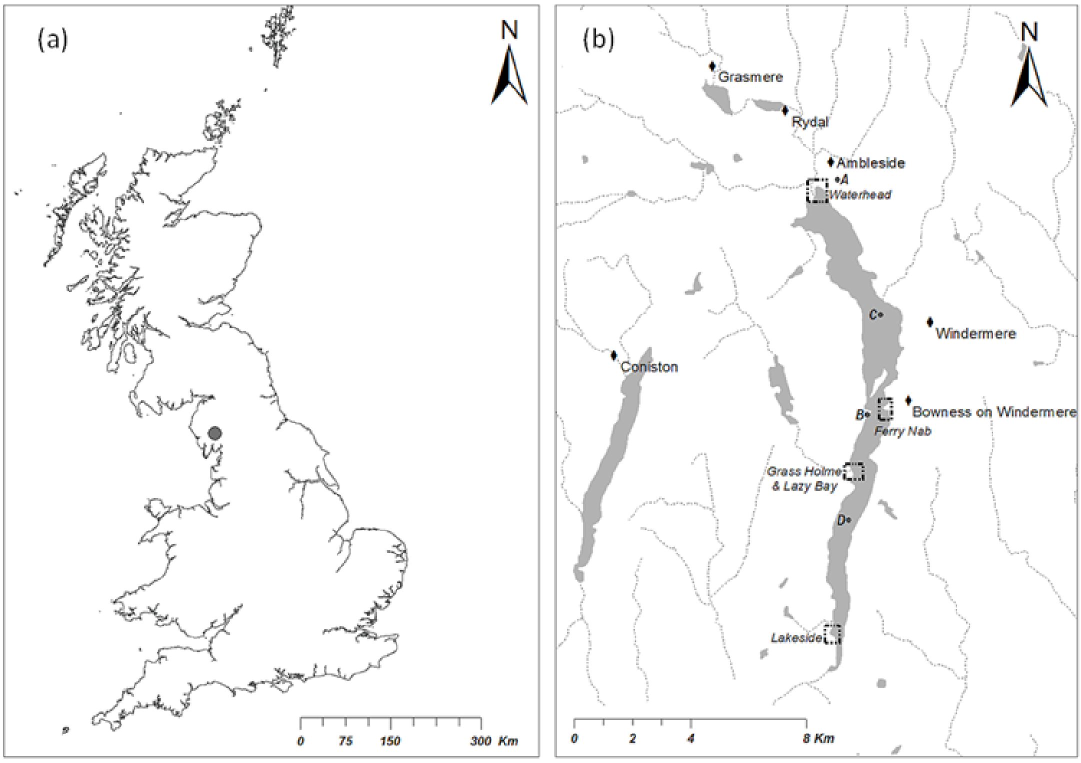


Figure 3.1 These maps illustrate the location of Windermere within the United Kingdom (a) and the relative positions of sample and survey locations (b). Ferry Nab is the location of the shallow sill separating the North Basin from the South Basin. ([squares] = reedbed survey locations, [A] = the Met Office weather station for rainfall and air temperature data, [B] = the Environment Agency gauging station for lake level data, [C] and [D] = the approximate CEH sample locations for the North and South basins respectively)

accommodation, and leisure facilities) have been linked to significant increases in human activity within the lake and surrounding area (Collingwood, 1902; Hamilton-Taylor, 1979; Bell, 2000; Pickering, 2001). The resultant urban expansion that began during the early part of the nineteenth century led to the development of sewage treatment facilities after 1886. Improvements in the sewage system throughout the catchment have continued throughout the last century, including major upgrades in the 1960s and 1990s. During this period agriculture has continued to be dominated by pastoral sheep farming. Since the 1950s, sheep numbers and the application of nitrogen fertilisers increased, and mechanisation led to a decline in horse numbers (M^{c}Gowan *et al.*, 2011).

Monitoring and research of Windermere began in the 1930s and continues to the present day (Maberly and Elliott, 2012). Numerous studies have investigated long-term changes in the structure and function of Windermere in response to ‘external stressors’ (*e.g.,* climate change and nutrient enrichment) and ‘internal interactions’ such as predator-prey interactions. This research has focussed upon the pelagic zone, and in particular the ecological response to long-term changes in physicochemical determinants such as water temperature and plant nutrients (Thackeray *et al.*, 2008; M^{c}Gowan *et al.*, 2011; Maberly and Elliott, 2012; Elliott, 2012). Unfortunately, little is known regarding the causes and consequences of changes within the littoral zone. The earliest recorded expression of concern regarding the loss of *Phragmites* reedbed habitat within Windermere was made during the 1920s by local wildfowl enthusiasts. It has been speculated that possible causes of reedbed decline within Windermere are nutrient enrichment, hydrological changes, grazing by wildfowl, shoreline erosion due to boating activity, disease, and climate change (Pickering, 2001). However, investigations into the causes and consequences of reedbed loss and other long-term changes (*e.g.,* lake level) are lacking.

3.4 Method

3.4.1 Data collection

To investigate all three hypotheses, existing data were collated from a number of different organisations. As part of the Heritage Lottery funded ‘Restore the Shore’ project the Freshwater Biological Association (FBA), Lake District National Park Authority (LDNPA), South Cumbria Rivers Trust (SCRT), and Windermere Reflections worked in partnership to produce a map detailing estimated changes in reedbed coverage throughout Windermere since the 1870s. Long-term reedbed analysis was derived from records located within local archives including maps, photographs, and descriptions of individual reedbeds within academic papers. Contemporary reedbed data were based upon a boat survey carried-out during November 2012 (Alvarez-Codesal, 2012). Changes reported by ‘Restore the Shore’ were investigated using historic and present day Ordnance Survey (OS) maps to identify key changes in shore-line development. These included the building of roads and buildings on or close to the shore-line (<50 m) and boat launching areas (slipways, marinas, piers, jetties, and boat houses). Specific locations in which this research focussed are highlighted in Figure 3.1.

Physicochemical, hydrological, and climate data originated from contemporary long-term monitoring programmes (fortnightly collection). However, long-term physicochemical monitoring carried out by the FBA and latterly the Centre of Ecology and Hydrology (CEH) was restricted to the pelagic zone of each basin. The analytical methods used are described by

George *et al.* (2004). In 2010, the range of pollutants monitored within lakes throughout the Windermere catchment was expanded to include metals and micro-organic pollutants. Samples of surface water within the pelagic zone of lakes were analysed for 7 metals (aluminium, cadmium, chromium, copper, nickel, lead, and zinc) and 128 different organic pollutants (Maberly *et al.*, 2011). Single samples were collected over 7–9 days per month during January, April, June, and October 2010. Data relating to the accumulation of metals, and organic compounds within historic sediments were obtained from published accounts (Hamilton-Taylor, 1979; Cranwell and Koul, 1989). Mean daily lake level data was collected from a gauging station by the Environment Agency (EA) at a point approximately equidistant between the centre of the two basins (54.352302^{o} N 2.936951^{o} W, Figure 3.1). Lake level was expressed in metres Above Ordnance Datum (height relative to the average sea level at Newlyn, Cornwall, UK). The Met Office collects air temperature and rainfall data from a weather station located at Ambleside (54.432130^{o} N 2.957272^{o} W, Figure 3.1) within 3 km of the lake.

3.4.2 Data analysis

Data sets for physicochemical determinants within the littoral zone of Windermere (water and sediments) are lacking. In contrast, long-term data sets for surface water in the pelagic environment were available along with published accounts of key changes (*e.g.*, Maberly *et al.*, 2011; M^{c}Gowan *et al.*, 2011). While conditions in the pelagic may not reflect those within the littoral zone, trends in the pelagic have the potential to provide insights into changes in sediment chemistry within the littoral zone that are relevant to reedbeds. For example, increased eutrophication in the pelagic zone is associated with increased sedimentation, which can lead to phytotoxin release due to anoxic conditions within littoral sediments (Armstrong *et al.*, 1996b). In addition, there is a lack of quantitative data for many physical stressors (*e.g.,* grazing pressure is lacking). Consequently, the analytical approach of this chapter was to carry out metadata analysis that included a range of different potential stressors rather than performing detailed time-series analysis (*e.g.,* spectral analysis) on individual data sets (*e.g.,* water temperature).

To test H_1 and $H_{3,}$ moving averages were calculated to smooth reedbed surface area, hydro-meteorology, and chemical data and identify general trends in the annual means of physicochemical data (*sensu* Schwartz *et al.*, 1996). Five year means of annual values were plotted at the median year. For example, the data point plotted for the year 2000 was the mean of annual values from 1998–2002, thus reducing the influence of single years. Trends in semi-continuous data sets (*e.g.,* alkalinity) were described with time-series plots. For key variables (nutrient levels, surface temperature, and lake level) at the North Basin, temporal changes within years were investigated.

There were clear mismatches between reedbed loss data and other variables. For example, reedbed loss data consisted of 4 data points from 1920 to 2009, whereas the alkalinity datasets consisted of 39 yearly means collected between 1969–2014. Consequently, meaningful correlations between reedbed loss and other variables were not possible. Instead the multi-factorial nature of reedbed loss ($H_{1,}$ H_2, and H_3) was investigated by fitting reedbed surface area, hydro-meteorology, and chemical data to a simple linear regression model ($\gamma = \alpha + \beta x$) using the ‘Mass’ library in the R statistical environment. The Durbin-Watson test within the ‘lmtest’ library was used to test for autocorrelation. Time series data that demonstrated autocorrelation (*e.g.,* nitrate and phosphate-phosphorus data) was excluded from regression modelling (*sensu* Legendre, 1993). In addition, the assumptions necessary for applying the Pearson product-moment correlation coefficient to investigate the influence of rainfall on chemical factors were also violated (Harrell, 2001).

Historic and contemporary annual means for chemical determinants were compared with reference values in order to test the hypotheses (H_2 and H_3) that assert continued reedbed loss is likely to trigger adverse chemical conditions for reedbeds. Reference values for water quality (TP, Secchi depth, and chlorophyll *a*) within Windermere were obtained from Maberly *et al.* (2011). For other stressors (nitrate, alkalinity, and pH) reference values were generated from a review of literature from across Europe (van der Putten, 1994; Armstrong and Armstrong, 1999; DEFRA, 2002).

Quintiles (and not seasons) are commonly used as statistical descriptors of temporal changes in climatic determinants (Trewin *et al.*, 2007). For example, the Intergovernmental Panel on Climate Change (IPCC) utilises monthly climate data arranged by quintiles (Parry *et al.*, 2007). In order to investigate the likely mechanisms for a future switch to chemically induced die-back syndrome (H_3), seasonal changes were analysed. For each year, data relating to climate (lake level and surface water temperature) were grouped into quintiles (Table 3.2). For example, ‘Quintile 1’ contains data collected from 1st January to 14th March and ‘Quintile 2’ contains data collected from 15th March to 26th May. Yearly means for each quintile were compared with means of quintiles within a reference period. The standard reference period used to investigate the impact of climate changes as set by the World Meteorological Organisation (WMO) is 1961–1990 (Parry *et al.*, 2007). Due to a lack of data before 1975, the present study set considers 1975–1990 as the reference period. Anomalies from the reference for each quintile were displayed as stacked values for each year as column charts. This approach was also applied to total phosphorus (TP) and nitrate data. The relative influence of changes in reedbed coverage upon nutrient levels and vice versa were investigated by selecting reference periods that took account of changes in nutrient loading at the whole lake scale. Phosphate stripping at Ambleside sewage treatment works (North Basin) began in April 1992; therefore, the reference period for TP was limited to 1946–1991. Similarly, changes in nitrate concentrations within the North Basin were contextualised using the period 1946–51 as a reference, on the basis that nitrate fertilisers were widely used throughout the UK after 1951 (M^{c}Gowan *et al.*, 2011).

Table 3.2 Using data from Haslam (1975) the life history of *Phragmites* was related to quintiles in order to facilitate the investigation of seasonal changes in hydro-meteorological and physicochemical determinants.

Quintile	Start	End	Dominant growth phase
Q1	1st January	14th March	Dormant
Q2	15th March	26th May	Vegetative (shoot emergence ~April)
Q3	27th May	7th August	Vegetative (end of rapid growth ~July)
Q4	8th August	19th October	Reproductive (efflorescence formation and consequent senescence)
Q5	20th October	31st December	Dormant

3.5 Results

3.5.1 Reedbed decline and shoreline development

Fringing *Phragmites* reedbeds are no longer a dominant feature of Windermere's shores and islands. There has been a severe decline in reedbed surface area within both basins from the earliest records (~1870) to the present day (Figures 3.2–5). The proportion of shoreline (including islands) with reedbed habitat has reduced, as has the extent of reedbed expansion into the littoral zone (Pickering, 2001; Alvarez-Codesal, 2012). From the late nineteenth century to the present day, most of the large scale shore-line development structures within Windermere (*e.g.,* commercial and residential buildings, piers, jetties, slipways, gardens, recreational parks, and roads) have been centred around three locations (Figure 3.1): (1) the northeastern shore near Waterhead (Figure 3.2a), (2) the eastern shore adjacent to the where the two basins confluence (Figure 3.2b), and (3) the southern extreme of the lake near Lakeside (Figure 3.3). These locations provide the majority of lake users with access to the lake via ferry or cruiser terminals, mooring facilities (*e.g.,* marinas), and launch points for pleasure crafts. These three hubs are linked by frequent daily cruise boats. The key feature of lake user hubs is that shoreline developments (*e.g.,* piers and jetties) extend across the littoral zone. Smaller structures that impinge upon the littoral zone to a lesser degree (*e.g.,* small boat houses and slipways belonging to private residences and membership clubs) are distributed throughout the lake.

The majority of present day structures (*e.g.,* roads and buildings) were already in place in some form by 1890, and by 1970 the shoreline closely resembled its present day configuration. The main changes between 1890 and 1970 were the expansion of boat mooring facilities at Ferry Nab (Figure 3.2b) into both basins and the southern expansion of launch facilities at Waterhead (Figure 3.2a). Visual observations indicated that the majority of roads, buildings, recreational areas, and private gardens located on or close (<50 m) to the shore are typically associated with bank protection structures (*e.g.,* walls, riprap, gabions, and groynes). Hence, building near the shoreline has had an indirect impact on the shoreline that was beyond the resolution of OS maps.

Large scale reedbed loss was not restricted to areas where building on the shore/littoral zone has occurred. For example, Lazy Bay and the adjacent island of Grass Holme are both free of human-development (Figure 3.4); nonetheless, Grass Holme has lost its entire historic reedbed, and at Lazy Bay only small fragments of the original (~1920) reedbed coverage remains. The shores of both these sites are relatively inaccessible due to a complete lack of human development; in addition, Lazy Bay is protected by woodland, boggy areas, and a steep gradient from the nearest road or path. Boats are prohibited from landing on Grass Holme which is now dominated by woodland. The key difference between these two sites is that Lazy Bay is relatively sheltered from wave and wind action.

3.5.2 Hydro-meteorological and chemical determinants

There was a significant linear decrease in reedswamp area over the last 90 years (Figure 3.5, Table 3.3). In addition, there were general increases in the annual means of temperature, lake levels (Figure 3.6), alkalinity, pH, nitrate (Figure 3.7), and chlorophyll *a* as well as decreases in Secchi depth and TP (Figure 3.8). However, with the exception of lake level and rainfall, the majority of variables demonstrated autocorrelation. As result it was not possible to investigate the relationship between rainfall and water quality factors (*e.g.,* turbidity) commonly associated with increased land runoff (*sensu* Sharpley *et al.*, 1992). Over recent decades there has been a general trend for annual means of alkalinity and pH to increase (Figures 3.7a,b). There has also been a clear increase in nitrate concentrations since the 1950s; furthermore, annual means of nitrates have become increasingly variable over recent decades (Figure 3.7c). In the initial period (~12 years) following the implementation of phosphate stripping at Ambleside and Tower Wood sewage treatment works in 1992, TP and chlorophyll *a* levels decreased and Secchi depth increased. These improvements in water quality were not sustained after 1996 (Figure 3.8).

Analysis of quintile data indicated that a number of seasonal changes have occurred over the last century. Since 1975─1990 mean surface water temperature for the North Basin increased across all quintile time periods (Figures 3.9a). In addition, lake level increased over the last four decades due mainly to increases from June to January (Figure 3.9b). However, there was no consistent pattern in mean annual rainfall over time, and seasonal patterns of rainfall varied little over the period during which they were measured (1965–2004) (Figure 3.10, Table 3.3). For the mid October─June period there was an upward trend in nitrate levels over time. Although, for the June─mid October period, nitrate levels peaked during 1970─1980 (Figure 3.11a). Within the North Basin, TP quintile means within years were broadly similar and varied little over the decades (Figure 3.11b).

Throughout the study period nitrate concentrations and alkalinity within the pelagic zone have been at levels much lower than those associated with published accounts of reed-die back syndrome (Table 3.4). Unfortunately, levels within the littoral zone are unknown. In addition, historic levels of pH (within the pelagic zone) have been outside the range associated with phytotoxin production, and they continue to increase away from critical levels (Table 3.4, Figure 3.7). Trophic and Water Framework Directive (2010) classifications described in Maberly *et al.* (2011) indicate that eutrophication (a risk factor associated with die-back) is not severe (Table 3.5). While TP levels have declined post 1991, trends in chlorophyll *a* and Secchi depth following phosphate stripping were variable (Figure 3.8).

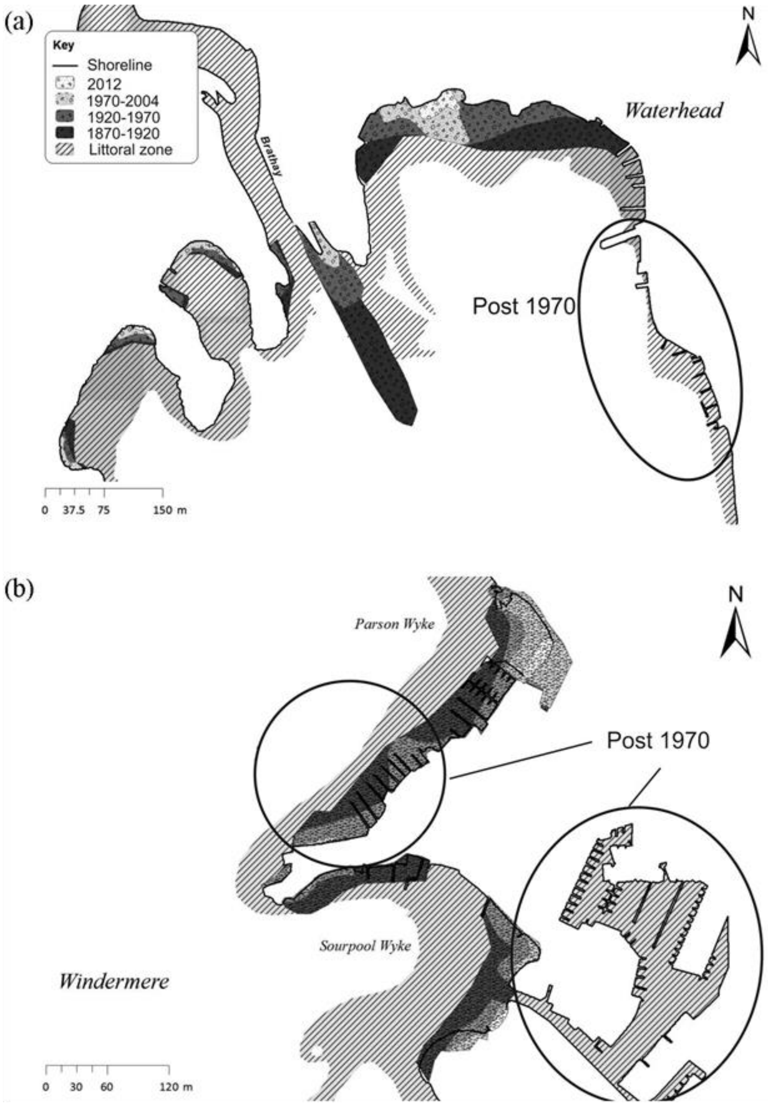


Figure 3.2 These maps depict temporal changes in shoreline development (jetties and piers only) and reedbed coverage from 1870 to 2012 near (a) Waterhead and (b) Ferry Nab, redrawn from Alvarez-Codesal (2012). Circles indicate areas developed post-1970. Shading with dates refers to contemporary (2012) and historic reedbed coverage (estimated for the time periods, 1870–1920, 1920–1970, and 1970–2004) within the littoral zone, a potential habitat for reeds.

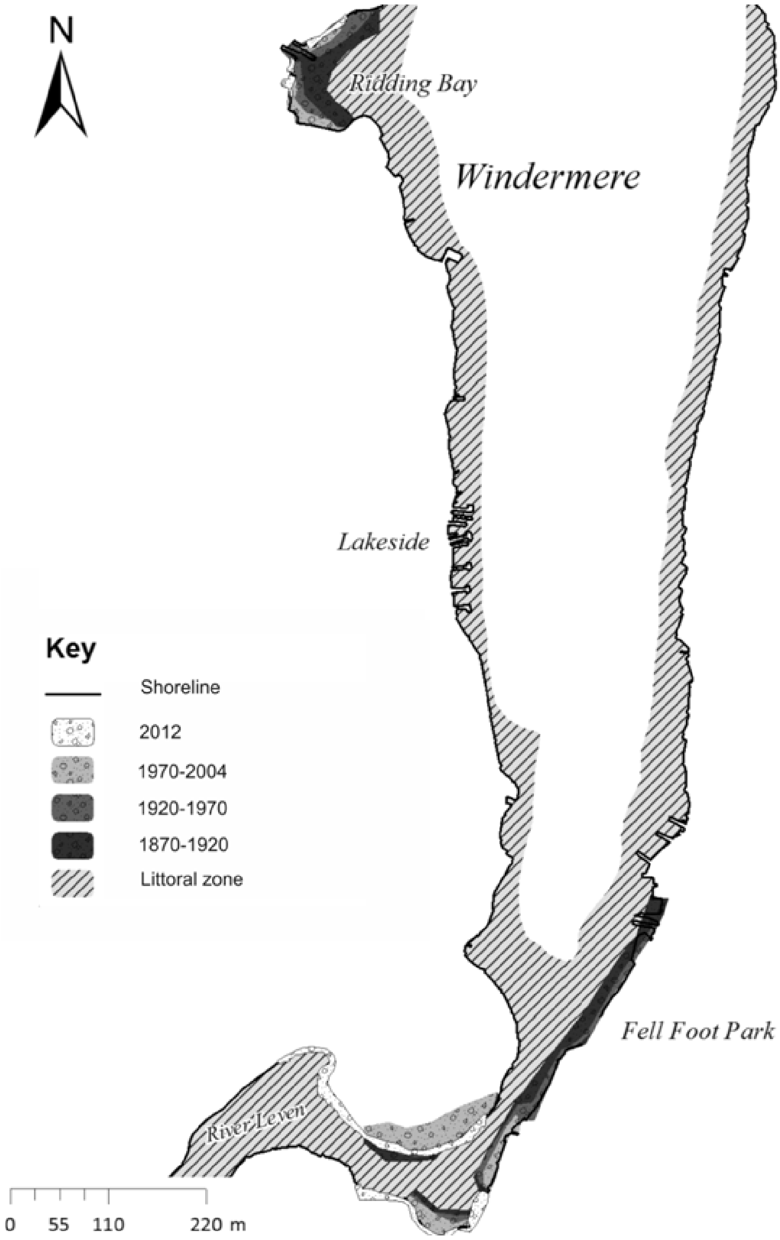


Figure 3.3 This map depicts temporal changes in reedbed coverage near Lakeside (Southern end of Windermere) from 1870 to 2012, redrawn from Alvarez-Codesal (2012). Shading with dates refers to contemporary (2012), and historic reedbed coverage (estimated for the time periods: 1870–1920, 1920–1970, and 1970–2004) within the littoral zone. Structures in the littoral zone at Lakeside are landing stages that have existed in some form since the late 1800s.

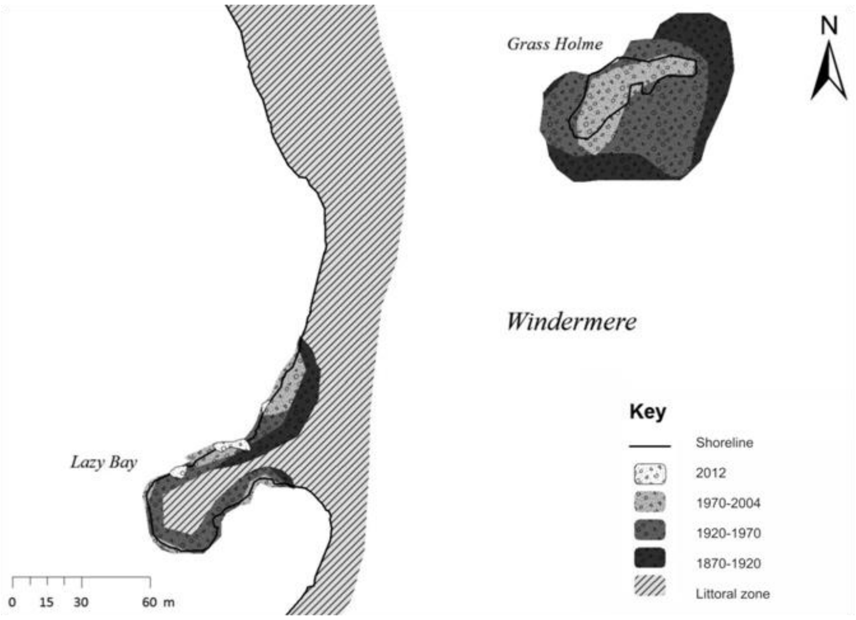


Figure 3.4 This map depicts temporal changes in reedbed coverage at Lazy bay and Grass Holme, Windermere South Basin, redrawn from Alvarez-Codesal (2012). Shading with dates refers to contemporary (2012) and historic reedbed coverage (estimated for the time periods: 1870–1920, 1920–1970, and 1970–2004) within the littoral zone. There are no records of landing stages (*e.g.,* jetties and piers) at this location during these time periods.

Table 3.3 Regression analysis indicated that declines in reedbed surface were the only environmental factors to demonstrate linearity over time for the North Basin (N), South Basin (S), and at a location equidistant between basins (W). Factors that demonstrated autocorrelation were omitted.

	Date range	n	*F*	R^2	*p*
Physical factors					
Surface area of reeds (N)	1920–2012	4	$F_{1,2}$ = 786.7	1.0	<0.0001
Surface area of reeds (S)	1920–2013	4	$F_{1,2}$ = 489.0	1.0	<0.0001
Surface area of reeds (W)	1920–2014	4	$F_{1,2}$ = 680.0	1.0	<0.0001
Annual mean rainfall	1965–2004	33	$F_{1,31}$ = 0.29	-0.02	0.59
Lake Level minimum (W)	1969–2012	39	$F_{1,37}$ = 5.01	0.1	0.03
Lake Level maximum (W)	1969–2013	39	$F_{1,37}$ = 7.12	0.2	0.02
Lake Level mean (W)	1969–2014	39	$F_{1,37}$ = 7.11	0.2	0.02
Water quality					
pH (S)	1975–2009	18	$\mathrm{F}_{1,16}$ = 2.17	0.1	0.16

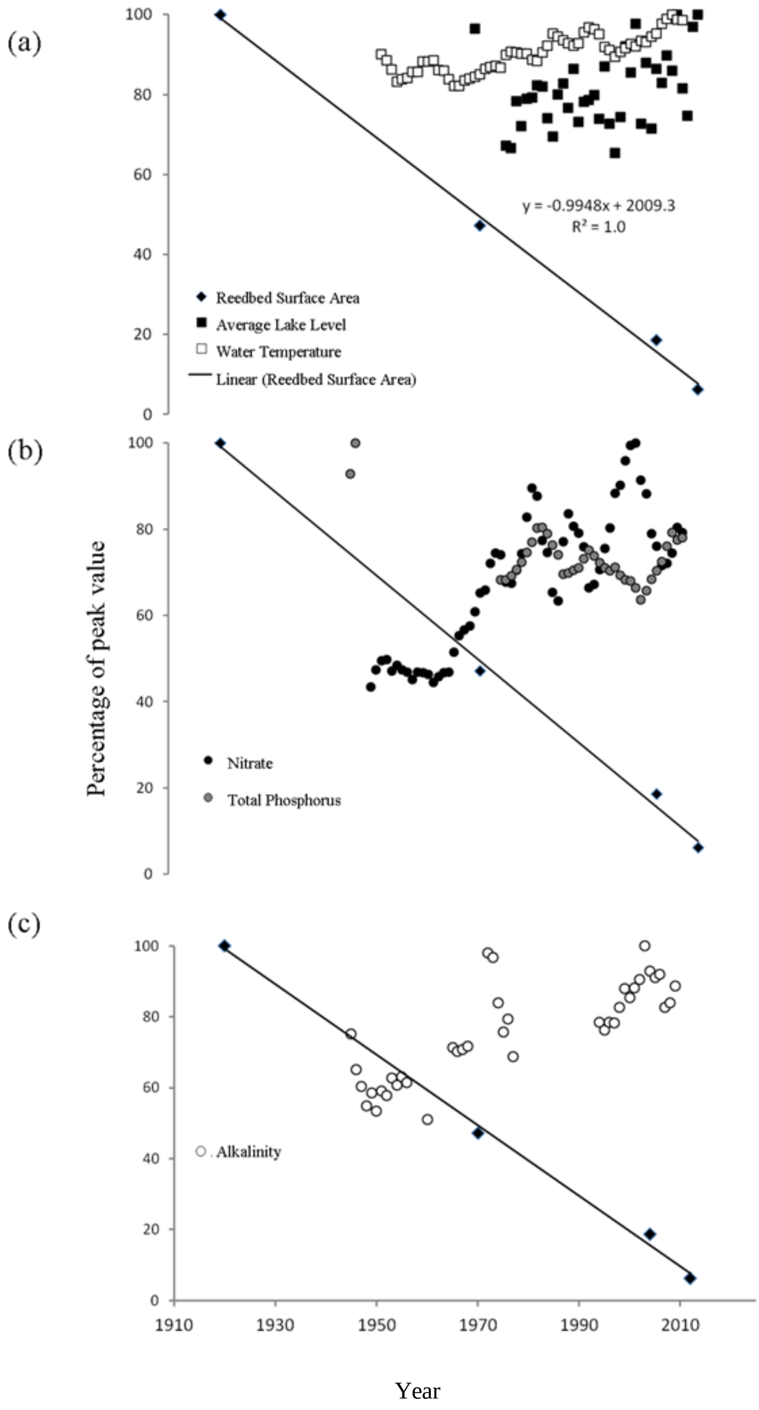


Figure 3.5 A comparison of trends in yearly means of physical (squares) and chemical factors (circles) for the North Basin of Windermere is depicted above. With the exception of reedbed surface area, all data points represent 5 year moving averages. Significant linear correlation (just under unity) is observed for changes in reedbed surface area.

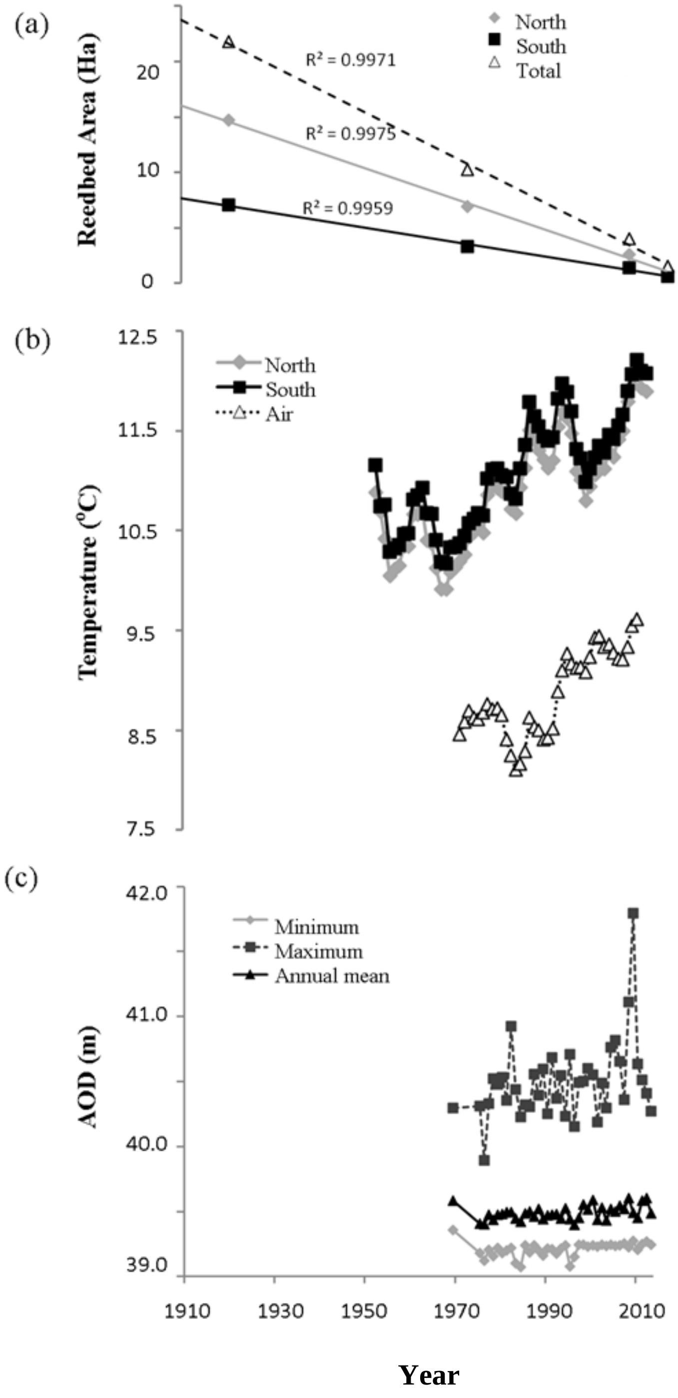


Figure 3.6 These graphs enable a comparison of trends in (a) reedbed surface area across both basins and (b) 5 year moving averages of annual means for temperature as well as (c) monthly values of minimum, maximum, and mean lake level above ordnance datum. Significant linear correlation is observed for changes in reedbed surface area.

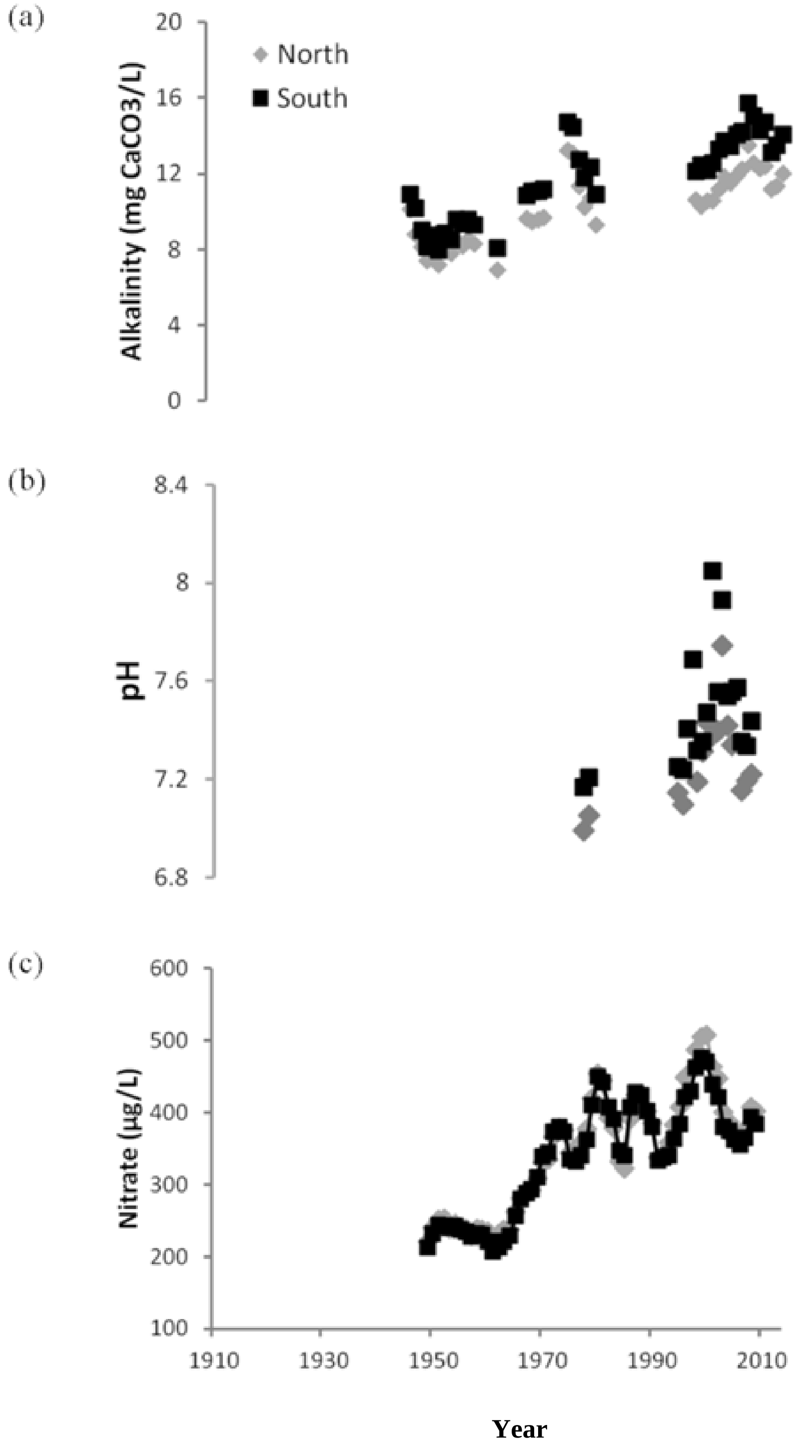


Figure 3.7 These graphs allow a comparison of trends in the annual means of chemical determinants for both basins.

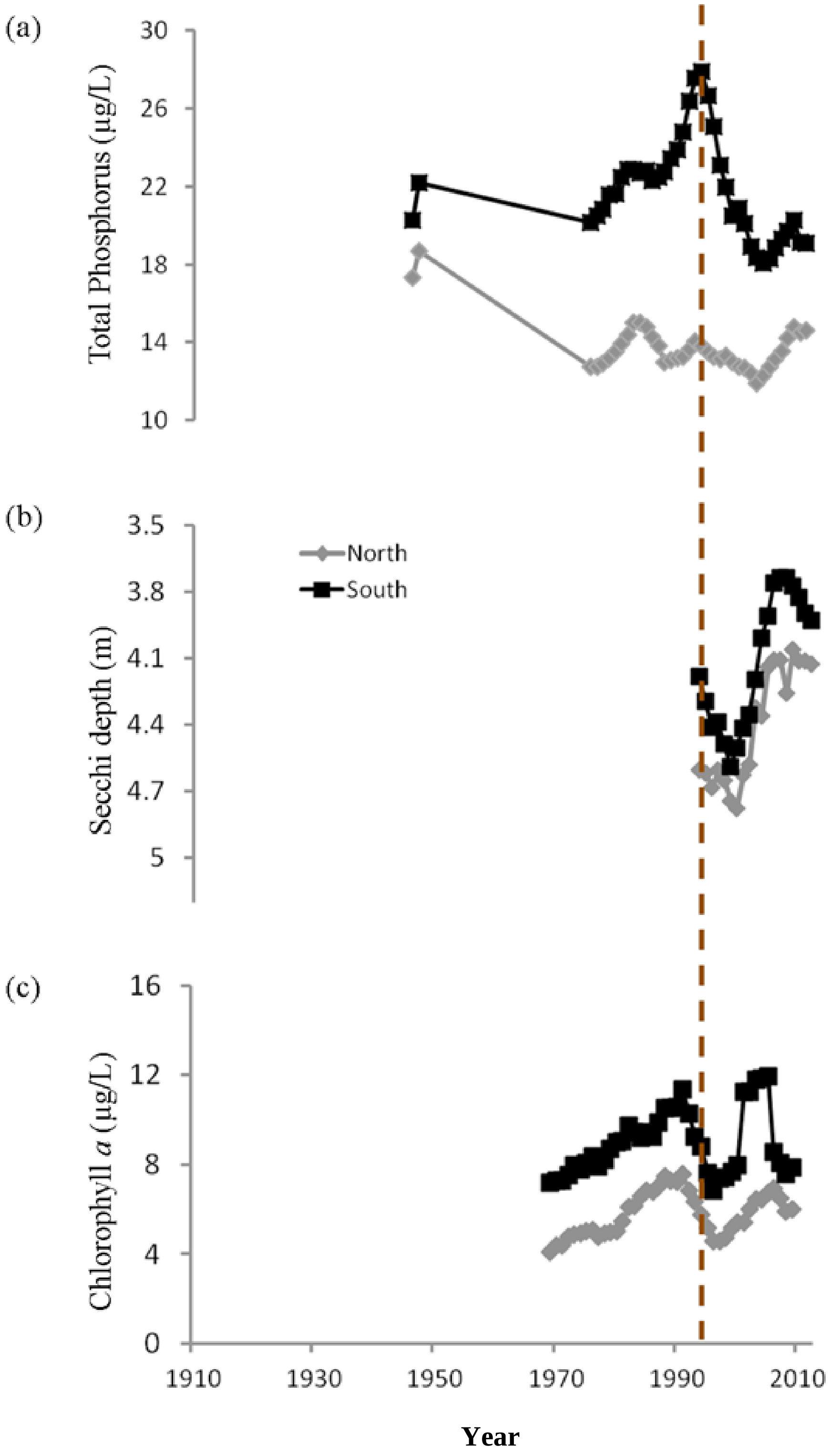


Figure 3.8 These graphs illustrate the response of key water quality indicators (five year moving averages of annual means), before and after phosphate stripping, at Ambleside and Tower Wood sewage treatment works (vertical dashed line). Secchi depth was inverted to reflect an initial improvement in water quality.

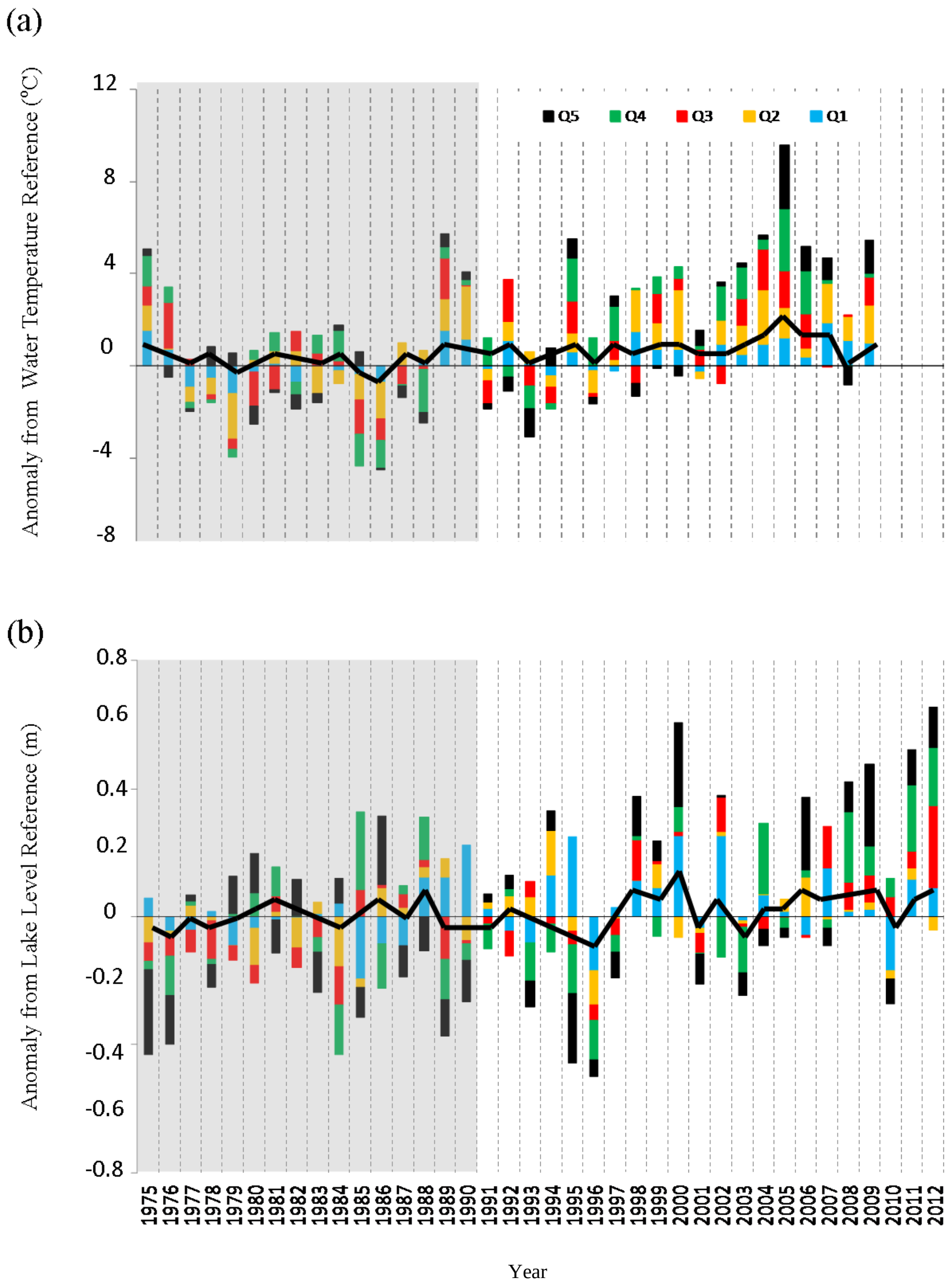


Figure 3.9 Seasonal changes in key hydro-meteorological factors were used to assess their influence upon reedbed habitat. Anomalies from mean values derived from a reference period (1975–90) for each year are displayed. The trend lines represent anomalies from annual means for (a) daily water temperature and (b) lake level. Stacked values represent anomalies for individual quintiles (*e.g.,* Q1 = 1st January – 14th March) by year. Shaded areas represent the reference period used to calculate anomalies.

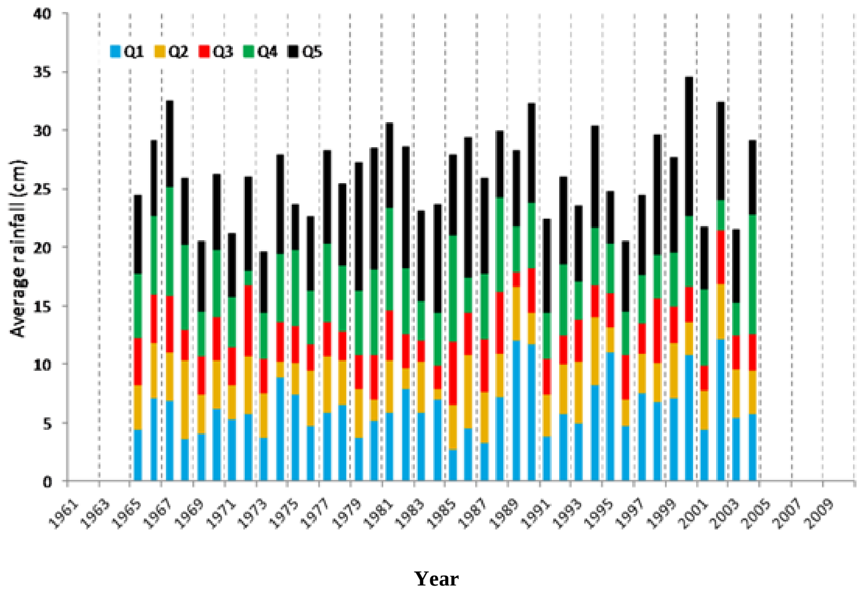


Figure 3.10 Seasonal rainfall patterns recorded at Ambleside by the Met Office weather station were used to assess their possible influence upon variations in water chemistry and hydrology. Stacked values represent mean values for each quintile (*e.g.,* Q1 = 1st January—14th March).

Table 3.4 This table allows for comparisons between Windermere and published data on factors associated with chemically mediated die-back from locations throughout the world. (* = Nitrate Vulnerable Zone [NVZ] designation, ø = data from sites within UK, Denmark, Germany, Czech Republic, and Hungary, Δ = data from controlled laboratory conditions, and + = general increase at Windermere over time)

	Source	Published value	Windermere (range of annual means)	Trend
Level of Nitrate (μg/L) associated with eutrophication*	DEFRA (2002)	>11, 300	208–507	+
Value of Alkalinity ($CaCO_3$ mg/L) associated with die-back ø	van der Putten (1997)	~850	6.1–17.8	+
pH at which phytotoxin release occurs Δ	Armstrong and Armstrong (1999)	4.5–6	6.5–9.7	+

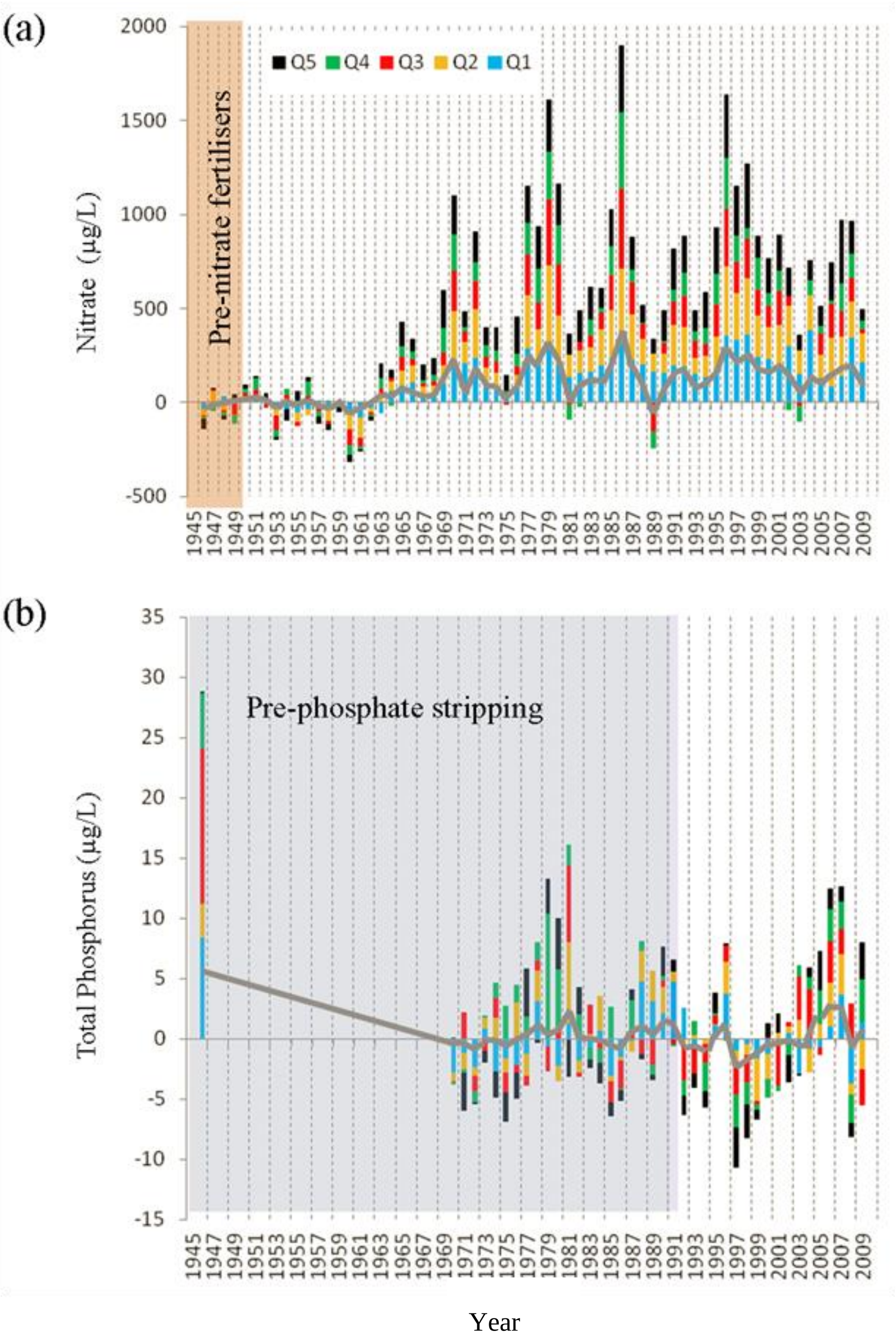


Figure 3.11 Seasonal variations in plant nutrient concentrations within Windermere were used to assess the influence of changes in nutrient loading. Stacked values represent anomalies from mean values derived from a reference period (shaded areas) for individual quintiles (*e.g.,* Q1 = 1st January – 14th March) by year. Shaded areas represents the reference period used to calculate anomalies for the period before nitrate fertilisers were widely used (orange) and pre-phosphate stripping at Ambleside STW (grey) respectively. Trend lines represent anomalies from annual means for (a) daily water temperature and (b) lake level.

Table 3.5 Contemporary Water Framework Directive (WFD) and trophic classifications for Windermere North and South Basins in 2010 (Maberly *et al.*, 2011) in the context of 5 year rolling averages recorded at each basin, refer to Figure 3.8 for details of long-term trends.

	North Basin		**South Basin**	
	5 year Rolling average	Classification (2010)	5 year Rolling average	Classification (2010)
Mean TP (µg/L) (1945–2009)	11.9–18.7	11.2 Mesotrophic Good (WFD)	17.3–27.9	12.6 Mesotrophic Moderate (WFD)
Mean Chl *a* (µg/L) (1969–2009)	4.1–7.6	16 Eutrophic	6.9–11.9	6.1 Eutrophic
Arithmetic observed Chl *a* (µg/L) (1969–2009)	-	12.3 Moderate (WFD)	-	6.3 Good (WFD)
Mean secchi depth (m) (1991–2009)	4.1–4.8	3.2 Oligo–Mesotrophic	3.7–4.6	3.9 Mesotrophic

In 2010, metals (*e.g.,* zinc, copper, and lead) were at undetectable levels throughout the year for Windermere and the majority of other lakes in the catchment. Diazinon (an organophosphorus insecticide) and 4-chlorophenoxyacetic acid (an artificial plant hormone) were the only micro-organic pollutants to exceed maximum allowable concentrations (UKTAG WFD Annex VIII substances). These levels were detected in the north and south basins respectively (Maberly *et al.*, 2011). Analysis of historic sediments by Hamilton-Taylor (1979) indicated that relatively high amounts of zinc, lead, and copper had been deposited into the south basin of Windermere over the previous 130 years (Figure 3.12). This was attributed to increases in human activities over that period. It was speculated that key causes of anthropogenic metal accumulation were: anthropogenic atmospheric deposition, metal/quarry mine run-off (via rivers), sewage, road run-off, and boating activity (Aston *et al.*, 1973; Hamilton-Taylor, 1979). Furthermore, the influence of seston (living and non-living suspended organic matter) in the cycling of metals throughout the lake is likely to have changed significantly over the last 130 years due to nutrient and organic enrichment of the lake (Pennington, 1973; Sholkovitz and Copland, 1982).

Phragmites rhizome-root systems typically occupy the upper layer (~50 cm) of sediments (Haslam, 2010). Metal-sediment concentrations (top 50cm) within the south basin of Windermere were relatively low compared to levels of contamination under which *Phragmites* has been shown not to display any adverse effects (Hamilton-Taylor, 1979; Weis *et al.*, 2004; Table 3.6). Studies of the historic accumulation of persistent organic compounds within the sediments of Windermere have been limited to changes in petroleum-derived aromatic hydrocarbons (PAH) within the north basin. Cranwell and Koul (1989) found that flux rates for polycyclic aromatic hydrocarbons in the north basin began to increase in the early part of the 20th century and peaked in the 1970s at ~4 $\mu g.\ cm^{-2}.\ year^{-1}$. It was estimated that levels in 1984 were ten times greater that pre-industrialisation levels; and that the mean concentration of total anthropogenic PAH within the top 53 cm of sediment was 38 ppm.

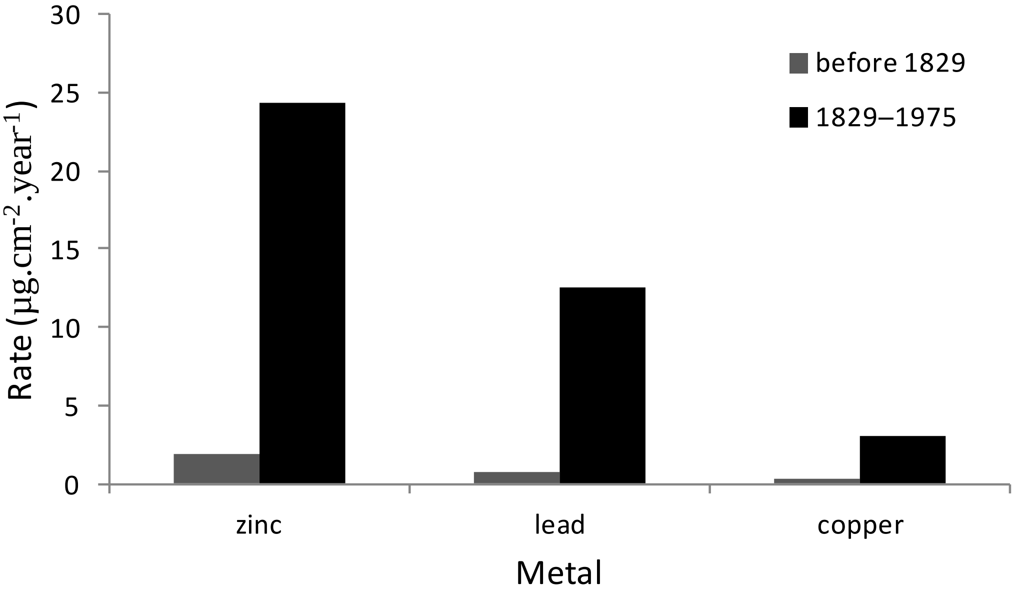


Figure 3.12 This graph illustrates differences in the rates of sedimentary flux over time for 3 commonly occurring metals within the south basin of Windermere, and is based upon data from Hamilton-Taylor (1979).

Table 3.6 This is a comparison between mean concentrations of metals within the top 50 cm of sediment in the profundal zone of the south basin of Windermere (Hamilton-Taylor, 1979), and the concentrations within an artificial substrate (vermiculite) in a greenhouse experiment (Weis *et al.*, 2004). The experiment included monocultures, and combinations of metals; no adverse effects upon *Phragmites* growth were observed.

Metal	Windermere concentrations (ppm)	Greenhouse experiment concentrations (ppm)
Zinc	454.2	1000
Lead	335.8	1000
Copper	42.2	1000

3.6 Discussion

Studies of recent environmental change (post-1920s) within Windermere at the whole lake scale have focussed upon long-term changes in physicochemical determinants within the pelagic zone (*e.g*., Maberly *et al.*, 2011) and their ecological consequences (*e.g*., Thackeray *et al.*, 2008). A novel aspect of this study was its focus upon the littoral zone through integration of a broad range of data derived from monitoring programmes, historic maps and photographs, academic papers, and government reports. By comparing changes in reedbed coverage to trends in multiple physical and chemical factors, this study implicated shoreline development and other physical stressors (*e.g.,* elevated water level) as responsible for reedbed decline. Long-term trends in water quality within the pelagic zone are not consistent with those trends associated with reed die-back syndrome (*sensu* Armstrong *et al.*, 1996b). However, these trends may not have been fully representative of conditions within the littoral zone. This highlights the need for further information on physicochemical conditions within the littoral zone (sediments, and water quality) of Windermere. Herein the discussion considers the underlying reasons for reedbed loss by investigating (H_1) physical stressors, (H_2) chemical stressors, and (H_3) the possible consequences of reedbed loss for chemical factors. Finally, the implications for conservation and management are discussed.

3.6.1 Physical causes of reedbed loss

Quantitative (*e.g.,* lake level) and qualitative data (*e.g.,* boat traffic) supported the hypothesis (H_1) that multiple physical stressors were associated with long-term reedbed decline (*sensu* Ostendorp *et al.*, 1995; Armstrong *et al.*, 1996b). Human shoreline developments have displaced pre-existing reedbeds and reduced the number of sites available for natural colonisation, and replanting. Most of the shoreline development was in place by 1900, albeit in more primitive forms than many of the contemporary structures. This implies that the impact of development over the last century (especially post-1970) had little influence on reedbed distribution. However, human activity associated with historic structures (*e.g.,* jetties and other access points) has changed in nature and increased in intensity. For example, visitor numbers have increased (Pickering, 2001), and since 2005 speed boating (*e.g.,* water skiing) has been superseded by pleasure craft boating (residential mooring, and ferry and cruise boats) as the characteristic boating activities. In addition, evidence from a recent oral history project 'Clear Waters' suggests that boating activity within Windermere has increased dramatically since the 1970s. While these stressors are not easily quantified, they have the potential to negatively impact the shore and littoral zones (Mosisch and Arthington, 1998; Bell, 2000; Gabel *et al.*, 2008).

One of the most ecologically significant changes within Windermere has been a progressive increase in water temperature over recent decades across all seasons (Thackeray *et al.*, 2008). Within warmer latitudes elevated water temperature can result in anoxic conditions that can lead to reed die-back syndrome (Armstrong *et al.*, 1996b). However, within the UK, warmer conditions have the potential to be beneficial. Summer temperatures are important, as warmth and elevated photosynthetically active radiation

(PAR) promote vigorous growth and seed production (Lessmann *et al.*, 2001). In addition, the production of viable seeds within the UK must occur before the first frosts, otherwise sexual reproduction will fail (M^{c}Kee and Richards, 1996). Also, young shoots (from established rhizomes) and seedlings are susceptible to frost, droughts, and floods (Haslam, 1975). Unfortunately, historic changes in the timing and duration of frosts are unknown. In addition, there was no evidence of the expected positive influence of warmer temperatures on reedbed sustainability and expansion into new areas. This may be because the positive effects of warmer temperatures may have been counteracted by other stressors. Consequently the net influence of warming on *Phragmites* within Windermere is unknown.

The retreat of reedswamps within Windermere towards the shore is consistent with elevated water tables. Within the littoral zone, high water levels can flood the broken stems of *Phragmites* and impede aeration (Gries *et al.*, 1990). Hence, elevated water level is likely to have had a negative influence on reedbed sustainability within deeper waters (*sensu* Gries *et al.*, 1990; Armstrong *et al.*, 1996b). Nearer to the shoreline, summer drought conditions can accelerate the displacement of reeds by scrub and amphibious macrophytes (Armstrong *et al.*, 1996b). As a result, flooding can have a negative influence upon reedswamp and a positive influence on fen reedbed habitat. However, the response of reedbeds to hydro-meteorological changes is complex (Armstrong *et al.*, 1996b; Lessmann *et al.*, 2001). This is due in part to physiologically distinct geographic biotypes that are adapted for different climates, such as short summers at northern latitudes (*e.g.,* UK). *Phragmites* have a number of physiological and anatomical adaptations to withstand droughts and flooding that vary across biotypes (Gries *et al.*, 1990). In addition, phenotypic variation allows *Phragmites* reedbeds to expand across ecotonal gradients (*e.g.,* water depth). However, the ability of phenotypic variation to cope with changes in water level is restricted to gradual changes or short lived events, rather than sudden and/or prolonged events (Vretare *et al.*, 2001).

There was no evidence that variations in water level were driven by changes in annual rainfall. The downstream flow of water across the lake is modified by abstraction for potable water supply, and by a Crump-style weir located near its outflow on the River Leven (Reynolds and Irish, 2000). Consequently, Windermere is classified as a ‘heavily modified water body’ under the Water Framework Directive (Environment Agency, 2013). Rainfall and associated run-off can also have an influence upon water quality, and sediments within reedbeds (Johnston *et al.*, 1996). However, annual rainfall did not vary significantly over time and was therefore unlikely to have influenced any water quality determinants. Rainfall can also have a direct influence upon the sustainability of reedbeds by disrupting pollination (Haslam, 1975).

Even transient flooding (minimum of several hours) can result in oxygen depletion sufficient to produce reduced conditions within the soil (redox potential <200 mV). This can trigger the release of nutrients, sulphides, and organic acids into the water column (Ponnamperuma, 1972), which can have a negative influence on *Phragmites*. Biological processes and physical disturbance can reverse this process by oxygenating flooded sediments (Drew and Lynch, 1980). For example, during the summer months *Phragmites* roots provide oxygen rich conditions at the surface of their rhizomes (Armstrong, 1967). In addition, wind and boat induced waves can oxygenate the sediments of shallow water (Hayes and Anthony, 1958). Oxygen rich conditions mimic the conditions within non-flooded reedbed habitat and allow nutrient uptake from the sediments during vegetative growth (Klopatek, 1977; Ho, 1980; Keddy, 2010). Consequently, physicochemical determinants near the surface of the water at the centre of each basin are not representative of conditions within the littoral zone sediments. Nonetheless, data collected from the centre of each basin do provide an indication of long-term trends in water quality that are relevant to the littoral zone and the organisms within.

3.6.2 Additional physical stressors associated with reedbed decline

Reedbed loss occurred at both sheltered and exposed sites and was not restricted to areas of shoreline development, proximity to launch facilities, or other categories of human activity. A possible explanation for loss at these sites, is that an initial loss of reedbed habitat across the lake due to shoreline development ~1900 resulted in a decline in the genetic diversity of *Phragmites.* As a result the ability of the population to respond to a range of physical, biological, and chemical changes over the long-term was restricted (*sensu* Clevering and Lissner, 1999; Vretare *et al.*, 2001). In addition, a lack of human activity or other types of physical disturbance may have facilitated natural succession at some locations and led to the displacement of reeds by deciduous woodland (*sensu* Keddy, 2010; RSPB, 2011). Indirect consequences of human activity, such as the introduction of alien invasive species (*e.g.,* bird species) are also likely to be important.

Studies throughout the world have demonstrated that high numbers of geese and other grazing wildfowl can have an adverse influence upon water quality and reedbed coverage (Pehrsson, 1988; Feare *et al.*, 1999; Unckless and Makarewicz, 2007). At Windermere, long-term increases in non-native Canada Geese (*Branta canadensis*) have been linked to losses in reedbed coverage due to grazing (Pickering, 2001). In addition, it has been speculated that defecation may have an impact on organic, nutrient, and bacterial (*e.g., Escherichia coli*) loading of the lake (Pickering, 2001; LDNPA, 2012). Unfortunately, analytical investigations into the impact of wildfowl grazing and defecation upon Windermere are lacking.

By 1970 reedbed decline was already advanced (Alvarez-Codesal, 2012), however, at this time numbers of Canada Geese were much lower than their current level. These low numbers continued into the 1980s; for example, in 1983 there were no recorded Canada Goose sightings within Windermere. The non-native goose population of Windermere has now reached nuisance proportions with an estimated 1164 individuals recorded in 2011, the majority (69%) of these birds were residents rather than regional migrants (LDNPA, 2012). While there is little evidence that Canada Geese have been major factors in the historic loss of reeds, they are a clear threat to the survival and expansion of remnant and replanted reedbeds within Windermere.

3.6.3 Chemical causes of reedbed loss

There was a lack of support for the hypothesis (H_2) that historic and contemporary chemical conditions within Windermere were consistent with reed die-back syndrome. Genetic diversity (biotypes) has allowed *Phragmites* to colonise a broad range of chemical environments (Tomimatsu *et al.*, 2014). Despite this, reed die-back syndrome and retarded growth have become prevalent throughout Europe (Brix, 1999a; Gigante *et al.*, 2011). Understanding the influence of organic and nutrient enrichment upon declining reedbed sustainability is particularly challenging because reedbeds are associated with a broad range of enrichment conditions within natural and constructed wetlands. Increased organic loading promotes anoxic conditions within sediments which results in depressed pH, increased nutrient and metal solubility, and phytotoxin production (Armstrong and Armstrong, 1999; Moss, 2009). High nutrient conditions are often associated with reedbed loss. However, it is the often the factors associated with high nutrient environments (*e.g.,* high salinity, altered soil chemistry, and phytotoxins) that have been identified as the main stressors and not the nutrients directly (Čížková-Končalová *et al.*, 1992; Armstrong and Armstrong, 1999). Historic and contemporary data from the pelagic environment indicated that physicochemical determinants within Windermere were not consistent with those associated with die-back. Unfortunately, contemporary and historic accounts of chemical changes in Windermere's littoral sediments are lacking.

Despite a long-term decline in TP, Windermere remains phosphate-phosphorus enriched (Reynolds and Irish, 2000; Elliott, 2012). This has had different impacts on each basin (Elliott, 2012). The North Basin is mesotrophic and is less productive than the South Basin which is at the mesotrophic–eutrophic border (Maberly *et al.*, 2011). While TP levels in the water column are not currently at eutrophic levels, the impact of historic enrichment upon reedbed decline is unknown. Unfortunately, data regarding sediment bound phosphorus within Windermere is lacking. Consequently, it is important to determine the contribution of phosphate-phosphorus enrichment to organic loading within the sediments of Windermere. In addition, long-term nitrate enrichment has also occurred within both basins. Increases in nitrate concentration are likely to have been driven by changes in land use and agriculture, as deposition of nitrogen has changed little over the last century (Tipping *et al.*, 1998). It has been proposed that nitrate enrichment can lead to an increase in nitrogen to carbon ratios within the tissues of *Phragmites*. This has been linked to adverse changes in reed morphology and growth which makes them more vulnerable to uprooting during physical disturbance (Kuhl and Kohl, 1993; Armstrong *et al.*, 1996b). However, evidence is limited to a relatively small number of studies. Furthermore, the carbon and nutrient requirements of *Phragmites* biotypes within Windermere are key gaps in knowledge.

The trend of increasing pH within the pelagic zone of Windermere was consistent with a decline in hydrogen ion and nonmarine sulphur deposition that began in the late 1970s (Tipping *et al.*, 1998). *Phragmites* die-back due to phytotoxin release from sediments occurs at pH 4.5–6 (Armstrong and Armstrong, 1999) and values near the surface ranged from pH 6.5 to 9.66 between 1974 and 2009. However, within littoral sediments pH is likely to have been lower compared with the surface water due the accumulation of CO_2 as a result of relatively anoxic conditions (Jones and Simon, 1981; Moss, 2009). Consequently, the influence of phytotoxin related die-back syndrome due to pH may have been a key factor in the past; however, its influence is likely to have diminished over recent decades.

If alkalinity levels become excessively high due to increasing pH and soil erosion (Sutcliffe *et al.*, 1982) they have the potential to harm reeds. Studies within transitional waters suggest that elevated alkalinity has the potential to limit photosynthesis and to restrict growth (Yang *et al.*, 2008; Deng *et al.*, 2011). Alkalinity data from sediments within freshwater *Phragmites* beds located throughout northern and central Europe indicate that vigorous growth occurs at ~250mg $CaCO_3/L^{-1}$, and die-back at ~850mg $CaCO_3/L$ (van der Putten, 1997). Unfortunately, alkalinity values within the littoral zone sediments of Windermere are unknown. However, the trend for increases within the pelagic zone suggests that the risk of alkalinity acting as stressor is increasing.

Comprehensive studies into reed die-back syndrome within natural wetland habitats across Europe (Ostendorp, 1989; van der Putten, 1997; Brix, 1999a) have not focussed upon the potential of non-nutrient pollutants to cause reed pathologies. Furthermore, published accounts of phytoremediation featuring natural or constructed wetlands in the treatment of contaminated soil and water do not suggest that adverse impacts upon reeds are common (Schwitzguébel *et al.*, 2002; Weis and Weis, 2004; Chu *et al.*, 2006; Derr, 2008; Matamoros *et al.*, 2012). Data relating to the south basin, and published accounts of phytoremediation do not suggest that metal pollution is a likely cause of reedbed loss within Windermere. For example, it has been demonstrated that plants from a wide range of non-contaminated locations can be successfully used for the phytoremediation of metals (Alkorta *et al.*, 2004; Marchand *et al.*, 2010). However, the response of different *Phragmites* biotypes (*e.g.,* metal distribution within tissues) to contamination has been shown to be highly variable (Ye *et al.*, 1997; Batty and Younger, 2004). Unfortunately, it is rare for studies of phytoremediation to publish data relating to contamination levels within effluents and/or sediments.

Evidence from natural and constructed wetlands throughout the world suggests that adverse impacts upon *Phragmites* reedbeds from organic pollutants are rare. For example, it has been demonstrated that the intentional control of *Phragmites* stands by herbicides (*e.g.,* glyphosate) is not effective without other measures such as mowing (Derr, 2008). Furthermore, *Phragmites* has demonstrated its utility in the phytoremediation of herbicides (Schröder *et al.*, 2005). Phytoremediation of wastewaters contaminated with di-azo dyes (*e.g.,* diazinon) using *Phragmites* is a relatively new approach. Consequently, research is in an early stage; however, there is no robust evidence of adverse impacts upon reedbed sustainably (Sharma *et al.*, 2005; Ferreira *et al.*, 2014). Similarly, data from

Matamoros *et al.* (2012) indicated that restored wetland (including *Phragmites*) within a small lake in Denmark was implicated in the mitigation of high concentrations of 4-chlorophenoxyacetic acid and other emerging contaminants associated with agricultural run-off. Adverse impacts upon wetland habitats were not reported. For petroleum pollution, a laboratory experiment by Nei *et al.* (2010) demonstrated that *Phragmites* responds by modulating the distribution of its biomass; but did not report any adverse consequences. Overall, Windermere data in combination with published accounts of reed die-back, and phytoremediation did not support the hypothesis (H_2) that changes in chemical conditions were responsible for reedbed decline. However, the high degree of genetic diversity typically associated with *Phragmites* populations means that caution must be exercised when making generalisations regarding the influence of chemical changes upon reedbeds (*sensu* M^{c}Kee and Richards, 1996; Marchand *et al.*, 2010).

3.6.4 Potential limitations of the physicochemical dataset

The long-term physicochemical monitoring programme for Windermere was originally designed to investigate factors relevant to the study of phytoplankton and its response to climate change and nutrient enrichment (Maberly *et al.*, 2011). This type of data (*e.g.,* temperature, and TP) has the potential to provide valuable insights into the relationship between reeds and the wider environment (*sensu* van der Putten, 1994). However, the Windermere dataset has a number of important deficiencies for the study of reedbed persistence. Firstly, data relating to long-term trends in non-nutrient pollutants are lacking. Secondly, pelagic data may not be representative of conditions within adjacent littoral sediments. Finally, sampling frequency (*e.g.,* fortnightly) may not be sufficient to detect important environmental changes.

For the current study, the investigation of possible causes of reedbed loss was based on the assumption that physicochemical trends in the pelagic zone are similar to those in the littoral zone. However, this assumption needs to be tested by detailed scientific monitoring of the littoral zone, which was beyond the scope of this study. Pelagic surface water data may not accurately reflect chemical conditions throughout the whole lake. For example, the redistribution of phosphate-phosphorus throughout an individual lake is a dynamic process (Boar *et al.*, 1989; Wetzel and Likens, 2000; Kim *et al.*, 2003). Phosphorus readily switches between soluble and insoluble forms in response to environmental change. These forms have contrasting affinities for the water column, and sediments. Soluble forms are readily incorporated into organic matter, which has a tendency to accumulate in the sediment phase. Within sediments, organic-phosphorus complexes are susceptible to anoxic conditions which can lead to the release of soluble phosphorus (Moss, 2009). Cycling of metals (*e.g.,* copper, lead, and zinc) occurs in a similar way (Sholkovitz and Copland, 1982).

Chemical exchanges between sediments and overlying water are determined by complex interactions between benthic organisms (*e.g.,* heterotrophic bacteria), macrophytes, sediment characteristics (*e.g.,* organic content), physical disturbance, and water chemistry and temperature (Cyr, 1998). Within the profundal-pelagic (deep water) zones of both Windermere basins, thermal stratification occurs during the summer months of most years (Pickering, 2001). During stratification, the transport of chemical elements (*e.g*., oxygen and nutrients) between the upper layer (~10 m) of the water column and the underlying water is relatively low (Thackeray *et al.*, 2008). In contrast, mechanical disturbance of littoral sediments and associated mixing throughout the water column is likely to be relatively high during the summer, due a peak in the intensity of boat usage. Consequently, stratification and human activity have the potential to have a strong influence upon chemical cycling throughout the lake (*sensu* Boers *et al.*, 1984; Wetzel and Likens, 2000; Kim *et al.*, 2003). Hence, pelagic-surface water data does not allow a robust investigation of changes in the key characteristics of littoral zone sediments (*e.g.,* redox potential).

It has been suggested that the resolution of the physicochemical dataset for Windermere (*e.g.,* fortnightly sampling) is sufficient for investigating the significance of trends in water quality and climate for phytoplankton populations (George *et al.*, 2004; Thackeray *et al.*, 2008; Maberly and Elliott, 2012). However, the resolution of the dataset may be less suitable for the study of *Phragmites*. There are key biological differences between reeds and phytoplankton. Compared to populations of phytoplankton, reedbeds are sedentary, slow growing, reproduction is less efficient, and genetic diversity is much lower (Haslam, 1973; Thackeray *et al.*, 2008). Both organisms are sensitive to deviations from seasonal norms (*e.g.,* late frosts, and summer floods) and associated physicochemical changes. However, the capacity of reed populations to recover from short duration impacts (<14 days) is considerably lower (Van der Toorn and Mook, 1982; Padisák, 1993; Dinka *et al.*, 2004; Conroy *et al.*, 2011).

The dataset derived from the monitoring of physicochemical trends within Windermere originated in 1945, as consequence it is based upon traditional sampling approaches which have changed little over the last 69 years (George *et al.*, 2004; Maberly and Elliott, 2012). Spot sampling (*i.e*., once every two weeks in Windermere) has the potential to miss important short-duration changes (*e.g.,* anoxic episodes). Hourly monitoring (or similar resolution) of physicochemical variables within sediments throughout the annual cycle over multiple years is required for the robust investigation of reedbed health. This is now feasible given recent technological developments (*e.g*., continuous monitoring using a redox probe). High resolution monitoring of physicochemical determinants and selected chemicals (*e.g.,* zinc, copper, lead, diazinon, 4-chlorophenoxyacetic acid, and PAHs) within littoral sediments and overlying water should be a research priority for Windermere.

3.6.5 The relationship between physical and chemical stressors

Trends in reedbed loss and chemical conditions within the pelagic zone do not support the hypothesis (H_3) that a continued decline in reedbed dominance will result in a shift in chemical conditions to those associated with die-back (*e.g.,* anoxia). This was unexpected given the effectiveness of *Phragmites* in the amelioration of water quality and chemical conditions within sediments (Ostendorp, 1993). Compared with the rate of chemical changes (*e.g.,* alkalinity) within the pelagic zone, decline in reedbed area has been rapid. In addition, contemporary chemical conditions in the pelagic zone are not approaching those associated with die-back. This is despite widespread reedbed recession and fragmentation. However, due to a lack of littoral data it is possible that reedbed loss due to physical pressures has or will lead to a shift in chemical conditions within the sediments to those associated with die-back. Given the broad range of potential stressors it is important to consider multiple physical and chemical factors when investigating the interaction between reedbeds and environmental factors (Figure 3.13).

Within Windermere it was difficult to assess the relationship between changes in reedbed surface area and water quality. This was because water quality determinants were influenced by major independent changes in nutrient loading (*e.g.,* phosphate stripping) and hydro-meteorological factors (*e.g.,* temperature) (Thackeray *et al.*, 2008). Throughout the world, reedbeds have been shown to have an inhibitory effect on deteriorations in water quality related to phytoplankton biomass. For example, *Phragmites* beds have been shown to be important refuges for zooplankton grazers that regulate phytoplankton blooms (Okun and Mehner, 2005; Cazzanelli *et al.*, 2008). However, studies of planktonic organisms suggest that the loss of reedbed habitat as a refuge for zooplankton was not a key factor in the deterioration in water quality within Windermere following a initial improvement linked to phosphate stripping. Instead it was strongly linked to

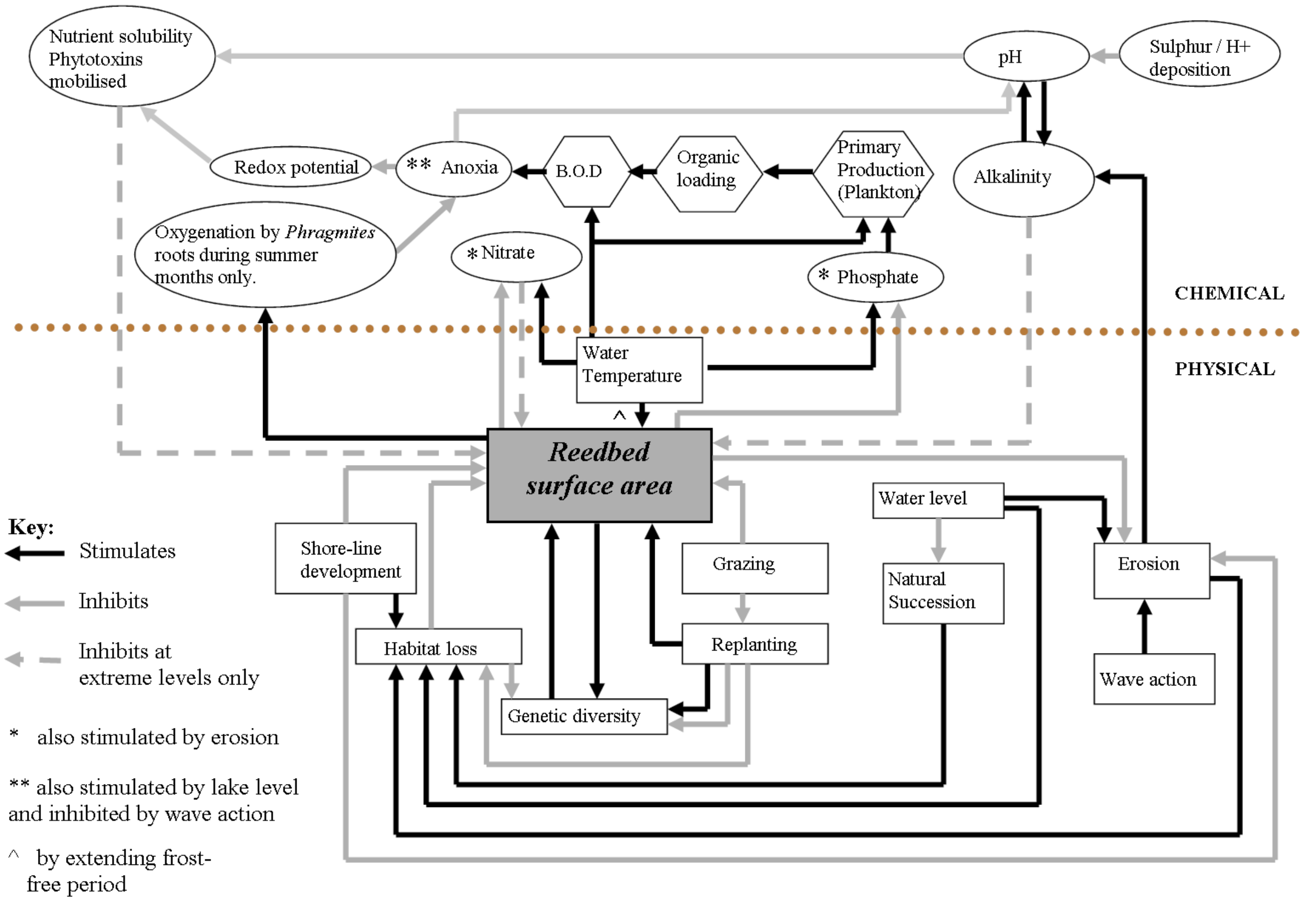


Figure 3.13 A conceptual model was used to illustrate the possible ways in which physical (rectangles), biological (hexagonals), and chemical factors (ovals) combine to influence reedbed sustainability within lakes.

the effect of increasing water temperature upon phytoplankton (Thackeray *et al.*, 2008). The influence of warming was supported by George and Harris (1985) who found that within Windermere, zooplankton biomass was more closely correlated to fluctuations in temperature rather than to numbers of planktivorous fish. In addition, variations in grazing pressure from zooplankton have been shown to have a relatively small influence on spring blooms of diatoms within Windermere when compared to the influence of temperature and phosphate-phosphorus enrichment (Thackeray *et al.*, 2008).

Analysis of seasonal changes in nutrients within the pelagic zone has the potential to provide insights into the ways in which fringing reedbeds act as buffer strips, and the consequences of their loss. Reeds are deciduous perennial grasses (Hubbard, 1982); consequently they can have a strong influence on seasonal variations in local nutrient levels within the littoral zone (Klopatek, 1977; Ho, 1980; Keddy, 2010). Rainfall data suggests that within reedbeds, the majority of nutrients bound to soil (from runoff) accumulate outside of the summer months. In contrast, sewage effluent discharge is likely to be at its highest during the summer months due to a peak in transient visitors (tourists) (Pickering, 2001). During the summer months nutrients associated with reedbed habitat become insoluble and are incorporated into reed tissues (Klopatek, 1977; Ho, 1980). After this period of vegetative growth, nutrients leach out of reed tissues into the aquatic environment (Polunin, 1982). It is probable that the influence of this natural cycle of phosphate-phosphorus loading and cycling within Windermere was disrupted by the temporal dynamics of sewage effluent discharges. This may explain why there were no clear changes in the seasonal patterns of nutrient concentrations during a period of reedbed loss. The general lack of information regarding key processes (*e.g.,* nutrient cycling) within the littoral zone, and their interaction with the pelagic zone and deep water sediments, is a key research gap.

3.6.6 Conclusions

Reedbed loss is one of the most noticeable and potentially ecologically significant environmental changes to occur within Windermere over the last century. Diminished persistence of reedbed habitat is associated with increases in a number of different stressors (*sensu* Ormerod *et al.*, 2010). Available evidence suggests the majority of stressors were likely to have been physical rather than chemical in nature. However, some physical trends within Windermere (*e.g.,* increasing water temperature) may enhance reedbed sustainability (sensu M^{c}Kee and Richards, 1996). The ability of *Phragmites* to adapt to rapid change (*e.g.,* elevated water table) is likely to have been compromised by a potential loss of genetic diversity due to the shoreline development of Windermere and consequential widespread loss of reedbeds (sensu M^{c}Kee and Richards, 1996; Vretare *et al.*, 2001; Lambertini *et al.*, 2006). Due to the multi-factorial nature of reedbed loss (*sensu* Ormerod *et al.*, 2010) the conclusions within this chapter are speculative. In addition, the datasets utilised were collected by others (*e.g.*, Maberly *et al.*, 2011) and were not designed to investigate changes within the littoral zone. This chapter highlights the need for addressing major unknowns within the littoral zone of freshwater lakes, including the role of *Phragmites* genetic diversity and phenotypic plasticity in reedbed resilience. This would require long-term multiple factorial experiments. In addition, comparative studies of the genetics of healthy and unhealthy reedbeds would also be beneficial. Understanding the genetics of reeds within Windermere and their environmental tolerances is essential for the conservation of this important habitat.

3.6.7 Implications for conservation and management

From a technical perspective many of the physical stressors linked to reedbed loss within Windermere are relatively easy to ameliorate (Pickering, 2001). For example, water level is regulated by a weir managed by a government body (the Environment Agency), and control of non-native wildfowl numbers should reduce grazing pressure. In addition, there are current planning applications for new shoreline development projects within Windermere that would impinge upon current reedbed habitat. Unfortunately, support for the protection of reedbed habitat is lacking due to a number of political considerations that relate to local socioeconomic issues. For example, there was widespread public opposition, on the grounds of animal welfare, to a proposed plan to cull Canada Geese in 2011. The findings of this study have the potential to persuade the general public, regulators (*e.g.,* the Environment Agency), owners of the lake (*e.g.,* South Lakeland District Council), and other stakeholders (*e.g.,* United Utilities PLC) of the importance of reedbed habitat in the sustainable use of the lake (*sensu* Ostendorp, 1993). In particular, this study highlights a number of adverse environmental changes and demonstrates the need for management at the whole lake scale. By identifying some of the risk factors associated with reedbed sustainability, this study provides important guidance on how to manage the lake. It also highlights the need for research to focus upon the littoral zone.

3.7 Summary

Historically, Windermere has been characterised by extensive *Phragmites* reedbeds that have fringed its shores and islands (Alvarez-Codesal, 2012). Unfortunately, this ecologically important habitat is now under threat due to an extensive decline that was underway as early as the 1920s (Pickering, 2001). Long-term (~70 years) trends in a number of different potential stressors upon Windermere (*e.g.,* elevated lake level, increased water temperature, nutrient enrichment, and number of grazers) are consistent with conditions associated with reedbed loss throughout Europe (*sensu* Ostendorp *et al.*, 1995; Armstrong and Armstrong, 2001; Ormerod *et al.*, 2010). However, a robust and comprehensive understanding of reedbed loss within Windermere was prevented by deficiencies in the Windermere dataset. Important aspects of physical pressures were qualitative (*e.g.,* the impact of boating, and grazing), and physicochemical data was restricted to the pelagic zone. This was compounded by key gaps in knowledge regarding reed die-back syndrome (*e.g.,* the role of genetic diversity), and inconsistent evidence, such as the influence of nutrient status upon reedbed health across different lakes (Ostendorp *et al.*, 1995). Furthermore, little has been published about how multiple factors combine to influence reedbed persistence. This thesis proposes a conceptual model (Figure 3.13) which explores the complex relationship between multiple physical (*e.g.,* wave-washing) and chemical factors (*e.g.,* pH), and reedbed coverage. The model integrates published information and observations from Windermere, and needs to be tested. A key aspect of this model is the importance of genetic diversity in reedbed resilience to both physical and chemical changes (*sensu* Clevering and Lissner, 1999). It is recommended that detailed case studies at the regional scale (*e.g.,* northwest England) are used to investigate the relationship between genetic diversity and multiple environmental factors within Windermere and other lakes.

CHAPTER 4 Macroinvertebrate biodiversity in reedswamp habitat

4.1 Chapter Introduction

Chapters 2 and 3 reviewed the importance of reedswamp habitat and its changing status within Windermere, and throughout the world. This chapter uses primary survey data to investigate the consequences of variations in reedswamp habitat for macroinvertebrate biodiversity across 2 lakes.

4.1.1 Introduction

Ecosystems are dynamic systems driven by various factors at scales from global to local (Vitousek *et al.*, 1997; Tilman and Lehman, 2001). The ‘habitat heterogeneity hypothesis’ is central to our understanding of ecology (Simpson, 1949; MacArthur and Wilson, 1967). It predicts that structural complexity drives biological diversity and ecosystem stability by providing niches and diverse opportunities to utilise environmental resources (Bazzaz, 1975). The movement of species between mesohabitats (structurally distinct patches) is thought to be an important mechanism for determining the dynamics and sustainability of ecosystems (van Nes and Scheffer, 2005). Thus, an enhanced understanding of the ways in which ecosystems respond to external change (*e.g.,* habitat fragmentation) over a range of temporal and spatial scales remains a key research theme in ecology (Resh and Rosenberg, 1989; Vitousek *et al.*, 1997; van Nes and Scheffer, 2005).

Freshwater ecosystems are particularly vulnerable to a variety of external pressures, many of which are terrestrial in origin (Lake *et al.*, 2000). Natural wetland transitional zones (ecotones) act as an important buffer between the aquatic and terrestrial habitat (Ferrati *et al.*, 2005; Keddy, 2010), mitigating the impact of urban, industrial, and agricultural run-off upon the aquatic environment (Brüsch and Nilsson, 1993; Harbor, 1994; Bratli *et al.*, 1999). In addition, they enhance biodiversity within both environments (Ward *et al.*, 1999) by providing habitat for wildlife that include macroinvertebrates, fish, and migratory birds (Vander Zanden and Vadeboncoeur, 2002; RSPB, 2011). However, freshwater biodiversity is facing "unprecedented and growing threats from human activities" (Dudgeon *et al.*, 2006, p.164), and the effects of structural changes in transitional aquatic environments are largely unknown (White and Irvine, 2003; Brauns *et al.*, 2007b). Studies across the world suggest that anthropogenic deterioration of the structural heterogeneity and complexity of lacustrine ecotones is likely to increase in the future (Ostendorp, 1989; Tscharntke, 1999; Saltonstall, 2002; Brauns *et al.*, 2007b).

Changes in macrophyte community structure at local and regional scales have a particularly strong influence upon habitat structure/complexity within lacustrine ecotones (Lodge *et al.*, 1988; Chick and McIvor, 1994; Weaver *et al.*, 1997; Weatherhead and James, 2001). Such changes can have a profound impact upon aquatic biodiversity by modifying the niches available to a broad range of organisms (Cole and Weigmann, 1983; Tscharntke, 1992; Tolonen *et al.*, 2001; Peeters *et al.*, 2004; Stoffels *et al.*, 2005). Across the globe, changes in reedswamp prevalence within the littoral zone have been implicated in biodiversity and ecosystem functioning declines (Ostendorp, 1993; Brix, 1999b; Saltonstall, 2002; Schmieder, 2004; Rogalski and Skelly, 2012). Unfortunately, the consequences of changes in the structure, distribution, and dynamics of reedswamp habitat upon whole lake biodiversity remain unknown.

Assemblages of familiar and well-studied groups of organisms are commonly used to investigate changes in biodiversity, habitat heterogeneity, and water quality (Noss, 1990; Dufrêne and Legendre, 1997; Wright *et al.*, 1998; White and Irvine, 2003). For example, the use of littoral macroinvertebrate assemblages in the assessment of ecological status of lakes is on the increase (Heino, 2008; Tolonen and Hamalainen, 2010; Schreiber and Brauns, 2010). They are central components of food chains and contribute significantly to the energy budget of the whole lake (Strayer and Likens, 1986; James *et al.*, 1998; Vadeboncoeur *et al.*, 2002).

Macroinvertebrate assemblages within the shallows of lakes and ponds are sensitive to differences in habitat structure (Dvořák and Best, 1982; Tolonen *et al.*, 2001; White and Irvine, 2003; Schreiber and Brauns, 2010) and their relative position along the ecotone (Dvořák, 1970; Mason and Bryant, 1974; Sychra *et al.*, 2010). At the local scale (<30 m) macroinvertebrate metrics (*e.g.,* alpha diversity) have been shown to respond to changes in reedswamp extent and structure (Mason and Bryant, 1974; Sychra *et al.*, 2010). However, research into the influence of structural heterogeneity upon macroinvertebrates within ecotones has been limited to a small number of lake types based upon a combination of their dominant limnological features (*e.g.,* oligotrophic or eutrophic, monomictic or polymictic, and temperate or tropical) and mesohabitat categories, such as coarse woody debris or stony substratum.

Substratum and macrophyte structure can have a stabilising influence upon a habitat and its macroinvertebrate assemblages (Gabel *et al.*, 2008; Schreiber and Brauns, 2010). The influence of habitat upon community stability (*e.g.,* refuge from wave washing) is determined by the interaction of habitat structure and the environment (Gabel *et al.*, 2008). However, across a range of environments the relationship between habitat stability and biodiversity is not consistent; for example, increases in habitat stability have been associated with both increases and decreases in biodiversity (Huston, 1979). Little is known regarding the influence of changes in habitat stability along the reedswamp ecotone upon macroinvertebrate diversity, due in part to a lack of studies into macroinvertebrate seasonal community dynamics. Furthermore, little has been published regarding the influence of spatial variations in environmental factors not driven by ecotonal gradients upon reedswamp biodiversity. Further work is required to enhance the evidence base here because habitat structure and stability can have a strong influence upon biodiversity (Cobb *et al.*, 1992; Death and Winterbourn, 1994; Zimmermann and Death, 2002). A more complete understanding of the relationship between macroinvertebrate biodiversity and reedswamp habitat at the whole lake scale is highly desirable to influence whole lake management decisions (White and Irvine, 2003). However, this requires an extensive understanding of how common features of reedswamps (*e.g.,* structural heterogeneity) influence macroinvertebrate diversity at the local scale (*sensu* Huston, 1979).

4.2 Aim and hypotheses

The overall aim was to assess the contribution of reedswamp habitat to macroinvertebrate biodiversity within lakes. Three hypotheses were tested: (H_1) spatial differences in macroinvertebrate community structure within individual reedswamps are driven by ecotonal gradients (Dvořák, 1970; Mason and Bryant, 1974; Sychra *et al.*, 2010); (H_2) macroinvertebrate communities of different reedswamps within the same lake will be more similar to each other compared to those within reedswamps located in other lakes (Allan and Johnson, 1997; Johnson and Goedkoop, 2002; Johnson *et al.*, 2004); and (H_3) temporal variations in diversity, richness, total abundance, and biomass will be minimal at the middle of reedswamp ecotones and stony-littoral ‘open’ environments because they provide relatively stable environments for macroinvertebrate communities (Gabel *et al.*, 2008; Schreiber and Brauns, 2010).

4.3 Study area

Important descriptors of European reedswamps include: trophic status, reed species composition, and substratum structure (Table 4.1, and references therein). In order to produce a dataset that was representative of these different features, the original study area (Windermere only) was expanded

Table 4.1 This table compares the dominant characteristics of the study sites (shaded area) with those described in published accounts of the macroinvertebrate-reedswamp interaction for lakes throughout Europe (England, Ireland, Finland, Hungary, Netherlands, Germany, and Italy); see Tables 2.1–2.3 for further details. (A–F = indicate similarity to study sites A to F, * = Windermere, Rs = reedswamp, O = stony-littoral, + = dominant feature of the site, ∞ = studies that only included reedswamp sites, Meso = mesotrophic, Eu =eutrophic, ≠ = also included hypertrophic lakes, ∂ = also included oligotrophic lakes, *Phrag* = *Phragmites australis*, *T. ang* = *Typha angustifolia*, [under] =underlying, [over] = overlying)

		Reed species			**Substratum features**				
Data source	Trophic status	*Phrag*	*T. ang*	Stability	Stony	Sand	Reed litter	Silt (under)	Silt (over)
Study sites									
A) Swan stone (Rs)	Meso-Eu	+		Ss				+	+
B) RW-N (O)	Meso-Eu			St	+				+
C) White Moss (Rs)	Meso-Eu	+	+	Ss			+	+	+
D) RW-S (O)	Meso-Eu			Us	+	+			
E) Borrans (Rs)*	Meso	+		St	+		+		+
F) Borrans (O)*	Meso			St	+				
Other studies									
England									
Moon (1936) *	E,F	A,C,E	C	B,D,E,F	B,D,E,F	D	C,E	A,C	A,B,C,E
Mason & Bryant (1974)∞	A,B,C,D	A,C,E	C	A,C	-	-	C,E	A,C	A,C,E
Mainland Europe									
White and Irvine (2003)	A,B,C,D ∂	A,C,E	-	E	B,D,E,F	-	C,E	A,C	A,B,C,E
Varga (2001) (2003)	E,F	A,C,E	-	A,C	-	-	C,E	A,C	A,C,E
Heino (2000)	A–F ∂	A,C,E	-	B,D,E,F	B,D,E,F	D	C,E	A,C	A,B,C,E
Sipkay *et al.* (2007) ∞	Eu	A,C,E	C	A,C	-	-	C,E	A,C	A,C,E
Dvořák and Best (1982) ∞	Eu	A,C,E	C	A,C	-	-	C,E	A,C	A,C,E
Brauns *et al.* (2007a)	A–F ≠∂	A,C,E	-	A,C	B,D,E,F	D	C,E	-	-
Brauns *et al.* (2007b)	A–F ≠	A,C,E	-	B,D,E,F	B,D,E,F	D	C,E	-	-
Schreiber and Brauns (2010)	E,F ∂	A,C,E	-	B,D,E,F	B,D,E,F	D	C,E	-	-
Mancinelli *et al.* (2007)	E,F	A,C,E	-	A,C	-	-	C,E	-	-

to include sites within Rydal Water. This allowed investigation of a number of different factors that Windermere in isolation could not provide. These factors included the influence of: *Typha angustifolia* (a different reed species), higher trophic status, soft sinking substratum, and different reedswamp sizes. The only remaining remnant of reedswamp habitat on the northern shore of Windermere (‘Borrans’) was selected because of: (1) its suitability for macroinvertebrate sampling, (2) the structural heterogeneity of its substratum, (3) ease of access, and (4) its relative proximity to suitable reedswamps within an adjacent lake located in the same catchment (Rydal Water). Within Rydal Water, the ‘White Moss’ reedswamp provided information on *Typha angustifolia* and deep deposits of detritus; and ‘Swan Stone’ facilitated the investigation of reedswamp size and the influence of deep deposits of silt.

Semi-quantitative macroinvertebrate samples were collected from fifteen reedswamp and three non-reedswamp locations within six sites distributed across two lakes in the northwest of England, Windermere and Rydal Water. Figure 4.1 and Table 4.2 describe the locations and key physical features of all sample sites. Windermere is the largest lake in England and divided into two deep basins by a strip of relatively shallow water (average depth 10 m) at a narrowing of the lake. The North Basin is limnologically distinct from the South Basin into which it flows (Pickering, 2001). The nutrient status of the North Basin is mesotrophic and is less productive than the South Basin which is at the mesotrophic–eutrophic border (Maberly *et al.*, 2011). Located on the northern shore of the North Basin, approximately 100 m to the east of the River Rothay/Brathay confluence, is a large bay (54.421286^{o} N

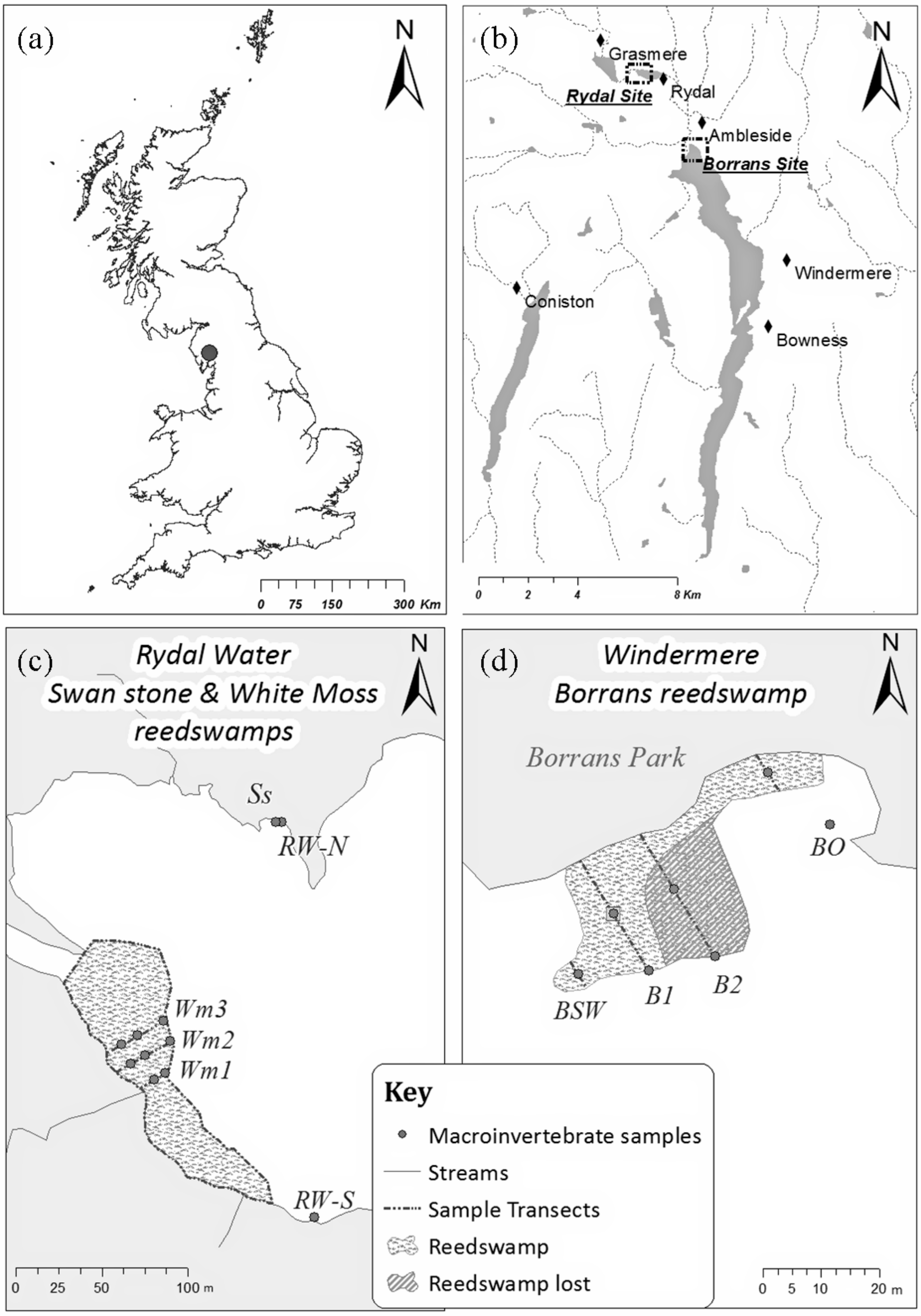


Figure 4.1 These maps illustrate the distribution of sample locations within: (a) the United Kingdom, (b) Cumbria, (c) Rydal Water, and (d) Windermere. Reedswamp lost relates to an area destroyed by physical damage (underlying mechanism unknown) during October 2011 ─ January 2012.

Table 4.2 Differences in the dominant physical features of sample sites reflect the high degree of structural heterogeneity within the littoral zone of the Windermere catchment. O = stony-littoral 'open' sites, Rs = reedswamp sites, RW = Rydal Water, Wi = Windermere, L = local, W = widespread, and E = extensive.

Site	Decimal Degrees	Lake	Shore	Surface area	Number of sample locations	Reed species	Distance along ecotonal axis	Stability	Underlying Substratum	Overlying silt
Borrans (Rs)	54.421286 N 2.964726 W	Wi	North	820 m^2	6	*P. australis*	9 to 26 m	Stable	Cobble Pebbles	L
Borrans (O)	54.421286 N 2.964728 W	Wi	North	-	1	-	-	Stable	Cobble Pebbles	L
Swan Stone (Rs)	54.450650 N 3.000889 W	RW	North	12 m^2	1	*P. australis*	1.6 m	Soft Sinking	Silt	E
RW-N (O)	54.450650 N 3.000887 W	RW	North	-	1	-	-	Stable	Cobbles Pebbles	W
White Moss (Rs)	54.441651 N 3.002409 W	RW	West	6,019 m^2	8	*P. australis* *T. angustifolia*	12.5 to 60 m	Soft Sinking	Silt Detritus	L
RW-S (O)	54.447967 N 2.999281 W	RW	South	-	1	-	-	Unstable	Cobbles Pebble Sand	L

2.964726^o W) hereafter referred to as 'Borrans'. Long-term records (~1870–2013) indicate that a *Phragmites australis* swamp (hereafter referred to as Borrans [Rs]) has existed within Borrans Bay throughout this period. GIS mapping techniques estimate that around 1870 *P. australis* swamp dominated the littoral zone of the bay, but that since 1870 the surface area of ~28,000 m^2 of continuous swamp has reduced down to a single stand of ~820 m^2, a loss of 98% (Alvarez-Codesal, 2012). At the time of this study (June 2011–April 2012) the swamp extended along 50 m of the shore. The distance from the mean shoreline to the deep water extremes of the swamp ranged from 8 to 22 m. A stony-littoral 'open' site was positioned to the northwest of the centre of Borrans, hereafter referred to as 'Borrans (O)'.

Rydal Water is a smaller lake with a surface area of 0.31 km^2 (Parker, 2002); located ~3 km upstream of the North Basin of Lake Windermere, to which it is connected by the outflowing River Rothay. The nutrient status of Rydal Water is mesotrophic to eutrophic (Maberly *et al.*, 2011). Sample sites were located off the western, northern, and southern shores. The western shore of Rydal Water is dominated by a mixed reedswamp consisting of *T. angustifolia* and *P. australis*. Due to its proximity to White Moss Common the reedswamp is hereafter referred to as 'White Moss'. White Moss was flanked by the inflowing River Rothay to the north and an area of deeper (>1 m) water to the south. Since 1956 the surface area of ~15,160 m^2 of continuous reedswamp has reduced down to a single stand of ~6,019 m^2, a loss of 60% (Alvarez-Codesal, 2012). Historically, reedswamp habitat extended along the majority of the northern shore, but since 1956 it has become fragmented, and in 2012 it consisted of several isolated small remnants (≤12 m^2) of reedbeds (Alvarez-Codesal, 2012). A second Rydal Water reedswamp site was located off the northern shore, 6 m to the west of a small peninsula. Due to its proximity to the Swan Stone area the reedswamp is hereafter referred to as 'Swan Stone (Rs)'. Since 1956 the surface area of ~4400 m^2 of the Swan Stone reedswamp has reduced down to a single monospecific stand of *P. australis* of ~12 m^2, a loss of 99.7% (Alvarez-Codesal, 2012). Field observations from 2010 to 2012 combined with Ordnance Survey maps from 1920 and 1956 indicate that reedswamp habitat has not been a dominant feature of the southern shore. Stony-littoral 'open' sites were positioned off the northern and southern shores of Rydal Water, hereafter referred to as RW-N (O) and RW-S (O) respectively.

4.4 Methods

4.4.1 Macroinvertebrate sample collection

A hand net sampling technique was used to investigate the relationship between reedswamp habitat and the taxonomic composition of their macroinvertebrates communities. A preliminary investigation of sampling efficacy was carried-out to determine appropriate sample size. Data collected from a 1 m^2 patch of reedswamp indicated that an individual sample consisting of a group of 5 x 0.1 m^2 randomly selected replicates from within a 2 m^2 sample area would provide a reliable estimate of community composition (Figure 4.2). Consistency in sample effort was demonstrated by comparing samples within individual reedswamps. For example, there were no significant differences in community composition between samples

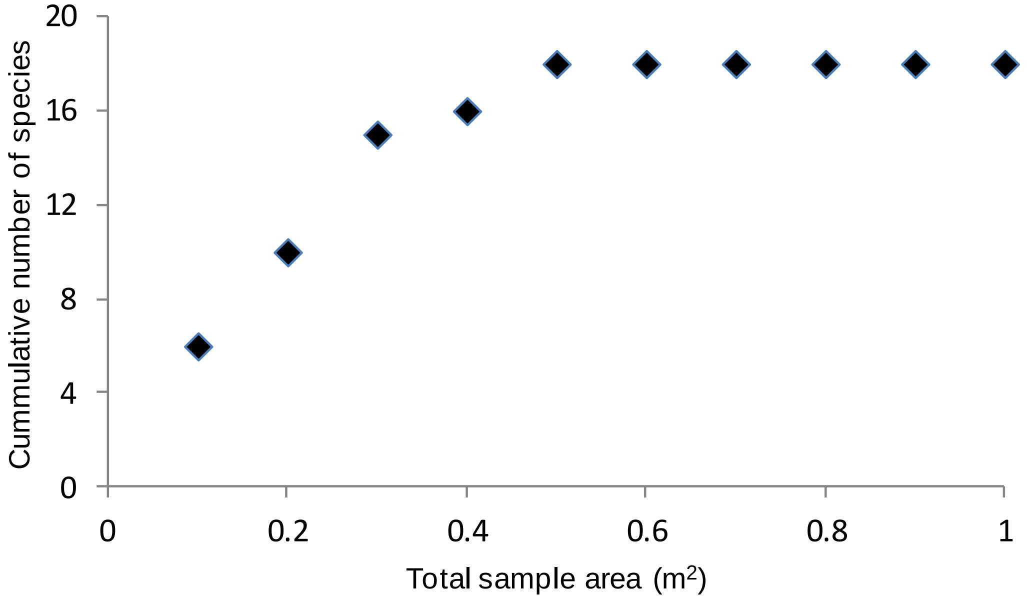


Figure 4.2 This data suggests that 5 replicates samples of 0.1 m^2 were sufficient to provide representative community composition data for the centre of the White Moss reedswamp during April 2011.

distributed across the middle, and landward locations of structurally similar reedswamp habitats (Table 4.7). This indicates that data generated by the sample procedure is reproducible. Furthermore, the sampling procedure was sensitive enough to detect differences in invertebrate assemblages between distinct habitat types. This was demonstrated by variations in community composition across the ecotonal axis, and between different reedswamps. A higher level of sample replication was not possible due to a combination of small reedswamp size and the large amount of structural heterogeneity between reedswamps. This was the case for locations within the study area and those throughout the catchment. The limited amount of spatial sample replication within this study restricted the statistical validity of the findings. However, given the representative nature of the study sites (*e.g.,* reedswamp size and structure) these findings are relevant to the investigation of reedswamps throughout Europe (Table 4.1).

During June and September 2011 all sample locations were sampled to assess spatial variation in macroinvertebrate communities. Seasonal changes at selected locations were investigated by collecting additional samples during January and April 2012 (Table 4.3). Survey areas within reedswamps were selected due to their suitability for sampling on foot using a hand-net. Due to safety considerations the available survey area within the White Moss reedswamp was restricted to ~15% of its total surface area (Figure 4.1). However, the survey areas at Borrans (Rs) and Swan Stone (Rs) encompassed the whole reedswamp. The number and spatial distribution of sample positions within survey areas were based upon: (1) survey area extent, (2) length of reedswamp ecotone, and (3) structural heterogeneity. For example, a single sampling position was located within the Swan Stone reedswamp due to its relatively small surface area of 12 m^2 and lack of heterogeneity. At each sample location, samples were collected from five randomly distributed quadrats of 0.1 m^2 from within an area of 2 m^2.

A bespoke hand-net (16 [W] × 45 cm [H], 250 µm mesh), designed for sampling within reed stands, was used to collect samples over a 30 second period. The netting procedure within reedswamp habitat followed a defined sequence: (1) several rapid swipes from the water surface downwards; (2) starting at the base of reed stems, the net-head was scraped along the reeds up towards the surface; (3) vigorous sweeps through the immersed reed shoots (to dislodge any remaining invertebrates); and (4) several sweeps through the top 3 cm of reed detritus deposits, or if the detritus was sparse, through the silty substratum. For firm or consolidated substrates it was necessary to kick the substrate to dislodge organisms. The netting procedure within stony-littoral 'open' habitat consisted of a vigorous kick

Table 4.3 Differences in the number and distribution of sample locations within individual sites reflected variations in reedswamp shape and size (Figure 4.1c, d). Furthermore, seasonal variation was assessed by sampling throughout the year at key locations. (O = stony-littoral 'open', l = landward, m = middle, e = edge, Y = sample collected, * = included estimates of total biomass of all macroinvertebrates combined, ** = reedswamp habitat lost post September 2011)

			Sample dates			
Sample locations Within sites	Distance from edge (m)	Distance between transects (m)	7/6/11	23/9/11	18/1/12	2/4/12
Borrans						
BO (O)	-	-	Y	Y	Y	Y
BSW	2	10	Y	Y	-	-
B1e	2	10	Y	Y	Y	Y
B1m	12	10	Y	Y	Y	Y
B2e **	2	10	Y	Y	-	-
B2m **	12	10	Y	Y	-	-
BNE	2	27	Y	Y	-	-
Swan Stone						
RW-N (O)	-	-	Y	Y	Y	Y
Ss	2	-	Y	Y	Y	Y
White Moss						
RW-S (O)*	-	-	Y	Y	Y	Y
Wm1e	2	15	Y	Y	-	-
Wm1m	10	15	Y	Y	-	-
Wm2e*	2	12	Y	Y	Y	Y
Wm2m*	18	12	Y	Y	Y	Y
Wm2l*	28	12	Y	Y	Y	Y
Wm3e	2	12	Y	Y	-	-
Wm3m	18	12	Y	Y	-	-
Wm3l	28	12	Y	Y	-	-

sample within the quadrats. Preliminary testing indicated that the sample method was effective in collecting a variety of taxa throughout a range of different niches. For each sample replicate (stony-littoral, and reedswamp) a suite of quantitative and qualitative habitat measurements were made following a bespoke procedure designed for this study (Table 4.4). Assessment of qualitative variables (*e.g.,* substratum particle size) was based upon the RIVPACS method (*sensu* Wright *et al*., 1998). Following collection, macroinvertebrate samples were immediately preserved in 70% ethanol. The majority of individuals were identified to species level. Chironomidae were identified to tribe and Oligochaeta to family level. To assess the influence of the reedswamp ecotone upon total macroinvertebrate biomass, ash-free dry mass (AFDM) was determined for macroinvertebrates at selected locations (RW-S, Wm2e, Wm2m, and Wm2l) by drying in an oven at 58 ^{o}C for 8 hours followed by combustion at 550 ^{o}C for 6 hours.

4.4.2 Data analysis

The R programming language and associated statistical and graphical packages were used for data analysis. Macroinvertebrate data were converted into five commonly used metrics: AFDM, total abundance (A), taxon richness (S), Shannon index (H), and Simpson’s index (1-D). Simpson’s and Shannon indices are widely used measures of alpha diversity (Magurran, 2004; Keylock, 2005) that take account of both abundance and evenness of the taxa present (Hill, 1973; Peet, 1974). The assumptions necessary for applying parametric tests of homogeneity were assessed.

Normality was tested using Q-Q probability plots, and the Shapiro-Wilks test. Bartlett's and Levene's tests were used to assess homogeneity of variances (Bartlett and Kendall, 1946; Rao, 1952). For RM-ANOVA, the R package *Car* was used to apply Mauchly's Test of Sphericity and to make corrections using Greenhouse Geisser correction where sphericity was violated (*sensu* von Ende, 2001). Due to a significant departure from normality for the majority of individual samples, commonly used data transformations were applied and the data were re-tested for normality. Consequently, parametric statistical analysis was applied to Log_{10} (x + 1) transformed AFDM, A, S, H, and 1-D data. To detect spatial differences (H_1 and H_2), one-way repeated measures ANOVA (RM-ANOVA) with time as a random factor was performed separately on all metrics using the command 'aov'. One-way ANOVA was used to detect differences over time at individual sample locations (H_3). Significant differences (spatial and temporal) between pairs of means were investigated using the 'TukeyHSD' command in the *Car* package (H_1, H_2, and H_3).

Beta diversity is an important component of all three hypotheses. A number of alternative definitions of beta diversity have been proposed (Anderson *et al.*, 2011). In the context of this study, beta diversity is the amount of spatial variability in community composition within given spatial and temporal scales (Anderson *et al.*, 2006). Bray-Curtis Dissimilarity index (BC) is a multivariate ordination method (Bray and Curtis, 1957; Beals, 1984) and is commonly used in the measurement of beta diversity (Clarke, 1993; Clarke *et al.*, 2006). It can also be used to investigate changes in community composition

Table 4.4 The procedure used for the assessment of structural heterogeneity for each sample replicate (based upon the RIVPACS method [Wright *et al*., 1998]), SA = surface area.

Habitat variable	Details
1) Quantitative (continuous) variables	Measurements of distance were rounded to the nearest centimetre.
Water depth (cm)	Distance between the surface of the substratum and the water surface
Distance to open water edge (cm)	Measured from the centre of the sample area to the reedswamp-open water interface
Distance to fen/shore (cm)	Measured from the centre of the sample area to the reedswamp-fen interface
Shoot density (shoots 0.1 m^{-2})	Total numbers of erect (live or dead) shoots were counted
Ratio of *Phragmites* to *T. angustifolia*	The proportion of *Phragmites* shoots (live or dead) per 0.1 m^2 was calculated
2) Qualitative ordinal variables	These variables were allocated to discrete categories which were ordered in a meaningful sequence.
Substratum stability	Degree of resistance to disturbance on a scale from 1 to 4 with increasing resistance: 1) “Soft sinking” *i.e.,* difficult to walk across (*e.g.,* deep silt) 2) “Unstable” *i.e.,* shifts under foot (*e.g.,* gravel) 3) “Stable” *i.e.,* easily disturbed by kick sampling (*e.g.,* pebbles) 4) “Consolidated” *i.e.,* none of the above (*e.g.,* embedded cobbles)
Substratum particle size (longest axis)	Characterisation of substratum based upon dominant particle size on a scale from 1 to 3 with increasing size: 1) Silt (<2 mm) and/or fine reed detritus (<5 mm) 2) Gravel/pebbles (<64 mm) 3) Cobbles/boulders (≥64 mm)
Detritus	Detritus at or near the surface of the substratum on a scale from 1 to 4 with increasing dominance: 1) None/trace amounts (depth <0.5 cm) 2) Local (depth >0.5 cm and SA>10%) 3) Widespread (SA = 10-60% and depth >0.5 cm) 4) Extensive (SA >60%, or SA >40% combined with depth >3 cm)
Silt deposits	Silt at or near the substratum surface on a scale from 1 to 4 with increasing dominance: 1) None (depth <0.5 cm) 2) Local (SA <10%, depth >0.5 cm) 3) Widespread (SA ≥10%, depth >0.5 cm) 4) Extensive (SA >10%, depth >2 cm)

over time. BC was calculated using the ‘vegdist’ command within the vegan library (Oksanen *et al.*, 2012). All three hypotheses were tested by applying tests of homogeneity to BC data. Spatial variations in BC were tested within individual reedswamps (H_1), and between reedswamps/lakes (H_2). Comparisons of temporal variations in BC between different categories of sample location (*e.g.,* middle vs edge), and changes in beta diversity over time were used to test H_3. Beta diversity and temporal changes in community composition were investigated by performing permutational multivariate analysis of variance (PERMANOVA) and analysis of similarity (Anosim) upon BC. Both of these tests are non-parametric permutation techniques designed to perform multivariate analysis upon Euclidean distance matrices (Tanner, 2006). However, they are now commonly used to perform univariate tests of homogeneity upon dissimilarity coefficients such as BC (Chapman and Underwood, 1999; Anderson, 2005; Jones *et al.*, 2007). PERMANOVA compares centroids for each individual sample with the centroid of the whole data set (Anderson, 2006). It analyses actual coefficient values, and can be used to partition variability in within multi-factorial data sets in similar way to analysis of variance (ANOVA) (Anderson, 2005). However, unlike the ANOVA technique, PERMANOVA does not rely upon *p*-tables that assume normality.

An additional advantage of PERMANOVA and Anosim techniques over ANOVA is that they measure dissimilarity between multiple pairings of replicates across different samples; whereas, ANOVA only allows comparison between groups of individual BC values (*e.g.,* sets of replicates).

Hence, permutational techniques provide a more comprehensive measure of dissimilarity between samples that consist of replicates. PERMANOVA was applied to a matrix of BC arranged by spatial factors (lake, reedswamp, and ecotonal position) and sample time. One-way PERMANOVA was performed using the ‘Adonis’ command and ‘Strata’ function (based on 1000 permutations). For those individual data sets which departed from homology, Anosim was used as a *post hoc* test to analyse differences between the centroids of pairs of samples based on 1000 permutations. Anosim compares the centroids of pairs of samples using permutations based upon coefficient rankings to calculate *p*-values (Chapman and Underwood, 1999). In addition, homogeneity between variances was tested using the ‘Betadisper’ command, a multivariate analogue of Levene’s test (Levene, 1960). For data sets which departed from homology the Tukey HSD test was used to make pair-wise comparisons of variance between samples.

BC is frequently used in combination with the Non-metric Multidimensional Scaling (NMDS) technique to produce a graphical representation of dissimilarity relationships, and was used to illustrate beta diversity with regard to all three hypotheses. The NMDS technique is a type of unconstrained ordination in which dissimilarity data is plotted independently of environmental data (*e.g.,* relative position within the ecotone) (O'Dowd *et al.*, 2003). H_1 was investigated using an NMDS plot to illustrate relative dissimilarities between all sample locations during June 2011. In addition, selected sample locations across all sample times were plotted in order to investigate spatial variations across different lakes and reedswamps (H_2), and to investigate differences in temporal responses across the reedswamp ecotone (H_3). For NMDS, all five replicate samples for each sample time and location were combined to produce a single taxa list. The ‘metaMDS’ command was used to plot differences in community taxonomic dissimilarity (BC). Gradients in environmental factors were subsequently superimposed over the dissimilarity plot using the ‘Envfit’ command from the vegan library (Cao *et al.*, 2002; Clarke *et al.*, 2006; Oksanen *et al.*, 2012).

4.5 Results

In total 30,356 macroinvertebrates were collected from 270 samples over an eleven month period (Appendix A1). The majority of samples were collected from Rydal Water, where mean total abundance (A) per 0.1 m^2 was higher compared to Windermere locations (Table 4.5). Differences in richness and diversity between the lakes were less marked. Ninety-two different taxa were identified. The main taxonomic groups within the study area were Mollusca, Crustacea, Oligochaeta, and Diptera (Figure 4.3). The dominant families were Crangonyctidae (36% of individuals sampled), Chironomidae (29%), and Sphaeriidae (13%). *Crangonyx pseudogracilis* was the single species of Crangonyctidae, and *Sphaerium* was the dominant (77%) genus of Sphaeridae. Chironomidae consisted of 3 subfamilies; Chironominae (51%), Orthocladiinae (32%), and Tanypodinae (17%).

4.5.1 Differences within reedswamps

Spatial variation in abundance across the Borrans site was lacking. In addition, spatial differences in alpha diversity and taxon richness were limited to a small proportion of pair-wise comparisons within the Borrans study area (Table 4.6, Figure 4.4a–c). For individual sample positions within the Borrans site, spatial replicates did not demonstrate significant variations in dissimilarity. However, dissimilarity (beta diversity) across both the ecotonal and lateral (perpendicular to ecotone) axes of the Borrans site

Table 4.5 These summary statistics highlight key differences in biotic metrics between lakes and includes all samples collected during this study. All values relate to sample areas of 0.1 m^2; bracketed values indicate number of samples.

	Rydal Water (170)	Windermere (100)	All Sites (270)
Abundance (A)			
Range	3-609	7-492	3-609
Median	92	48	77
Mean	130	82	112
Standard deviation	91	88	92
Taxon Richness (S)			
Range	3-19	4-24	3-24
Median	11	9	11
Mean	11	9	11
Standard deviation	2.6	4	3.3
Shannon Index (H)			
Range	0.5-2.1	0.5-2.2	0.5-2.2
Median	1.8	1.7	1.7
Mean	1.7	1.6	1.7
Standard deviation	0.3	0.4	0.3
Simpsons Index (1-D)			
Range	0.2-1	0.2-0.9	0.2-1
Median	0.8	0.8	0.8
Mean	0.7	0.7	0.7
Standard deviation	0.1	0.1	0.1

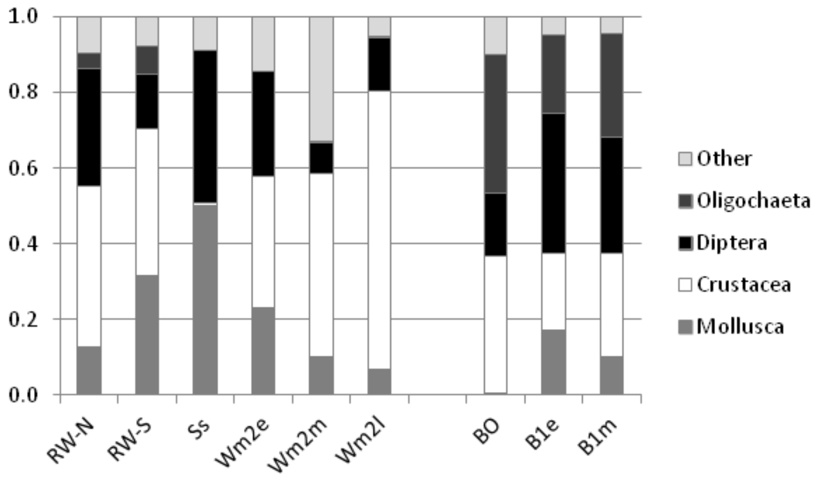


Figure 4.3 This graph illustrates spatial variation in community composition (mean relative taxonomic abundances) throughout the study area during June 2011. (RW = Rydal Water, Ss = Swan Stone, Wm = White Moss, B = Borrans, N = north, S =south, e = edge, m = middle, l = land, O = stony-littoral 'open', and 1-2 = transect numbers)

Table 4.6 RM-ANOVA (time as a random factor) in combination with Tukey HSD *post hoc* testing identified significant differences ($p < 0.05$) in the means of macroinvertebrate metrics across groups of sample locations. (* = significantly different (higher) than at other locations, ** = Wm2l significantly different [higher] to other locations except for Wm2m)

Sample location grouping	Macroinvertebrate response	Survey period	df	*p*
Rydal Water: RW-S (O) RW-N(O) Wm2e Wm2m Wm2l**	Abundance (A)	June to April	$F_{3,80} = 7.8$	0.002
Windermere, Borrans: B2m* B2e	Richness (S)	June to September	$F_{1,16} = 8.14$	0.02
Windermere, Borrans: BSW B1e* B2e BNE	Shannon Index (H)	June to September	$F_{1,32} = 11.21$	0.04

was significant (Table 4.7, Figure 4.5). Exceptions were the pairings of the stony-littoral ‘open’ site (BO) versus B1m (Rs), and BNE (Rs) versus BSW (Rs). Within the White Moss reedswamp, spatial variation in abundance was restricted to the ecotonal axis. Abundance was highest at the landward position (Wm2l) of the ecotone (Table 4.5, Figure 4.4d). Throughout Rydal Water spatial variations in biomass, alpha diversity, and taxon richness were lacking. However, beta diversity was present throughout Rydal Water (Table 4.7). Within the White Moss reedswamp lateral beta diversity was limited to the edge positions (Wm2e vs Wm3e). Significant differences in beta diversity were present along two of the three transects (Wm1 and Wm2) (Table 4.7, Figure 4.5).Both Rydal Water ‘open’ sites were significantly dissimilarity to all reedswamp locations within Rydal Water.

4.5.2 Differences between reedswamps

At equivalent locations within the ecotone (*e.g.,* Wm2m vs B1m) there were no significant differences in abundance, taxon richness, or alpha diversity between reedswamps (Table 4.8). However, across the stony-littoral ‘open’ sites, alpha diversity was significantly lower within Windermere (Borrans) compared to each of the two ‘open’ sites within Rydal Water. Analysis of mean BC scores indicated that beta diversity was significant across all sites for equivalent sample positions. In contrast, significant differences in the variance of BC scores for spatial replicates across equivalent positions were limited to the ‘open’ sites (Table 4.9). NMDS plots of Bray Curtis scores grouped sample locations by lake and by individual reedswamps (Figure

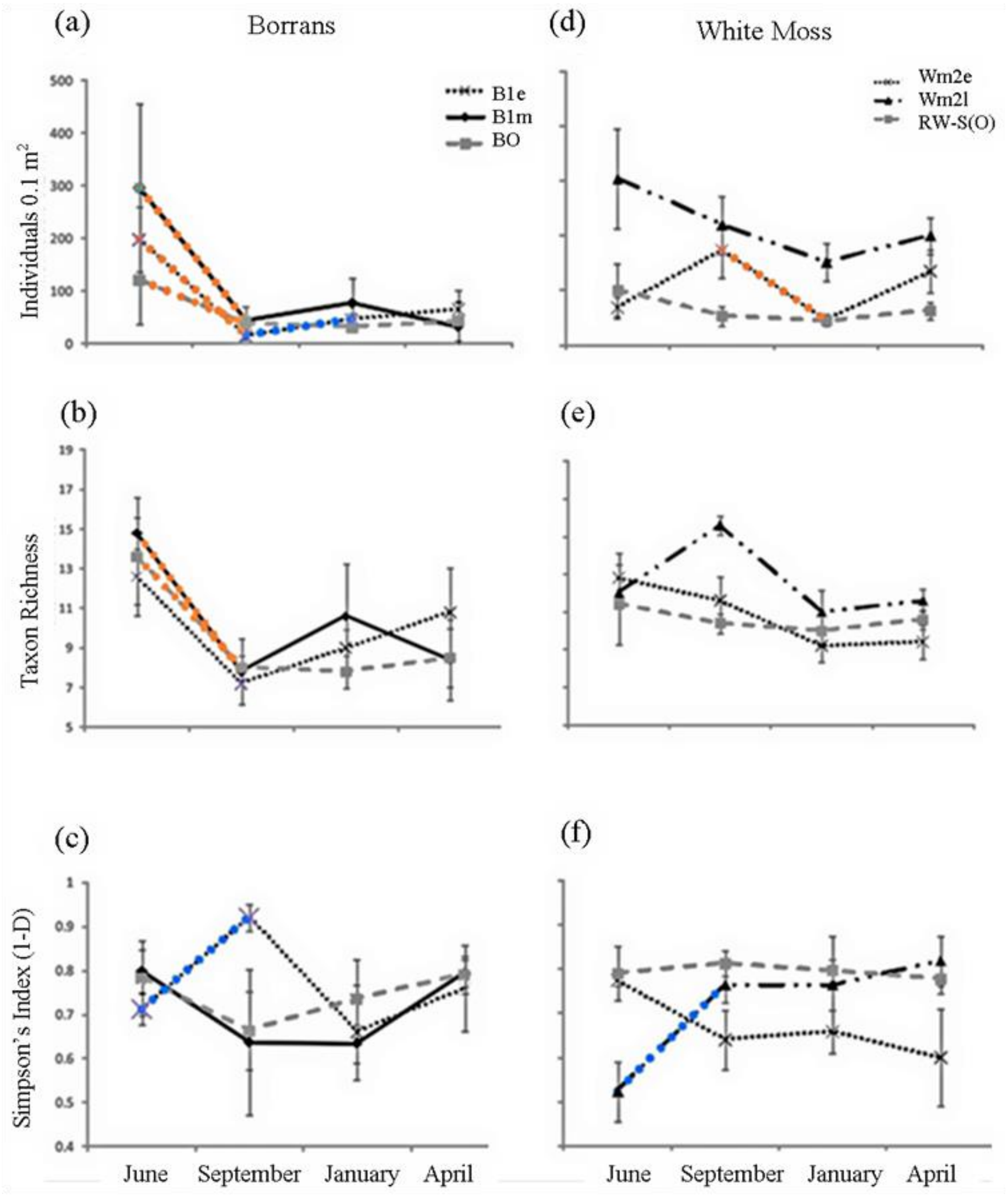


Figure 4.4 Comparisons of mean (± 1 SE) macroinvertebrate responses over space and time were carried out at (a–c) Borrans and (d–f) White Moss reedswamps. Key responses were: (a, d) abundance; (b, e) taxon richness; and (c, f) Simpson's Index. Orange dots indicate a significant (*p* < 0.05) decrease over time, blue dots indicate an increase over time.

Table 4.7 Pair-wise comparisons (Anosim) of Bray Curtis dissimilarity index were made between different sample locations within individual lakes and reedswamps ($p < 0.05$ only).

Location comparisons	*R*	*p*
Windermere, Borrans		
BNE vs B1e	0.6	0.01
BNE vs B2e	0.7	0.01
B1e vs BSW	0.4	0.01
B1e vs B2e	0.3	0.03
B2e vs BSW	0.3	0.04
BO vs B2m	0.7	0.01
BO vs B1e	0.9	0.01
BO vs B2e	1	0.01
BO vs BNE	0.5	0.01
BO vs BSW	0.7	0.01
Rydal Water		
Wm2e vs Wm3e	0.6	0.01
Wm1m vs Wm1e	0.2	0.01
Wm2l vs Wm2e	0.4	0.001
Wm2m vs Wm2e	0.4	0.02
RW-S(O) vs Ss	0.7	0.01
RW-S(O) vs Wm1e	0.5	0.01
RW-S(O) vs Wm1m	0.7	0.01
RW-S(O) vs Wm2e	0.6	0.01
RW-S(O) vs Wm2m	0.7	0.004
RW-S(O) vs Wm2l	0.7	0.003
RW-S(O) vs Wm3e	0.7	0.01
RW-S(O) vs Wm3m	0.7	0.01
RW-S(O) vs Wm3l	0.6	0.01
RW-N(O) vs Ss	0.6	0.01
RW-N(O) vs Wm1e	0.5	0.001
RW-N(O) vs Wm1m	0.7	0.01
RW-N(O) vs Wm2e	0.6	0.01
RW-N(O) vs Wm2m	0.7	0.01
RW-N(O) vs Wm2l	0.7	0.005
RW-N(O) vs Wm3e	0.7	0.005
RW-N(O) vs Wm3m	0.7	0.01
RW-N(O) vs Wm3l	0.6	0.01

4.5). Large gradients in taxon abundance rankings were associated with environmental gradients across all three reedswamps, and across all three ‘open’ sites. The environmental gradients most associated with groupings of sample locations were substratum stability, accumulations of detritus, and the distance between land and the reedswamp edge. Relatively high numbers of *Gyrinus marinus* and *Ancylus fluviatilis* characterised Windermere (Borrans reedswamp and ‘open’ locations) samples; whereas, *Dugesia tigrina* and *Hesperocorixa linnaei* were characteristic of Rydal Water (White Moss, Swan Stone, and ‘open’ sites). Compared to White Moss, Borrans reedswamp sample positions were more widely distributed (dissimilar) across the NMDS plot (Figure 4.5). Middle samples from both reedswamps were grouped together while edge sample positions were much more widely distributed. These sample positions were distributed along an environmental gradient that included variations in substratum stability and overlying detritus. For example, most middle and landward samples were associated with greater amounts of reed detritus and were characterised by *Athripsodes aterrimus* rather than Tubificidae.

4.5.3 Differences in temporal responses

Within the Borrans site, each of the three sample positions sampled over the full eleven month period demonstrated significant ($p < 0.05$) temporal variations in abundance, alpha diversity and similarity (Table 4.10). Total abundance (A) at all three positions decreased significantly from June to September; however, temporal variations in S, H, 1-D were less consistent between sample positions (Figure 4.4a, b and c, Table 4.10). Significant changes in similarity (BC means) occurred between June and September for all three Borrans sites; the only other progressive change was at B1e from September to January (Table 4.11, Figure 4.6). Within Rydal Water, temporal changes in abundance and diversity over eleven months were limited to a smaller proportion of sample positions and times (Table 4.10).

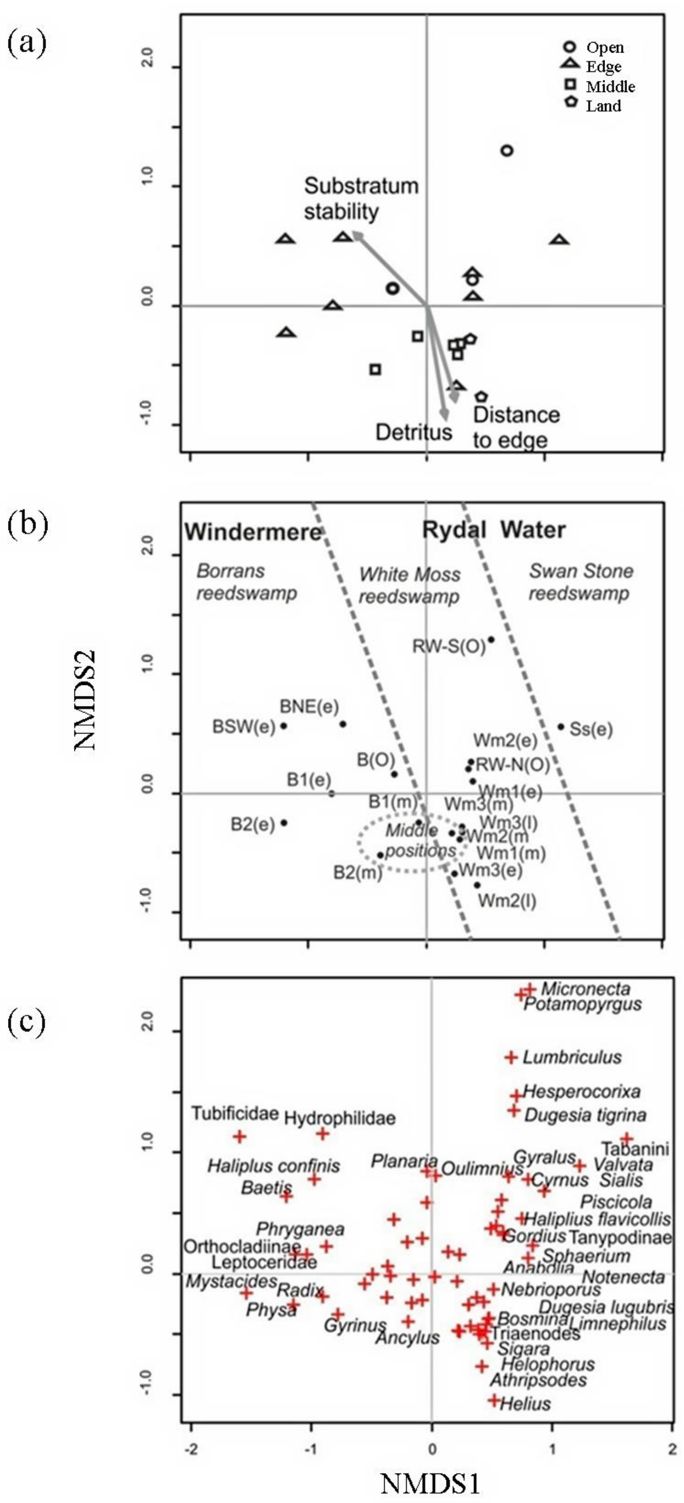


Figure 4.5 This NMDS plot based upon Bray Curtis dissimilarity data (replicate samples combined) illustrates spatial differences across all sites during June 2011: (a) environmental variables ($p < 0.05$ only); (b) relative positions of sample locations; and (c) red crosses indicate position of individual taxa, taxa on the periphery of the plot are labelled by genus or species (where more than one single species was recorded for that genus).

Table 4.8 RM-ANOVA (time as a random factor) testing identified differences between means of macroinvertebrate metrics across reedswamps, and lakes between June 2011 ─ April 2012. (* = Tukey HSD *post hoc* testing indicated that diversity was lowest at Borrans)

Sample location	df	*F*	*p*
B1m vs Wm2m			
Richness (S)	3,32	1.676	0.286
Abundance (A)	3,32	1.853	0.267
Shannon Index (H)	3,32	0.728	0.456
Simpson's Index (1-D)	3,32	0.164	0.713
B1e vs Wm2e vs Ss			
Richness (S)	3,48	0.644	0.558
Abundance (A)	3,48	0.655	0.553
Shannon Index (H)	3,48	1.035	0.411
Simpson's Index (1-D)	3,48	1.306	0.338
BO vs RW-N (O) vs RW-S (O)			
Richness (S)	3,48	2.38	0.173
Abundance (A)	3,48	4.361	0.068
Shannon Index (H)	3,48	35.78	<0.001*
Simpson's Index (1-D)	3,48	125.2	<0.001*

Table 4.9 One-way PERMANOVA (Adonis) and analysis of multivariate homogeneity of variances (Betadisper) were used to test for differences across 'open', and reedswamp sample positions between June 2011 ─ April 2012. Pair-wise comparisons using Anosim as a *post hoc* test indicated that the means of all location pairings within each grouping were significantly different to each other ($p <$ 0.05). The Tukey HSD *post hoc* test indicated that for the 'open location grouping' variance was only homogeneous ($p >$ 0.05) for the pairing of BO vs RW-N ([a]).

Sample location groupings	Adonis			Betadisper	
	R^2	*F*	*p*	*F*	*p*
Middle B1m Wm2m	0.2	$F_{1,38} = 5.4$	0.002	$F_{1,38} = 3.9$	0.06
Edge B1e Wm2e Ss	0.2	$F_{2,57} = 7.5$	0.001	$F_{2,57} = 0.6$	0.6
Open[a] BO RW-S RW-N	0.2	$F_{2,57} = 4.0$	0.001	$F_{2,57} = 5.8$	0.005

Progressive changes in abundance and diversity were less widespread compared to the Borrans site (Figure 4.4). In contrast, significant changes in similarity over time occurred at all Rydal Water sites (Table 4.10). With the exception of three positions (RW-N, Ss, and Wm2e) progressive changes in similarity occurred within Rydal Water throughout the sample period (Table 4.11, Figure 4.6).

NMDS indicated that for Borrans and White Moss reedswamps the edge positions were more variable over time compared to the adjacent middle and ‘open’ positions (Figure 4.7). However, the range of dissimilarity at the edge location within the Swan Stone reedswamp was similar to that at the adjacent ‘open’ position (RW-N). In general, samples taken at the same time and sample position (*e.g.,* edge) were not clustered together. Temporal changes in detritus deposits and substratum stability were associated with changes in community similarity at the edge and stony-littoral ‘open’ positions. At the middle positions, temporal changes in community structure were not strongly associated with any single environmental factor.

Table 4.10 Significant (p<0.05) temporal variations (June 2011–April 2012) in macroinvertebrate metrics were tested using ANOVA (Richness, abundance, diversity), Adonis (BC means) and betadisper (BC variance).

Sample location	Wm2e	Wm2m	Wm2l	Wm-S (O)	Ss	RW-N (O)
Richness	$F_{3,16}$=2.3 p=0.11	$F_{3,16}$=0.7 p=0.61	$F_{3,16}$=7.9 p=0.002	$F_{3,16}$=0.03 *p*=1.01	$F_{3,16}$=2.5 *p*=0.13	$F_{3,16}$=0.6 *p*=0.64
Abundance	$F_{3,16}$=5.0 *p*=0.01	$F_{3,16}$=1.6 *p*=0.21	$F_{3,16}$=0.3 *p*=0.80	$F_{3,16}$=0.1 *p*=1.03	$F_{3,16}$=3.2 *p*=0.05	$F_{3,16}$=0.4 *p*=0.85
Shannon Index	$F_{3,16}$=2.1 *p*=0.26	$F_{3,16}$=1.6 *p*=0.22	$F_{3,16}$=7.7 *p*=0.002	$F_{3,16}$=1.0 *p*=0.42	$F_{3,16}$=0.6 *p*=0.68	$F_{3,16}$=0.4 *p*=0.86
Simpson's Index	$F_{3,16}$=1.1 *p*=0.41	$F_{3,16}$=2.4 *p*=0.11	$F_{3,16}$=10 *p*=0.001	$F_{3,16}$=0.1 *p*=12	$F_{3,16}$=1.2 p=0.34	$F_{3,16}$=0.4 p=0.75
Biomass	$F_{3,16}$=4.2 *p*=0.02	$F_{3,16}$=2.6 *p*=0.08	$F_{3,16}$=3.6 *p*=0.04	$F_{3,16}$=5.3 *p*=0.01	-	-
BC (means)	$F_{3,16}$=4.2 *p*=0.001 R^2=0.4	$F_{3,16}$=4.1 *p*=0.001 R^2=0.4	$F_{3,16}$=4.2 *p*=0.001 R^2=0.4	$F_{3,16}$=5.5 *p*=0.001 R^2=0.5	$F_{3,16}$=6.3 *p*=0.001 R^2=0.5	$F_{3,16}$=5.4 *p*=0.001 R^2=0.5
BC (variance)	$F_{3,16}$= 0.8 *p*=0.54	$F_{3,16}$= 0.7 *p*=0.64	$F_{3,16}$=0.7 *p*=0.64	$F_{3,16}$= 1.5 *p*=0.34	$F_{3,16}$= 3.7 *p*=0.035	$F_{3,16}$=0.5 *p*=0.75

Sample location	B1e	B1m	BO
Richness	$F_{3,16}$=2.6 p=0.09	$F_{3,16}$=5.2 p=0.01	$F_{3,16}$=6.6 p=0.04
Abundance	$F_{3,16}$=2.6 *p*<0.001	$F_{3,16}$=7.8 *p*=0.02	$F_{3,16}$=7.2 *p*=0.003
Shannon Index	$F_{3,16}$=1.4 *p*=0.34	$F_{3,16}$=2.1 *p*=0.15	$F_{3,16}$=4.7 *p*=0.02
Simpson's Index	$F_{3,16}$=3.6 *p*=0.03	$F_{3,16}$=1.8 *p*=0.26	$F_{3,16}$=6.8 *p*=0.004
Biomass	-	-	-
BC (means)	$F_{3,16}$=7.7 *p*=0.001 R^2=0.6	$F_{3,16}$=3.4 *p*=0.001 R^2=0.4	$F_{3,16}$=4.5 *p*=0.001 R^2=0.5
BC (variance)	$F_{3,16}$=5.7 *p*=0.01	$F_{3,16}$=0.8 *p*=0.53	$F_{3,16}$= 0.1 *p*=1.11

Table 4.11 Pair-wise comparisons of progressive temporal variations in Bray Curtis Index using Anosim were used to identify the timings of changes.

	B1e	B1m	BO	Wm2e	Wm2m	Wm2l	RW-S (O)	Ss	RW-N (O)
Means									
June vs September	*R*=1.00 *p*=0.01	*R*=0.70 *p*=0.01	*R*=0.90 *p*=0.01	*R*=0.90 p=0.01	*R*=0.50 *p*=0.01	*R*=0.50 *p*=0.01	*R*=0.60 *p*=0.01	*R*=1.00 *p*=0.01	*R*=0.80 *p*=0.01
September vs January	*R*=0.80 *p*=0.01	*R*=0.04 p=0.5	*R*=0.10 p=0.2	*R*=0.90 *p*=0.01	*R*=0.70 *p*=0.01	*R*=0.70 *p*=0.01	*R*=0.90 *p*=0.01	*R*=1.00 *p*=0.01	*R*=0.70 *p*=0.01
January vs April	*R*=0.17 p=0.06	*R*=0.26 *p*=0.06	*R*=0.23 *p*=0.06	*R*=0.10 *p*=0.1	*R*=0.30 *p*=0.03	*R*=0.30 *p*=0.03	*R*=0.50 *p*=0.01	*R*=0.20 *p*=0.06	*R*=0.20 *p*=0.10

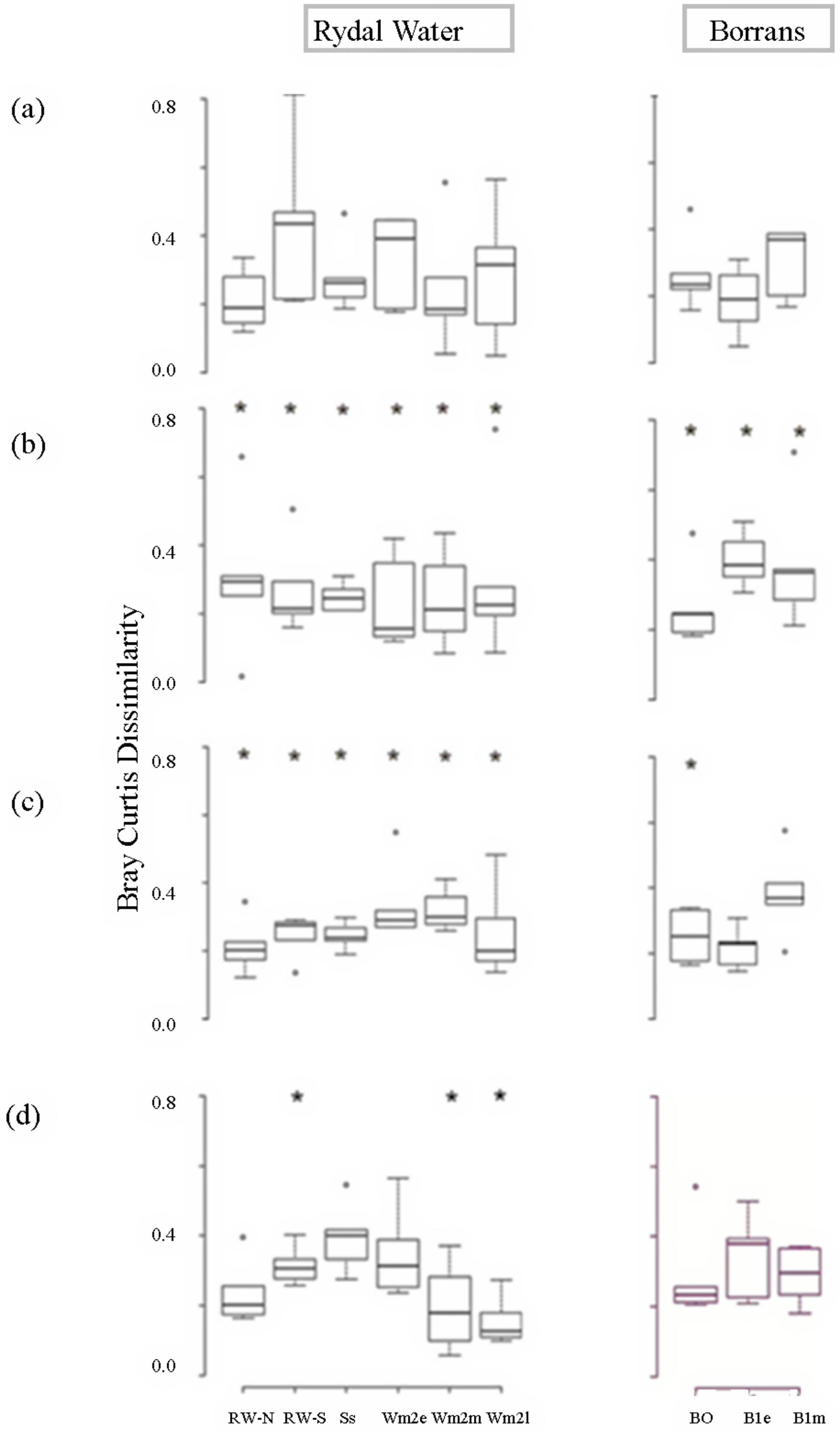


Figure 4.6 Changes in beta diversity across selected sites over time are shown for the following: (a) June 2011, (b) September 2011, (c) January 2012, and (d) April 2012. An asterisk * above plots indicates significant change ($p < 0.05$) in BC mean over time from the previous collection date.

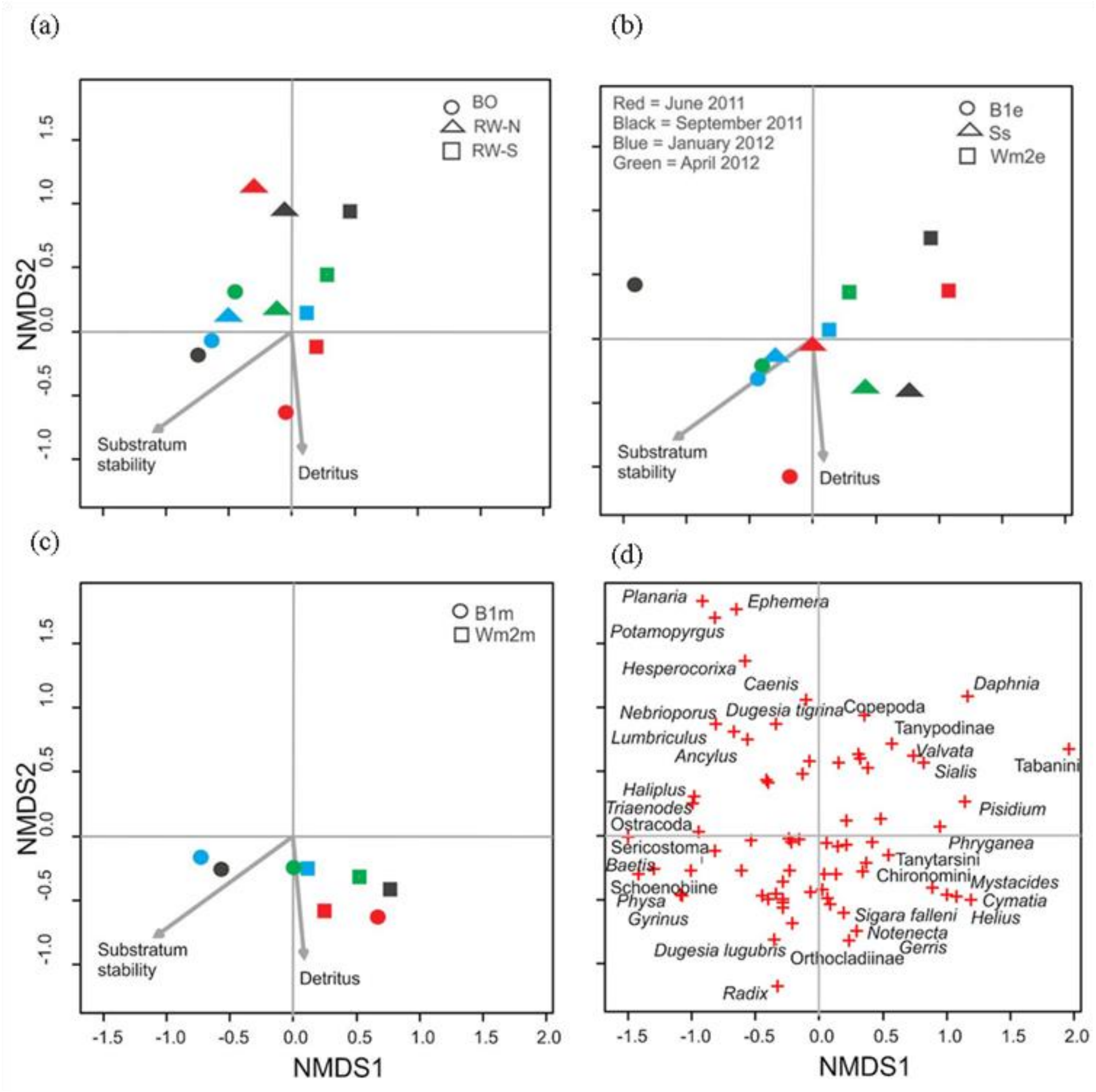


Figure 4.7 These NMDS plots illustrate temporal variations in Bray Curtis Dissimilarity scores across reedswamps (replicate samples combined) by sample position relative to the reedswamp ecotone: (a) = ‘open’ locations, (b) = edge positions, and (c) = middle positions. Environmental variables for each location category are superimposed ($p < 0.05$ only). Red crosses in panel (d) indicate position of individual taxa, taxa on the periphery of the plot are labelled by genus, or species (where more than one single species were recorded for that genus). Species details are listed in Appendix A1.

4.6 Discussion

Previous studies of macroinvertebrate diversity within reedswamps focused solely on change along the ecotonal axis (*e.g.,* Mason and Bryant, 1974). By investigating structural heterogeneity throughout reedswamps, this study found that the relationship between reedswamp habitat structure and macroinvertebrate diversity was stronger along the ecotonal axis (*i.e.,* land to water). This suggests that structural heterogeneity in isolation had a relatively weak influence upon diversity compared to structural heterogeneity combined with other environmental gradients (*e.g.,* changes in refuge and physicochemical determinants). A novel aspect of this study was the investigation of macroinvertebrate seasonal dynamics across the reedswamp ecotone. Temporal changes in abundance and diversity were not consistent across individual ecotonal transects. For example, statistically significant progressive temporal changes in diversity throughout the study period (11 months) at White Moss, only occurred within the inner reedswamp and not at the ‘open’ or edge locations. Furthermore, spatiotemporal responses across the ecotones of physically distinct reedswamps were inconsistent. Hence, reedswamp habitat is a highly variable and dynamic habitat for macroinvertebrates. Herein the discussion considers the underlying reasons for the following: (1) spatial variations within individual reedswamps, (2) spatial differences across lakes and reedswamps, and (3) differential temporal responses across the reedswamp ecotone. Finally, the implications for conservation and management are discussed.

4.6.1 Spatial variations in biodiversity and abundance within individual reedswamps

Results from the two larger reedswamps support the hypothesis (H_1) that local variations in structure (*e.g.,* substratum composition) have less of an influence upon macroinvertebrate community composition than ecotonal gradients. This is an important finding given the long-term decline in reedswamp surface area within the study area and throughout Europe. Borrans, Swan Stone, and White Moss reedswamps are fragments of what were much larger reedbeds and have receded towards the shore over the last few decades. A lack of historic macroinvertebrate data from these reedswamps prevents quantification of the impact of this change upon biodiversity. In addition, published accounts of reedswamp ecotones of similar sizes (> 36 m) to those of historic reedswamps are lacking. Consequently, it was not possible to estimate the impact of reedswamp recession upon diversity. However, data from this study suggest that it is likely that biodiversity within these reedswamps has declined as they have receded towards the shore. This is because reedswamp recession is likely to have reduced the number of niches for macroinvertebrates.

A lack of significant spatial variation in total macroinvertebrate abundance across the ecotonal axis within Borrans reedswamp was consistent with the findings of Sychra *et al*. (2010) for a similar size stand of *Phragmites* reedswamp. However, within the White Moss reedswamp there was evidence that abundance increased with proximity to the shore. Compared to Borrans, White Moss is a much larger reedswamp and consequently its landward zone has relatively deep litter deposits; it also provides greater refuge from fish predation and disturbance from wind and waves. Dvořák (1970) reported a progressive increase in total macroinvertebrate abundance away from the shore for a less extensive stand of *Glyceria*, which only extended 20 m into a pond. This suggests that the influence of reedswamp ecotones upon total macroinvertebrate abundance is variable.

Variations in alpha diversity along the ecotonal axes of Borrans and White Moss reedswamps were not significant. This might be due to high levels of variability across replicates within individual samples from both reedswamps. Within Borrans a stable substratum facilitated a consistent sample effort between replicate samples. This suggests that although reedswamp appears to be a relatively uniform habitat there can be a high degree of spatial heterogeneity in biodiversity even at the local scale (2 m^2). In contrast, Sychra *et al*. (2010) and Mason and Bryant (1974) found significant peaks in alpha diversity along the reedswamp ecotone; however, the patterns of variation between the two studies were distinct. Despite a lack of variation in alpha diversity within the Windermere catchment, analysis of similarity data indicated that beta diversity was relatively high across the reedswamp ecotones of Borrans and White Moss reedswamps. This anomaly is likely to be due to taxonomic turnover along the ecotones reflecting changes in habitat conditions. This highlights the importance of using similarity techniques to investigate spatial and temporal variations in biodiversity, and because published accounts of beta diversity across other reedswamp ecotones are lacking, this should be seen as a priority for future research.

Within reedswamp habitat, wave action generates a gradient in detritus and silt which increases towards the shore. This provides a habitat for macroinvertebrates with a preference for organic matter and associated physicochemical conditions (Learner *et al.*, 1978; Polunin, 1984; Sychra *et al.*, 2010). Within this study, spatial changes in substratum stability and detritus accumulation were the only measures of habitat structure to correlate significantly with invertebrate change across the ecotonal axis. During flood conditions nearby rivers may disrupt these gradients by depositing silt and macroinvertebrates throughout the length of the ecotone (*sensu* Junk *et al.*, 1989). Habitat structure variables and macroinvertebrate data at the ecotonal transect of White Moss adjacent to the confluence of the River Rothay were consistent with a strong riverine influence. Within the study area and adjacent areas, reedswamp habitat is a common feature at or near the confluence of rivers and lakes. This highlights the importance of developing a more complete understanding of the interactions between rivers and lacustrine reedswamps at tributary-lake confluences.

Within the White Moss and Borrans reedswamps there was an apparent absence of lateral environmental gradients sufficient to drive differences in macroinvertebrate community (*sensu* Heino, 2000; White and Irvine, 2003; Schreiber and Brauns, 2010). This was despite the influence of the River Rothay at White Moss, and marked differences in habitat structure at Borrans. Within the Borrans reedswamp the only pairing of communities not to be significantly dissimilar were at the southwestern edge (BSW) versus the northeastern edge (BNE). This was unexpected given the clear structural differences between these two patches of reedswamp located at opposite corners of the reedswamp (*sensu* White and Irvine, 2003). The substratum (lake bottom) at the two corners were distinct; one was unstable and silt dominated, while the other was firm set and dominated by boulders and cobbles. Macroinvertebrate data for these locations suggests that substratum structure did not have a significant impact upon community composition, in contrast to much of the literature (Moon, 1936; Dvořák, 1996; Schmude *et al.*, 1998; White and Irvine, 2003; Schreiber and Brauns, 2010). A likely explanation for this is that the influence of the wider habitat overrode the local influence (<5 m^2). These structurally distinct patches were separated by a single and relatively large mesohabitat, whose species pool may have had a strong influence upon the taxonomic composition of these distinct mesohabitats. In addition, the close proximity of both BNE and BSW to the open water environment may have minimised the influence of local habitat upon macroinvertebrate community assembly.

4.6.2 Spatial variations in biodiversity and abundance across lakes and individual reedswamps

The results broadly supported the hypothesis (H_2) that macroinvertebrate communities of different reedswamps within the same lake will be more similar to each other compared to those within reedswamps located in other lakes (*sensu* Allan and Johnson, 1997; Johnson and Goedkoop, 2002; Johnson *et al.*, 2004). A survey of twenty two Irish lakes by White and Irvine (2003) found that for similar categories of littoral habitat, macroinvertebrate assemblages could be reliable indicators of differences between lakes. In general, the current study supported the findings of White and Irvine (2003).

However, despite clear structural differences between the middles of White Moss and Borrans reedswamps, NMDS indicated that dissimilarity data relating to the middle of the reedswamp ecotone did not discriminate between the two lakes. This suggests that the reedswamp ecotone reduced the impact of differences between the two lakes (*sensu* Poff, 1997). A lack of dissimilarity between the middles of structurally distinct reedswamps is further evidence of the importance of physicochemical gradients in driving beta diversity. It suggests that it is position relative to the ecotone that determines macroinvertebrate diversity and not differences at the whole lake and individual reedswamp scales. Hence, the influence of the ecotone has the potential to reduce beta diversity across different reedswamps that are located within and between individual lakes. The mechanisms underpinning variations in dissimilarity from open water to shore are investigated further in chapter 5.

4.6.3 Differences in temporal response across the reedswamp ecotone

The degree to which the provision of refuge from wind and waves influences macroinvertebrate assemblages is likely to vary over an annual cycle. Spatial patterns of temporal variations in total macroinvertebrate abundance were distinctly different between the two lakes, and inconclusive. Similarity data failed to support the hypothesis (H_3) that temporal variations in community composition were relatively low at the middle and stony-littoral 'open' locations (*e.g.,* Gabel *et al.*, 2008; Schreiber and Brauns, 2010). Patterns of temporal change in macroinvertebrate assemblages within the inner (middle/landward) positions of White Moss were distinct to those at the edge and ‘open’ positions. The main feature of this differential response was a significant increase in dissimilarity at the middle and landward positions between January and April. This was an unexpected finding; the sheltered conditions within the inner reedswamp were expected to smooth the response of macroinvertebrates to change (*sensu* Schreiber and Brauns, 2010). A possible explanation is that the more stable conditions within the inner reedswamp allowed biotically mediated variations (*e.g.,* competition) to occur, while physical conditions at the edge disrupted some biotic interactions.

At certain times of year (*e.g.,* spring and summer), sheltered conditions facilitate biological succession (*sensu* Pickett and White, 1985; Boulton *et al.*, 1992; Hobbs and Huenneke, 1992). For example, increased diatom growth triggered by an increase in photosynthetically active radiation (PAR) during early summer (*sensu* Pickering, 2001) is enhanced by habitat stability, as is subsequent succession by green algae (Grimes *et al.*, 1980). This is significant because diatoms and other epiphytic photo-autotrophs can have a significant impact upon community composition by acting as an important food resource (Mazumdlr *et al.*, 1989; Hann, 1991). Macroinvertebrate community dynamics can also be influenced by the seasonal migration of predatory fish into reedswamps during the summer months (Suthers and Gee, 1986; Tolonen *et al.*, 2001; Mancinelli *et al.*, 2007). During this period the reedswamp ecotone (from open water to shore) provides some refuge from fish predation for macroinvertebrates (Sychra *et al.*, 2010).

The influence of reedswamp ecotones upon macroinvertebrates is complex and highly dynamic (Mason and Bryant, 1975b; Suthers and Gee, 1986; Mancinelli *et al.*, 2007). Horizontal gradients in dissolved oxygen and pH have been measured across reedswamp ecotones (Polunin, 1984). In addition, diel fluctuations in dissolved oxygen within dense stands of emergent vegetation have been demonstrated (Suthers and Gee, 1986). Both of these responses are more pronounced in the warmer months. Consequently, habitat structure is only one of a number a factors that influence temporal variations in beta diversity across the ecotonal axis of reedswamps. The current study demonstrates that macroinvertebrate assemblages located at different positions across the reedswamp ecotone respond to seasonal variations in different ways. Macroinvertebrate data allied with detailed descriptions of habitat structure provide valuable insights into the ways in which reedswamp habitat influences macroinvertebrate dynamics.

4.6.4 Implications of findings

Spatiotemporal variations in macroinvertebrate assemblages observed in this study imply that seasonal changes in climate and ecology can have a profound effect upon reedswamp macroinvertebrates and the ways in which they influence key processes such as carbon cycling (*sensu* Polunin, 1982; Mancinelli *et al.*, 2007). Dramatic changes in the global distribution of extensive stands of lacustrine reedswamps over the last century (Ostendorp, 1993; Brix, 1999b; Saltonstall, 2002; Schmieder, 2004; Rogalski and Skelly, 2012) and the influence of these changes upon key processes within individual lakes (Polunin, 1982; Birkett *et al.*, 1996; Marcot and Vander

Heyden, 2001; Carpenter, 2001) may have had a net influence upon global processes (*e.g.,* nutrient cycles). Lacustrine reedswamp habitat is distributed within both tropical and temperate zones (Haslam, 2010). Hence, there is a clear need to enhance current understanding of the ways in which climate and seasonal dynamics influence the functioning of reedswamp habitat.

At the local scale, evidence of the relative importance of reedswamp length across the ecotonal axis in supporting biodiversity will facilitate the conservation and restoration of reedswamp habitat (Mace and Baillie, 2007). However, while the length of the ecotonal axis has an important influence upon the animal community of reedswamps (Sychra *et al.*, 2010) the lateral extent of reedswamps is likely to be important for the resilience of the reedbed. The lateral extent of reedbeds along the shore also plays an important role in reducing bank erosion and providing cover for wildlife (Ostendorp, 1993; Báldi and Kisbenedek, 1999). Measures of diversity facilitate the conservation and management of biodiversity by informing policy and management actions (Mace and Baillie, 2007). They are particularly effective when there are implications for the status of legally protected or commercially important species. For example, evidence of macroinvertebrate biodiversity and abundance increasing along the length of the reedswamp ecotone can be used to imply a similar response from their vertebrate predators (*e.g.,* endangered birds, such as the bittern, and edible fish, such as trout [RSPB 2011]). Using variation in diversity to highlight key features of reedswamps (*e.g.,* ecotone length) will assist in the protection, management, and restoration of important but undervalued reedswamp habitat.

4.7 Summary

Spatiotemporal patterns of macroinvertebrate biodiversity seen in this study have demonstrated the dynamic responsiveness of this group to changes in the physical structure of the littoral zone of lakes (*sensu* Tolonen *et al.*, 2001; Aroviita and Hämäläinen, 2008; Gabel *et al.*, 2008). Current understanding of influence of the freshwater reedswamp ecotone upon environmental factors and biota (Dvořák, 1970; Mason and Bryant, 1974; Sychra *et al.*, 2010) is based mainly upon data related to the summer months within the temporal zone. Data from this study suggests that these models of ecotone function (*e.g.,* Sychra *et al.*, 2010) are over simplistic and may not fully explain the contribution of reedswamp ecotones to key processes (*e.g.,* carbon cycling) at the whole lake scale (*sensu* Strayer and Likens, 1986; Wetzel, 1990; Vadeboncoeur *et al.*, 2002). Spatiotemporal changes in macroinvertebrate assemblages indicated that the direction and magnitude of environment gradients generated across ecotones can fluctuate over an annual cycle. Hence, the influence of the freshwater reedswamp ecotone should not be thought of as a biological constant when making policy and management decisions that affect lake littoral habitats.

CHAPTER 5 Biological and functional traits assessment of invertebrate communities

5.1 Chapter Introduction

Chapter 4 described the relationship between biological diversity and habitat heterogeneity. This chapter uses the same datasets but adopts trait-based analysis of macroinvertebrate assemblages to investigate the mechanistic basis for community composition across distinct reedswamp habitats.

5.1.1 Introduction

Understanding the processes that underpin ecosystem functioning is an important challenge for applied ecologists (Verberk *et al.*, 2013). This requires quantification of the ecological response to natural and anthropogenic variables over a broad range of spatiotemporal scales (Statzner and Beche, 2010). Traditionally, the characterisation of ecological communities has relied on taxonomic structure (Statzner *et al.*, 2004). Unfortunately, observational approaches that relate taxa to their environment are empirical in nature and do not facilitate a mechanistic understanding of why certain species are found in a given location or provide any insights into potential ecosystem functioning (Lawton and Brown, 1993; Weiner, 1995). More recently, methods based on multiple functional-biological traits have come to the fore (Statzner *et al.*, 2004). The measurable and well-defined properties (*e.g.,* morphology, behaviour, ecology, and life-history) of an organism are known as its traits (M^{c}Gill *et al.*, 2006). Traits that strongly influence the ability of an organism to sustain its biomass over multiple generations are known as functional traits (M^{c}Gill *et al.*, 2006). Consequently functional trait-based approaches have facilitated recent investigations into interactions between ecosystem functioning, biodiversity, and environmental degradation (Kinzig *et al.*, 2001; Loreau *et al.*, 2001; Bai *et al.*, 2010; Mora *et al.*, 2011). In addition, approaches that emphasise traits rather than taxonomy aids comparison between sites with different species assemblages and makes findings meaningful to scientists unfamiliar with local species (Weiher and Keddy, 1995).

The functional trait approach is well established. The century old Saprobic Index (Pantle and Buck, 1955), based upon the oxygen requirement of benthic macroinvertebrates, was used to assess the impact of organic pollutants (Statzner and Beche, 2010). Trait-based approaches are underpinned by the concept of environmental filters (Poff, 1997). This idea can be considered as an expansion of the original concept of habitat templates (Heino, 2008). Southwood (1977) based his habitat templates theory on the hypothesis that certain combinations of environmental factors allow species with compatible functional traits to coexist with the other members of their local community. Rather than considering how local scale spatial and temporal heterogeneity selects (filters) species based on their traits, environmental filter approaches consider ecological features at multiple scales. To pass through filters at each scale, a species requires traits that enable it to exist in the target environment (Poff, 1997) (Figure 5.1).

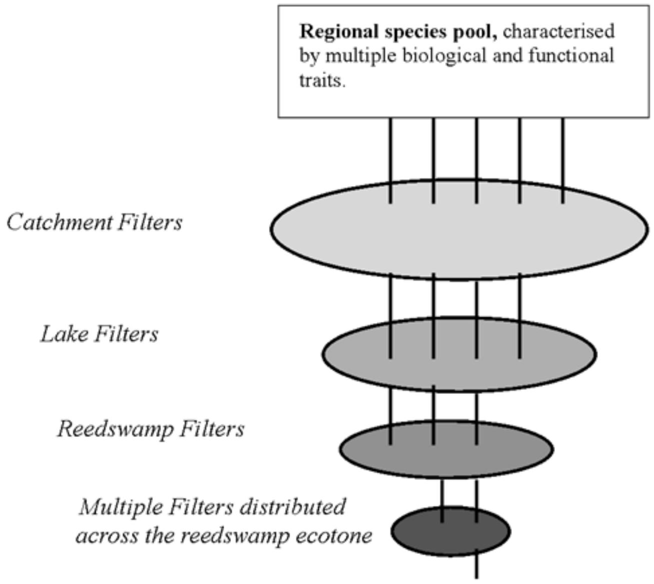


Figure 5.1 This conceptual diagram illustrates how multiple environmental filters distributed across a range of spatial scales may influence community assembly within lacustrine reedswamps. Straight lines represent the passage of individual species through filters. This diagram was adapted from Poff (1997), who proposed a similar model for river systems.

While the application of trait-based approaches in applied ecology is expanding (Verberk *et al.*, 2013), there are relatively few examples from the littoral zones of lakes, ponds, and other types of wetlands (Heino, 2000; King and Richardson, 2002; van Kleef *et al.*, 2006; Sychra *et al.*, 2010). Theoretically, an improved understanding of multiple landscape filters should enable scaled predictions of community composition in the littoral zone of lakes (Poff, 1997; Johnson and Goedkoop, 2002; Tolonen *et al.*, 2003). In freshwater systems the most influential filters that determine the functional characteristics of community often include ecosystem size, habitat structure, trophic state, and biotic interactions (Tonn *et al.*, 1990; Poff, 1997).

Investigation of these filters requires detailed information on organism traits (*e.g.,* substrate preferences and tolerance to saprobity) and multiple stressors over a broad range of spatiotemporal scales (Poff, 1997). Collection of this data is time consuming and expensive, requiring sophisticated analysis and interpretation techniques. Consequently, trait-based approaches often focus upon single groups of organisms and ecosystems that are relatively well known. For example, previously published information on benthic macroinvertebrates (*e.g.*, Tachet *et al.*, 2000) has been used effectively to relate changes in the ecology of lotic systems to anthropogenic impacts (Dolédec *et al.*, 1999; Lamouroux *et al.*, 2004; Finn and Poff, 2005).

The macroinvertebrate traits most likely to be important to the functioning of a lake littoral ecosystems are dietary in nature and include detritus processing, animal-microbial interactions, and herbivory. Where and how food resources are obtained, allied with the functional roles of macroinvertebrates, determines how a freshwater ecosystem functions (Covich *et al.*, 1999). Moog (1995) recognised that some aquatic macroinvertebrates move through different feeding guilds during their life cycles and devised a ten-point weighting scale for guilds. This ‘fuzzy coding’ method has now been adopted across multiple traits for European macroinvertebrates (Chevene *et al.*, 1994; Tachet *et al.*, 2000). In the absence of published databases of macroinvertebrate traits specifically for lakes, lotic databases (Tachet *et al.*, 2000) are often used (Heino, 2000; van Kleef *et al.*, 2006; Sychra *et al.*, 2010) although the validity of applying these data to lakes is untested.

Macroinvertebrate trait-based approaches can provide important information regarding the management of the littoral zone within lakes (Heino, 2008). The majority of published studies include dietary traits with additional traits selected on the basis of the environmental filters under investigation. For example, a study of four shallow lakes in the Netherlands by van Kleef *et al.* (2006) successfully predicted the response of littoral macroinvertebrate community composition to different phases of habitat restoration (*e.g.,* improvements in trophic status) using biological traits related to diet, life history, locomotion, habitat preference, and respiration (*sensu* Tonn *et al.*, 1990; Poff, 1997). Sychra *et al.* (2010) demonstrated that the integration of information on macroinvertebrate traits (diet and habitat preference), structural heterogeneity, and associated physicochemical gradients could be used to explain progressive changes in macroinvertebrate assemblages across the ecotonal axis (~30 m) of a fish pond reedswamp. However, the limited number of traits utilised (functional feeding groups and microhabitat preferences) prevented a mechanistic understanding of the influence of reedswamp habitats on macroinvertebrates.

Concerns have been raised regarding the consequences of anthropogenic changes in reedswamp coverage for the functioning of lakes throughout the world (Ostendorp, 1989; Tscharntke, 1992; Saltonstall, 2002). While the influence of macrophytes upon key functional traits such as oviposition have been described in detail (Cattaneo, 1983; Rooke, 1984; Lodge, 1985; Usseglio-Polatera *et al.*, 2000; Scheffer, 2004), the integrated response of macroinvertebrates to spatiotemporal changes in reedswamp habitat within lakes (*sensu* van Kleef *et al.*, 2006) has received little attention. Sychra *et al*. (2010) demonstrated the potential for macroinvertebrate traits to reflect functionally significant changes in reedswamp coverage. However, a more complete understanding of how multiple macroinvertebrate traits interact with intraspecific and interspecific reedswamp gradients (filters) will facilitate a mechanistic understanding of how reedswamp influences key processes such as carbon cycling (*sensu* van Kleef *et al.*, 2006).

5.2 Aim and hypotheses

The overall aim was to assess the potential of multiple traits as a tool for inferring the influence of reedswamp habitat upon the processing of organic matter by macroinvertebrates. Three hypotheses were tested. The first hypothesis (H_1) asserts that spatial successional changes in functional feeding traits, substrate relation, and related traits (*e.g.,* saprobity and reproduction) will occur across the reedswamp ecotone (Sychra *et al.*, 2010). For example, inner (landward) reedswamp locations, and stony-littoral habitats will be characterised by traits consistent with habitat stability and refuge from fish predation (Tolonen *et al.*, 2001). Assemblages at these two habitats will be differentiated from each other by dietary and substrate relation traits (*e.g.*, interstitial deposit-feeders in stony-littoral habitats vs crawlers and shredders in reedswamp). The second hypothesis (H_2) asserts that compared to structural variation between individual reedswamps (*e.g.,* silt accumulation), differences in trophic status at the whole lake scale will have a stronger influence upon trait composition by changing the relative abundance of traits related to saprobity and filter-feeding (*sensu* Allan and

Johnson, 1997; Johnson and Goedkoop, 2002; Johnson *et al.*, 2004). The third hypothesis (H_3) asserts that the mechanisms that underpin environmental filters vary over time; for example, variations in trait composition reflect seasonal changes in food availability (*e.g.,* epiphytes), saprobity, and disturbance (*sensu* Ripl, 1976; Dvořák and Best, 1982; Mazumdlr *et al.*, 1989; Hann, 1991; Varga, 2003; van Kleef *et al.*, 2006).

5.3 Study area

Semi-quantitative macroinvertebrate samples were collected from one stony-littoral (non-reedswamp) and five reedswamps locations distributed across two lakes in the northwest of England, Windermere and Rydal Water (Figure 5.2). Windermere is the largest lake in England with a surface area of 14.76 km^2 and divided into two deep basins by a strip of relatively shallow water (average depth 10 m) at a narrowing of the lake (Pickering, 2001). Rydal Water is a smaller lake with a surface area of 0.31 km^2 (Parker, 2002) and is located ~3 km upstream of the North Basin of Lake Windermere, connected by the River Rothay. Refer to Chapters 3 and 4 for detailed descriptions of the study area.

Figure 5.2 and Table 5.1 describe the locations and key physical features of all sample sites. White Moss was the largest reedswamp within the study area and dominated the western shore of Rydal Water. Samples were collected along the land-water axis of White Moss: (1) adjacent to the shore (Wm2l), (2) at the middle of the reedswamp (Wm2m), and (3) at the ‘edge’

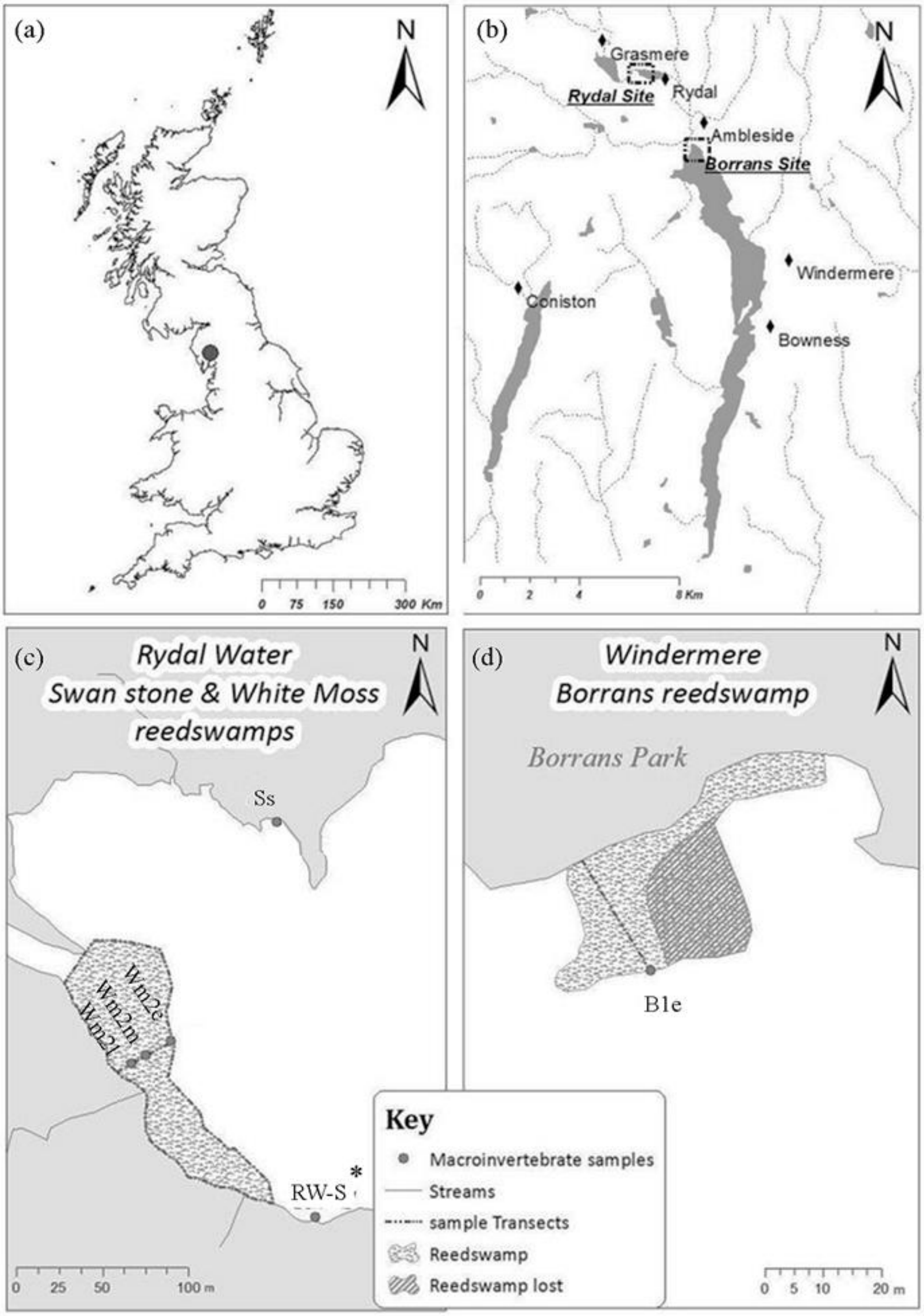


Figure 5.2 These maps illustrate the distribution of sample locations within: (a) the United Kingdom, (b) Cumbria, (c) Rydal Water, (d) and Windermere; * = stony-littoral site. Reedswamp lost relates to an area destroyed by physical damage (underlying mechanism unknown) between October 2011 and January 2012.

Table 5.1 Differences in the dominant physical features of sample sites within the littoral zone of the Windermere catchment. (O = stony-littoral 'open' sites, Rs = reedswamp sites, RW = Rydal Water, Wi = Windermere, L = local, W = widespread, and E = extensive)

Site	Latitude/ Longitude	Lake	Shore	Surface area	Number of sample locations	Reed species	Distance along ecotonal axis	Stability	Underlying Substratum	Overlying silt
Borrans (Rs)	54:25:15.674N 2:57:59.693W	Wi	North	820 m^2	1	*P. australis*	9–26 m	Stable	Cobble Pebbles	L
Swan Stone (Rs)	54:26:55.244N 3:0:5.015W	RW	North	12 m^2	1	*P. australis*	1.6 m	Soft Sinking	Silt	E
White Moss (Rs)	54:26:51.456N 3:0:9.198W	RW	West	6,019 m^2	3	*P. australis* *T. angustifolia*	12.5–60 m	Soft Sinking	Silt Detritus	L
RW-S (O)	54:26:48.155N 3:0:1.511W	RW	South	-	1	-	-	Unstable	Cobbles Pebble Sand	L

i.e., the reedswamp-open water interface (Wm2e). The distances between White Moss sample locations are described by Figure 5.2c and Table 5.2. Other sample locations within Rydal Water were at the edge of the Swan Stone reedswamp (Ss) on the northern shore of Rydal Water, and at a stony-littoral 'open' position (RW-S) off the southern shore. A single location within Windermere was sampled at the edge of Borrans reedswamp (B1e); which was located on the northern shore (Figure 5.2d). Refer to Table 5.2 and Chapters 3–4 for detailed descriptions of these reedswamps.

Table 5.2 The influence of ecotonal position upon multiple macroinvertebrate traits was investigated by collecting samples along the land-water axis near the centre of the White Moss reedswamp. Differences across reedswamps and lakes were investigated by comparing edge locations at three reedswamps distributed across two lakes (Figure 5.2c–d).

Sample location	Lake	Ecotonal position	Distance from reedswamp edge (m)
RW-S	Rydal Water	Open	-
White Moss:	Rydal Water		
Wm2e		Edge	2
Wm2m		Middle	18
Wm2l		Landward	28
Swan Stone:	Rydal Water		
Ss		Edge	2
Borrans:	Windermere		
Be1		Edge	2

5.4 Methods

5.4.1 Macroinvertebrate sample collection

A bespoke hand-net sampling technique was used to sample all six sample locations during June 2011, September 2011, January 2012, and April 2012. The same approach was used to sample both reedswamp and ‘open’ stony-littoral habitat. At each location, individual samples were collected from five randomly distributed quadrats of 0.1 m^2 from within an area of 2 m^2 over a 30 second period. Preliminary testing indicated that the sample method was effective in collecting a variety of taxa throughout a range of different niches for both habitat types. Refer to Chapter 4 for a detailed description of the sample protocol.

The number and spatial distribution of sample positions within the study area was based upon the findings of Chapter 4, which highlighted the importance of variations in taxonomic composition along the land-water axis, and across reedswamps. Transect 2 of White Moss reedswamp (Wm2l, Wm2m, and Wm2e) was selected in combination with a stony-littoral site off located the southern shore of Rydal Water (RW-S) for the investigation of changes in the trait composition of macroinvertebrate assemblages along the reedswamp ecotone (H_1). This transect was chosen because of the relatively long distance by which it extended out into the lake, and for its proximity to the centre of the reedswamp. In order to investigate differences in macroinvertebrate trait composition between reedswamps and across lakes (H_2) samples were also collected from the edges of Swan Stone (Ss) and Borrans (B1e) reedswamps. The collection of samples from all sites between

June 2011 to January 2012 allowed the investigation of seasonal changes in environmental filters throughout the littoral zone (H_3).

5.4.2 Data analysis

A bespoke traits database was created by integrating published information regarding *Daphnia* traits (Koivisto and Ketola, 1995; Weber and Declerck, 1997; Urabe and Sterner, 2001) into an existing traits database for riverine macroinvertebrates (Tachet *et al.*, 2000). A fuzzy coding approach (*cf*. Chevene *et al.*, 1994) was applied to the bespoke traits database to establish a link between each taxon and its affinity to 63 trait categories (Table 5.3). Trait composition per sample was calculated by multiplying taxon trait affinities with the relative abundance of each taxon. Furthermore, trait richness was summarised as the number the trait categories represented in each replicate sample. Differences in richness and composition across the reedswamp ecotone (H_1) and between the three reedswamps (H_2) were tested. Trait richness data was Log_{10} (x + 1) transformed in order to conform to normality and analysed using repeated measures analysis of variance (RM-ANOVA) with time as an independent factor (H_1 and H_2). Refer to Chapter 4 for details of RM-ANOVA, and associated *post hoc* tests.

For all three hypotheses, dissimilarity of trait composition data was analysed by applying one-way permutational multivariate analysis of variance (PERMANOVA), Betadisper, and ordination techniques based upon the dissimilarity coefficient, the Bray Curtis Index (BC). Refer to Chapter 4 for details of BC and the tests of homogeneity (PERMANOVA, Betadisper, and

Table 5.3 Trait richness and composition was calculated by allocating the following categories of traits to each macroinvertebrate taxon (*sensu* Tachet *et al.*, 2000) using a fuzzy coding approach (*cf.* Chevene *et al.*, 1994).

Traits	**Categories**	**Categories per trait**
Feeding habits	Absorber, deposit-feeder, shredder, scraper, filter-feeder, piercer, predator, and parasite	8
Food	Microorganisms, detritus (<1 mm), dead plant (≥1 mm), living microphytes, living macrophytes, dead animal (≥1 mm), living microinvertebrates, living macroinvertebrates, and vertebrates	9
Locomotion and substrate relation	Flier, surface swimmer, full water swimmer, crawler, burrower, interstitial, temporarily attached, and permanently attached	8
Maximum potential size	≤0.25 cm	7
	0.25–0.5 cm	
	0.5–1 cm	
	1–2 cm	
	2–4 cm	
	4–8 cm	
	>8 cm	
Life cycle duration	≤1 year	2
	>1 year	
Potential number of cycles per year	<1	3
	1	
	>1	
Substrate (preference)	Flags/boulders/cobbles/pebbles, gravel, sand, silt, macrophytes, microphytes, twigs/roots, organic detritus/litter, and mud	9
Reproduction	Ovoviviparity, isolated eggs (free), isolated eggs (cemented), clutches (cemented or fixed), clutches (free), clutches (in vegetation), clutches terrestrial), and asexual reproduction	8
Saprobity	Xenosaprobic, oligosaprobic, beta–mesosaprobic, alpha-mesosaprobic, and polysaprobic	5
Respiration	Tegument, gill, plastron, and spiracle	4
All traits		**63**

associated *post hoc* tests) applied upon it. Macroinvertebrate community traits were related to the habitat measurement data for selected sites along the reedswamp ecotonal axis (H_1 and H_3), and in a separate analysis across three different reedswamps (H_2). The multivariate ordination technique RLQ analysis was used to generate a graphical representation of the ordination of individual taxa and traits upon habitat gradients (Dolédec *et al.*, 1996) in order to test all three hypotheses. Subsequent fourth corner permutation tests were carried-out to provide statistical information for the relationship between each individual trait and individual habitat measurements (*sensu* Dray and Legendre, 2008).

RLQ is a relatively new multivariate approach designed to facilitate simultaneous analysis of data from more than two different tables of environmental data. It is a double constrained ordination that is commonly used for the integrated analysis of environmental factors, taxonomic abundance, and trait data (*sensu* Dolédec *et al.*, 1996). As a result, RLQ ordination facilitates application of the habitat template (Southwood, 1977) and environmental filter concepts (Poff, 1997). The RLQ approach uses eigenvalue analysis to combine three individual ordinations. For the current investigation these ordinations consisted of: (1) Correspondence Analysis (CA) of abundance data for individual taxa by sample location and time (L table); (2) Principal Components Analysis (PCA) for habitat measurements by sample location and time (R table); and (3) Fuzzy Correspondence Analysis (FCA) ordination (Chevene *et al.*, 1994) of taxa and their traits (Q table). These data were combined to form a matrix 'R^TLQ'. Eigenanalysis consisting of 1000 random repetitions was performed upon rows of traits and habitat measurements located within the matrix '$R^T LQ$' (*sensu* Dolédec *et al.*, 1996). Separate and independent RLQ plots were produced for ecotonal (White Moss only), and inter-reedswamp analysis.

The fourth-corner permutation test is a univariate method that can be applied to abundance data (*sensu* Dray and Legendre, 2008). It utilises Pearson's coefficient to test for correlation between taxon abundance and environmental factors. Models of fourth corner testing are characterised by the different ways in which location and time data within the L-table is analysed. For this investigation, the correlation between individual traits and each habitat variable (*e.g.,* water depth) were tested by analysing the abundances of each individual taxa per sample (all five replicates combined) independently using 1000 permutations (model 1, Legendre *et al.*, 1997). Results were plotted in a 'fourth table', where the direction of significant correlations ($p < 0.05$) were illustrated. For example, whether or not individual trait categories increase or decline significantly with increases in habitat variables such as water depth. All statistical analysis was performed using the statistical environment R. Both RLQ and fourth corner analysis were carried using the 'ade4' package (Dray and Dufour, 2007).

5.5 Results

In total 13,490 macroinvertebrates were collected from 120 samples over an 11 month period. A fuzzy coding approach (*cf*. Chevene *et al.*, 1994) indicated that 71 different taxa contributed to all 63 trait categories. There were no significant ($p < 0.05$) differences in trait richness across the following categorisations: (1) all sample locations, (2) the reedswamp ecotone, and (3) different reedswamps (Table 5.4). However, nested one-way PERMANOVA based upon Bray Cutis dissimilarity data indicated that trait composition varied significantly across the ecotone and between reedswamps (Table 5.5). There were clear differences in feeding and mobility traits between lakes and across the ecotone; for example, the dominance of shredders increased away from open water while the relative abundance of filter-feeders decreased (Figure 5.3). In addition, free swimming filter-feeders were less dominant within the Windermere reedswamp (Borrans) compared to the Rydal Water reedswamps (Figure 5.3). The relative abundances of trait categories within most traits were highly variable over time. At the majority of locations, free swimming filter-feeders were dominant during September, but by April crawling shredders predominated (Figure 5.3). However, variations in trait composition across reedswamp spatial axes were not consistent over time (Table 5.6, Figures 5.4 and 5.5). Progressive significant spatial variations in trait composition occurred from June to January across the ecotone, and from June to September across reedswamps (Table 5.6). In general, variance in trait composition over time was homogeneous (Table 5.6, Figures 5.4 and 5.5).

The RLQ plot samples relating to the reedswamp ecotone were clustered by sample position along the primary (x) axis. Positions along the ecotone were ordered sequentially from the shore towards the open environment (Figure 5.6b). The only habitat variable closely associated with the primary axis was detritus accumulation, which declined distally from the landward site position

Table 5.4 These statistics describe trait richness data across the ecotone at White Moss (locations: RW-S, Wm2e, Wm2m, and Wm2l) and across the edges of all three reedswamps (locations: Ss, Wm2e, and B1e) from June 2011 to April 2012. Repeated Measures ANOVA analysis (with time as an independent factor) demonstrated that trait richness was not significant across the ecotone, reedswamp edges, and all sites.

	Ecotone	Edges	All sites
Mean	53.9	53.1	53.5
Standard deviation	3.4	3.2	3.3
Range	43–62	47–60	43–63
Median	54.0	53.5	54.0
RM-ANOVA	$F_{3,64} = 2.4$ $P = 0.14$	$F_{3,48} = 0.8$ $P = 0.50$	$F_{3,96} = 1.34$ $P = 0.30$

Table 5.5 These results of one-way nested PERMANOVA (1000 permutations) for trait composition demonstrated that significant dissimilarity in trait composition occurred along the White Moss ecotone (locations: RW-S, Wm2e, Wm2m and Wm2l) and across all three reedswamps (locations: Be1, Ss, and Wm2e) from June 2011 to April 2012.

	R^2	F, *p*
Ecotone	0.05	$F_{1,79} = 4.4$, $p = 0.001$
Reedswamps (Edges)	0.06	$F_{1,59} = 4.9$, $p = 0.005$

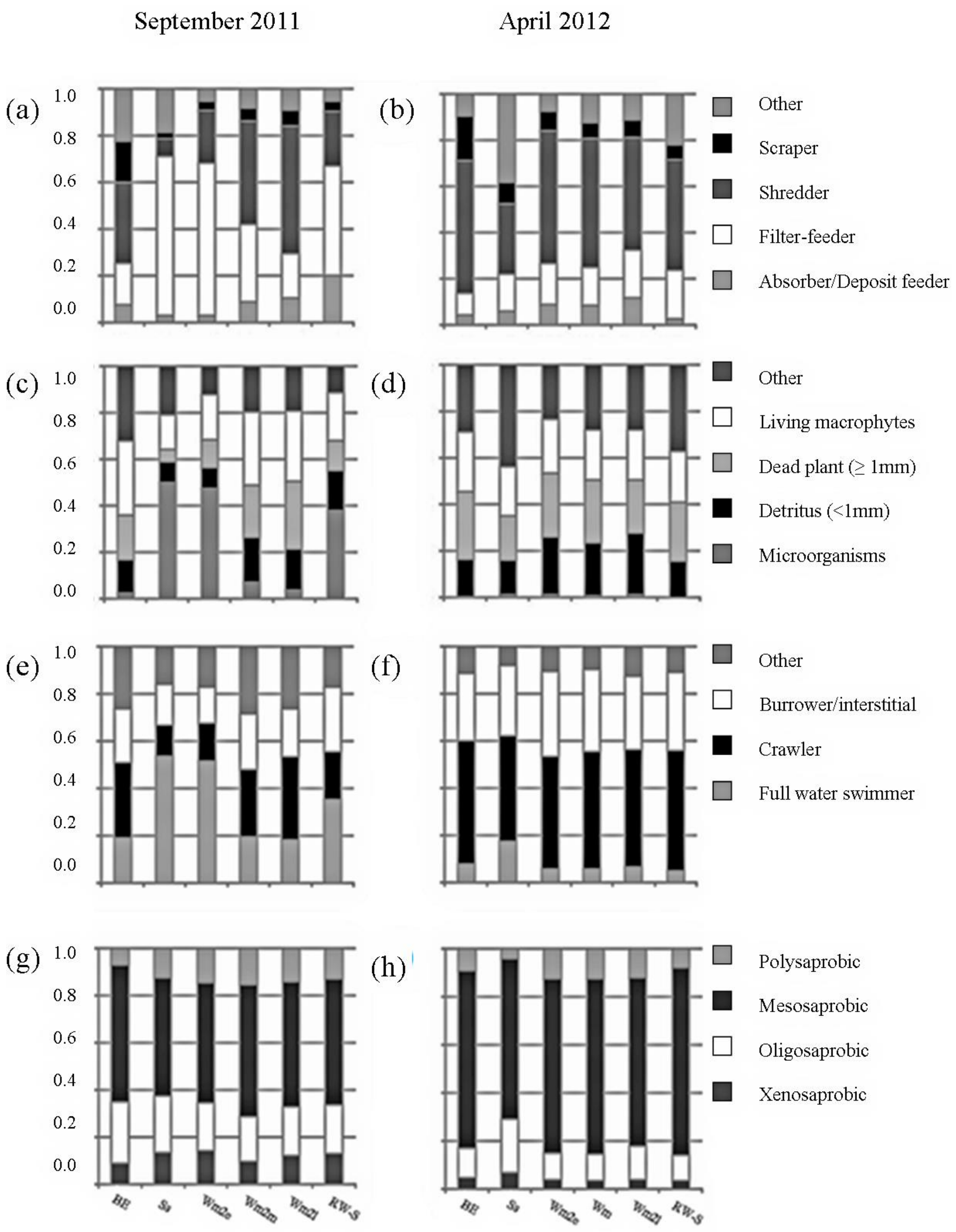


Figure 5.3 These graphs illustrate spatial variations in mean relative abundances for key trait categories from September 2011 to April 2012: (a, b) feeding, (c, d) food preference, (e, f) motility, and (g, h) saprobity. Sample locations relate to the following: (BE, Ss, Wm2e) the edge at three reedswamps, (Wm2m, and Wm2l) the middle and landward locations for White Moss reedswamp respectively, and (RW-S) a stony-littoral location adjacent to White Moss reedswamp.

Table 5.6 These results of one-way PERMANOVA (Adonis) and analysis of multivariate homogeneity of variances (Betadisper) identified the sample times during which dissimilarity was significant across the White Moss ecotone, and between edge locations at all three reedswamps. *Post hoc* analysis for PERMANOVA and Betadisper, Analysis of similarity (Anosim) and Tukey HSD respectively identified dissimilarity between pairs of samples. (* = *Post hoc* analysis [Tukey HSD] indicated no significant differences between pairs of locations, ** = Both White Moss and Swan Stone were significantly different [$p < 0.001$] to Borrans, and N/A = pair-wise comparisons not applicable)

	June	September	January	April
1) Ecotone				
i) PERMANOVA for all locations (Adonis)	$R^2 = 0.6$ $F_{3,19} = 8.5$ $p = 0.001$	$R^2 = 0.5$ $F_{3,19} = 6.6$ $p = 0.001$	$R^2 = 0.3$ $F_{3,19} = 2.7$ $p = 0.03$	$R^2 = 0.2$ $F_{3,19} = 1.7$ $p = 0.1$
ii) Pair wise comparisons by location (Anosim)				
Stony-littoral vs Edge	$R = 0.4$, $p = 0.02$	$R = 0.3$, $p = 0.04$	$R = 0.4$, $p = 0.03$	N/A
Stony-littoral vs Middle	$R = 0.9$, $p = 0.01$	$R = 0.8$, $p = 0.005$	$R = 0.3$, $p = 0.06$	N/A
Stony-littoral vs Land	$R = 0.9$, $p = 0.005$	$R = 0.9$, $p = 0.001$	$R = 0.5$, $p = 0.01$	N/A
Edge vs Middle	$R = 0.5$, $p = 0.01$	$R = 0.5$, $p = 0.04$	$R = 0.1$, $p = 0.2$	N/A
Edge vs Land	$R = 0.7$, $p = 0.004$	$R = 0.7$, $p = 0.01$	$R = 0.4$, $p = 0.03$	N/A
Middle vs Land	$R = 0.1$, $p = 0.13$	$R = 0.01$, $p = 0.4$	$R = -0.02$, $p = 0.4$	N/A
iii) Betadisper for all locations	$F_{3,19} = 1.1$ $p = 0.4$	$F_{3,19} = 0.7$ $p = 0.6$	$F_{3,19} = 0.2$ $p = 0.9$	$F_{3,19} = 3.7$ $p = 0.03$*
2) Across Reedswamps (Edges)				
i) PERMANOVA for all locations (Adonis)	$R^2 = 0.3$ $F_{1,13} = 7.0$ $p = 0.006$	$R^2 = 0.3$ $F_{1,13} = 6.7$ $p = 0.002$	$R^2 = 0.1$ $F_{1,13} = 2.3$ $p = 0.08$	$R^2 = 0.1$ $F_{1,13} = 1.3$ $p = 0.26$
ii) Pair wise comparisons by location (Anosim)				
Borrans vs Swan Stone	$R = 1.0$, $p = 0.005$	$R = 0.9$, $p = 0.01$	N/A	N/A
Borrans vs White Moss	$R = 1.0$, $p = 0.01$	$R = 0.8$, $p = 0.007$	N/A	N/A
Swan Stone vs White Moss	$R = 0.9$, $p = 0.01$	$R = 0.5$, $p = 0.006$	N/A	N/A
iii) Betadisper for all locations	$F_{2,12} = 1.2$ $p = 0.34$	$F_{2,12} = 22.2$ $p < 0.001$**	$F_{2,12} = 0.5$ $p = 0.63$	$F_{2,12} = 0.9$ $p = 0.42$

(Figure 5.6a). The trait categories with a positive relationship to detritus included shredding, and preference for organic litter. Trait categories negatively correlated with detritus included absorbers, asexual reproduction, and cementing isolated eggs (Figure 5.6c). Temporal variation within individual sample locations deceased along the secondary (y) axis; samples closely associated with the shore and stony-littoral location demonstrated the least degree of progressive temporal variation (Figure 5.6b). Variables most closely associated with the secondary axis were proximity to the pelagic zone (Figure 5.6b). However, only one trait (increase in laying of free isolated eggs with distance from land) demonstrated significant ($p < 0.05$) correlation with ecotonal position (Table 5.7). Many habitat vectors occurred along both axes, and the largest of these was water depth. Water depth was significantly correlated (negatively or positively) with seventeen different trait categories (Table 5.7). For the other main vectors, shoot density was negatively correlated with eight trait categories and positively with one. Correlations between substratum particle size and significant trait categories were mainly positive (Table 5.7).

Samples relating to different reedswamps were clustered by individual reedswamps along the primary (x) axis of the RLQ plot, Swan Stone was followed by White Moss, and then Borrans. In addition, the three reedswamps were arranged by lake (Figure 5.7b). The habitat vectors most closely associated with the primary axis were silt deposits (negative) and substratum particle size (positive) (Figure 5.7a). Trait categories significantly

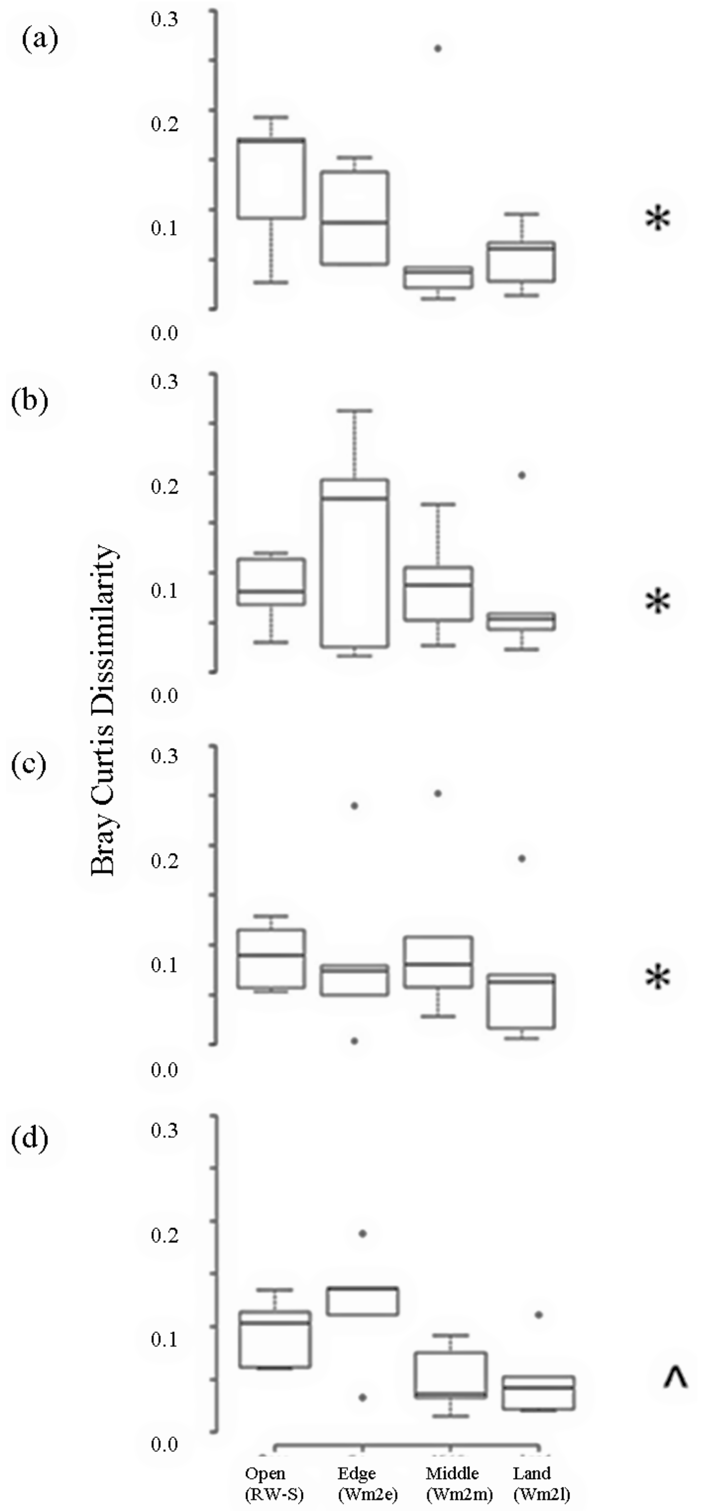


Figure 5.4 These box plots illustrate how spatial variations in trait composition across the ecotonal axis of White Moss changed over time. Text in brackets indicates sample location. (Panels a-d: [a] June 2011, [b] September 2011, [c] January 2012, [d] April 2012; * = means significantly different [$p < 0.05$] across the ecotone and ^ = variance significantly different [$p < 0.05$] across the ecotone)

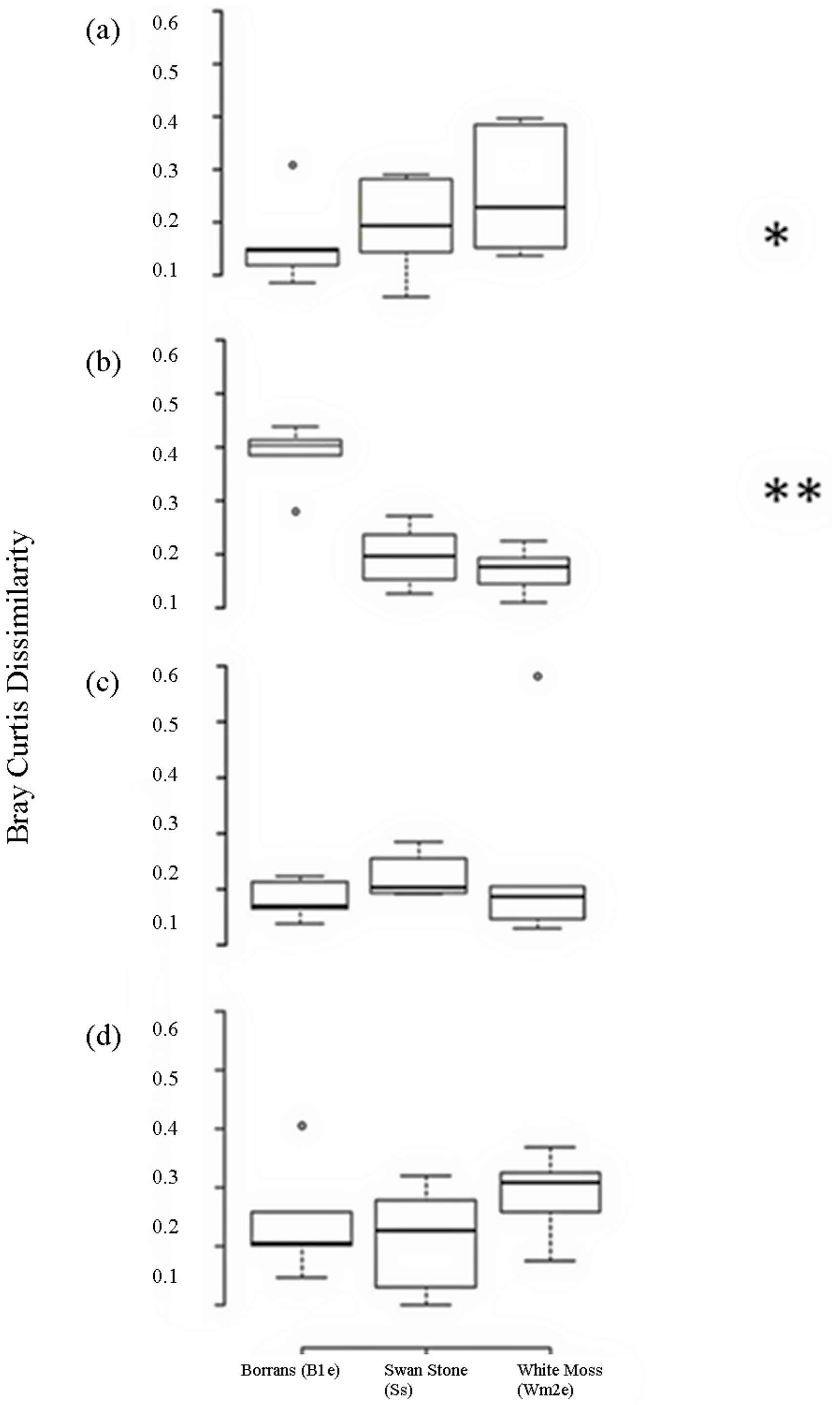


Figure 5.5 These box plots illustrate how spatial variations in trait composition across reedswamps (at the deep water edge) changed over time. Text in brackets indicates sample location. (Panels a-d: [a] June 2011, [b] September 2011, [c] January 2012, [d] April 2012, * = means significantly different [$p < 0.05$] across the ecotone, and ** = means and variance significantly different across reedswamps)

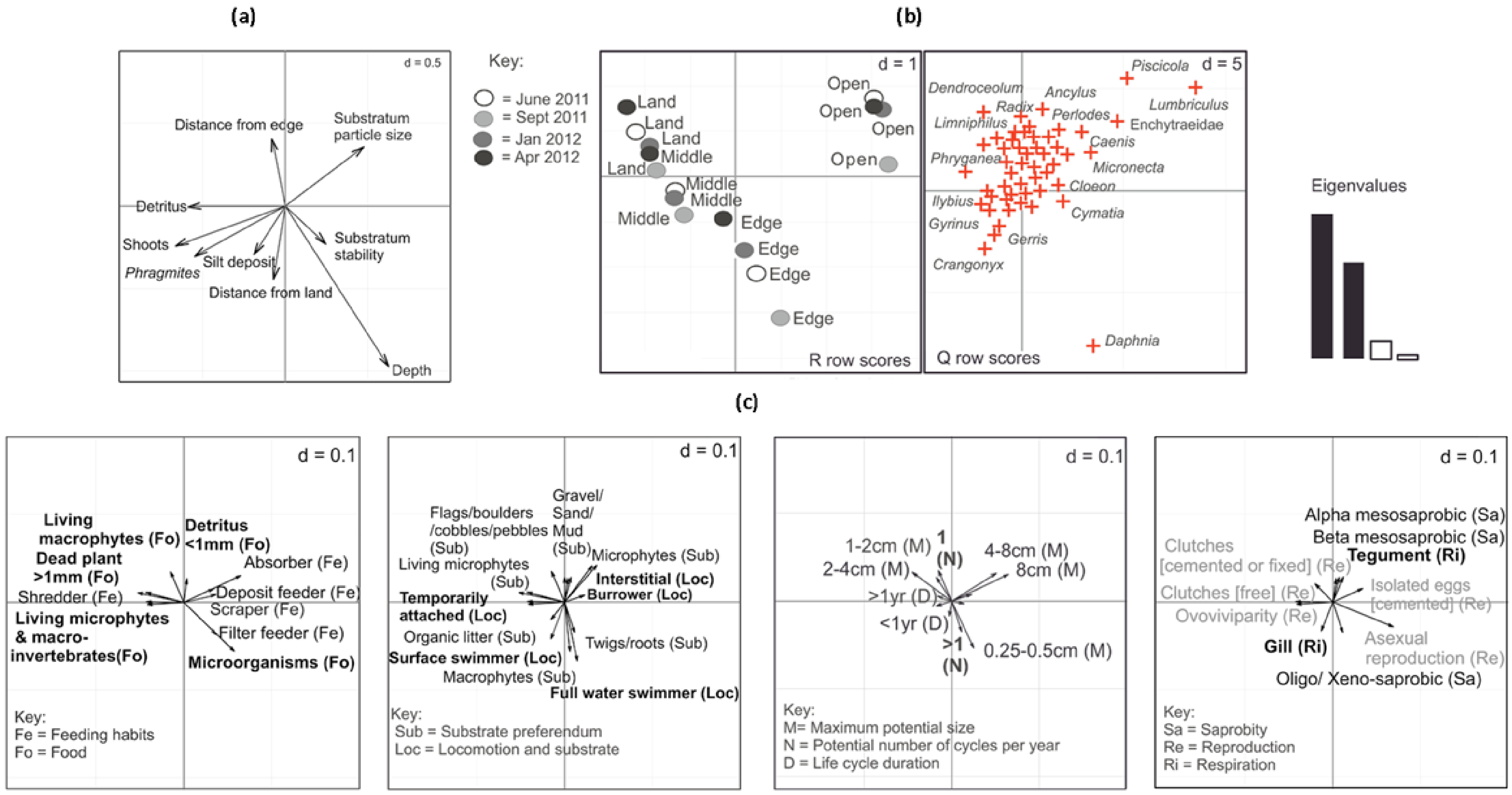


Figure 5.6 These plots of RLQ ordinations illustrate differences across the reedswamp ecotone from September 2011 to April 2012. (a) Gradients in habitat variables are represented by R-table canonical weights, (b) site and taxa ordinations are represented by plots of R and Q row scores, and (c) trait ordinations are represented by Q canonical weights. Ordination plot scale is indicated by d.

Table 5.7 This table presents the results of fourth corner analysis, which tested correlations between individual trait categories (rows) and habitat variables (columns) at locations across the White Moss ecotone from September 2010 to April 2011. Only traits categories correlated with at least one of the habitat variables were included. (- = negative correlation, + = positive correlation, blank = No significant [$p > 0.05$] correlation, Fe = feeding, Fo = food, Lo = locomotion and substrate relation, Sub = substrate preference, Sa = saprobity, Ri = respiration, M = maximum potential size, D = life cycle duration, N = potential number of cycles per year, and Re = reproduction)

Trait categories (traits in brackets)	Water depth	Shoot density	*Phragmites* :*Typha*	Substratum stability	Substratum size	Silt	Reed litter	Distance to land	Distance to edge
Absorber (Fe)		-	-		+	-	-		
Shredder (Fe)	-			+			+		
Filter-feeders (Fe)	+								
Microorganisms (Fo)	+								
Dead plant [≥1 mm] (Fo)	-								
Living macrophytes (Fo)	-								
Full water swimmer (Lo)	+								
Crawler (Lo)	-								
Flags/boulders/cobbles/pebbles (Sub)	-								
Gravel (Sub)		-	-		+				
Macrophytes (Sub)	+								
Microphytes (Sub)	-								
Organic detritus/litter (Sub)		+					+		
Alpha-mesosaprobic (Sa)	-								
Polysaprobic (Sa)			+						
Spiracle (Ri)			+						
>4–8 cm (M)		-	-		+	-			
>8cm (M)		-	-		+				
<1 (N)		-		+			-		
1 (N)	-								
>1 (N)	+								
Isolated eggs [free] (Re)					+			-	
Isolated eggs [cemented] (Re)		-	-		+	-	-		
Clutches [free] (Re)	-	+	+		-		+		
Asexual [reproduction] (Re)	+	-					-		

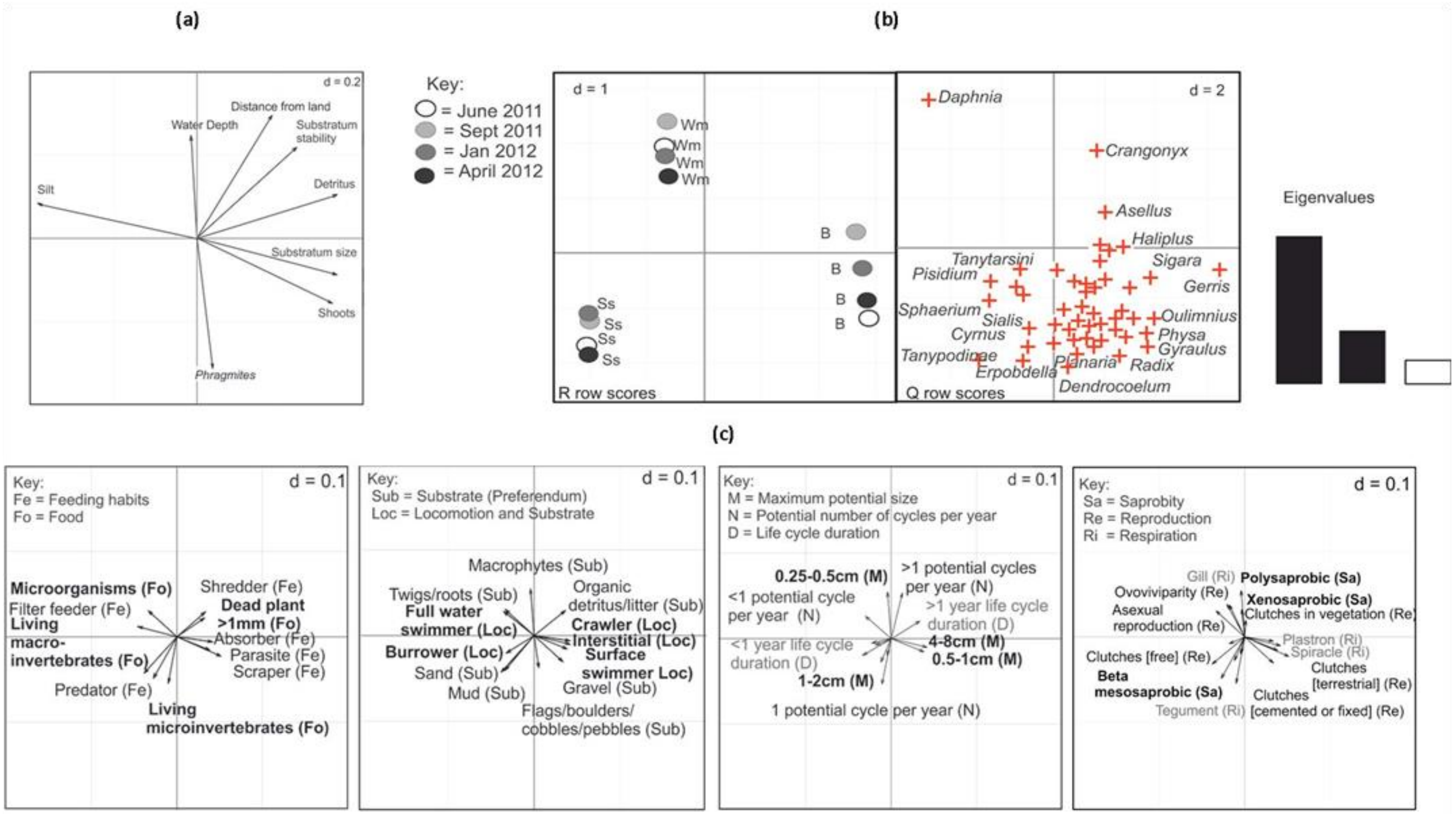


Figure 5. 7 These plots of RLQ ordinations illustrate differences across all three reedswamps ([Wm] White Moss, [Ss] Swan stone, and [B] Borrans) from September 2011 to April 2012. (a) Gradients in habitat variables are represented by R-table canonical weights, (b) site and taxa ordinations are represented by plots of R and Q row scores, and (c) trait ordinations are represented by Q canonical weights. Ordination plot scale is indicated by d.

Table 5.8 This table presents the results of fourth corner analysis, which tested correlations between individual traits categories (rows) and habitat variables (columns) at locations across the edges of all three reedswamps from September 2010 to April 2011. Only trait categories correlated to at least one of the habitat variables were included. (- = negative correlation, + = positive correlation, blank = No significant [*p* > 0.05] correlation, Fe = feeding, Fo = food, Lo = locomotion and substrate relation, Sub = substrate preference, Sa = saprobity, Ri = respiration, M = maximum potential size, D = life cycle duration, and N = potential number of cycles per year)

Trait categories (traits in brackets)	Water depth	Shoot density	*Phragmites*: *Typha*	Substratum stability	Substratum particle size	Silt	Reed litter	Distance to land
Shredder (Fe)				+				
Scraper (Fe)		+	+		+	-	+	
Filter-feeder (Fe)		-			-	+	-	
Piercer (Fe)	+	+		+	+	-	+	
Predator (Fe)				-			-	-
Detritus <1 mm (Fo)	-							
Dead plant (≥1 mm)							+	
Living microphytes (Fo)	-							
Dead animal (≥1 mm) (Fo)			+					
Living microinvertebrates (Fo)				-				-
Living macroinvertebrates (Fo)								-
Flier (Lo)		+			+	-	+	
Surface swimmer (Lo)		+		+	+	-	+	
Crawler (Lo)		+		+	+	-	+	
Gravel (Sub)		+	+		+	-	+	
Sand (Sub)				-	-	+	-	-
Microphytes (Sub)	-	+			+	-		
Organic detritus/litter (Sub)							+	
Mud (Sub)				-	-	+	-	-
Oligosaprobic (Sa)	+							
Alpha- mesosaprobic (Sa)	-							
Polysaprobic (Sa)			-					+
Tegument (Ri)		-						
Gill (Ri)		-	-					
Plastron (Ri)		+			+	-	+	
Spiracle (Ri)		+			+	-	+	
>1–2 cm (M)	+							
<1 (N)				-	-	+	-	
1 (N)			+	-				-
>1 (N)			-					+
Isolated eggs [free] (Re)				-			-	-
Isolated eggs [cemented] (Re)		+			+	-	+	
Clutches [cemented of fixed] (Re)		+	+		+	-	+	
Clutches [free] (Re)				-	-	+	-	-
Clutches [in vegetation] (Re)		+						

correlated with silt deposits included feeding by scraping (negative) and filter-feeding (positive). Crawling (positive) and burrowing (negative) were correlated with substratum size (Figure 5.7c). The secondary (y) axis represented temporal variation associated with changes in depth within individual reedswamps (Figure 5.7a,b). Furthermore, spatial variation between reedswamps along the secondary axis was associated with differences in the dominance of *Phragmites* shoots. *Phragmites* dominance was negatively correlated with scrapers and positively correlated with polysaprobic traits. Water depth was correlated with alpha mesosaprobity (negative) and piercers (positive). In contrast to the ecotonal RLQ plot, all habitat vectors were similar in magnitude. Furthermore, traits were evenly distributed across all habitat vectors (Table 5.8).

5.6 Discussion

By investigating the distribution of multiple categories of macroinvertebrate traits, this study found evidence of a broad range of different types of environmental filter associated with reedswamps (*sensu* van Kleef *et al.*, 2006). A novel aspect of this study was the investigation of changes in spatial filters over time. For example, seasonal changes in reed litter deposition and phytoplankton productivity appeared to be related to changes in the distribution of trait categories across the reedswamp ecotone. The findings of this study enhance current understanding (Sychra *et al.*, 2010) of the mechanistic ways that reedswamp habitat influences key processes such as decomposition. It was clear that the influence of reedswamp habitat upon macroinvertebrates and their role in key processes was highly complex due a combination of spatial and temporal drivers. Herein the discussion considers the underlying reasons for the following patterns: (1) spatial variations along the reedswamp ecotone, (2) spatial differences across lakes and reedswamps, and (3) differential temporal responses across the reedswamp ecotone. Finally, the implications for conservation and management are discussed.

5.6.1 Ecotonal variations in trait composition

There was strong support for the hypothesis (H_1) that significant variations in environmental factors across the reedswamp ecotone were reflected by changes in multiple macroinvertebrate trait categories. This was consistent with the findings of Sychra *et al*. (2010) who utilised fewer traits (functional feeding groups and microhabitat preference only) in the study of a reedswamp ecotone; the use of additional traits (*e.g.,* reproductive strategies, respiration method, and maximum potential body size) in the current study facilitated a more comprehensive mechanistic understanding of the influence of the reedswamp ecotone upon key ecological processes. The efficacy of using these additional traits to reveal complex changes in environmental factors within lakes was also demonstrated by van Kleef *et al*. (2006) for non-reedswamp habitat. This highlights the importance of carrying out comprehensive multi-trait based investigations into changes in the extent of the reedswamp ecotone within lakes, and should be seen as a priority for future research.

Published studies of variation along the reedswamp ecotone have focussed on organic matter and its impact on feeding and microhabitat preference traits (Dvořák, 1996; Sychra *et al.*, 2010). In the current study, changes in the relative amount of detritus across the reedswamp ecotone were positively correlated with shredder and crawler abundance. Although there was general consensus with published results, the expected positive relationship between silt deposits and both deposit-feeders and burrowers (Sychra *et al.*, 2010) was not observed. This suggests that understanding the ecological significance of differences in organic matter would benefit from the integration of multi-trait information regarding food preference (*e.g.,* living microphytes), feeding strategies (*e.g.,* shredding, filter feeding, *etc.*), saprobity, and substrate relation (*e.g.,* crawling) traits.

Considering the underlying reasons for differences in food resource availability was useful for understanding the influence of the reedswamp ecotone upon important ecological processes. For example, compared to reedswamp locations, habitat at the stony-littoral site was characterised by relatively small amounts of dead plant material. The substratum at this site was characterised by relatively large and stable interstitial spaces, which probably facilitated the interception and retention of relatively small (<1 mm) organic particles. Reedswamp substratum was dominated by larger litter particles (≥1 mm) due to aerial deposition of reed litter and subsequent retention by the reed stand (*sensu* Bedford, 2005). Within the stony-littoral site, the aerial deposition of large particles of litter was assumed to be negligible.

The structure of the stony-littoral ‘open’ site provided niches for invertebrates with a preference for soft sediments (fine litter and silt) trapped within interstitial spaces (*sensu* Learner *et al.*, 1978). These included burrowing deposit-feeders (*e.g., Caenis*) and absorbers (*e.g., Lumbriculus*) that are adapted for mesosaprobic to polysaprobic conditions. Conditions at the surface of the stony substratum were suitable for invertebrates that obtain most of their energy by scraping (*e.g., Ancylus fluviatilis*) rather than shredding or deposit feeding (*e.g., Crangonyx pseudogracilis)* (*sensu* Tachet *et al.*, 2000), reflecting more algal growth due to relative stability and a lack of shading (Müller, 1994). In contrast, reedswamp supported relatively high numbers of shredders by providing leaf litter and associated microorganisms as a source of food, in accordance with the findings of others (Egglishaw, 1964; Mason and Bryant, 1975a; Polunin, 1982; Jones *et al.*, 1994; Sychra *et al.*, 2010).

Across the reedswamp there were clear differences in substratum structure and stability between the inner locations and the edge, similar to those observed in pond reedswamps by Dvořák (1970) and Sychra *et al*. (2010). However, the strongest environmental gradient across the reedswamp ecotone was an increase in water depth from shore to open water. Water depth has a strong influence upon lake littoral macroinvertebrates (Weatherhead and James, 2001), and was significantly correlated ($p < 0.05$) with a large number of different trait categories (17) compared to distance from land or edge (1 trait category). This study therefore demonstrates the value of ‘spot checking’ water depth in conjunction with reedswamp macroinvertebrate sampling; it is recommended that future investigations include continuous temporal monitoring of hydrological data (*sensu* Bedford and Powell, 2005).

The main biological variation across the reedswamp was an increase in the dominance of *Daphnia* from shore to open water. Large numbers of *Daphnia* and other large zooplankton species migrate into reedswamps and other structurally complex and dense habitats during the daytime in order to avoid pelagic planktivorous fish (Timms and Moss, 1984; Lauridsen and Buenk, 1996; Burks *et al.*, 2001). Consequently there was a rise in the dominance of small body size, free swimming, asexual reproduction, and filter-feeding trait categories at the reedswamp edge. If *Daphnia* are actively feeding while using the reedswamp as refuge, then the reed shoots would be facilitating the utilisation of food resources above the substratum (Rooke, 1984; Scheffer, 2004).

Across the reedswamp ecotone, distance from the pelagic environment was associated with progressive increases in the provision of shelter and refuge (Sychra *et al.*, 2010) with a consequent increase in the dominance of epiphytic and benthic macroinvertebrates. The key trait categories of these invertebrates were feeding by shredding, crawling, relatively large body size, long-life, and univoltine reproduction. The trait of laying clutches of eggs directly into the water column within inner reedswamp was evidence of a relatively stable habitat (Dolédec *et al.*, 1999; Usseglio-Polatera and Beisel, 2002; Diaz *et al.*, 2008). It is clear from this ecotonal data that macroinvertebrates have an integrated response to changes in food resource, habitat structure and stability, shelter and refuge across the reedswamp ecotone. This highlights the need to develop and test multiple-trait based techniques across a wide range of different types of reedswamps, and lakes.

5.6.2 The influence of trophic status upon traits

Trait composition data supported the hypothesis (H_2) that trophic status at the whole lake scale has a strong influence on differences in macroinvertebrate communities between reedswamps located within different lakes. It is likely that trophic status drives macroinvertebrate community composition by influencing reedswamp structure rather than acting as an independent factor, consistent with the findings of van Kleef *et al.* (2006). They found that the responses of multiple macroinvertebrate traits to improvements in the trophic status of shallow lakes were related to associated changes in habitat structure (*e.g.,* siltation, and growth of macrophytes and algae). Reed communities are dependent upon the trophic status of lakes (Pieczyńska *et al.*, 1999), as are other elements of reedbed habitat such as silt deposits, detritus, periphyton, plankton, macrophytes, and microbes (Papas, 2007). This investigation indicates that analytical methods based upon multiple macroinvertebrate traits are an effective way of assessing the influence of differences between individual reedswamps and across lakes (*e.g.,* trophic status).

Published information on spatial variations in saprobity trait categories for macroinvertebrates within reedswamps and the wider lacustrine environment is lacking. Furthermore, evidence of a close relationship between saprobity trait categories and trophic status of rivers has been inconsistent between different studies (Archaimbault *et al.*, 2005; Lecerf *et al.*, 2006). In the present investigation, macroinvertebrate saprobic trait categories did not discriminate between differences in trophic status across the two lakes. In contrast, spatial variation in filter-feeder dominance was particularly effective in discriminating between Rydal Water and Windermere sample locations. This is relevant because filter-feeder abundance increases with planktonic productivity, which has a positive relationship with trophic status (*sensu* Gulati, 1983; Bays and Crisman, 1983; Elser and Goldman, 1991; Nalepa *et al.*, 1998). Therefore, the relatively numerous filter-feeders recorded at Rydal Water were consistent with its elevated trophic status compared to Windermere, as reported by Maberly *et al*. (2011).

The influence of environmental changes along the vertical axes of reedswamps may help to explain why the trait of filter-feeding was discriminatory between lakes. There were key functional differences between the dominant species of filter-feeders at the two Rydal Water sites. *Daphnia* is a free swimming filter-feeder and was relatively dominant at White Moss. In contrast, the burrowing filter-feeder *Sphaerium* was dominant at Swan Stone. The trait of regulating vertical position within the water column (full water swimming) allowed *Daphnia* to access food resources throughout the water column at White Moss. Whereas, at Swan Stone the majority of filter-feeders fed upon suspended organic matter from within a substratum that consisted of soft deposits of fine sediments (*sensu* Learner *et al.*, 1978). Unfortunately, accounts of changes in macroinvertebrate trait composition along vertical axes within freshwater are lacking. Consideration of the ways in which multiple traits allow macroinvertebrates to respond to differences in habitat structure and physicochemical variables along the vertical axis of lakes was a novel aspect of the current study.

5.6.3 Temporal variations in environmental filtering

There was support for the hypothesis (H_3) that the mechanisms underpinning environmental filters vary over time; for example, variations in trait composition were associated with seasonal changes in food availability and physical disturbance. During June, September, and January there were significant variations in community composition (dissimilarity) across the reedswamp ecotone. In contrast there was no evidence of environmental filters acting across the ecotone during April. Because the majority of reed shoots within a reedbed persist throughout the year, it is likely that some form of environmental filtering occurs year round. However, the influence of environmental filtering is at its strongest during the summer to autumn period, as macroinvertebrate activity (*e.g.,* feeding) and growth is at or near its peak during this period (Ward and Cummins, 1979; James *et al.*, 1998). Unfortunately, the majority of published evidence is based upon data relating to June through September (Dvořák, 1970; Mason and Bryant, 1974; Polunin, 1984; Sychra *et al.*, 2010), and there are no published accounts of environmental conditions within reedswamp habitat (or similar) during the winter months. Hence, little is known about the seasonal dynamics of lacustrine macroinvertebrates.

A shift in trait composition from September to April was evidence of a strong seasonal influence upon reedswamp macroinvertebrates. For example, the trait categories associated with macrophyte litter (shredding, feeding upon detritus and crawling) increased in dominance across all ecotone positions. This is consistent with the findings of chapter 6 that indicated that a combination of reed shoot senescence in autumn, and weather conditions during winter drives an increase in reed leaf litter accumulation within mixed (*Phragmites* and *Typha*) reedswamps in the spring months (Polunin, 1984; Findlay *et al.*, 2002). Furthermore, progressive increases in shredder numbers from edge to landward positions with reedswamp habitat were observed in September but not in April. This suggests that seasonal factors (*e.g.,* the life history of reeds) established a temporary filter that was driven by reed litter distribution. Filter-feeders also demonstrated a similar type of response to seasonal changes (*e.g.,* changes in phytoplankton) (Dvořák, 1996). In contrast to shredders, filter-feeder dominance decreased from September to April. During September there was a temporary spatial gradient in filter-feeders, characterised by high relative abundance at the reedswamp edge and stony-littoral environments. This is evidence that the nature and distribution of multiple environmental filters across the reedswamp ecotone are transient in nature and strongly influenced by seasonal changes in both climate and biology.

There was a relatively low level of temporal variation in trait dissimilarity at stony-littoral, and inner reedswamp habitats across the entire 11 month sample period. This indicated that compared to the reedswamp edge they provided food and refuge for macroinvertebrates in a relatively stable environment. It is important to distinguish between physical and chemical stability. The landward extremes of reedswamps are protected from physical disturbance but are susceptible to fluctuations in dissolved oxygen due to the presence of large deposits of organic material in a sheltered environment. Dissolved oxygen decreases over the warmer summer months due to increased microbial activity (*sensu* Mann, 1956; Polunin, 1982). However, associated changes in saprobity trait categories over time within landward extreme of the reedswamp were inconclusive, suggesting that macroinvertebrates were adapted for wide fluctuations in dissolved oxygen. While numerous studies have identified several possible influences upon the temporal dynamics of reedswamps (Canedo-Arguelles and Rieradevall, 2009), the current study demonstrated the need to measure the actual ecological response to seasonal changes in biotic and abiotic factors.

5.7 Summary

This chapter shows that novel datasets collected from lake littoral zones support the theory of Weiher and Keddy (1995) that differences in multiple-traits are associated with habitat heterogeneity at different spatial and temporal scales. Uniquely, this study demonstrated that even at small spatial scales (~8 m) within relatively structurally homogenous habitats, multiple traits can demonstrate a differential respond to temporal changes. Spatiotemporal patterns of multiple macroinvertebrate traits seen in this study demonstrated the dynamic responsiveness of this group to changes in the physical structure of the littoral zone of lakes (sensu Heino, 2005; van Kleef *et al.*, 2006; Sipkay *et al.*, 2007; Brauns *et al.*, 2007a). These patterns imply that changes in physical structure related to reedswamp habitat act as environmental filters and determine macroinvertebrates assembly (Poff, 1997). Understanding the seasonal dynamics of filters has the potential to reveal the ways in which macroinvertebrates link primary production and vertebrate consumers, and how they influence the decomposition rates of organic matter and the translocation and cycling of nutrients (Murkin and Wrubleski, 1988). However, traits related to the utilisation of food resources (mobility and feeding strategy) were not the only ones that were shown to be valuable. These traits in combination with saprobity and reproductive strategy traits provided valuable insights in the spatiotemporal dynamics of ecotonal filters. This investigation facilitates the effective management of lakes by highlighting the role of reedswamp habitat in regulating key processes within the littoral zone. Consequently, it demonstrates the importance of monitoring and protecting key features within the littoral zone. In particular it promotes the need for reedbed conservation and restoration.

CHAPTER 6 The relationship between reed community composition and detritivores: an experimental test

6.1 Chapter Introduction

The ecological significance of interspecific differences in detritus structure is relatively simple to investigate in isolation. This information facilitates the interpretation of spatial and temporal variations in macroinvertebrate assemblages within and between reedswamps and across lakes (Chapters 4 and 5).

6.1.1 Introduction

The functioning of reedswamps is underpinned by the breakdown of reed material (Mason and Bryant, 1975b; Brinson *et al.*, 1981; Polunin, 1984; Gessner, 2000). Detailed assessment of the functional significance of decay and its associated processes requires information on litter availability. However, research into the influence of detritus within reedswamps has mainly focused on the aquatic phase of decay in isolation. Consequently, the processes that underpin the formation and distribution of reed detritus across a range of reedswamp types are poorly understood. The biological significance of the dynamics of reed detritus creation, deposition, and distribution remains unresolved. A more complete understanding of the role of seasonal dynamics of detritus is likely to benefit the management of reedswamps including, for example, the impact that the common practice of harvesting or burning stands of dead reeds (Haslam, 2010) has upon the processes underpinned by detritus.

A combination of shoot growth and the structure of dead shoots determine detritus loading within reedswamps. Reeds have high levels of decomposition-resistant structural fibres, which enable living and dead shoots to resist wind damage (Polisini and Boyd, 1972; Polunin, 1984). At the end of the growing season (autumn) reed shoots (*e.g., Typha angustifolia* and *Phragmites australis*) dieback, leaving behind stands of dead shoots, which may persist for a couple of years (Mason and Bryant, 1975b; Komínková *et al.*, 2000). The impact of differences in reed shoot size, structure, life cycles, growth rates, and resistance to grazing and disease upon detritus dynamics has received little attention. This is unfortunate, as there is often a high degree of variability, even within a single species at the same reedswamp (Haslam, 1971b; Clevering and Lissner, 1999; Sharma *et al.*, 2008). Across the common reedswamp forming plants there is a wide range of functionally significant differences. For example, the dead aerial shoots of *P. australis* are more resistant to physical damage and persist longer than those of *T. angustifolia* and *Schoenoplectus lacustris* L. Palla (Ostendorp, 1993). In addition, *P. australis* and *T. angustifolia* are distinct in their life histories, morphologies, and chemical composition (Mason and Bryant, 1975b; Grace and Harrison, 1986; Haslam, 2010). While both species emerge during April, shoot density for *T. angustifolia* peaks earlier than *P. australis* (May *cf*. July; Mason and Bryant, 1975b). *Phragmites australis* net productivity is lower than *T. angustifolia*, plus there are differences between the species in both nutrient content and dynamics (Mason and Bryant, 1975b). However, detailed information on interspecific responses has been limited to a small range of lakes and environmental conditions. Little is consequently known regarding the effect of climate change and habitat loss upon detritus dynamics.

The majority of reed litter that enters the water column is comprised of fragments of dead aerial shoots (Mason and Bryant, 1975b; Pieczyńska, 1993). When dead reed material enters freshwater systems it begins to decay almost immediately. This initial phase of decay results in rapid loss of mass due to the leaching of nutrients and other soluble components. The influence of leaching is determined by abiotic factors (*e.g.,* temperature and pH) rather than by biological activity (Polunin, 1982). Following leeching, the biological process of decomposition becomes dominant. The biotic decomposition of reed litter is driven by the interaction of microbes and detritivorous macroinvertebrates (Lewin *et al.*, 2004; Okun and Mehner, 2005; Mancinelli *et al.*, 2007). However, it is the breakdown of detritus by macroinvertebrates that forms part of the main pathway for nutrient and carbon cycling of reed tissue (Imhof, 1973; Skuhravy, 1978). The distribution and dynamics of breakdown products within reedswamps are influenced strongly by the structure of macroinvertebrate communities (Mason and Bryant, 1975b; Carpenter and Adams, 1979; Polunin, 1982; Bärlocher, 1990). For example, leaf litter is progressively broken down into finer particles by a succession of different macroinvertebrate species (Cummins, 1973). The ways in which macroinvertebrates interact with reedswamp detritus can be highly variable not just between lakes (Danell and Andersson, 1982) but also within individual reedswamps (Mason and Bryant, 1975b; Polunin, 1982; Polunin, 1984; van Dokkum *et al.*, 2002).

Valuable contributions to understanding the importance of macroinvertebrates to reed decay with reedswamps have been made by Mason and Bryant (1975b) and Polunin (1982). Both studies used a combination of laboratory and field techniques to investigate biotic and abiotic influences upon reed decay within reedswamps. Most studies into the role of macroinvertebrates in reed detritus decay within reedswamps have focussed upon *P. australis* litter, perhaps because of its role in nutrient cycling and the organisms it supports (Sabetta *et al.*, 2000; Mancinelli *et al.*, 2006; Quintino *et al.*, 2009). The influence of other reed species is less well known. Consequently, the focus has been upon decay within monospecific stands of *P. australis*. Many of the other reedswamp forming plants (*e.g., T. angustifolia*) are widely distributed and commonly occur along with *P. australis* as mixed stands (Haslam, 1971b; Mason and Bryant, 1975b; Dvořák and Best, 1982; Kulesza *et al.*, 2008) and these require research attention.

Interspecific differences between reeds can underpin contrasting decomposition and colonisation rates by macroinvertebrate shredders and scrapers (Mason and Bryant, 1975b). However, little is known regarding the ways that reed detritus influences macroinvertebrate structure and functioning. Studies carried out within streams suggest that the primary role of tree leaf detritus is to provide food (Egglishaw, 1964; Drake, 1984;

Richardson, 1992). However, there is some evidence that within the lentic environment, shredders and scrapers can be influenced more by microhabitat rather than food. For example, Street and Titmus (1982) studied the colonisation of different materials by macroinvertebrates within a gravel pit in England. All of the materials were structurally similar but only some acted as a food source for macroinvertebrates. However, there were no significant differences between the macroinvertebrate assemblages associated with food and non-food materials. Enhancing our knowledge of the ways in which reeds influence macroinvertebrate assembly is essential if we are to understand the role of reedswamps in key lake processes. Hence, a more complete understanding of reed detritus dynamics and its relationship with macroinvertebrates will facilitate the management of this important habitat.

6.2 Aim and hypotheses

The overall aim was to investigate the ecological significance of differences in *P. australis* and *T. angustifolia* life history and properties of their leaf litter (breakdown rates and structure). Three hypotheses were tested: (H_1) increases in reed litter biomass over the winter months will be more pronounced in a mixed reedswamp compared to a monoculture of *P. australis* (*sensu* Mason and Bryant, 1975b); (H_2) interspecific differences in detrital mass loss will be accompanied by differences in macroinvertebrate assemblages (*sensu* Mason and Bryant, 1975b); and (H_3) interspecific differences in the provision of food, rather than microhabitat or refuge, drive differences in macroinvertebrate colonisation between the litter types (*sensu* Egglishaw, 1964; Drake, 1984; Richardson, 1992).

6.3 Study area

Aspects of reed leaf litter decay were studied in two structurally distinct reedswamps within two lakes in the northwest of England: Windermere (*P. australis* monoculture) and Rydal Water (*T. angustifolia* and *P. australis*) (Figure 6.1). Refer to chapters 3 and 4 for detailed descriptions of study area.

6.4 Methods

6.4.1 Estimation of standing crops

Counts of living reed shoots were made in five randomly distributed quadrats of 0.1 m^2 located near the centres of both reedswamps during July 2012. All green shoots were identified to species and enumerated separately. Data from Mason and Bryant (1975b) was used to estimate the peak standing crops of each reed species at both reedswamps. Quantitative samples of detritus were collected from the centre of Borrans and White Moss during the same days on 15th October 2012 and on the 25th March 2013. Five randomly distributed replicate samples of 0.03 m^2 were collected from within an area of 1 m^2. Areas from which samples were taken were enclosed by an open ended box (17.5[L] × 15[W] × 17.5 cm [D]). The enclosure was pushed firmly into the bottom of the reedswamp, and prior to sampling the enclosed contents were agitated by a vigorous figure of eight motion using the handle of a small pond net. The net aperture (16 × 16 cm, 250 µm mesh) was used

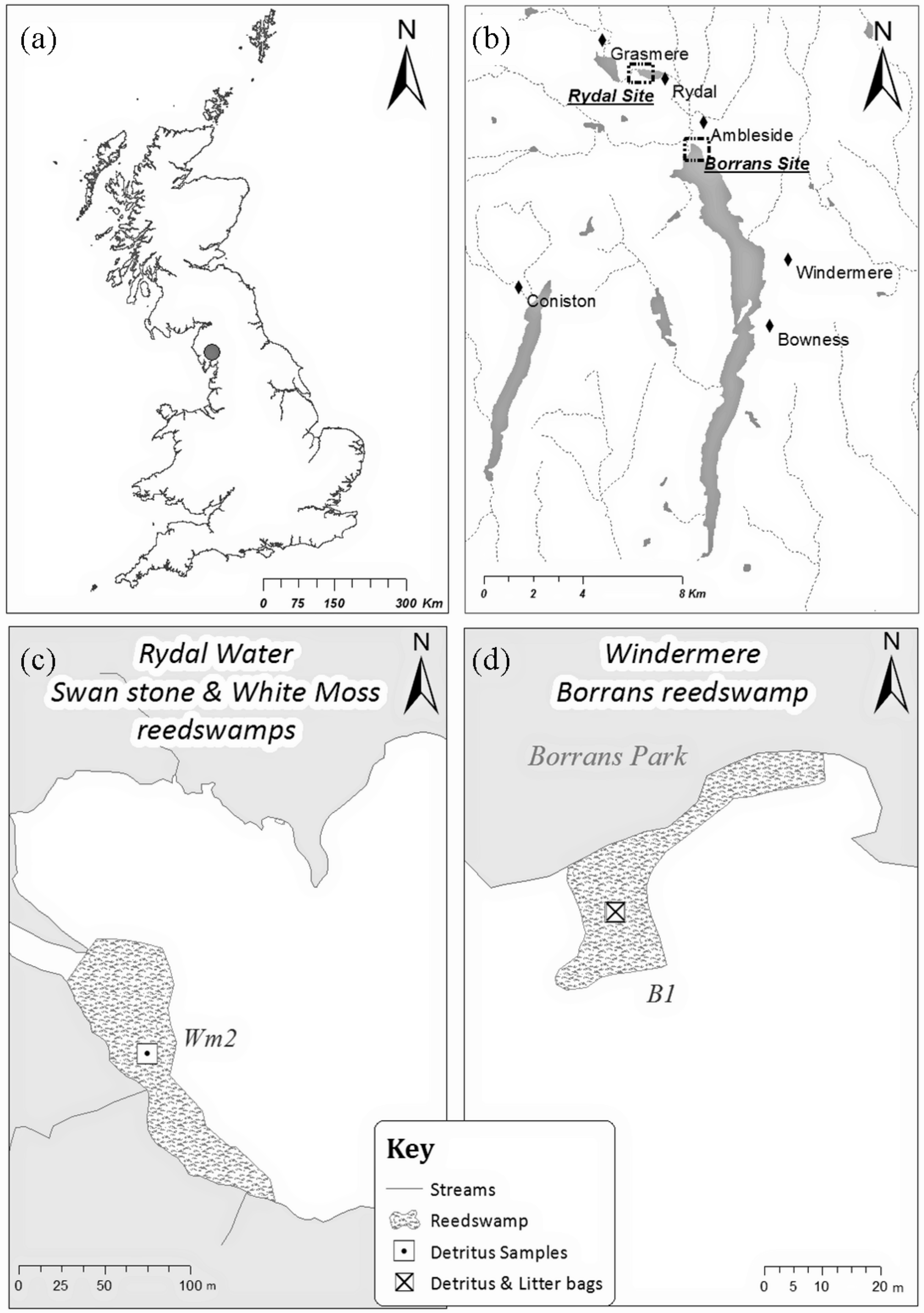


Figure 6.1 These maps illustrate the distribution of sample locations within (a) the United Kingdom, (b) Cumbria, (c) Rydal Water, and (d) Windermere.

to scoop out the contents of the enclosure. Woody debris (including leaves), stems and pond weeds were removed. Samples were sieved into two size fragments (≥1 mm and 0.5–1 mm) and allocated to the nearest ‘general’ detritus category (*sensu* Cummins, 1974). Litter of length ≥1 mm was allocated to the category of coarse particulate organic matter (CPOM). Litter of lengths < 1 mm and > 0.5 mm were classified as fine particulate organic matter (FPOM). Ash-free dry mass (AFDM) was determined for all fragment sizes by drying in an oven at 58 °C for 7 hours followed by combustion at 550 °C for 5 hours.

6.4.2 Litter breakdown experiment

A decomposition experiment was undertaken within the Borrans reedswamp between 24th September 2012 and 19th November 2012. Litter bags were used to make comparisons between *P. australis* and *T. angustifolia* leaf litter decay and their associated macroinvertebrate assemblages. Living (green) leaf blade material (hereafter leaves) was collected from *T. angustifolia* and *P. australis* shoots located within the White Moss reedswamp on 30th July 2012 and air dried for a period of eight weeks. Lengths of dried leaves were standardised across species by removing and retaining the tips of the much longer *T. angustifolia* leaves. Breakdown resistant mimics of reed leaves were made from 0.76 mm thick 100% virgin polypropylene sheets produced commercially by Kimberley Clark as Kimtech® prep process wipes (‘Kimtech’ hereafter). Air dried whole leaves of *P. australis*, tips of *T. angustifolia* leaves, and Kimtech were divided into subsamples weighing

5.00 ± 0.33 grams. Single litter types (*i.e.* Kimtech, *P. australis*, or *T. angustifolia*) were placed into tetrahedral shaped litter bags. Bags with a mesh size of 1 cm (‘coarse mesh’ hereafter) were selected to allow macroinvertebrate colonisation and to retain the majority of leaf litter of lengths in excess of 1 cm. In addition, bags with apertures of 250 µm (‘fine mesh’ hereafter) were used in an attempt to exclude macroinvertebrates and thus assess microbially mediated breakdown processes. Fine mesh bags also retained the majority of solid leaf material throughout the duration of the experiment. In total, forty-five coarse and fifteen fine mesh bags were deployed, consisting of fifteen coarse bags per litter type and five fine bags per litter type. Five subsamples of *P. australis* and *T. angustifolia* were retained to estimate the AFDM of samples prior to immersion.

On 24th September 2012, all sixty litter bags were installed into the centre of the Borrans reedswamp (Figure 6.1d). Litter bags were arranged into bundles consisting of one bag each of *P. australis*, *T. angustifolia,* and Kimtech. Five replicate bundles were distributed linearly along transects at intervals of 0.1 m, weighed down by stones and placed on the lake bed. Five sets of bundles were placed in transects parallel to each other at a distance of 0.15 m. To facilitate pair-wise comparisons each bag was labelled sequentially along transects. One randomly selected set of coarse mesh bags (5 replicates of each litter type) was removed after 3, 21 and 56 days of immersion. All fine litter bags were retrieved after 56 days.

Following retrieval, litter was frozen and stored at -18 °C. Within one month of freezing, samples were thawed at room temperature, and then rinsed over a 250 µm sieve to remove loosely attached silt, sand and macroinvertebrates. Macroinvertebrates were identified immediately without further preservation. The majority of individuals were identified to species level. Chironomidae were identified to tribe and Oligochaeta to family level. Macroinvertebrates were enumerated and assigned to functional feeding groups (FFGs) using Tachet *et al*. (2000). Ash-free dry mass (AFDM) was determined for litter material and macroinvertebrates by drying in an oven at 58 ^{o}C followed by combustion at 550 ^{o}C. Refer to Chapter 4 for further details on the determination of AFDM.

6.4.3 Data analysis

The R programming language and associated statistical and graphical packages were used for data analysis.

6.4.3.1 Standing crop

Nonparametric hypothesis testing (Wilcoxon matched-pair test) was used to test for differences in shoot density and peak standing crop between the two reedswamps.

6.4.3.2 Decay within litter bags

Lines of best fit were drawn using exponential regressions of mass loss over time and used to calculate half-lives (T_{50}) for *P. australis* and *T. angustifolia*. Mass loss rate, k (day^{-1}) was estimated with the formula $k = ln2/T_{50}$ based on Olson's (1963) exponential model. Despite arcsine transformation, the mass loss data did not conform to normality, so the preferred test of Analysis of Covariance (ANCOVA) was not appropriate. Instead the non-parametric test, Wilcoxon matched-pair test was applied to identify inter- and intra-specific differences in mass loss.

6.4.3.3 Macroinvertebrate data

Bray Curtis dissimilarity indices (BC) were calculated for the taxonomic dataset using the vegan library in R (Oksanen *et al.*, 2012). Vegan was also used to investigate differences in BC across litter types, immersion times, and a combination of the two. Permutational multivariate analysis of variance (nested one-way PERMANOVA) via the Adonis command and ‘Strata’ function based on 1000 permutations was used to investigate the effects of litter type and immersion time on the means of BC (*sensu* Anderson, 2001). *Post hoc* tests were carried-out using Anosim (based on 999 permutations) to make pair-wise comparisons between the means of different litter types and different immersion periods. Furthermore, tests of equality of variance for BC between all sets of litter were performed using the ‘Betadisper’ command. Non-metric Multi-Dimensional Scaling (NMDS) using the ‘metaMDS’ command was used to illustrate differences in taxonomic composition.

Taxonomic data relating to macroinvertebrates were converted into Functional Feeding Groups (FFGs). A fuzzy coding approach (*cf*. Chevene *et al.*, 1994) was applied to establish a link between each taxon and its affinity to different FFGs. For example, the gastropod, *Physa fontinalis* L. has a greater affinity for scraping than shredding and so 75% of its abundance was allocated to scraper and 25% to shredder groups. Macroinvertebrate data were summarised by calculating biomass (AFDM), abundance, taxonomic richness and diversity. Simpson's Index of diversity (1-D) and Shannon Index (H) are widely used measures of diversity that take account of both abundance and evenness of the taxa present.

The assumptions necessary for applying RM ANOVA to macroinvertebrate data were tested using tests of normality and sphericity (*sensu* Chapter 4). Subsequently, macroinvertebrate data relating to coarse mesh bags was Log_{10} (x + 1) transformed. Overall differences across all three types of litter for the means of transformed macroinvertebrate responses (AFDM, abundance, S, 1-D, and H) were tested using one-way repeated measures ANOVA (RM ANOVA) with time as a random factor. Significant differences were investigated using the *post hoc* test Tukey's HSD to identify differences between pairs of samples across litter types and immersion times. The fine mesh bag data did not conform to normality, so Wilcoxon matched-pair tests were used to identify differences within datasets that included fine mesh data.

6.5 Results

6.5.1 Estimates of reed standing crops

Borrans was a monospecific stand of *P. australis*, whereas 70% of reed shoots at White Moss were *P. australis* and 30% were *T. angustifolia*. There were no significant differences in total shoot density and total peak standing crop between the two reedswamps (Table 6.1). During October, differences in detrital standing crop between the reedswamps for CPOM or FPOM were lacking. The only significant change in detrital standing crop over time (p = 0.04) was an increase in CPOM at White Moss. This resulted in a significantly higher biomass of CPOM at White Moss (*p* = 0.02) compared to Borrans during March (Figure 6.2).

Table 6.1 This table demonstrates the contribution of individual reed species to mean (± 1 SD) total shoot density and peak standing crop at Borrans and White Moss reedswamps; *p* values represent the significance of differences between the two reedswamps using non-parametric testing. (*T. ang* = *T. angustifolia, P. aust* = *P. australis*)

	Shoot density (m^{-2})			Peak Standing Crop (Dry Mass g m^{-2})		
	P. aust	***T. angust***	**Total**	***P. aust***	***T. angust***	**Total**
Borrans	62 (21.68)	0	62 (21.68)	459.42 (160.64)	0	459.42 (160.64)
White Moss	38.00 (14.70)	16.00 (20.60)	54 (13.56)	281.58 (108.9)	178.56 (229.80)	460.14 (184.19)
p-value			1.00			0.05

6.5.2 Litter mass over time

The estimated mass loss rate (*k*) for *P. australis* was 1.2 times greater than that estimated for *T. angustifolia* (Figure 6.3, Table 6.2). Within coarse mesh litter bags, the percentage loss in *P. australis* leaf litter AFDM at 21 days immersion was significantly higher than *T. angustifolia* loss over the same period. However, there were no significant differences at 3 or 56 days. Furthermore, *P. australis* leaves within coarse mesh bags at 56 days lost 1.6 times more AFDM than within the corresponding fine bags (Figure 6.4; Table 6.3). In comparison, the average AFDM loss for *T. angustifolia* leaves at 56

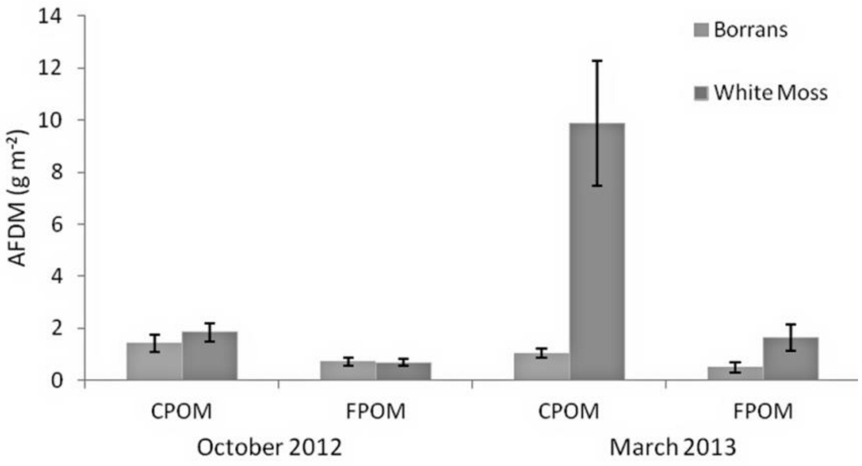


Figure 6.2 This graph illustrates differences in means (± 1 SD) for size based fractions of detritus between Borrans and White Moss reedswamps over time. (CPOM = Coarse Particulate Organic Matter [length ≥1 mm]; FPOM = Fine Particulate Organic Matter [length 0.5–1 mm] [*sensu* Cummins, 1974])

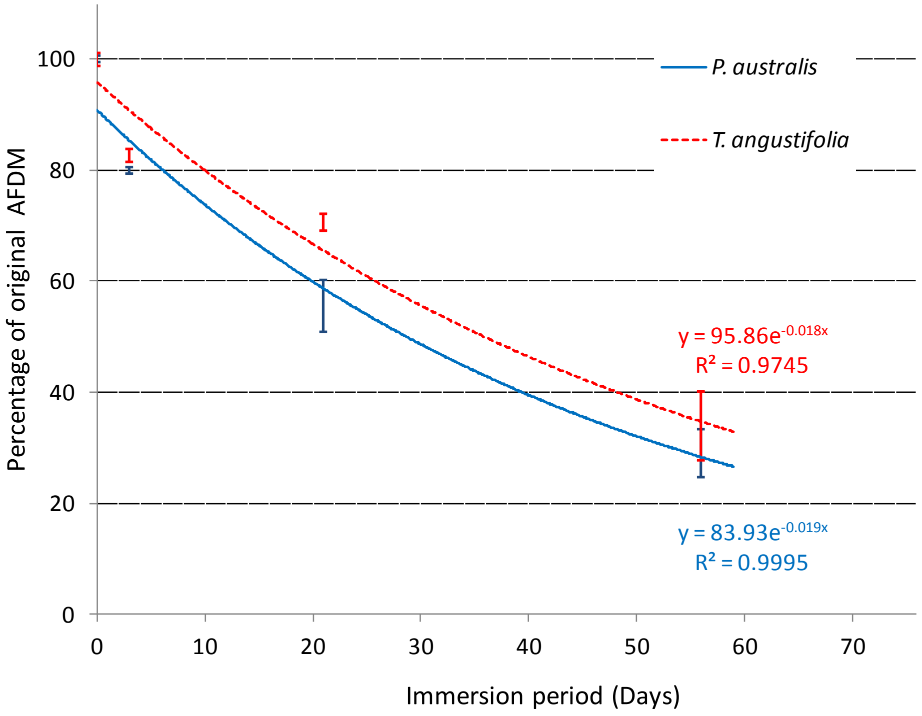


Figure 6.3 This illustration of exponential regression represents the decay of *P. austrailis* and *T. angustifolia* leaf litter within coarse mesh litter bags. Immersion period relates to the number of days that elapsed following litter bag installation. Bars represent standard error (1 SE) for the percentage of AFDM remaining after immersion. (Blue = *P. australis,* Red = *T. angustifolia*)

Table 6.2 This is a comparison of percentage change in mass (± 1 SE) and associated descriptors that highlight differences in decay between sets of substrates within coarse mesh litter bags. Reed data is based upon AFDM and Kimtech DM.

	3 days (coarse)	21 days (coarse)	56 days (coarse)	56 days (fine)	Half-life (days)	Mass Loss rate, *k* (day^{-1})
P. australis	-20.0 ± 3.2	-44.5 ± 18.6	-71.0 ± 3.5	-45.4 ± 3.5	30	0.023
T. angustifolia	-17.4 ± 3.5	-29.3 ± 5.4	-66.1 ± 21.6	-35.9 ± 5.7	37	0.019
Kimtech	-	-	0.274 ± 0.12	0.076 ± 0.072	-	-

Table 6.3 Wilcoxon matched-pair test hypothesis testing was used to investigate differences in percentage change in AFDM between sets of litter bags for all three immersion periods. Litter bags containing *P. australis* or *T. angustifolia* were compared by mesh size, immersion period, and reed species; C and F indicate coarse mesh and fine mesh bags, respectively. Where there were significant differences, the variable with the greatest mass loss is underlined.

	W	*P*
Post 3 days immersion		
P. australis (C) vs *T. angustifolia* (C)	20	0.152
Post 21 days immersion		
<u>*P. australis* (C)</u> vs *T. angustifolia* (C)	25	0.008
Post 56 days immersion		
P. australis (C) vs *T. angustifolia* (C)	16	0.548
<u>*P. australis* (F)</u> vs *T. angustifolia* (F)	25	0.008
P. australis (F) vs <u>*P. australis* (C)</u>	0	0.008
T. angustifolia (F) vs <u>*T. angustifolia* (C)</u>	0	0.008
Kimtech (F) vs <u>Kimtech (C)</u>	25	0.008

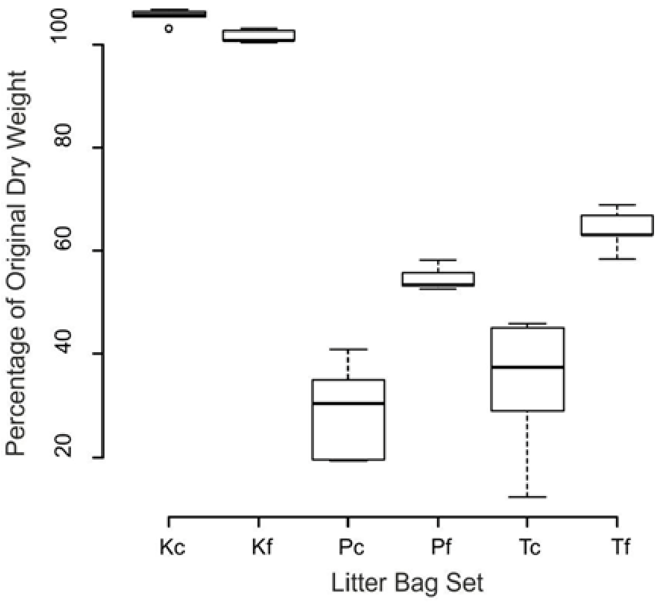


Figure 6.4 This box plot illustrates the percentage of original DM lost after 56 days immersion by litter type and litter bag mesh size. (K = Kimtech, P = *P. australis,* T = *T. angustifolia,* c = coarse mesh bags, and f = fine mesh bags)

days within coarse mesh bags was 1.8 times greater than in the corresponding fine mesh bags.

6.5.3 Macroinvertebrates

6.6.3.1 Analysis of community structure

Nineteen taxa belonging to seven FFGs were found (Appendix A2). No single taxon was present across all twelve sets of litter bags. Following the initial period of immersion (three days) the shredder *Crangonyx* was present within all sets of bags. Across litter types and immersion periods, shredder was the dominant FFG within the majority of bags, mainly due to the dominance of *Crangonyx*. The majority of fine bags were colonised by small macroinvertebrates due to deterioration of bag seals. Key differences between coarse and fine mesh bags were that taxon richness was lower, and shredder abundance was higher within fine mesh bags (Appendix A2, Figure 6.5, Table 6.4).

For coarse mesh litter bags, RM-ANOVA suggested that there were no significant differences across litter types for total abundance, total AFDM, contribution of shredders to AFDM, Simpson’s Index, and Shannon Index (Figure 6.6). However, there were significant differences across litter types for number of taxa ($p < 0.04$) and number of FFGs ($p < 0.03$). Tukey’s HSD *post hoc* test indicated that there were no significant differences between *T. angustifolia* and *P. australis* for both taxon richness and number of FFGs (Table 6.5). Taxon richness and the number of FFGs were significantly higher in *Phragmites* litter compared to Kimtech. For *Typha*, only FFGs were higher compared to Kimtech.

Table 6.4 Differences in macroinvertebrate net migration for coarse (5) and fine mesh bags (5) for each substrate after 56 days immersion is demonstrated.

	P. australis	*T. angustifolia*	Kimtech
Coarse bags (56 days)			
No. bags with macroinvertebrates	5	5	5
Total abundance per bag	4–12	2–9	3–35
Fine bags (56 days)			
No. bags with macroinvertebrates	4	2	3
Total abundance per bag	0–61	0–43	0–38

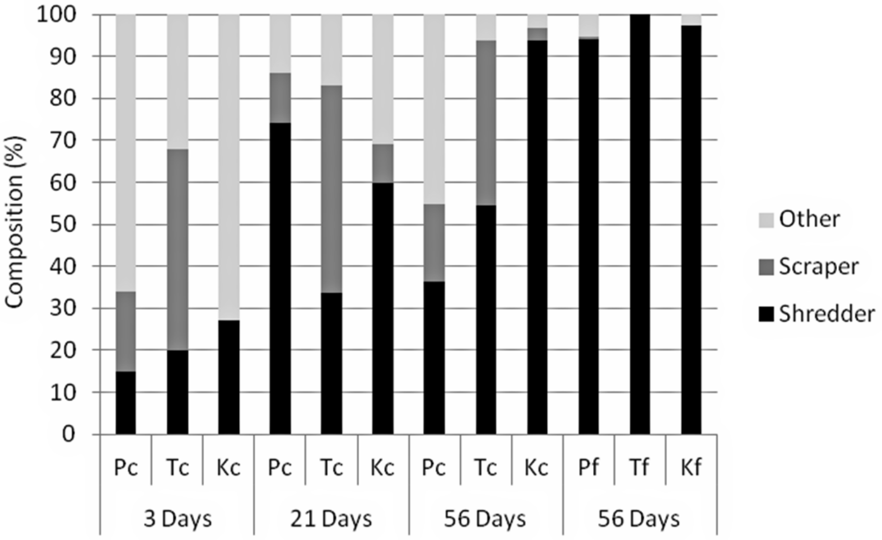


Figure 6.5 This graph illustrates differences in the relative contribution of shredders and scrapers to total abundance for each set of litter bags by immersion period, litter type, and litter bag design. (P = *P. australis* leaves, T= *T. angustifolia* leaves, K = Kimtech cut into leaf shapes, c = coarse mesh bags, f = fine mesh bags)

Table 6.5 Pair-wise comparisons of transformed taxon richness data (Log$_{10}$ [S + 1]) and number of FFGs (Log$_{10}$ [FFG + 1]) for coarse litter bags using Tukey's HSD test are demonstrated. Where there are significant differences ($p < 0.05$), the variable with the greatest value is underlined.

	Difference	**Lower**	**Upper**	***p***
Log$_{10}$ (S + 1)				
P. australis vs T. angustifolia	-0.133	-0.308	0.041	0.164
P. australis vs Kimtech	0.267	0.093	0.442	0.002
T. angustifolia vs Kimtech	0.134	-0.040	0.309	0.160
Log$_{10}$ (FFG + 1)				
P. australis vs T. angustifolia	-0.005	-1.121	0.110	0.993
P. australis vs Kimtech	0.286	0.170	0.402	0.001
T. angustifolia vs Kimtech	0.281	0.165	0.397	0.001

6.6.3.2 Dissimilarity data

The effects of litter type and immersion time within coarse mesh bags upon BC were significant (PERMANOVA, $p = 0.001$). Pair-wise comparisons using Anosim indicated that for each reed species there were significant differences between immersion times (Table 6.6). However, for Kimtech there were no significant differences between immersion periods. At each immersion time there were significant differences between all three litter types. Parametric analysis of variance (Betadisper) of BC data based upon taxonomic composition indicated that there were no significant differences in variance between any of the litter bag sets. Pair-wise comparisons using Anosim detected a number of differences between fine mesh and coarse mesh litter bags for each litter type (Table 6.7). The communities associated with *P. australis* within fine mesh bags at 56 days immersion were significantly dissimilar to coarse bags at 3 and 56 days, but not 21 days. For *T. angustifolia*, fine mesh bag communities were not significantly different to the corresponding coarse mesh bags at 3, 21, and 56 days immersion. The fine bag communities associated with Kimtech, only differed from those in the coarse bags at 3 days immersion. NMDS ordination indicated that communities within sets of *T. angustifolia* (based upon immersion periods) were distinct from each other and from the other litter sets (Figure 6.7). At 21 days immersion, community composition within *P. australis* was distinct to that at 3 and 56 days, which were grouped together. The communities of Kimtech at 21 and 56 days immersion periods were similar. However, Kimtech at day 3 was excluded from the NMDS plot due to insufficient data.

Overall, R statistics (Anosim) for Kimtech at different immersion periods were relatively low ($R < 0.12$), which indicated a high level of variation in similarity within sets of Kimtech at different immersion periods compared to reed litter. When all of the sets of coarse mesh bags were arranged by immersion times only and litter type only, there were considerable overlaps in ellipses (Figure 6.7).

6.6.3.3 Relationship between shredder, scrapers, and litter decay

Abundance per gram of litter (hereafter density) was significantly higher for shredders compared to scrapers for *P. australis* ($p = 0.006$) and Kimtech ($p = 0.002$). However, within *T. angustifolia* there was no significant difference ($p = 0.45$) in abundance between the two FFGs. Trends in shredder density were significantly different for all three litter types (Figure 6.8). Shredder density reached an peak at 21 days within *P. australis*, reached a plateau after 21 days within *T. angustifolia,* and only increased within Kimtech after 56 days. For scraper density, changes within the reed material followed similar trends to that of shredders. However, for *P. australis* the decline in scrapers after 21 days was less marked than that observed for shredders. For all immersion periods, there were no significant differences in scraper density between the two reed species, but both exhibited higher density than did Kimtech (Figure 6.8).

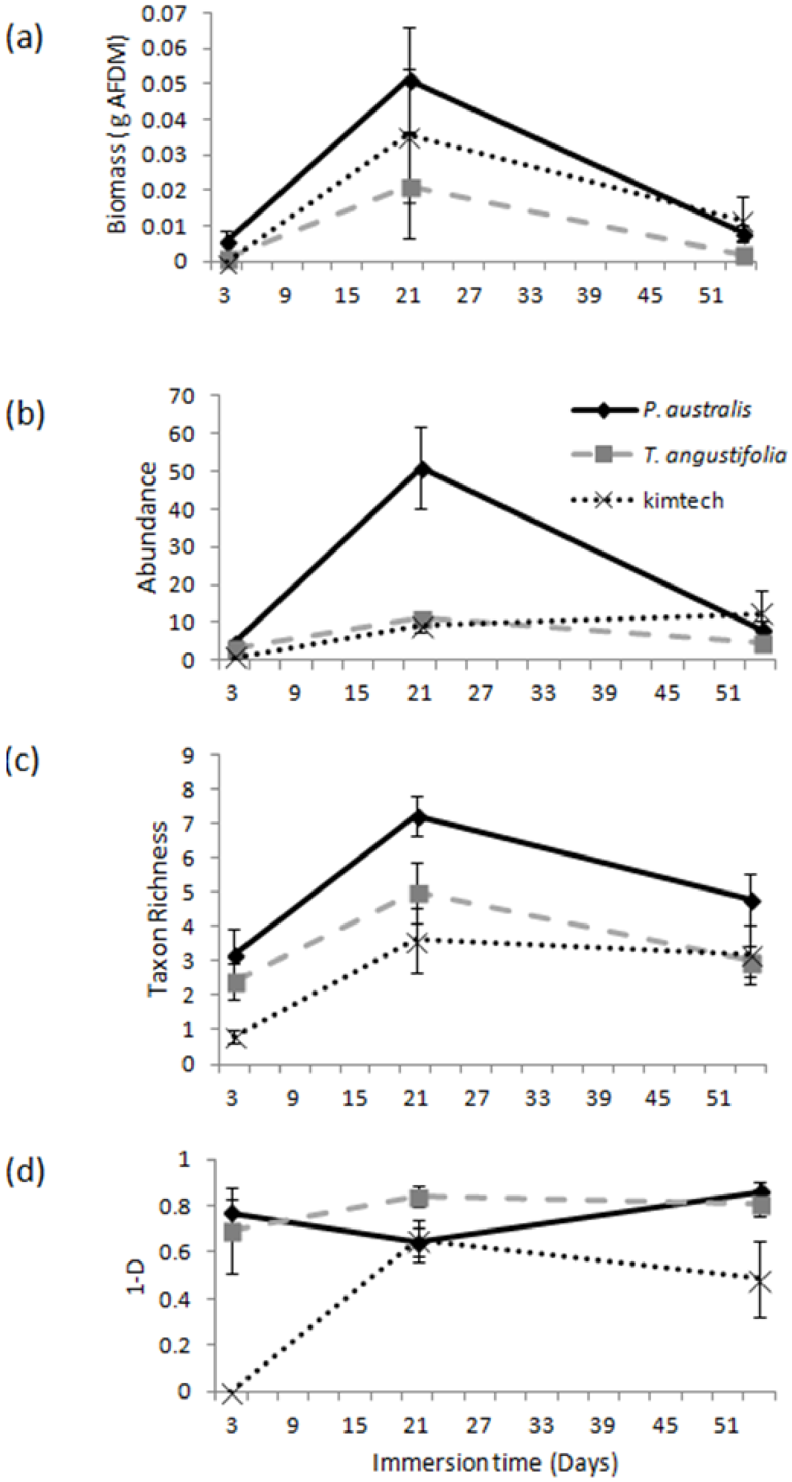


Figure 6.6 These graphs demonstrate variations in mean (± 1 SE) macroinvertebrate variables across different immersion times. Data are presented for (a) total macroinvertebrate biomass for coarse litter bags, (b) total abundance, (c) taxa richness, and (d) Simpson's Index (1-D).

Table 6.6 The results of pair-wise analysis of similarities (Anosim) based on 99 permutations for coarse litter bags based on Bray Curtis dissimilarities are demonstrated.

	R	*p*
P. australis		
3 vs 21 days	0.968	0.008
3 vs 56 days	0.760	0.006
21 vs 56 days	1.000	0.011
T. angustifolia		
3 vs 21 days	0.630	0.008
3 vs 56 days	0.642	0.012
21 vs 56 days	0.700	0.010
Kimtech		
3 vs 21 days	-0.209	0.726
3 vs 56 days	-0.154	0.718
21 vs 56 days	0.132	0.066
3 days immersion		
P. australis vs *T. angustifolia*	0.682	0.006
P. australis vs Kimtech	0.554	0.146
T. angustifolia vs Kimtech	0.909	0.048
21 days immersion		
P. australis vs *T. angustifolia*	0.786	0.007
P. australis vs Kimtech	0.670	0.012
T. angustifolia vs Kimtech	0.810	0.011
56 days immersion		
P. australis vs *T. angustifolia*	0.440	0.022
P. australis vs Kimtech	0.584	0.017
T. angustifolia vs Kimtech	0.670	0.020

Table 6.7 The results of Anosim pair-wise comparisons (means) comparing Bray Curtis dissimilarity for fine bags at 56 days to coarse mesh bags at different periods of immersion are demonstrated.

	R	*p*
Phragmites australis		
3 days	0.981	0.013
21 days	0.319	0.069
56 days	1.000	0.010
Typha angustifolia		
3 days	0.065	0.370
21 days	0.037	0.390
56 days	0.398	0.118
Kimtech		
3 days	0.889	0.032
21 days	0.062	0.326
56 days	-0.145	0.899

6.6 Discussion

Previous studies of the ecological significance of reed litter decay have focused mainly on the aquatic phase of decay in isolation (Mason and Bryant, 1975b; Brinson *et al.*, 1981; Polunin, 1984; Gessner, 2000). By investigating reed litter characteristics and their influence upon macroinvertebrates, this study found that interspecific differences in litter deposition and the physical structure of reed tissue had a strong influence upon key ecological processes (*e.g.*, decomposition). This suggests that models of reedswamp functioning need to include information on reed species composition. A novel aspect of this study was the investigation of

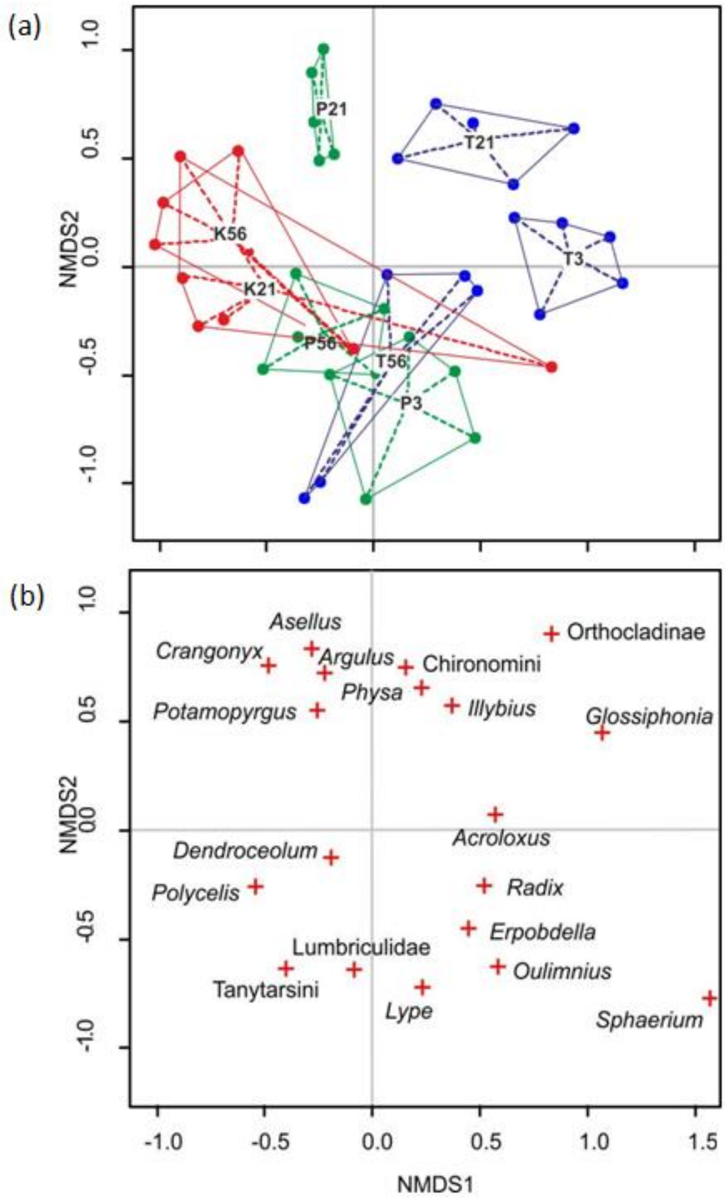


Figure 6.7 The associations between individual taxa and a combination of immersion time and substrate type for coarse litter bags are demonstrated by this NMDS plot which was based upon a Bray Curtis dissimilarity matrix. Panel (a) demonstrates relative positions of litter bags, ellipses are drawn around data with a common immersion time and litter type: P = *P. australis*, T = *T. angustifolia*, K = Kimtech, 21–56 = immersion periods (days), Red = Kimtech, blue = *T. angustifolia*, and green dots = *P. australis.* Panel (b) demonstrates relative positions of taxa (taxonomic and FFG details, Appendix A2). Kimtech at day 3 is omitted because an in sufficient number of bags were colonised.

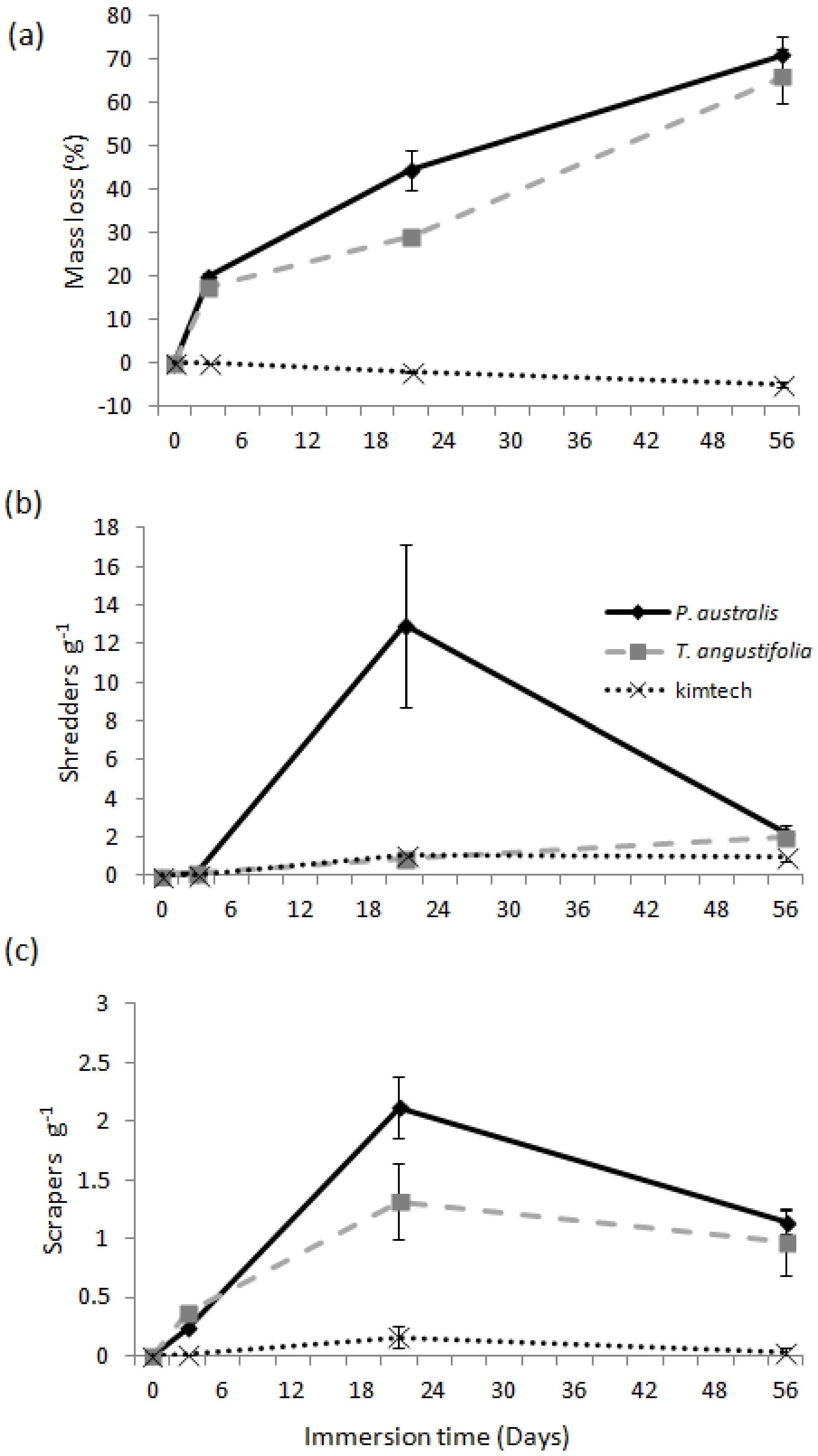


Figure 6.8 These graphs illustrate changes in mean (± 1 SE) values over time for (a) percentage substrate mass loss and associated changes in net colonisation of (b) shredders and (c) scrapers.

interspecific differences in litter deposition and its influence upon macroinvertebrate seasonal dynamics. Furthermore, the relative importance of reed litter as refuge versus as a food resource was investigated. Herein the discussion considers the underlying reasons for the following: (1) interspecific differences in detritus dynamics, (2) interspecific differences in decay and associated macroinvertebrate responses, and (3) the importance of reed detritus for macroinvertebrates. Finally, the implications for future research into reedswamp function are discussed.

6.6.1 Interspecific differences in detritus dynamics

This study has provided strong evidence that differences in the relative dominance of reed species between beds drives detritus dynamics in littoral reedswamps. Mason and Bryant (1975b) estimated that the standing crop for a single shoot of *T. angustifolia* was 1.56 times greater than for *P. australis* within the same lake. Hence, it was hypothesised (H_1) that differences in reed detrital standing crop would be linked to differences in reed community composition. Field-based observations supported this hypothesis, but not some of the underpinning reasons. Differences in reed community composition between White Moss and Borrans reedswamps were not sufficient to generate the expected difference in peak shoot standing crop. However, a slight increase in *T. angustifolia* dominance at White Moss would have produced a significantly higher peak shoot standing crop compared to Borrans (*P. australis* only). For estimates of shoot standing crop, standard deviations were large compared to the means. Unfortunately, accurate estimates of shoot biomass are difficult to obtain. This is due to wide ranging inter- and intra-specific variations in growth rates, and the timing and magnitude of maximum biomass within and between reedswamps (Haslam, 1971b; Dykyjová and Hradecká, 1973; Ho, 1980; Kuehn and White, 1999). However, estimating peak biomass based on published data is a time efficient and cost effective way of estimating the relative contributions of each species to peak shoot standing crop.

Interpretation of the detritus sample data focused upon variations in CPOM. In contrast to FPOM, the constituents of CPOM are readily separated into reed and non-reed material. Hence, CPOM provides a more accurate estimate of the contribution of reeds to detrital standing crop. Due to the ability of reedswamps to retain particulate organic matter, it is likely that a significant proportion of FPOM was derived from the long-term (>1 year) decay of CPOM within the aquatic phase. A lack of spatial (between reedswamps) and temporal variation in FPOM provided additional justification for focussing upon CPOM data. Division of CPOM into species and reed organs (*e.g.,* leaf sheaths, shoots, *etc.*) would have provided useful information regarding litter decay (Hietz, 1992; Gessner, 2000); however, this process would have been technically difficult and time consuming, and the results would have lacked statistical confidence.

Following the onset of senescence, differences in CPOM mass between reedswamps became significant. It had been hypothesised (H_1) that a combination of shoot senescence and winter weather conditions would drive an increase in reed CPOM at both reedswamps (Polunin, 1984; Findlay *et al.*, 2002). The predicted increase occurred within the mixed (White Moss) reedswamp but not within mono-specific stand of *P. australis* (Borrans). It is likely that the influence of *T. angustifolia* at White Moss was responsible for this differential response. Data from the litter bag experiment indicated that *P. australis* and *T. angustifolia* decay rates would not have been significantly different over the period of detritus collection (five months). This suggests that differences in 'detrital' standing crop dynamics were driven by factors other than interspecific differences in 'shoot' standing crop and aquatic decay rates. For example, interspecific differences in the physical structures of erect shoots may have driven differences in detritus formation (Fiala, 1973; Ho, 1980; Komínková *et al.*, 2000).

Shoot morphologies of *P. australis* and *T. angustifolia* are very different (Grace and Harrison, 1986; Lansdown, 2009; Haslam, 2010). The shoots of *P. australis* consist of mainly cane-like breakdown resistant stems with paper-like leaves that only represent approximately 6.5% of the total dry weight for the whole shoot (Dvořák, 1996). In contrast, leaves of *T. angustifolia* have a spongy texture and are typically much longer (>1 m) and more numerous than *P. australis* leaves. The vegetative stems of *T. angustifolia* are not as structurally distinct to the rest of the shoot as with *P. australis* and consist of tightly packed leaves. Following senescence, the shoots of *P. australis* and *T. angustifolia* can persist for up to 2 years, during this time loss of material from the erect shoots is partial before they collapse fully (Fiala, 1973; Komínková *et al.*, 2000). Examination of dead *in situ* reed shoots and litter detritus during March 2013 suggested that it was mainly whole leaves of *P. australis* that had entered the water, while it is likely that most *T. angustifolia* litter had entered the water as leaf fragments. At White

Moss during March 2013, intact *P. australis* stems were common but stems with one or more leaves were rare. In contrast, the upper portions (at least one third) of most *T. angustifolia* shoots were absent.

There is some published evidence that the shedding of leaves from ‘living’ shoots has a significant impact upon detritus load. Ho (1980) found that within a Scottish loch, the shedding of leaves from *P. australis* shoots gradually increased from April to a peak in June/July. Data from the Borrans reedswamp indicated that the mass of *P. australis* entering the base of the reedswamp was similar during the summer and the winter months. Little has been published on the leaf fall dynamics of common reedswamp forming macrophytes such as *T. angustifolia*. Therefore, this study provides novel data on the influence of reed community structure upon seasonal changes in detritus loading within reedswamps and their contribution to key ecological processes at the whole lake scale. Data from this investigation indicates that there was a prolonged release of organic matter from *P. australis*, whereas the majority of *T. angustifolia* mass was shed over the winter months. There are also interspecific differences in timing of key events such as peak shoot density and onset of senescence (Mason and Bryant, 1975b). In a seasonal context these are broadly similar. Whereas, the structures of *P. australis* and *T. angustifolia* shoots (living and dead) are distinct (Lansdown, 2009). It can be concluded that detritus dynamics with the study area were driven mainly by differences in the ways in which living reed material was converted into detritus.

6.6.2 Interspecific differences in decay and associated macroinvertebrate responses

Initial rates of rapid mass loss (leaching) for both reed species were not significantly different from each other and were both consistent with published values (Planter, 1970; Howard-Williams, 1979; Polunin, 1982; van Dokkum *et al.*, 2002). However, comparing mass loss rates (*k*) with published values was problematic. Firstly, *P. australis* decay has received considerably more attention than *T. angustifolia*, and interspecific comparisons within the same reedswamp are rare. Secondly, published values of *k* for *P. australis* are wide ranging. This is related to variations in experimental design (*e.g.,* timing and duration of the experiment, and litter bag design) and prevailing environment conditions (*e.g.,* salinity, temperature, and reedswamp size and structure). Unfortunately, detailed descriptions of important environmental factors are often lacking (Polunin, 1984). Findlay *et al.* (2002) found that within a tidal marsh in the USA, *T. angustifolia* and *P. australis* litter decomposed at the same rate. However, Mason and Bryant (1975b) used regressions of mass loss to show that within a lacustrine reedswamp in southeast England, *P. australis* decomposed at a faster rate. Regressions of the Borrans litter bag data also indicated that *P. australis* decomposed faster than *T. angustifolia*. However, at the end of the experiment (56 days immersion) there was no significant difference in mass loss between reed species. It is important to note that the short lived interspecific difference in mass loss at 21 days may still be functionally significant. The relationship between macroinvertebrate responses and litter mass loss were used to investigate the functional significance of differences in mass loss between reed species.

Macroinvertebrates influence litter decomposition by: (1) breaking down litter during ingestion by shredding or scraping; (2) influencing particle production and mineralisation via digestion; and (3) regulating microbial activity by ingestion and digestion of detritus (Mason and Bryant, 1975b; Polunin, 1982; Polunin, 1984). The influence of different macroinvertebrate taxa on the decay of reed litter in the lentic freshwater environment is highly variable (Mason and Bryant, 1975b; Polunin, 1982). Even within shredders there is considerable variation in the ways macroinvertebrates influence breakdown. For example, *Limnephilus marmoratus* cut reed leaf litter, whereas *Crangonyx pseudogracilis* influence breakdown by the removal of veins and fibres at the broken ends of leaves (Mason and Bryant, 1975b; Polunin, 1982). Hence, the rate of decomposition of leaf litter is influenced strongly by the taxonomic structure of macroinvertebrate communities (Mason and Bryant, 1975b; Carpenter and Adams, 1979; Bärlocher, 1990).

The influence of macroinvertebrates upon the decay of both species of reed was demonstrated by the litter bag experiment. Compared to coarse litter bags, leaf litter decay in fine mesh bags for both reed species was slowed by approximately 35 days. This is likely to be an underestimate because fine mesh litter bags only partially restricted the access of macroinvertebrates to reed litter. Bedford (2004) suggested that fine mesh litter bags are particularly susceptible to contamination by Chironomidae and other small invertebrates. However, for the current investigation, net colonisation by chironomids for all litter types and bag designs was low compared to those of the dominant taxa (*Crangonyx pseudogracilis* and *Asellus aquatica)*. This suggests that contamination was due to damage or deterioration of the bags (*e.g*., the seals), rather than a failure of the intact mesh to exclude smaller invertebrates. Furthermore, the tribes of Chironomidae found within fine mesh bag were predominately deposit feeders, and not shredders or grazers. Litter mass loss data suggests that significant contamination by detritivores (mainly shredders) occurred relatively near to the end of the 56 days immersion period, as it did not appear to have a strong influence upon the results of this experiment. The inclusion of additional immersion periods for reed detritus within fine mesh bags (*e.g.,* 21 days) would have been beneficial in the assessment of macroinvertebrate exclusion and associated differences in reed decay.

The hypothesis (H_2) that changes in macroinvertebrate communities would be related to changes in reed litter mass loss was upheld. The timing of the divergence in mass loss (21 days) coincided with the most striking difference in macroinvertebrate response between *T. angustifolia* and *P. australis*. At 21 days, *P. australis* supported much higher numbers of macroinvertebrates compared to *T. angustifolia*. The majority of these invertebrates were shredders. However, in the context of all immersion periods the response of macroinvertebrate communities to mass loss were not as wide ranging as expected. For example, interspecific differences in detrital decay were not strongly related to differences in total macroinvertebrate biomass, species richness, number of FFGs, alpha diversity, number of scrapers, or taxonomic dissimilarity. In contrast, analysis of Bray Curtis dissimilarity data indicated that there was significant taxonomic beta diversity across the three litter types at each individual immersion time. Furthermore, each litter type demonstrated significant temporal changes in dissimilarity over time. This is an important finding because it suggests that mixtures of *T. angustifolia* and *P. australis* litter would support greater taxon diversity than monocultures of each species. Outside of the enclosed litter bag environment, shredder numbers may be more consistent due to the constant input of fresh *P. australis* detritus as indicted by the detritus sampling data. Comparing the colonisation dynamics of litter with published data was problematic due to wide variations between and within individual reedswamps (Mason and Bryant, 1975b; Polunin, 1982; Polunin, 1984; van Dokkum *et al.*, 2002) and across lakes (Danell and Andersson, 1982).

6.6.3 Detritus: food versus refuge

It has been suggested that the role of detritivores within reedswamps may be enhanced by the provision of refuge from predators by reed detritus (Lewin *et al.*, 2004; Okun and Mehner, 2005; Mancinelli *et al.*, 2007). However, the relative importance of reed detritus as a habitat rather than a food source has received little attention. The low numbers of detritivores within Kimtech compared to organic reed material supported the hypothesis (H_3) that provision of refuge exerts less of an influence than food. Differences in FFGs between *Phragmites* and *Typha* at 21 days immersion was further evidence of the relative importance of reed litter as food resource. This was collaborated by the findings of Mason and Bryant (1975b).

The peak and subsequent decline in shredder and scraper densities within *P. australis* indicates that its value as a food source is relatively short lived. Differences in shredder and scraper responses between *T. angustifolia* and *P. australis* indicated possible functionally significant differences in leaf litter tissue structure. Differences in shredder numbers indicated that *T. angustifolia* is relatively resistant to shearing forces, whereas both reeds responded similarly to rasping forces (*e.g.,* scrapers). These qualities are compatible with the differences in litter shedding dynamics discussed earlier in this chapter. The ability of *P. australis* to provide food for shredders is relatively short lived but fresh detritus continuously enters the system. In contrast, the majority of *T. angustifolia* litter enters the reedswamp at the same time (winter) and retains is ability to provide food for longer.

6.7 Summary

The ways in which reeds interact with the broader reedswamp environment has received little attention. In particular, little is known regarding the influence of seasonal changes in reed detritus production upon aquatic macroinvertebrate communities. A field-based experiment along with surveys of reeds and associated detritus was used to investigate the influence of two common reedswamp forming species upon aquatic detritivores. The timing and magnitude of litter production combined with the ability of detritus to resist macroinvertebrate shredding and scraping appear to be important factors in driving macroinvertebrate community assembly. By providing a mechanistic understanding of the influence of reed litter on macroinvertebrates this chapter facilitates future research into the consequences of changes in reedswamp habitat for whole lake functioning. Furthermore, it highlights the importance of seasonal variations in key processes (*e.g.*, decomposition).

There is an important distinction between the litter bag environment and the natural environment. Litter bags exclude inputs of fresh detritus and retain the majority of CPOM; within reedswamps the distribution of detritus is both patchy and dynamic due to a number of factors (*e.g.*, wind and wave action) (Mason and Bryant, 1975b; Pieczyńska, 1993). Also, natural detrital deposits may not be monocultures of single reed species and usually contain some allochthonous litter. Furthermore, the influence of detritus upon detritivores is determined by biotic (*e.g.*, predation) and abiotic (*e.g.*, dissolved oxygen) factors associated with spatial and temporal variations within reedswamps (Polunin, 1984). Chapters 4 and 5 subsequently relate seasonal and temporal variations in macroinvertebrate communities (including benthic detritivores) to differences in reed community composition and other environmental gradients (*e.g.*, across ecotones).

CHAPTER 7 Research synthesis, wider implications and future opportunities

7.1 Research synthesis

This thesis examined historic and contemporary changes in reedswamp wetland and the likely consequences for aquatic macroinvertebrate communities within Windermere, England's largest lake. The primary goals of the research were to relate changes in the intensity of multiple potential stressors to a long-term decline in reedswamp habitat, and to assess the influence of changes in the structure and coverage of reedswamp habitat upon macroinvertebrates and their contribution to key ecological processes.

Notably, this research demonstrated that identifying the principal reasons for reedswamp loss requires the integration of data relating to changes in reed genetics and environmental conditions (*e.g.,* hydro-meteorological, physicochemical, and mechanical factors) that occur throughout the lake. A lack of data for seasonal variations in physicochemical conditions within littoral zone sediments, and an absence of information on the physiological characteristics of Windermere biotypes prevented a robust assessment of the causes of reedbed loss. Furthermore, there were a number of key limitations with the chemical dataset. Firstly, trends in physicochemical determinants were based solely upon aqueous phase data collected at the surface of the pelagic zone. Secondly, sampling frequency was limited to fortnightly collection, and may have missed important environmental changes (*e.g.*, early frosts). Finally, comprehensive long-term datasets for non-nutrient pollutants (*e.g.,* metals, persistent organic compounds, and petroleum derived compounds) were lacking. There were also limitations with the physical dataset. Much of this data was qualitative, and only reflected general trends. For example, estimated increases in the numbers of Canada Geese were used to imply that grazing pressure had increased. However, despite these limitations in the dataset, a number of potential stressors for reedbeds at the whole lake scale are likely to have increased in intensity over recent decades. Potentially important changes include increases in: lake level, water and air temperature, grazing pressure, and boating activity. Furthermore, changes in reedswamp habitat are likely to have significant biological and functional consequences for the littoral zone, which can be effectively assessed by analysing spatiotemporal variations in macroinvertebrate assemblages.

More specific key findings in relation to individual aims can be summarised as follows:

Aim/Objective 1: to identify possible stressors and key gaps in knowledge for reedbed loss and its consequences for water quality within Windermere

Phragmites australis has been, and continues to be the dominant species of reed within Windermere. As early as 1920, there was steady decline in the ability of this cosmopolitan species to withstand change. Based upon general trends in multiple factors, key stressors are likely to include one or more of the following: (1) impoundment by a weir; (2) shoreline development; (3) proliferation of alien invasive species (*e.g.,* Canada Geese); and (4) physical disturbance by humans (*e.g.,* boating and trampling of marginal vegetation). Robust assessment of the causes and consequences of reedbed loss would require detailed research into the physicochemical characteristics of littoral zone sediments throughout Windermere. In addition, there is a clear need to quantify the environmental tolerances and ecological requirements of Windermere’s *Phragmites* biotypes.

Aim/Objective 2: to assess the contribution of reedswamp habitat to macroinvertebrate biodiversity within lakes

At the local scale (~8 m), spatial variations in the physical structural of littoral zone habitat had a strong influence upon macroinvertebrate species composition. While structurally distinct patches (mesohabitats) had similar values of alpha biodiversity, and species richness the cumulative effect of different mesohabitats to total biodiversity was significant. However, within individual reedswamps structural variation had a relatively small influence on biodiversity. In contrast, the distance by which a reedswamp extended along its ecotonal axis (*i.e.* towards the centre of lake) had a strong influence on diversity. Furthermore, differential responses to seasonal conditions across the ecotone underpinned differences in community composition, and made important contributions to biodiversity. The strong influence of reedswamp length across the ecotonal axis explained why macroinvertebrate species composition at the centre of two structurally distinct reedswamps located within different lakes was relatively similar (compared to differences between other categories of mesohabitat types across lakes).

Aim/Objective 3: to assess the potential of multiple traits as a tool for inferring the influence of reedswamp habitat upon the processing of organic matter by macroinvertebrates

Analysis of multiple traits provided a mechanistic understanding of the ways in which reedswamp habitat influences spatiotemporal variations in the processing of organic matter by macroinvertebrates. This approach identified the features of reedswamps (size, shape, and structural heterogeneity) responsible for the generation of environmental filters which act upon the composition of functional feeding groups (*sensu* Poff, 1997). Important filters included the distributions of various categories of organic matter that act as food resources (*e.g.,* reed litter, and epiphytes) across the ecotone. Other important filters were variations in the provision of shelter and refuge across the ecotone, which influenced the different ways in which organic matter was processed by macroinvertebrates. A key finding was that ecotonal position determined the response of macroinvertebrates to seasonal changes, and that this was associated with spatial differences in the processing of organic matter over a yearly cycle.

Aim/Objective 4: to investigate the ecological significance of interspecific differences in leaf litter

Macroinvertebrates play a vital role in the decomposition of reed litter within the aquatic environment. Furthermore, reed leaf litter influences macroinvertebrates by providing food rather than refuge. There were differences in the community composition of macroinvertebrate assemblages associated with the litter of two common reedswamp forming species, *Typha* *angustifolia* and *P. australis.* This was underpinned by differences in standing crop, litter deposition dynamics, and litter structure. These findings suggest that models of ecosystem functioning may also benefit from the quantification of spatial variations in the seasonal dynamics of macroalgae, epiphyton, phytoplankton, fungi, bacteria, and archaea assemblages.

Aim/Objective 5: to recommend a conceptual outline for investigating spatiotemporal variations in macroinvertebrate assemblages within the littoral zone

A comprehensive review of published macroinvertebrate sample and survey techniques within the littoral zone identified the need for a standardised approach to surveying. The requirements for sampling within reedswamp habitat include: (1) collection of samples representative of key niches, (2) rapid collection of a large number of samples ~15–60 per reedswamp, (3) minimal habitat damage and disturbance, (4) standardised sample effort, and (5) to be suitable for making comparisons to non-reedswamp mesohabitats. In addition, the equipment required needs to be low cost, and readily available or easy to construct. The bespoke sample method designed for this thesis was effective in meeting these requirements. Consequently, it is recommended that semi-quantitative hand net approaches should form the basis of future investigations into macroinvertebrate biodiversity and functioning within reedswamps and throughout the littoral zone.

7.2 Implications for future research: key drivers for reedswamp loss

Windermere has been the focus of a great deal of scientific investigation including continuous monitoring of physicochemical variables since the 1930s (M^{c}Gowan *et al.*, 2011), and more is known about long-term changes in key stressors (*e.g.,* water level, and temperature) in this lake than for most others. Consequently, retrospective analysis of Windermere data has the potential to identify the main reasons for reedbed decline. However, a comprehensive assessment of the causes of reed die-back within Windermere was not possible, due mainly to a lack of historic and contemporary physicochemical data for littoral zone sediments. This has implications for the study of lakes that have received less attention over the long-term. An absence of relevant historic data is one of the main reasons why survey methods in isolation are not effective ways of investigating reed die-back. As a result, current knowledge of reed die-back syndrome is based mainly upon data from laboratory based multiple factorial experiments, which have revealed the importance of genetic diversity in reedbed resilience (Armstrong and Armstrong, 1999).

Unfortunately, temporal changes in the genetic diversity of *Phragmites* and other reed species within the natural environment are unknown for the majority of lakes (including Windermere). In the absence of historic data, comparison of genetic diversity between different reedbed populations (*e.g.,* healthy vs unhealthy reedswamps) within a particular region has the potential to reveal key reasons for die-back. It is important that these studies include an assessment of the ability of different biotypes to reproduce by seed, as this provides important information on population dynamics. For example, within the study area (northwest England) the ability to reproduce by seed is highly variable even between biotypes within the same population (M^cKee and Richards, 1996). Windermere has the potential to provide a useful model for assessing the influence of genetic diversity in reed die-back for a number of reasons: (1) its proximity to a relatively large and healthy *Phragmites* wetland *i.e.,* Leighton Moss; (2) other lakes in the catchment have reedbeds with different characteristics to those in Windermere; (3) there are maps detailing changes in reedbed distribution for Windermere since the late 19th century; and (4) there is long-term data for hydro-meteorological variables.

7.3 Implications for future research: consequences for macroinvertebrates

This thesis demonstrated the effectiveness of using macroinvertebrate data to assess the consequences of structural changes within the littoral zone for biodiversity and key ecological processes. Reed die-back within Windermere is likely to have had a significant impact upon macroinvertebrate communities and their potential to influence key processes at the local scale. The priority of this thesis was to focus on the relationship between reed litter and macroinvertebrates and its significance for energy flux and carbon cycling. Furthermore, multiple trait analysis also highlighted the importance of biological processes involving other types of organic matter, such as grazing and filter-feeding. Consequently, there is a need for future work on the quantification of spatiotemporal changes in periphyton, plankton, fine organic sediments, macroalgae, macrophytes, fungi, bacteria, and archaea. Conceptual models provided by this thesis for spatial (Section 7.3.1) and temporal (Section 7.3.2) variations provide a platform for a more complete assessment of how environmental filters (*e.g.,* changes in physical structure) influence the contribution of macroinvertebrate processes to functions at the whole lake scale.

7.3.1 A conceptual model of spatial variation

Two important components of spatial variation with littoral zones are structural heterogeneity, and progressive changes along the reedswamp ecotone. It was demonstrated that key influences on macroinvertebrate diversity and functioning within the littoral zone are: (1) macrophyte bed size and shape; (2) macrophyte community composition and standing crop; (3) substratum structure and composition (*e.g.,* silt or stone); and (4) environmental conditions at the whole lake scale (*e.g.,* trophic status). The relative influence of different habitat conditions upon macroinvertebrates varied along the ecotone. This was due to a combination of structural differences (*e.g.,* open water vs reed shoots) and relative position along the reedswamp ecotone. A novel and effective aspect of this thesis was to use multiple trait analysis to investigate changes in the vertical distribution of macroinvertebrate niches across the reedswamp ecotone.

Survey data was used to generate a conceptual model of the integrated response of macroinvertebrate communities to mesohabitat structure and position along the ecotone (Figure 7.1). Changes in the dominance of different macroinvertebrate niches across the ecotone were characterised by: (1) the distribution of different types of organic matter, (2) gradients in physicochemical conditions, and (3) differences in refuge and shelter. Non-reedswamp habitat was characterised by stony substratum with trace amounts of macroalgae and macrophytes. This habitat provided niches for burrowing deposit-feeders within the substratum; as a consequence of which there was significantly more deposit-feeders within stony-littoral habitat than there were in reedswamp habitat. This was unexpected, as visual inspections indicated that fine organic matter was much more prevalent in reedswamp. However, compared to the bottom of reedswamps, interstitial spaces within stony substratum provide deposit-feeders with: (1) refuge from avian and piscivorous predation; (2) stable habitat; (3) shelter from wave washing; and (4) aeration (Tolonen *et al.*, 2001). In addition, the surface of the substratum provides a suitable substrate for epilithic algae (Kahlert *et al.*, 2002), and points of attachment for filter-feeders (Johnson *et al.*, 2004). The lack of refuge and shelter above the substratum surface means that the majority of macroinvertebrates were located in or near the substratum. Consequently, the influence of stony-littoral habitat upon the processing of organic matter is distinct to that of reedswamp habitat. Furthermore, total macroinvertebrate abundance at stony-littoral locations was significantly lower compared to reedswamp mesohabitats due to the relatively small volume of available living space and food resource.

Reedswamp habitat generates environmental gradients which act as filters across the ecotonal axis (Sychra *et al.*, 2010). At the reedswamp-open water edge, the majority of macroinvertebrates were located in the water column.

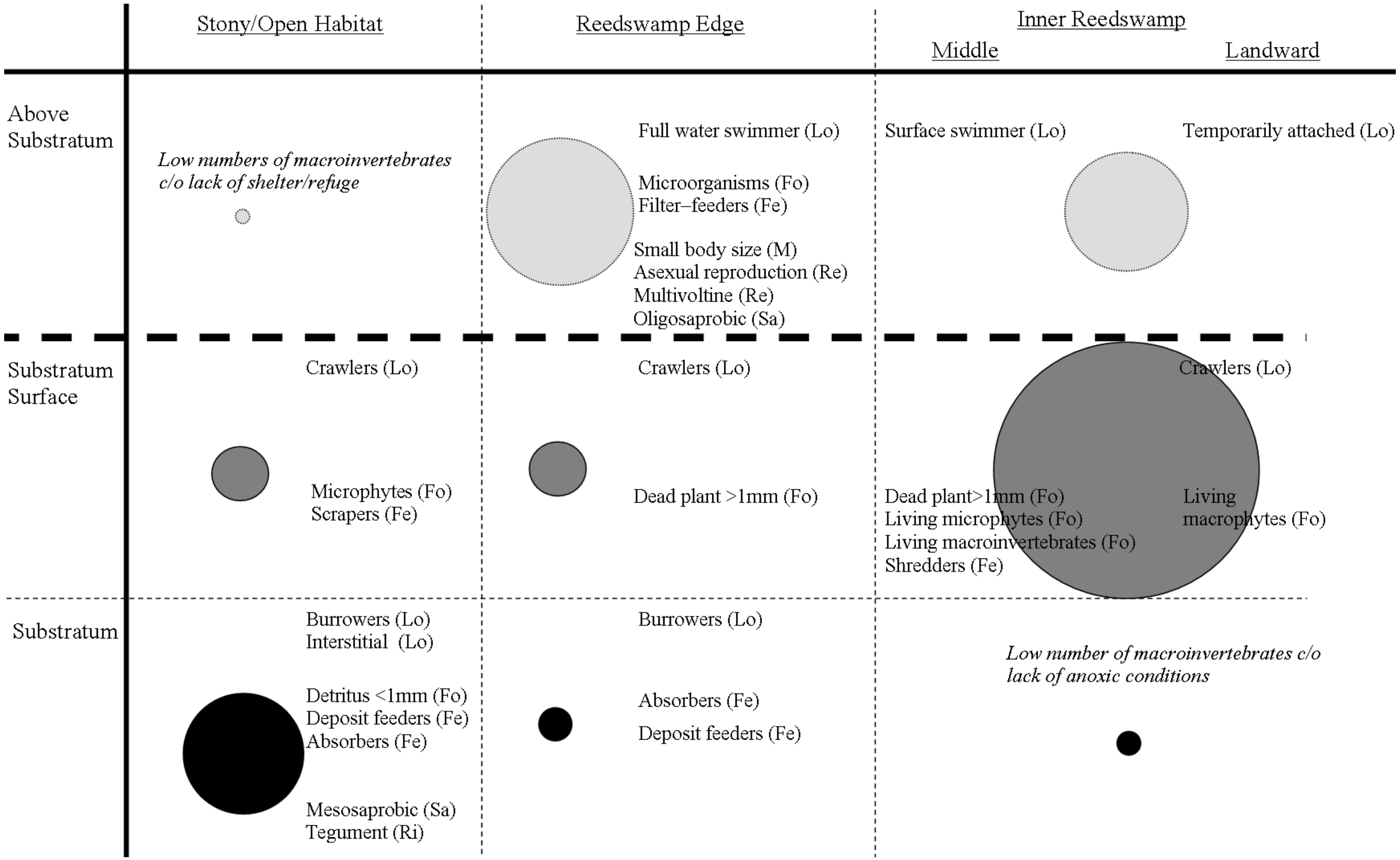


Figure 7.1 This conceptual diagram describes the influence of structural variations across the reedswamp ecotone upon macroinvertebrate abundance and characteristic traits. Different sizes of circles represent the relative abundance of macroinvertebrates within the substratum (black),at the substratum surface (dark grey), and attached to reed shoots or in the water column (light grey). Key trait categories were: (Lo) locomotion and substrate relation, (Fo) food, (Fe) feeding habits, (Sa) saprobity, (Ri) respiration, (M) maximum potential size, and (Re) reproduction.

These were filter-feeders with multiple-traits that are often associated with survival in areas of high predation, including free swimming, small body size, and multi-voltine reproduction (Gilinsky, 1984; Burks *et al.*, 2001). These traits were less dominant close to the shore, indicating that reedswamp provides a gradient of refuge from predation. In addition, an increase in the number of surface swimmers closer the shore was evidence of the provision of increased shelter from wave washing. However, the greatest influence upon macroinvertebrate assemblages was an increase in reed detritus deposits towards the shore. The abundance of macroinvertebrates (mainly crawling shredders) was greatest within these accumulations. Furthermore, the smothering effect of reed detritus had a negative impact upon the macroinvertebrates underneath (*e.g.,* burrowing deposit-feeders).

This model of spatial variation across the ecotone suggests that reedswamp recession within Windermere is likely to have had a strong influence on the ways in which macroinvertebrates influence energy transfer, and recycle nutrients (Figure 7.1). This is important information that will facilitate the future management of Windermere. However, this model would be enhanced by the inclusion of mesohabitats that reflect important changes at the whole lake scale. For example, the alien invasive pondweed, *Crassula helmsii* has colonised areas previously dominated by *Phragmites* reedbeds. Consequently, comparisons between reedswamp and other types of habitat (*e.g.,* pondweed dominated) along the land-water axis may enhance our understanding of the consequences for reedswamp loss.

7.3.2 A conceptual model of temporal variation

This research demonstrated the value of incorporating seasonal changes into models of reedswamp ecosystem functioning (Chapters 4–6). Given the deciduous nature of reeds it is surprising that this aspect of reedbed ecology has received little attention from other researchers. Macroinvertebrate survey data indicated that the direction and strength of spatial environmental filters associated with the reedswamp ecotone varied over an annual cycle. Furthermore, these changes were not consistent between structurally distinct reedswamps (Chapters 4–5). For example, there were significant differences in the seasonal dynamics of macroinvertebrate assemblages between a *Phragmites* reedswamp and a mixed (*Typha* and *Phragmites*) reedswamp. An experimental approach was used to investigate the role of interspecific differences in reed litter upon macroinvertebrates dynamics. Comparisons were made between the composition of different particle sizes of reed litter between reedswamps during October 2012 and March 2013. In addition, the relationship between reed litter mass loss and colonisation by macroinvertebrates was investigated during September to November 2012. These findings formed the basis of a conceptual model which illustrates the influence of interspecific differences in structure and seasonal dynamics in reed detritus upon macroinvertebrates (Figure 7.2). Survey data were used to make a complete estimate of changes throughout the year.

There were important functional interspecific differences between reeds that were related to the resilience and structure of their shoots and leaves. *Typha* has a greater standing crop and makes its greatest contribution to the detrital pool during the winter months, whereas the relatively persistent stems of *Phragmites* shed leaves throughout the year with a slight peak in the winter months (Figure 7.2). The majority of reed detritus enters the water as coarse particulate organic matter (≥ 1 mm) that is slowly broken down into fine particulate organic matter (>0.5 mm – <1 mm), at similar rates for both reed species. Although *Phragmites* generates less detrital biomass, its leaf litter has a stronger influence upon macroinvertebrate assemblages. For example, it supports relatively high numbers of invertebrates, the majority of which belong to the shredder functional feeding group. While the influence of freshly deposited *Phragmites* detritus on macroinvertebrates is short lived, input of fresh detritus is relatively steady compared to *Typha*. This demonstrates that there are ecologically significant interspecific differences in the ways reeds influence macroinvertebrate dynamics. The temporal model summarises the relative influence of different species of reed detritus on macroinvertebrate abundance, biomass, species richness, and functional feeding group composition (Figure 7.2).

The conceptual model of detritus-macroinvertebrate dynamics proposed by this thesis illustrates how spatial variations in physical structure can drive differences in invertebrate seasonal dynamics. Unfortunately, this thesis was less successful in identifying the mechanisms responsible for variations in seasonal dynamics across the reedswamp ecotone. This may have been due a lack of appropriate quantitative data for analysis of seasonal variations in biological variables (*e.g.,* changes in plankton, periphyton, and fish

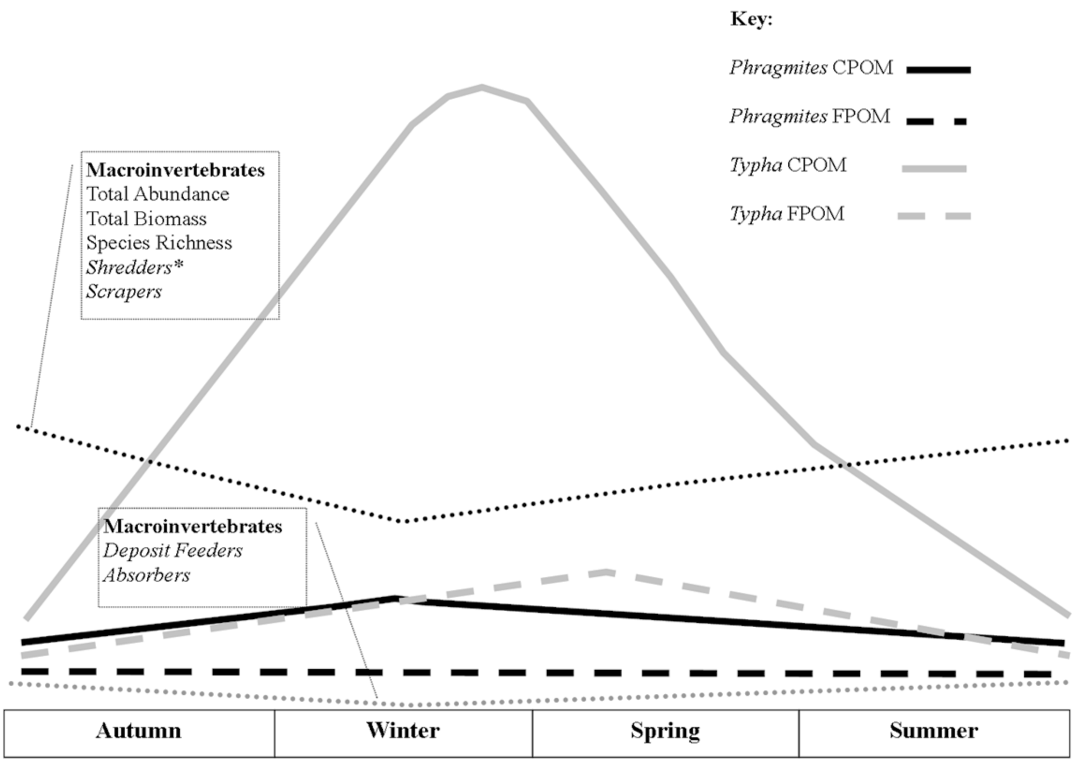


Figure 7.2 This conceptual diagram illustrates the response of macroinvertebrates to reed litter dynamics within a mixed (*Phragmites* and *Typha angustifolia*) reedswamp. Changes in key macroinvertebrate metrics and functional feeding traits (italics) are related to interspecific differences in coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM). The asterisk indicates that compared to *Phragmites, Typha* litter supports much lower numbers of shedders per gram of litter.

predation), and in physicochemical determinants such as temperature and alkalinity. In contrast the structural descriptors that were measured (*e.g.,* substratum composition and stability) were relatively unresponsive to seasonal changes. Based upon these findings it is recommended that future investigations of spatiotemporal changes in the littoral zone should include comprehensive measurements of biotic and abiotic variables.

7.4 Implications for future research: macroinvertebrate sample techniques

7.4.1 The need for a standardised survey approach

This thesis has developed a new suite of methods that shed new light upon the influence of reedswamp and other habitats on key processes throughout the littoral zone. Reedswamps and their associated environmental filters (*sensu* Poff, 1997) can be described by the composition and distribution of their component mesohabitats (van Nes and Scheffer, 2005). Mesohabitats are structurally distinct patches, which can be characterised by the nature of their substratum and the physical structure of their macrophyte communities. Unfortunately, published information on macroinvertebrate assemblages is limited to a small proportion of reedswamp mesohabitat types (*e.g., Phragmites* only reedswamp). In addition, the majority of reedswamp studies have not compared mesohabitats across different reedswamps and lakes. Furthermore, a lack of consistency in sample methods and data analysis has made it difficult to integrate mesohabitat information from different studies. Consequently, the implications for changes in littoral zone structure, and associated temporal changes, for whole lake functioning are poorly understood (Chapters 2, 4, 5 and 6). To address this issue, coordinated research across the globe will be necessary.

In recent decades the ecological assessment of lakes has focussed on the pelagic rather than the littoral zone (Chapter 2). However, the European Water Framework Directive (2000/60/EC) requires a broader approach to environmental assessment and has driven a recent renaissance in macroinvertebrate surveying within the littoral zone (White and Irvine, 2003).

The use of standard sample protocols for macroinvertebrates is an established approach in the investigation and classification of freshwater systems and an important feature of the Water Framework Directive classification tool (Wright *et al.*, 1998). However, standard protocols suitable for the investigation of spatiotemporal changes within the littoral zone of lakes are lacking. Therefore the priority for limnologists should be to develop a universal diagnostic tool capable of investigating the impact of changes in reedswamp dominance upon the ecosystem functioning of lakes throughout the world (White and Irvine, 2003; Solimini *et al.*, 2006; Tolonen and Hamalainen, 2010; Schreiber and Brauns, 2010). To encourage the development and consequent universal adoption of a standardised approach the following guidance is suggested (Section 7.4.2, Figure 7.3).

7.4.2 A detailed conceptual outline for investigating macroinvertebrate biodiversity and functionality within reedswamp habitat

i. Select qualitative or semi-quantitative approaches.
   a. Qualitative sampling (*e.g.,* timed sample collection) is suitable for scoping studies, and for estimating contributions to total biodiversity.
   b. Semi-quantitative sampling is suitable for studies of ecosystem functioning, water quality, and for the comparison of biodiversity and community composition within and between lakes. At individual sample locations, samples should be

collected from a known area, using a modified quadrat (two measuring sticks set at right angles). Data from the current investigation suggests that five isolated spatial replicates of 0.1 m^2 collected from within an area of 2 m^2 provide an adequate coverage.

ii. The frequency and timing of sample collection depends on the aims of the survey and the availability of resources. If only sampling once per year then consider sampling in the late spring to early summer period. During this time most functional groups of macroinvertebrates are relatively active.

iii. Identify structurally distinct patches of reedswamp (mesohabitats). Sample as many of these mesohabitats as is practical. Ideally this should include collecting samples from along the transitional axis (land to deep water). It is important to include at least one position that is equidistant between the landward edge and the deep water edge. There should also be one sample position near the deep edge. The latter only applies if the reedswamp extends out into the littoral zone beyond 15 m.

iv. Select adjacent reference sites within the littoral zone (*e.g.,* stony substratum and/or submerged macrophyte dominated mesohabitats).

v. Sample methods

    a. The use of a standard pond net to sample mesohabitats (both reedswamp and non-reedswamp) is an essential component of all surveys.

b. Where appropriate, complementary collection methods should be used. Recommended methods include: activity traps (Turner and Trexler, 1997); Chironomid Pupal Exuviae Technique (Ruse, 2010); and collection of adult beetles by sweeping in aerial shoots (Foster *et al.*, 2007). For a comprehensive review of alternative sample techniques see Jackson (1997).

c. Litter bag techniques are useful for assessing the influence of reed litter availability on macroinvertebrate assemblages (Bedford and Powell, 2005). Data from Chapter 6 indicates that 5 replicate litter bags of mesh size of 1 cm along with immersion times of 21, and 56 days are effective. Similar approaches could be used to assess differences between substrates (*e.g.,* pebbles vs detritus).

vi. For sampling within reedswamp habitat the recommendation is that netting procedure follows this sequence: (1) several rapid swipes from the water surface downwards, (2) starting at the base of reed shoots, scrape the head of the net along the reeds up towards the surface, (3) vigorous sweeps through the immersed reed shoots (to dislodge any remaining invertebrates), and finally (4) several sweeps through the top 3cm of the reed detritus, or if detritus sparse through the silty substratum. For firm or consolidated substrates it may be necessary to kick sample the substrate. When sampling non-reedswamp habitat, it is important that sample collection is carried out in a similar way to the approach used in the reedswamp.

vii. For each individual sample point make the following measurements and observations:

   a. Macrophyte species composition (reed and non-reed species)
   b. Estimate of substrate stability (soft, unstable, or consolidated)
   c. Percentage cover of overlaying: silt, reed detritus, coarse woody debris, *etc*.
   d. Water depth
   e. Local influences (*e.g.,* shading by trees, deposition of silt by rivers, wave washing from boats, *etc.*)
   f. Key physicochemical determinants (*e.g.,* temperature, and pH)

viii. Identify macroinvertebrates to species level where practical. Otherwise take species to a taxonomic level that enables the application of trait based analysis (typically genus).

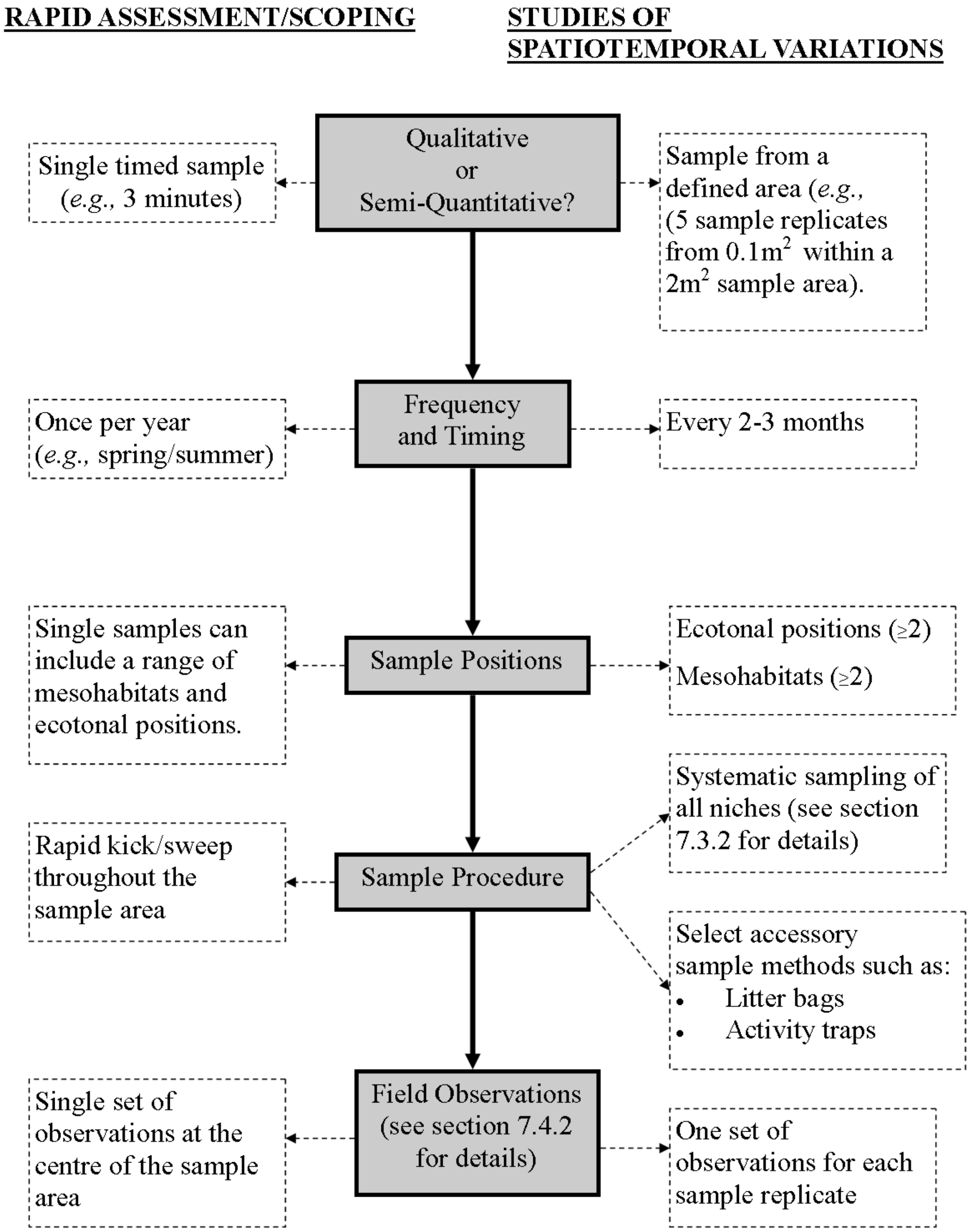


Figure 7.3 This schematic diagram summarises the proposed standard protocol for the collection of macroinvertebrate samples within the littoral zone of lakes. Solid boxes and arrows represent the order in which key decisions or actions need to be taken. Hashed boxes and arrows provide guidance on how to modify the approach for rapid assessment (left-hand side of diagram), and for more analytical studies of spatiotemporal variations (right-hand side).

7.4.3 Appraisal of thesis sample method

The design of the thesis sample method required a detailed assessment of the advantages and disadvantages of various techniques and approaches (Chapter 2). Quantitative approaches are relatively precise and useful for standardising sample effort (Metcalfe, 1989). In addition, quantitative sampling enhances the reliability of multivariate statistical techniques such as ordination techniques based upon the Bray Curtis Dissimilarity index (Lenat, 1988). However, it has been suggested that qualitative sample approaches are more suitable for the assessment of biodiversity, because they typically cover larger surface areas and encompass a greater range of niches (Sychra and Adámek, 2010). It was decided that the primary aim of the survey method should be to collect quantitative samples representative of a broad range of different niches. Existing methods were deemed unsuitable; for example, there are practical problems associated with collecting a large number of samples from reedswamp habitat with an enclosure device (Sychra and Adámek, 2010). The disturbance caused immediately before the placement of these cumbersome devices would have negated the advantage of an enclosure. Also this method is time consuming, and it is difficult to collect large numbers of samples within a short period of time. Instead an open quadrat (two sticks at right angles) was used to estimate the sample area before using a hand-net to sample within it. Due the low precision of this quantitative approach, this sample method should be considered to be semi-quantitative.

The semi-quantitative nature of the approach may have contributed to some of the large standard errors recorded for diversity, and total abundance for reedswamp and stony habitats. Alternatively these standard errors may have been a true indication of spatial variation within these superficially uniform mesohabitats. This was supported by survey data (Chapters 4 and 5) which indicated that significant variations could have occurred at the scale of the 2 m^2 sample area from which 5 replicates were collected. Unfortunately little is known regarding patchiness of macroinvertebrate data within the littoral zone. Seasonal variations are also a key knowledge gap, and require study over multiple years. However, describing variations over a single annual cycle was a novel aspect of this study, and provided an original insight into the dynamics of the reedswamp ecotone and other environmental filters.

Assessment of macroinvertebrate diversity and functioning within individual reedswamps is greatly enhanced by the collection of samples that are representative of a broad range of different niches (Chapters 2, 4, 5, and 6). Unfortunately, the majority of individual studies have focussed on a narrow range of niches (*e.g.,* detritivores associated with detritus at the surface of the substratum). Surprisingly, this has included other hand-net based sweep sample methods, for example Sychra *et al.* (2010) avoided sampling from the substratum. Consequently, it was necessary to design a bespoke sample approach for investigating the aims of this thesis. Survey data demonstrated the importance of sampling along vertical and horizontal axes within habitats dominated by emergent macrophytes. Systematic use of sweep and kick sampling from the water surface down to the substratum was effective in capturing a variety of macroinvertebrates associated with different niches. For example, the adult whirligig beetle, *Gyrinus* is restricted to the surface of the water and is fast moving and elusive; whereas the lake limpet, *Acroloxus* *lacustris* is associated with living and dead plant material, and is relatively difficult to dislodge (Tachet *et al.*, 2000). In addition, burrowing oligochaetes and chironomids were also detected.

Without consideration of the vertical distribution of macroinvertebrates, it would not have been possible to identify important functional differences between reedswamp and non-reedswamp habitat. The application of this approach across the reedswamp ecotone was particularly valuable. Given the retreat of reedswamp within the study area, this multi-directional sampling approach was key feature of the survey method. The holistic nature of the survey facilitated a mechanistic understanding of the ways in which reedswamps influence macroinvertebrate assembly within lakes. In particular, it provided a valuable insight into the relative importance of detritivores within what has been described as a detritus based ecosystem (Komínková *et al.*, 2000). In the context of existing knowledge of the reedswamp-macroinvertebrate relationship, the chosen sample and survey approaches were efficient and effective in delivering the thesis aims. The hand net approach was complemented by the litter bag method which facilitated a detailed understanding of the influence of leaf litter (Chapter 6).

Macroinvertebrates respond to multiple factors, and a mechanistic understanding of their relationship with a single factor (*e.g.,* reed litter) cannot be investigated by survey methods in isolation. Numerous studies have used litter bag techniques to investigate the role of macroinvertebrates in reed litter breakdown within lakes (Chapter 2). A novel aspect of this thesis was to complement a litter bag experiment with field data relating to interspecific differences in reed litter seasonal dynamics (Chapter 6). This was a successful approach and provided unique insights into the different ways in which two common reedswamp forming plants interact with macroinvertebrates to influence key processes (*e.g.,* energy transfer). By combining a range of different field-investigation techniques this thesis facilitated a mechanistic understanding of the ways in which different mesohabitats act as environmental filters and influence the role of macroinvertebrates in key processes (*e.g.,* decomposition).

7.4.4 Appraisal of data analysis method

Macroinvertebrate community data can be analysed on the basis of its taxonomic and trait composition (Statzner and Beche, 2010). Taxonomic approaches provide data that is readily understood by non-ecologists (*i.e.,* increasing biodiversity is good), whereas trait-based approaches require relatively complex statistical methods and provide a mechanistic understanding of the responses of macroinvertebrate to change (*sensu* van Kleef *et al.*, 2006). Both approaches provided key insights into the influence of spatiotemporal changes upon biodiversity and key ecological processes (Chapters 4–6). Investigations of spatial and temporal variations in alpha diversity and abundance using univariate analysis methods (*e.g.,* ANOVA) were a useful preliminary investigation technique. However, multivariate techniques (*e.g.,* ordination based on Bray Curtis Dissimilarity index) were more effective in identifying changes in diversity across structural and ecotonal gradients (beta diversity). Unconstrained ordination (NMDS) identified spatiotemporal variations in biodiversity, and RLQ ordination (constrained) and associated fourth corner analysis (correlation) facilitated a mechanistic understanding of the ways in which environmental filters influence macroinvertebrate traits.

7.5 Summary and research gaps

This thesis has increased knowledge of the spatiotemporal variation of macroinvertebrate communities within the littoral zone of lakes, by highlighting the diverse and dynamic nature of environmental conditions within these systems. Furthermore, macroinvertebrate assemblages and their contribution to key ecological processes were shown to be sensitive to changes in habitat structure related to declining reedswamp coverage. The reasons for reedswamp habitat decline within the study area were shown to be multi-factorial in nature. This study raises concern for the consequence of whole lake functioning due to the continued decline of reedswamp habitat within lakes throughout Europe, and provides information relevant to the management of the lacustrine littoral zone. Recommendations for future research are as follows:

- **Development of a standard protocol for investigating the littoral zone:** testing of the conceptual outline proposed in this thesis for investigating littoral macroinvertebrate biodiversity and functionality within a range of different lake types (Figure 7.3)
- **Genetic diversity of reeds**: assessment of the importance of different biotypes within the regional pool in-order to identify key reasons for reedbed loss, and the likelihood of natural (recolonisation) and assisted recovery (*e.g.,* planting) of reedbeds

- **Physicochemical conditions within the littoral zone:** examination of the relationship between surface water conditions in the pelagic zone with those in littoral sediments
- **Mesohabitats:** the physical, biological, and functional characterisation of a range of different littoral mesohabitats within the littoral zones of lakes including those dominated by alien invasive plant species
- **Ecotone:** comparison of changes in macroinvertebrate assemblages along the land-water axis of the littoral zone for different categories of mesohabitat (*e.g.,* reeds vs pondweed dominated areas)
- **Deep littoral zone:** extension of macroinvertebrate surveys into areas within the littoral zone too deep for reedswamp habitat
- **Other taxonomic groups:** assessment of the response of vertebrate, plant species, and microbes to structural heterogeneity within lakes
- **Food webs:** research into the interactions between organisms throughout the littoral zone (*e.g.,* the comparison of detailed food webs for reedswamp, stony-littoral and pondweed dominated habitats)
- **Whole lake functioning:** investigations into the impact of long-term reedswamp loss for whole lake functioning

Phragmites dominated wetlands are important but increasingly vulnerable habitats that make important contributions to biodiversity and ecosystem functioning. Concerns regarding reed-die back syndrome within Europe have led to an increase in research into the capability of *Phragmites* to respond to change (Brix, 1999a). Case studies of reedswamp decline within lakes are lacking, due partly to a lack of relevant historic data. This is unfortunate because understanding the reasons for long-term decline in the natural environment is essential if reed die-back is going to be managed successfully. Similarly, data relating to the adverse consequences of reedswamp loss is lacking for the majority of lakes. Collecting this evidence is crucial if managers, regulators and academics are to be persuaded to focus their attention upon this important but poorly protected habitat. Fortunately, the European Water Framework Directive has encouraged research into the influence of structural heterogeneity within the littoral zone on its macroinvertebrate assemblages (White and Irvine, 2003). In addition, there has been a renaissance in the use of trait-based analysis to assess functionally significant changes within riverine systems; data from these types of studies provided a useful baseline for the research delivered by this thesis. However, many important gaps in knowledge remain, and coordinated research is required before reedswamp loss and its consequences for whole lake functioning become irreversible.

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APPENDIX A1 Macroinvertebrate survey data

Number of individual taxa per 0.5 m^2 collected during June 2011 from selected sites. N = north shore, S = south shore

Lake:	Windermere			Rydal Water					
Sample position:	BO	B1e	B1m	RW-S (O)	RW-N (O)	Ss	Wm2e	Wm2m	Wm2l
Mollusca									
Acroloxus lacustris	-	1	5	-	-	-	-	-	1
Ancylus fluviatilis	-	-	-	3	-	-	-	-	-
Valvata piscinalis	-	-	-		4	7	-	11	-
Gyraulus albus	-	-	1	3	4	4	-	11	-
Planorbis carinatus	1	-	5	-	-	-	7	22	-
Physa fontinalis	-	13	-	-	-	-	-	-	-
Radix balthica	-	153	8	1	1	-	2	-	-
Potamopyrgus antipodarum	-	-	-	188	-	-	-	-	-
Sphaerium	-	17	154	123	44	189	61	28	99
Pisidium	2	-	-	-	1	-	10	28	-
Trichoptera									
Lepidostoma hirtum	1	-	-	-	-	-	-	-	-
Triaenodes bicolor	-	-	2	-	-	-	-	-	-
Mystacides azurea	-	-	-	-	-	2	-	-	-
Mystacides longicornis	1	1	3	-	-	-	1	-	4
Athripsodes cinereus	12	-	-	-	-	-	-	-	-
Tinodes waeneri	5	-	-	-	-	-	-	-	-
Lype reducta	-	4	-	-	-	-	1	-	1

Sample position:	BO	B1e	B1m	RW-S (O)	RW-N (O)	Ss	Wm2e	Wm2m	Wm2l
Limnephilus flavicornis/marmoratus	-	-	-	-	-	4	-	-	-
Limnephilus lunatus	1	-	5	2	4	-	10	-	21
Anabolia nervosa	-	-	-	-	3	10	3	-	1
Phryganea bipunctata	-	1	1	-	-	-	-	-	-
Cyrnus trimaculatus	-	-	-	-	-	-	2	2	-
Diptera									
Ceratopogoninae	3	-	-	1	-	-	-	-	-
Chironominae (Chironomini)	33	5	408	4	74	66	80	26	172
Chironominae (Tanytarsini)	11	9	19	0	18	21	10	26	15
Orthocladiinae	95	384	82	16	4	-	3	3	9
Tanypodinae	-	-	10	1	38	72	3	3	13
Tabanini	-	-	-	-	-	1	-	-	-
Helius	-	-	-	-	-	-	-	-	1
Megaloptera									
Sialis lutaria	-	-	3	-	13	12	1	-	1
Ephemeroptera									
Ephemera danica	-	-	-	2	-	-	-	-	-
Zygoptera									
Enallagma cyathigerum	1	-	-	7	3	2	8	-	-
Hemiptera									
Hesperocorixa linnaei	-	-	-	6	2	-	-	-	-
Sigara dorsalis	13	16	28	-	-	-	-	-	1
Sigara falleni	4	-	-	-	-	1	-	3	-
Sigara stagnalis	-	-	-	-	-	-	-	6	1
Notonecta glauca	-	-	-	-	-	-	3	-	32
Micronecta poweri	-	-	-	1	-	-	-	-	-

Sample position:	BO	B1e	B1m	RW-S (O)	RW-N (O)	Ss	Wm2e	Wm2m	Wm2l
Coleoptera									
Gyrinus marinus	-	1	-	-	-	-	-	-	-
Haliplus confinis	1	-	-	-	-	-	-	-	-
Haliplus ruficollis group	-	-	-	1	-	-	1	-	-
Haliplus flavicollis	-	-	-	-	2	1	1	-	-
Ilybius fuliginosus	6	-	-	-	-	-	2	-	-
Oulimnius troglodytes / tuberculatus	5	2	3	8	4	1	-	13	-
Crustacea									
Asellus aquaticus	141	36	84	6	3	3	5	-	7
Ostracoda	2	-	-	-	-	-	-	-	-
Crangonyx pseudogracilis	170	184	380	27	180	-	115	339	1088
Hirudinea									
Erpobdella octoculata	5	1	3	-	-	-	3	3	-
Glossiphonia complanata	4	1	-	1	-	1	-	-	-
Helobdella stagnalis	1	-	5	-	-	-	1	1	-
Piscicola geometra	-	-	-	-	1	-	-	1	-
Arachnida									
Hydracarina	-	12	4	2	4	1	5	-	-
Oligochaeta									
Lumbriculus	1	1	7	84	16	-	-	-	-
Enchytraeidae	1	5	15	3	-	-	-	3	4
Turbellaria									
Planaria torva	-	-	-	1	-	-	-	-	-
Dugesia lugubris / polychroa	4	-	-	-	-	-	-	18	8
Dugesia tigrina	-	-	-	5	3	-	2	18	-
Dendroceolum lacteum	2	-	4	-	2	-	1	-	4
Polycelis tenuis/nigra	19	14	15	1	-	-	1	1	5

APPENDIX A2 Macroinvertebrate data from litter bag experiment

Mean numbers of macroinvertebrates per bag within sets of litter bags are demonstrated. Where multiple dominant FFG feeding guilds are attributed to single taxa, the dominant FFG (*sensu* Cummins, 1973) is denoted first. (Sh = shredders, Sc = scrapers, F = filter-feeders, De = deposit-feeders, Ab = absorbers, Pi = piercers, Pr = predators, Pa = parasites. *Phrag* = *P. australis* leaves, *T. ang* = *T. angustifolia* leaves, Kim = leaf shaped strips of polypropylene)

Taxonomic groups	FFG	Coarse Bags 3 days			Coarse Bags 21 days			Coarse Bags 56 days			Fine Bags 56 days		
		Phrag	*T. ang*	Kim	*Phrag*	*T. ang*	Kim	*Phrag*	*T.ang*	Kim	*Phrag*	*T. ang*	Kim
Crangonyx pseudogracilis	Sh	0.4	-	-	30.4	0.6	3.8	2	0.4	9.2	19.4	6.8	9.6
Asellus aquaticus	Sh	-	-	0.2	4.4	0.6	1.4	-	0.2	-	5.2	3.8	2.4
Ilybius spp. Larvae	Sh/Pi	-	-	-	-	0.2	-	-	-	-	-	-	-
Lype reducta	Sh/F	-	-	-	-	-	-	1.6	2.6	0.2	0.6	0.6	-
Potamopyrgus antipodarum	Sh/Sc	-	-	-	0.2	-	-	-	-	-	-	-	-
Acroloxus lacustris	Sc/Sh	0.6	1.4	-	2.2	1.2	0.2	1.2	1.4	-	-	-	-
Radix peregra	Sc/Sh	-	-	-	-	0.2	0.4	-	-	-	-	-	-
Physa fontinalis	Sc/Sh	0.4	0.6	-	5.6	4	-	-	0.6	0.6	-	0.2	0.6
Oulimnius tuberculatus	Sc	-	-	-	-	-	0.2	0.2	-	-	-	-	-
Orthocladiinae	Sc	-	-	-	-	0.4	-	-	-	-	-	-	-
Sphaerium corneum	F	-	0.2	-	-	-	0.2	-	-	-	-	-	-
Tanytarsini	De	1.8	-	0.6	0.8	-	2	1	0.4	0.6	1.2	0.4	0.4

		Phrag	*T. ang*	Kim	*Phrag*	*T. ang*	Kim	*Phrag*	*T.ang*	Kim	*Phrag*	*T. ang*	Kim
Chironomini	De	0.4	0.6	-	5.2	1.4	-	0.2	-	-	0.2	0.2	0.2
Lumbriculidae	De/Ab	-	-	-	-	-	-	-	-	-	-	-	0.4
Erpobdella octoculata	Pr	1	0.2	-	0.8	-	0.6	-	-	-	-	-	-
Dendrocoelum lacteum	Pr	0.2	-	-	-	0.2	-	0.2	-	0.2	-	-	-
Polycelis tenuis	Pr	-	-	-	-	-	-	2.8	-	1.2	-	-	-
Argulus foliaceus	Pa	-	-	-	0.4	-	-	-	-	-	-	-	-
Glossiphonia complanata	Pi	-	-	-	0.2	0.6	0.2	-	-	-	-	-	-