The Ecology of Four Scarce Wetland Molluscs

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A Watson

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Keywords
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Research Contractor
This document was produced under R&D Project W1-038 by:
Prof. Stephen Omerod, Catchment Research Group, School of Biosciences, Main Building, Cardiff University, PO Box 915, Cardiff, Wales CF10 3TL

Tel: 029 20 875871 Fax: 029 20 874305 Email: ormerod@cardiff.ac.uk

Environment Agency's Project Manager
The Environment Agency's Project Manager for Project W1-038:
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THE ECOLOGY OF FOUR SCARCE WETLAND MOLLUSCS

Thesis submitted for the degree of Doctor of Philosophy

by

Alisa Watson, B.Sc., M.Sc.

School of Biosciences
Cardiff University

November 2002

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SUMMARY

1. In 1995, the United Kingdom (UK) Biodiversity Action Plan listed four wetland molluscs of Red Data Book (RDB) status that required urgent conservation measures to prevent further reduction in their distribution: *Segmentina nitida* (Muller 1774), *Anisus vorticulus* (Troschel 1834), *Valvata macrostoma* (Morch 1864) and *Pisidium pseudosphaerium* (Schlesch 1947). All four typically occur in drainage ditches of large lowland grazing marshes of southern Britain and have shown marked decline in range, particular *Segmentina nitida*. However, despite their relative rarity, little is known of their ecological requirements, the reasons behind their decline, nor the management measures that might benefit their numbers. This study used a blend of large-scale surveys, small-scale surveys and field experiments to assess likely biotic and abiotic effects on distribution and abundance.
2. Each of the RDB molluscs occurred in ditches with different ecological characteristics. *Segmentina nitida* occurred in shallow calcareous ditches choked with mainly emergent plants and occurred in locations with abundant amphibious vegetation; these features typified ditches at the advanced stages of vegetation succession. Ditches with *Valvata macrostoma* were dominated by floating plants but this species reached its greatest numbers within the emergent stands. *Anisus vorticulus* was recorded in less calcareous ditches than the other two snails, and typically occurred in channels with a high diversity of aquatic plants. *Pisidium pseudosphaerium* occurred in ditches with similar vegetation to both *Valvata macrostoma* and *Anisus vorticulus,* which were at a comparatively less advanced stage of vegetation succession.
3. Despite their higher abundance among certain vegetation types, the three snails were unaffected by location within a ditch, although each was scarce at the lower depths (>0.6m). Below 0.6m, ditches were almost anoxic with concentrations of dissolved oxygen at <1mg l^{-1}.
4. Classification and ordination showed that gastropod and bivalve assemblages in ditches strongly reflected vegetation characteristics. The three RDB snails are all potential ‘umbrella species,’ each representing and indicating the presence of a distinct associated assemblage. Gastropod responses to putative successional stages in vegetation were marked by changes in assemblage composition but there was no decline in the overall conservation interest. In contrast, increasing

vegetation cover appeared to result in reduced bivalve diversity, but with increasing abundance of the scarce *Pisidium pseudosphaerium*.

5. Based on the ditch vegetation and chemistry data, multiple logistic regression models indicated that *Segmentina. nitida* and *Valvata macrostoma* were absent from otherwise suitable ditches that had significantly higher concentrations of nitrate and nitrite than occupied ditches. *Pisidium pseudosphaerium* also appeared to be negatively affected by elevated concentrations of nitrogen.
6. A highly replicated field experiment was used to assess the short-term effect of nutrient loadings on *Segmentina nitida*, *Valvata macrostoma* and several other gastropod species. Elevated concentrations of ammoniacal-nitrogen occurred in response to nitrogen dosing but were not accompanied by variations in the biomass or abundance of any gastropod species.
7. Changes in the ecological character of drainage ditches can be attributed to the intensification of agriculture on grazing marshes, which has led to inappropriate ditch management, decreasing connectivity between ditches and increasing eutrophication. Based on work in this thesis, rotational management of ditches that maintained a full sequence of vegetation succession throughout a given grazing marsh would benefit all the target RDB molluscs and their associated assemblages. In addition, reduced agro-chemical use on grazing marshes is likely to assist the maintenance and recovery of three of the RDB species. Future work should aim to assess the long-term effects of ditch management and nutrient control on molluscs assemblages. Improved understanding of dispersal and persistence will also assist management of each of the RDB species.

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General introduction

1.1. Introduction

Among the richest habitats for freshwater molluscs in the United Kingdom (UK), are drainage ditches of grazing marshes that support at least 70% of all known freshwater molluscs in the country. Grazing marshes and, in turn, their drainage ditches are increasingly threatened by intensive drainage, conversion of grassland to arable land and also nutrient enrichment (Driscoll 1985, Palmer 1986, Hicklin 1986, Williams & Hall 1987). Typical of these ditches are four freshwater molluscs, *Segmentina nitida*, shining ram's-horn snail (Muller 1774), *Anisus vorticulus*, little whirlpool ram's-horn snail (Troschel 1834), *Valvata macrostoma*, large-mouthed valve snail (Mörch 1864) and *Pisidium pseudosphaerium*, false orb pea mussel (Schlesch 1947). These four mollusc species are all listed in the British Red Data Book (RDB) due to their increasingly scarcity in the face of the habitat deterioration and loss (Bratton 1991). They are all listed in the UK Biodiversity Action Plan (BAP), along with grazing marshes, as being in need of urgent conservation action (HMSO 1995). Information on the ecological requirements of the four species is still very scant for much of Europe as well as the UK, so that current conservation action cannot be optimised. This chapter introduces and reviews the current ecological information on the four molluscs and the final part presents the aims of the research along with background information on the study sites.

1.2. Classification of Molluscs

Mollusca is second to the Phylum Arthopoda in number of species known. Individuals are typically characterised by soft bodies and mantles (Pfleger 1990). The Phylum contains seven classes mostly restricted to the marine environment: the squids, cuttlefish and octopuses (class Cephalopoda), tusk shells (class Scaphopoda), chitons (class Polyplacophora), cones (class Monoplacophora) and solenogasters (class Aplacophora). The exceptions are the Gastropoda (slugs and snails) and Bivalvia (mussels and clams) which are able to survive also in freshwater (Fitter & Manuel 1994). Gastropod have also adapted to terrestrial habitats. A common estimate of number of molluscs is 135,000 species, of which the majority live in the sea and about 75% of this total are members of the Gastropoda (Pfleger 1990, Wells & Chatfield 1992, van Bruggen 1995). The freshwater fauna can be divided into three main groups: freshwater Bivalvia, freshwater Prosobranchia (Gastropoda) and freshwater Pulmonata (Gastropoda). The freshwater bivalves are distinguished into the larger freshwater bivalves belonging to the order Unionoidea and the smaller freshwater bivalves belongs to the order Veneroidea. A target species for this study, *Pisidium pseudosphaerium,* is a member of the family Sphaeriidae (order Veneroidea) (Dillon 2000).

Freshwater gastropods belong to one of two subclasses: Prosobranchia or Pulmonata. Freshwater prosobranchs are typically marine species that have invaded freshwater. They are characterised by their operculum and gills (Janus 1965). Most families of the freshwater prosobranchs have a worldwide distribution, however the Valvatidae which includes another of the target species of this study, *Valvata macrostoma,* are restricted to the northern hemisphere (Dillon 2000). The snails of the subclass Pulmonata have no gills and respire over the inner surface of their mantle, effectively a lung (Janus 1965, Dillon 2000). Most pulmonates are land snails, although some have reverted to aquatic habitats (Pfleger 1990). Both *Segmentina nitida* and *Anisus vorticulus,* the final two target species here, are members of the family Planorbidae which has a worldwide distribution (Dillon 2000).

1.2.1. Bivalvia, Sphaeriidae

Bivalves are defined by the presence of two laterally compressed shells, which are hinged together. They lack a defined head, although eyes are usually present somewhere on the body. Unlike the gastropods, they have no tentacles, jaws or radula and the mouth is simply an orifice at the anterior end of the body (Janus 1965). A muscular foot is always present which can be extended from the anterior and allows the bivalves some mobility (Fitter & Manuel 1994). Bivalves generally have two sets of gills enclosed in a large mantle cavity and water is circulated around the mantle using siphons (Janus 1965).

The majority of sphaeriids are simultaneously hermaphroditic and self-fertilisation has been observed in *Pisidium* species (Araujo & Ramos 1997). Sphaeriidae brood their larvae in the shell cavity, eventually releasing them as fully formed young mussels (Heard 1965, Mackie 1984). In *Pisidium* species, the brood is usually carried for one month before being released (Dillon 2000). The sphaeriids live buried in sedimentary substrate with just the posterior tip of the shell and the siphons protruding (Boycott 1936, Janus 1965, Kerney 1999, Dillion 2000). *Pisidium* species have been found among macrophtyes, where they are attached by temporary threads of mucus (Fitter & Manuel 1994). Some sphaeriids are excellent colonisers able to adapt to temporary habitats aided by their ability to self fertilise (Boycott 1936, Kerney 1999). *Pisidium* are more characteristic of calmer water with fine sediments, whereas *Sphaerium* species are more characteristic of coarse sediment at higher flows (Boycott 1936, Dillon 2000).

1.2.2. Gastropoda

Gastropoda, as well as being the largest class of the phylum Mollusca, occupies a diverse range of marine, freshwater or terrestrial habitats (Janus 1965). All gastropods retain a muscular foot, which allows them to be relative mobile. They have a primitive head bearing a pair of tentacles with an eye at the base of each and a fairly well developed nervous system. They all have shells, although in slugs this has disappeared or has been reduced to a rudimentary plate on the posterior surface (Pfleger 1990). Freshwater snails are mostly herbivorous. The radula, a flexible, toothed, ribbon-like tongue is used to gather food, often by scraping epiphytic growth. The structure of the radula will vary according to the food-source and the collecting mechanism of individual species (Stiglingh & van Eeden 1970, Thomas *et al.* 1985, Hickman & Morris 1985, Fitter & Manuel 1994, Dillon 2000). Freshwater gastropods can be divided according to whether they breathe free air by means of lungs or have gills (Dillon 2000).

1.2.2.1. Prosobranchia, Valvatidae

The prosobranchs are mainly a marine group, although several species have successfully invaded freshwater and some have even become terrestrial. When an aquatic prosobranch is moved into air, the support of the gills in water is lost and the gill filaments collapse. This feature makes it very difficult for freshwater prosobranchs to survive in fluctuating water levels or to colonise temporary aquatic habitats. There are ten native species of freshwater prosobranch in Britain. Boycott (1936) generalised that they prefer running water, which is well-oxygenated and free of particles. Most prosobranchs are gonochoristics with either female or male reproductive organs.

The Valvatidae have been little studied and there is virtually no literature on *Valvata macrostoma*. The American valvatids primarily inhabit deep lentic water with relatively low temperatures compared to other gastropods (Dillon 2000). In Europe, *Valvata piscinalis* is common in flowing water (Boycott 1936, Kerney 1999) and is considered to be a grazer of epiphytic algae (Fretter & Graham 1962, Cleland 1954). Unusually for prosobranch snails, valvatids are hermaphrodites (Janus 1965). The male system develops slightly in advance but in a mature specimen both egg and sperm are manufactured simultaneously so it is possible that valvatids could self fertilise but there is no evidence to support this (Cleland 1954). Valvatids have relatively large egg masses which are attached to vegetation or other hard surfaces. Heard (1963) suggested that breeding may require periodic migration to a vegetation mass, as *Valvata* populations typically inhabit the deeper water characterised by soft muddy substrate.

1.2.2.2. Pulmonata, Planorbidae

The subclass Pulmonata contains the most successful land snails as well as many freshwater forms. There are some primitive marine forms, which live in the littoral zone of marine environments. Their ability to breathe atmospheric air allows the pulmonates to colonise a range of aquatic habitats including those with low oxygen concentrations. The ability to live at high densities in shallow, even seasonal water bodies along with their ability as self-fertilising hermaphrodites makes pulmonates excellent pioneer colonists. Juveniles develop directly from the egg without any intervening larval stages (Janus 1965).

Most literature on Planorbidae has focused on the medically important species that carry bilharzia (Schistosomiasis) in Africa (Malek 1958, Appleton 1978, Brown 1994, Thomas 1987). The Planorbidae are widespread and are rarely restricted to one habitat. Research has shown that planorbids will use a range of food-sources. Carlow with his work on *Bathyomphalus contortus* (1973a & b, 1974, 1975, Carlow & Fletcher 1972) showed that this species prefers detritus to algae. The main characteristic of the family is its flat discoid shell. They are also unique amongst molluscs in having haemoglobin for storing oxygen (Pfleger 1990).

1.3. Distribution of freshwater molluscs

The distribution of molluscs can be described at three spatial scales: on a biogeographical scale (between geographical regions); within a geographical region (between water-bodies); and finally within water-bodies (among habitats). For each spatial level, different factors will be influential on the distribution and abundance of molluscs (Lodge *et al.* 1987, Crowl & Schnell 1990). Research on mollusc distribution is mostly carried out in rivers and streams (e.g. Cummins & Lauff 1969, Harman 1972, DeKock *et al.* 1989, Liu & Resh 1997, Crowl & Schnell 1990, Johnson & Brown 1997) or lakes and ponds (e.g. Dvørak & Best 1982, Brönmark 1985a, Lodge 1986, Bailey 1988, Brown & Lodge 1993, Costil & Clement 1996, Marklund *et al.* 2001). In comparison, molluscs in ditch habitats are poorly researched (Scheffer *et al.* 1984, Caquet 1990).

1.3.1. Abiotic factors affecting distribution

In the UK, the south eastern lowlands are richer in mollusc species than the cooler non-calcareous highlands of the north and west (Kerney 1999). Calcium is considered by many authors to be important in determining the distribution and abundance of freshwater molluscs (Boycott 1936, Macan 1950, Russell-Hunter 1978, Økland 1983, Aho 1966, 1978a & b). However, work by these latter authors focused on regions that are contiguous, geologically uniform and dominated by soft water (Ca = <5mg l^{-1}) so that the effects of calcium will be significant in influencing mollusc distribution. Experiments carried out in the laboratory and in the field have shown that calcium has an ecological role only at extremely low concentrations of less than 4.5mg 1^{-1}, which can affect snails physiologically (Williams 1970, Thomas *et al.* 1974, Young 1975, Nduku & Harrison 1976, Dussart & Kay 1980). At calcium levels above 5mg l^{-1}, other factors appear to have a greater influence the distribution and abundance of molluscs.

Temperature determines the onset and termination of reproduction in most freshwater snails (Russell-Hunter 1978), also affecting the development rates, fecundity and number of broods produced (Brown 1979a, McMahon & Payne 1980, El-Eman & Madsen 1982, McMahon 1983). It has been noted that the activities of freshwater snails increases significantly with temperature, with more time spent on feeding (Costil & Daguzen 1995, Costil & Bailey 1998).

Low oxygen concentrations may preclude some prosobranchs (Aldridge 1983, McMahon 1983). By contrast, the ability of pulmonates to use atmospheric oxygen provides clear competitive advantages in hypoxic situations (Cantrell 1981).

The role of pH in the distribution of freshwater molluscs appears to be varied. Dillon (2000) remarked that the uptake of calcium is likely to be influenced by pH levels. He suggested that the pH and buffering capacity might a critical variable in the distribution of freshwater molluscs. It has been demonstrated that low pH has an adverse effects on a pulmonate species independent of calcium concentration (Hunter 1990).

One abiotic factor, which is considered to be significant in influencing the distribution and abundance of freshwater molluscs on small spatial scales, is habitat disturbance or perturbation. The extent of perturbation is based on two criteria; the temporal availability of the habitat and the ability of a mollusc species to persist. Typical disturbances are seasonal drying of temporary ponds (Brown 1985), reduction in macrophytes (Lodge & Kelly 1985), waves, current velocity (Sousa 1984, Crowl & Schnell 1990) and other less well-researched disturbances such as winterkill (hypoxia under ice), salinity and flooding (Ruggerone 2000, Costil *et al.* 2001, Hughes & Rood 2001). The success of mollusc species to persist or to colonise disturbed habitats is a significant factor in their distribution and abundance (Pickett & White 1985, Townsend & Hildrew 1994, Death 1995).

1.3.2. Biotic factors affecting distribution

Abiotic factors such as disturbance, calcium, temperature and oxygen tend to set regional biogeographical limits to species' ranges. Biotic factors such as competition, predation, parasitism and habitat productivity are more likely to affect molluscs more locally, for example within waterbodies. Correlations have been found between mollusc diversity and the complexity of the habitats available (Harman 1972, Carlow 1973a, 1974, Soszka 1975, Pip & Stewart 1976, Bishop & DeGaris 1976, Mason 1978, Pip 1978, Ross & Ultsch 1980, Aldridge 1983, Brönmark 1985a, Lodge 1985, 1986, Thomas 1990, Thomas & Eaton 1996, Costil & Clement 1996). The habitats, in turn, will reflect rate of productivity, the type of food and the mollusc assemblage. It has been shown that snails often have species-specific habitat preferences and tolerance such as particular depths or vegetation structure (Lodge 1985,1986, Thomas

1990, Reavell 1980). Brown (1982) demonstrated that species that prefer detritus as a food source are common in woodland ponds whereas species that prefer algae are abundant in open ponds. Many authors have recently explored the effect molluscs can have on the food web in freshwater environments (Cuker 1983a & b, Brönmark 1985b, Cattaneo & Kalff 1986, Swamikannu & Hoagland 1989, Cattaneo & Mousseau 1995, Daldorph & Thomas 1995). Evidence shows that increasing the density of the snail population can significantly reduce the quality and diversity of epiphytic algae.

Where there are no disturbances and predation is minimal, thus allowing optimum size of mollusc populations, then competition could be a limiting factor in mollusc abundance and could possibly mediate patterns of distribution (Hairston *et al.* 1960, Fretwell 1987). *Ex situ* experiments have shown potential for inter-specific and intra-specific competition (Fenchel & Kofoed 1976, Madsen 1979, El-Eman & Madsen 1982). However, research in the field has shown that snail species tend to diverge in their food and habitat preferences and so avoid local competition (Brown 1982, Brown *et al* 1985, González-Solís & Ruiz 1996). The reproductive cycles of certain species have also been noted to be asynchronous, possibly to avoid competition between juveniles (Brönmark *et al.* 1991). While inter-specific competition might not be a significant factor affecting mollusc distribution and abundance, many authors have commented on effects of intra-specific competition (Eisenberg 1966, 1970, Brown 1979a, 1982, Brown & DeVries 1985, Barnes & Gandolfi 1998). Increasing the density of a population of one species will have a negative effect on snail growth and reproduction as the individuals all compete for the same food source. One area of competition largely neglected in research is inter-phyletic competition. For example, amphibian tadpoles have been shown to have a negative effect on the growth and reproduction rate of freshwater snails (Brönmark *et al*. 1991). In addition, molluscs can also have a negative effect on other aquatic invertebrates (Hawkins & Furnish 1987, Cuker 1983a & b).

The importance of predation appears to increase as the waterbody becomes bigger and more permanent (Lodge *et al.* 1987). Predation is an important source of mortality among molluscs and many freshwater species have evolved escape or defence mechanisms. Some species have developed stronger shells to dissuade shell-crushing predators (Stein *et al.* 1984, Brown & DeVries 1985, Vermeij & Covich 1978, Crowl & Covich 1990). The operculum in prosobranchs is believed to play a part in defence of shell invading invertebrates such as leeches and flatworms (Brönmark & Malmqvist 1986). Certain behaviours are apparent in some snails such as shell shaking (Townsend & McCarthy 1980), exiting water to escape predation (Brönmark & Malmqvist 1986) and burrowing into the substratum or crawling into the vegetation (Alexander & Covich 1991a, b). The length of habitat persistence is significant in whether predation is an important factor. In temporary water-bodies, the main predators are likely to be shell-invading invertebrates such as sciomizid fly larvae (Eckblad 1976), dytiscid beetles, belostomatid bugs (Eisenberg 1966), odonates, flatworms and leeches (Davies *et al.* 1981, Young 1981, Brönmark 1988, Brown & Strouse 1988). Predation rates are very low and unlikely to affect distribution and abundance in temporary habitats. In contrast, permanent bodies will also have predatory crustaceans (Covich 1977, 1981, Crowl & Covich 1990, Alexander & Covich 1991a & b, Lodge *et al.* 1994), fish (Crowder & Cooper 1982, Mittelbach 1984, Osenberg & Mittelbach 1989, Brönmark 1992, 1994, Turner 1996, Walker-McCollum *et al.* 1998) and birds (Fitzner & Gray 1994, Ntiamoa-Baidu *et al.* 1998) which can all have a high predation rates of molluscs species and hence will influence the mollusc communities.

The prevalence of parasites tend to be low in most freshwater molluscs, however there are known cases of larvae of digenetic trematodes (Liver fluke) in both pulmonates and prosobranchs snails (Holmes 1983, Nasincova *et al.* 1993), *Schistosoma* species in planorbid snails and *Fasciola* species in lymnaeid snails (Boyle 1981). Trematode infection causes an initial growth spurt in snails but with time it eventually depresses growth and reproduction (Brown 1978, Minchella & LoVerde 1981, Minchella *et al.* 1985). It is generally considered that parasitism is not an important factor of mollusc distribution (Lodge *et al.* 1987).

A concept model (Figure 1.1) has been produced to attempt to explain the extent of the influence on snails by individual abiotic and biotic factors (Lodge *et al.* 1987). The authors believed that the factors affecting distribution would vary over three spatial levels. Among regions it was expected that water chemistry would be the over-riding influence on molluscs distribution. Among waterbodies, it was suggested that water chemistry would still be significant but there would be a greater degree of influence by habitat availability and habitat disturbance. In the final spatial level, among habitats within a waterbody, the authors suggested that food selectivity would dictate the distribution of the molluscs assemblages, followed by predation.

1.4. Threats to freshwater molluscs

Given that the Mollusca are the second largest animal Phylum in terms of numbers of described species and that 40% of the recorded animal extinctions since 1600 are of molluscs, it is important that ecological information for the most threatened molluscs is collected before it is too late. The main threats to all freshwater molluscs are habitat loss and pollution (Wells & Chatfield 1992). Management of rivers such as channelisation and damming (Moss 1988, Seddon 1998a, Clifford 2001), and also the intensive drainage of floodplains and wetlands (Glaves 1998, Joyce & Wade 1998, Jeffereson & Grice 1998, Hughes & Rood 2001) cause loss of freshwater habitats. Freshwater environments are particularly threatened by pollution from acidification (Moss 1988, Edwards *et al.* 1990, Horne & Goldman 1994, Rabalais 2002) and eutrophication (Schindler 1974, Mulligan *et al.* 1976, Balls *et al.* 1989, Cartwright *et al.* 1993) as well as discharge of toxic substances such as oil and heavy metals (Meynell 1973, Muirhead-Thomson 1987, Jeffries & Mills 1990, Barnes & Mann 1991). In addition, there are also potential threats to aquatic ecosystems by the release of invasive or non-native species that can change the character of a habitat (Holdich & Reeve 1991, Maitland 1996, Dawson 1996, Khalanski 1997). Mollusc species, which are sensitive to slight changes in their chemical, physical, and/or biotic environment are potentially threatened by these frequent anthropogenic activities. To establish which mollusc species should have priority for nature conservation, it is important to indicate which species are currently rare or vulnerable to extinction. A species could be vulnerable due to natural abiotic/biotic requirements or because it has been severely affected by some anthropogenic activity. By prioritising freshwater mollusc species according to their vulnerability, research can focus on collecting ecological data on these vulnerable species and hopefully guide future management for nature conservation.

1.4.1. Vulnerability of freshwater molluscs

The identification of threatened molluscs depends on the spatial scale being assessed: local, regional, continental or global. There are many forms of rarity and a series of criteria has been described by several authors (Rabinowitz 1981, Mace 1994, Orians 1997, rey Benayas *et al.* 1999, Newman 2000). Current criteria of vulnerability are usually based on two or more of the following: geographical range (wide or narrow), habitat specificity (broad or restricted), local abundance (locally abundant or widespread but sparse), habitat occupancy (coloniser or sedentary), rate of production (high or low fecundity), life history (short or prolonged life cycle) and/or source of threats (natural or artificial). A threatened species will often satisfy a combination of criteria. The combinations of different criteria of vulnerability has led to a variety of lists identifying threatened molluscs.

Recent global Red Data Lists of Threatened Animals (IUCN 1996, Hilton-Taylor 2000) by the World Conservation Union (IUCN) have been classified based on three criteria (IUCN 1994b):

(1) **Known geographical range**. This can be seen in two ways. Firstly, the extent of occurrence, the total area in which the species occurs. Secondly, the area of occurrence, the absolute area in which the species lives. E.g. *S. nitida* has a Palaearctic distribution, which includes Britain. However, in the UK it is only present in 20 distinct marshes.

(2) **The rate of population decline**. The assessment of decline is dependent on the life cycle of the species. *Margaritifera margaritifera* can live up to 100 years so the assessment of the decline of the species is usually taken over 180 years. Whereas for *A. vorticulus* by contrast, only lives for 1-2 years and the assessment of decline needs to be taken over the last ten years.

(3) **Source of threat**. Examples include habitat decreasing/degradation or the impact of an introduced species. Both *V. macrostoma* and *P. pseudosphaerium* have a relict distribution. Neither species may not be particularly rare but both are threatened by their dependency on one habitat.

1.4.1.1. Global status

Out of the estimated 135,000 species of molluscs worldwide, 5,000 are freshwater, 35,000 are terrestrial and the remainder being marine (van Bruggen *et al.* 1995). The IUCN Red List (1996) defined threatened status for over 2,000 mollusc species of which most are terrestrial and freshwater species (Seddon 1998b). *S. nitida* was classified as vulnerable in the earlier Red Lists (IUCN 1979-1994a), but since the introduction of new IUCN Red List categories it is no longer included on the list (IUCN 1994b, 1996, Hilton-Taylor 2000, Bouchet *et al.* 1999). None of the other three British Red Data Book species being investigated in this thesis are listed under the current IUCN criteria (Table 1.1).

1.1.4.2. European status

Within Europe, there are approximately 3,200 species of land and freshwater molluscs (Bank *et al.* 1998) and at least 9% are considered to be threatened (Wells & Chatfield 1992). In Europe, the European Community (EC) Directive 92/43/EEC (the Conservation of Natural Habitats and Wild Fauna and Flora, European Commission 1992) is the most important legislation instrumental for protecting groups such as freshwater molluscs. EC countries have also become parties to the Berne Convention (European Commission 1979a) aimed at protecting European wildlife and habitats. Despite the long list of threatened molluscs listed on the IUCN Red List (1979), which has since been regularly reviewed and updated, not all are automatically listed under current European legislation (Seddon 1998b). The main components of the European list of threatened molluscs are endemic or near-endemic species. There have been proposals for the EC to expand the list of threatened species to molluscs regarded as widespread but declining (Wells & Chatfield 1992). There are many species in Europe that appear to be safe but are restricted to relict habitats which are scattered and generally under threat. A provisional list has been drawn up by Wells & Chatfield (1992) of 24 species which have been identified as widespread but declining European molluscs. All are wetland or marsh species whose habitats under increasing pressure from fragmentation, drainage and pollution. All four of the RDB molluscs species being studied in this thesis are included in this provisional list.

1.1.4.3. British status

In Britain there are about 220 mollusc species (excluding marine), of which approximately 15% are on the British Red Data Book list (Bratton 1991). Around 80% of the threatened UK molluscs are associated with wetland habitats. The British Red Data book includes all four of the molluscs discussed in this thesis (Table 1.1). The UK Wildlife & Countryside Act (HMSO 1981) included several Schedules of protected species based on the Berne Convention, but does not take into account the British Red Data list and therefore does not include the four RDB molluscs under investigation (Table 1.1).

Under the UK Biodiversity Action Plan published in 1995 (HMSO 1995), proposals to safeguard threatened habitats and species were made. This led to a list of threatened species and habitats for which an action plan has or will be written. The BAP list includes several molluscs species including *S. nitida, A. vorticulus, V. macrostoma* and *P. pseudosphaerium* (Table 1.1). However, currently Species Action Plans (SAPs) have only been drawn up for 'priority' species including *S. nitida* and *A. vorticulus.* The SAP provides a description of each snail, identifies threats to it, sets conservation targets and suggests future research priorities.

The initial aims of the SAPs in 1995 for *S. nitida* and *A. vorticulus* was to establish the current status of the molluscs, especially at stronghold areas in East Anglia and south east England (HMSO 1995, Killeen & Willing 1997). This was followed by more detailed survey and ecological work on *A. vorticulus* (Jackson & Howlett 1999, Willing & Killeen 1998, Abraham *et al.* 1998, Temple 1998, Willing 1999, Killeen 1999c) and on *S. nitida* (Jackson & Howlett 1999, Killeen 2000). There have been a very few surveys of *V. macrostoma* (Watson 1997) and *P. pseudosphaerium* (Jackson & Howlett 1999) both of which are not currently priority species under the Biodiversity Action Plan.

1.5. Known habitats of the four scarce molluscs

There is a large variety of freshwater habitats in Britain, and mollusc species have managed to colonise the majority (Boycott 1936). However, drainage ditches of grazing marshes are regarded as one of the richest mollusc habitats supporting 70% of all UK freshwater molluscs (Killeen 1994, Kerney 1999). Four RDB species (*S.*

nitida, A. vorticulus, V. macrostoma and *P. pseudosphaerium*) are all generally restricted to the ditches of traditional grazing marshes such as those found on the Pevensey Levels in East Sussex or the Broadlands in Norfolk (Boycott 1936, Hingley 1979, Bratton 1991, HMSO 1995). However, it is unusual to find any two RDB species, in particular *S. nitida* and *A. vorticulus,* together in the same ditch (Killeen 1994, Killeen & Willing 1997, Jackson & Howlett 1999). Jackson & Howlett (1998) suggested that each of the RDB species have specific habitat requirements and they rarely occur in similar ditches.

1.5.1. Grazing marshes

Grazing marshes are defined in the UK as periodically inundated pasture or meadows, with ditches that maintain high water levels. They can contain standing brackish or freshwater. Almost all areas are grazed and some are cut foray or silage. The extent of grazing marshes in Britain is approximately 300,000ha, with the highest proportion being in England (200,000ha) (English Nature 2000). Grazing marshes have declined by 40% in the last 60 years especially in the south east of England around London (RSPB *et al.* 1997). In terms of biodiversity, a grazed marsh is considered to be more favourable than arable floodplain (Driscoll 1985, Palmer 1986, Foster *et al.* 1990). Since the 1930's, the conversion of grazing marshes to arable land has been recorded on Pevensey Levels, Romney Marsh, Lewes Brooks, Gwent Levels, Somerset Levels, and many others (Hones 1953, Straw 1955, Jackman 1976, NCC 1977, Marshall *et al.* 1978, Hicklin 1986, Palmer 1986). A Habitat Action Plan (HAP) has been drawn up and aims to maintain and improve existing grazing marshes, and to create new grazing marshes in targeted areas of up to 5,000ha (HMSO 1995).

Grazing marshes were formed over 300 years ago by the drainage and associated embankments of estuarine mudflats, alluvial washland and fens (Harts 1994, Sutherland & Hill 1995). They are usually inundated seasonally by natural tidal movement or rainfall runoff but it is also common for such grassland to be maintained at a certain level of inundation by the use of sluice gates in which the water can be varied seasonally. Individual marshes are greatly influenced by underlying geology, the water source and the management of the marsh. The primary reason for grazing marshes being important sites for the conservation of freshwater molluscs is due to their drainage ditches.

1.5.2. Drainage ditches

Though ditches are 'artificial' habitats, on grazing marshes they are considered to be relict habitats of the previous landscape that existed before drainage. There are many wetland species that are confined to ditch habitats including the four RDB molluscs. Ditches are permanent linear bodies of water not exceeding 5 metres wide. Where there is a flow, it can be in either direction, but is erratic and often artificially induced. Ditches were constructed to drain water away from fens and marshy areas to permit grazing in the summer months. In the winter, excess water from the adjacent watercourses floods onto the fields. As an artificial habitat, ditches need continuous maintenance. Without periodic mechanical de-silting, the vegetation and sediment would gradually accumulate causing the ditch to dry out and revert to a terrestrial habitat (Kirby 1992, RSPB *et al.* 1997, Painter 2000). Prior to the introduction of mechanical machinery in the 1930's, the ditches were cleared on an annual basis by hand tools. Today the 360^{o} mechanical excavator is the most frequent method for managing ditches, usually on a 5-10 year cycle (Marshall *et al.* 1978).

The roles of ditches are varied and this influences the degree and frequency of management. Large drainage ditches under the management of Internal Drainage Boards (IDBs) or the Environment Agency (EA) are dredged every year, maintaining steep straight banks with minimal marginal and aquatic vegetation. The smaller ditches under private landowners are managed according to the objectives of the owners e.g. wildlife interest, field boundary or water supply. Today many of the remaining grazing marshes are being conserved either by conservation bodies or under the auspices of conservation action such as ESA schemes (Environmentally Sensitive Areas), the WES agreement (Wetlands Enhancement Scheme) or Countryside Stewardship Scheme (CSS) (Jefferson & Grice 1998, English Nature 2000).

After the excavation of a ditch, the channel is gradually colonised by submerged aquatic plants aiding the accumulation of silt. The accretion of silt is often exacerbated by the poaching effect of the livestock, silt from upland sources of water and from runoff on areas of arable cultivation. Emergent plants will start to dominate with increasing sediment levels, and with time the ditch will start to dry out and will be colonised by terrestrial plants. This classical hydroseral succession was first described by Storer (1972) and George (1976).

The stages of ditch succession often progress at different rates between ditches and are influenced by several factors:

(i) **Extent of excavation**. Some managers completely dredge out ditches and the recovery stage is prolonged. Others will only partially excavate a section of a ditch so that the ditch is rapidly colonised by aquatic plants in the untouched sections.
(ii) **Frequency of excavation**. Depending on the objectives of the landowner, some ditches are excavated on a regular basis to maintain drainage. Ditches with no particular functions were often last cleared 20-30 years ago.
(iii) **Adjacent land-use**. On grazing land emergent plants are reduced by livestock grazing pressure and poaching. By contrast, on arable land nutrient run-off due to the use of fertiliser may encourage prolific growth of dominant emergent vegetation.
(iv) **Water flows**. In the ditches, flows are controlled by the use of sluice gates and in some places pumping stations. Depending on the function of the ditch and the water level, the flow is mostly regulated. It may happen for a few minutes infrequently when farmers wish to top up the water in the ditches or it could be a continuous flow in a ditch responsible for feeding water to a network of ditches.
(v) **Underlying geology/soil**. This is an important factor in sedimentation. Water that runs off soft sediment such as peat will aid the rapid siltation of ditches.
Each stage of ditch succession will possess a distinct aquatic invertebrate assemblage and the challenge to conservation managers is to provide all stages of ditch succession simultaneously.

1.5.3. Segmentina nitida

S. nitida is fairly widespread in the lowland marshlands from southern Europe to southern Scandinavia, but is thought to be declining across its range (Chatfield 1998). It occurs in northern Asia and parts of Middle Asia including Israel (Zhadin 1965, Jaeckel 1962). It has been recorded from 19 of the 25 limnofaunistical regions of Europe (Willmann & Pieper 1978). Some literature has considered *S. nitida* to have a palaearctic distribution (Beran & Horsak 1999, Freitag 1962), i.e. Europe, North Africa, western Asia, Siberia, northern China and Japan (Lawrence 2000).

In the 1930's when Boycott (1936) produced his classic paper on the habitats of freshwater molluscs in Britain, *S. nitida* was regarded as a rare but widespread species. It was flourishing in drainage ditches in Sussex, Norfolk, Cambridgeshire and Lincolnshire. Populations were found as far as north as York and with outlying populations in the Severn Valley and Glamorgan. Boycott (1936) recognised that *S. nitida* was typical of habitats such as drainage ditches, bogs, meres and ponds that were relicts of larger marshes. In the early 20th century the snail was known from over 100 10-km grid squares in central and southern England. Since 1965, it has been recorded from only 14 10-km grid squares, a contraction of approximately 80%, and is now largely confined to two main regions in East Sussex on Pevensey Levels and on the Norfolk & Suffolk Broads (Figure 1.2, Kerney 1999). There are smaller colonies on the Somerset Levels, Lewes Brook and North Kent marshes. Due to the dramatic decline of *S. nitida* it has been classified in the British Red Data Book as endangered RDB species (Bratton 1991) and a priority BAP species for which a steering group meets annually to discuss progress.

It is broadly agreed that *S. nitida* is confined to ditches on traditional grazing marshes, living in shallow clean calcareous water at the advanced stages of ditch succession when choked with floating, emergent and marginal vegetation (Boycott 1936, Killeen 1992, 1994, 1999a-c, 2000, Killeen & Willing 1997, Willing 1997c, 1999, Jackson & Howlett 1999, Baker *et al.* 1998). It has been suggested that the presence of *S. nitida* indicates that the ditches have been neglected and no longer serve their primary function for drainage (Killeen 1994). Ditches with high abundance of *S. nitida* are either heavily poached by cattle, creating a substantial margin or alternatively they are found in very shallow ditches overgrown by floating grass-mats with little standing water (Jackson & Howlett 1999, Killeen & Willing 1997). Many previous molluscs surveys have recorded *S. nitida* in ditches choked with emergent plants such as *Phragmites australis*, *Sparganium erectum*, *Carex acutiformis* (NCC & SWA 1978, Hicklin 1986), *Glyceria maxima* (Hicklin 1986, Jackson & Howlett 1999), along with floating vegetation such as *Hydrocharis morsus-ranae*, *Lemna trisulca*, *L. minor* and *L. gibba* and algae (NCC & SWA 1978, Hicklin 1986, Killeen 1994, 2000, Jackson & Howlett 1999).

Currently there is no published autecology study for *S. nitida*. A studentship with the Open University is currently looking at the life history of *S. nitida*. It is currently believed that *S. nitida* can live up to two years and breeding occurs over several weeks in the late spring to early summer months (Cottingham-Hill pers.comm).

1.5.4. Anisus vorticulus

A. vorticulus has a widespread but scattered distribution throughout central and southern Europe to western Siberia. It is local throughout its range and is universally regarded as rare. It is known from 11 out of 25 limnofaunistical regions of Europe (Willmann & Pieper 1978). It is considered to have a Euro-Siberian distribution consisting of the whole of Europe from southern Scandinavia to northern Spain and Asia (Lawrence 2000, Beran & Horsak 1999, Freitag 1962).

The species is considered to be one of the rarest molluscs in Britain (Willing 1996a) and since 1965 has only been found at three main sites: the Arun Valley (West Sussex), Pevensey Levels (East Sussex) and the Waveney Valley (East Suffolk). It has been recorded in 15 10-km grid squares but since 1965 appeared to have disappeared from 5 of them (Figure 1.2, Kerney 1999). The species which can be difficult to distinguish from the similar but much commoner *Anisus vortex,* is under serious threat of extinction if the remaining habitats are destroyed or altered (Boycott 1936, Willing & Killeen 1999). Despite the threat to the snail, it is only classified in the British Red Data Book as vulnerable (Bratton 1991). In 1995, along with *S. nitida* it was placed on the priority species list for action and a steering group meets annually to discuss progress.

Willing and Killeen (1999) described *A. vorticulus* to be confined to traditional grazing marshes in ditches with clean, often calcareous water with a rich aquatic flora. It is acknowledged that *A. vorticulus* does not demand the same choked conditions as *S. nitida* (Killeen & Willing 1997, Jackson & Howlett 1999). Optimum populations of *A. vorticulus* occur in ditches on average between 1.3-3 metres wide and 0.15- >1.0 metres deep (Willing & Killeen 1998, 1999). On Waveney marsh, Jackson & Howlett (1999) considered the snail to prefer more exposed conditions than *S. nitida,* being fairly typical of ditches that were comparatively wider and deeper. It has been noted that the snail occurs in greatest abundance in the shallow margins of a ditch created by poaching or the encroachment of marginal vegetation (Long 1968, Abraham *et al.* 1998, Willing & Killeen 1998, 1999, Killeen 1999c). *A. vorticulus* does not have strong association with any particular plant species, instead being typical of ditches with diverse macrophtyes (Willing & Killeen 1999). National mollusc surveys from the last 10 years have recorded *A. vorticulus* mainly among floating and submerged vegetation such as *Lemna trisulca, Hydrocharis morsus-ranae*, *Ceratophyllum demersum* (Kerney 1999), *Myriophyllum verticillatum*, charophytes and algae

(Jackson & Howlett 1999). The snails are considered to be less tolerant of tall emergent and bankside vegetation (Willing & Killeen 1998, 1999, Abraham *et al.* 1998, Killeen 1999c).

Autecological studies have established that breeding occurs principally between early June and mid July, spread over several weeks and sometimes continuing into August (Killeen 1999c, Willing 1999, Willing & Killeen 1999). Temperature is also considered to be influential on population numbers, with greater abundances of *A. vorticulus* found in the shallow and warmer margins. It is believed that *A. vorticulus* has a 12 month life cycle. Over-wintering adults have rapid growth during the spring before breeding and dying in the early summer months. Throughout the summer there is often a significant juvenile mortality and by November less than half of the juveniles are likely to have survived (Willing 1999, Killeen 1999c).

1.5.5. Valvata macrostoma

V. macrostoma is present in central and northern Europe, however, the precise range is uncertain due to confusion with another valvatid species, *Valvata pulchella* (Kerney 1999). *Valvata macrostoma* has been recorded in 15 of the 25 limnofaunistical regions of Europe (Willmann & Pieper 1978). Its range is from Western Europe to Siberia and parts of the Far East (Zhadin 1965).

In Britain, it is a localised snail restricted to regions south of the Fenlands and at Pevensey Levels. There is a colony on the Somerset Levels. It has been recorded from 26 10-km grid squares and since 1965 it is still present in 21 grid squares. However, it is now presumed extinct from a number of these sites (Figure 1.2, Kerney 1999). It has been listed in the British Red Data Book as vulnerable (Bratton 1991).

The ecological requirements for *V. macrostoma* are not well researched compared to the two RDB planorbids. It is generally found in a range of ditches from those at a relatively early stage to those at the more advanced stages of the management cycle (Killeen 1999a & b). *V. macrostoma* is characteristic of long established aquatic habitats (Boycott 1936, Bratton 1991, Killeen 1994, Kerney 1999). Large populations of *V. macrostoma* were recorded just two years after ditch clearance (Hingley 1979). However they are found at their greatest abundance in ditches of late successional stages with a well-developed aquatic flora (Killeen 1994, Watson 1997, Killeen 1999a & b).

1.5.6. Pisidium pseudosphaerium

P. pseudosphaerium is a local mussel present throughout Europe in the lowlands between the Alps and Southern Scandinavia (Kerney 1999). It is present in 11 of the 25 limnofaunistical regions of Europe (Willmann & Pieper 1978). In southern England it is thought to be associated with other local molluscs such as *S. nitida*, *A. vorticulus* and *V. macrostoma* in particular in the Broadlands (East Anglia), North Kent Marshes, Pevensey Levels (East Sussex), Arun Valley (West Sussex) and Somerset Levels. It also occurs in a few localities in northern England. In all it has been recorded in 36 10-km grid squares in Britain and but has disappeared in 3 of the sites since 1965 (Figure 1.2, Kerney 1999). Due to its association with other local species, it is considered to be a relict species which does not readily disperse, hence it is noted in the British Red Data Book as rare (Bratton 1991). Of the four RDB molluscs, *P. pseudosphaerium* appears to be the most tolerant of polluted environmental conditions. The bivalve was found in comparatively wide ditches with a muddy substratum (Killeen 1994, Jackson & Howlett 1999). On Waveney, it was also typical of ditches with pronounced emergent cover and a high biomass of filamentous algae and duckweed (Jackson & Howlett 1999).

1.6. Decline in distribution and abundance of the scarce molluscs

Concerns for the four RDB molluscs were raised in the early 1990's, when the UK Biodiversity Action Plan was being drafted. Several reasons have been proposed as a cause of the decline of *S. nitida, A. vorticulus, V. macrostoma* and *P. pseudosphaerium* (HMSO 1995). Inappropriate management of the ditches in which the molluscs live, nutrient enrichment of water due to fertiliser applications, and conversion of grazing marshes to arable farming with associated water table lowering (Bratton 1991, HMSO 1995).

1.6.1. Changes in ditch management

As already discussed, ditches are artificial habitats and with time will be succeeded by terrestrial vegetation. Eventually the ditch will reach a state where no standing water is available and the ditch has to be excavated. The common consensus is that a ditch has to be left for at least 5 years or more without clearance to contain an RDB mollusc (Killeen & Willing 1997, Willing & Killeen 1998, Abraham *et al.* 1998). This has been noticed in all the grazing marshes with the RDB molluscs on Waveney Valley (Jackson & Howlett 1999), Arun Valley (Abraham *et al.* 1998), Stour Valley (Killeen 2000), Pevensey Levels and Lewes Brooks (Killeen & Willing 1997). However a neglected ditch will gradually dry out and this would eventually result in the disappearance of RDB molluscs. Conservation guidelines do exist, which recommend a rotational de-silting regime over a 5- 7 years cycle (RSPB *et al.* 1994, 1997, Jenman & Kitchen 1998). However, several authors believe that this does not attain optimum conditions for *S. nitida* (Killeen 1994, Killeen & Willing 1997). The re-colonisation of a newly de-silted ditch by molluscs can be rapid, but the rate varies between species. All the RDB species are considered to have relatively longer recovery rates (Hingley 1979, Palmer 1986). With sympathetic management, e.g. clearing vegetation from one side or leaving sections of the ditches un-dredged, it is possible to retain RDB molluscs population without losing a functional drainage ditch (Kirby 1992). This has been observed on Pulborough Brooks nature reserve, where the Royal Society for the Protection of Birds (RSPB) have adopted less intensive management policies to maintain and enhance floral biodiversity. Many of the best ditches for *A. vorticulus* were cleared the year before the surveying of the freshwater mollusc communities (Willing 1999, Willing & Killeen 1999). The frequency of clearance may not be as important as the intensity of the management. However, little is known of the exact mechanisms and timing of ditch management that may optimise the conservation of freshwater molluscs.

1.6.2. Changes in water chemistry

Water chemistry is generally uniform across a grazing marsh, and effects on the distribution of the macro-invertebrates between ditches only appears to be significantly affected by salinity (Wade 1977, Marshall *et al.* 1978, Clare 1979). On the Norfolk Broadlands in East Anglia, *S. nitida* has been recorded in both tidal and non-tidal waters (Ellis T. 1933 cited in Baker *et al.* 1998, Ellis A. 1941). However, recent surveys at Waveney Valley have not recorded *S. nitida* in any of the brackish ditches (Jackson & Howlett 1999). The low number of *S. nitida* at Stodmarsh NNR has been linked to the regular flooding of the reserve by saline water from the River Stour (Killeen 2000).

In comparison with other aquatic habitats, ditches are regarded as naturally eutrophic waterbodies (Rodwell 1995). In the Waveney Valley, the four RDB molluscs were recorded in ditches dominated by filamentous algae and duckweed species along with occasional *H. morsus-ranae* and *Ceratophyllum demersum* all characteristic of eutrophic conditions (Rodwell 1995, Jackson & Howlett 1999). In recent decades, increasing nutrient runoff from fertiliser applications has been accompanied by changing vegetation in drainage ditches. At high nutrient loading, there is usually an increase in phytoplankton and floating nuisance plants such as duckweed as well as a complete loss of submerged aquatic plants and sometimes the regression of emergent vegetation (Mason & Bryant 1975, De Groot *et al.* 1987, Moss 1988, Janse & van Puijenbroek 1998). The effects of eutrophication on molluscs is less well understood (Dalorph & Thomas 1991, 1995, Thomas & Dalorph 1991, 1994, Jones *et al.* 1999, 2000).

1.6.3. Changes in landuse and effects on water levels

The effects of water level on general biodiversity on grazing marshes has been a fairly contentious subject in the past 20 years. Many of the grazing marshes which are designated as Sites of Special Scientific Interest (SSSIs) are subjected to Water Level Management Plans (WLMPs). However, not all WLMPs have been implemented due to lack of resources and the requirement for landowner agreements. It has been argued that low water levels associated with the rise of arable farming in favourable mollusc sites is more harmful than nutrient enrichment (Hicklin 1986, Willing 1996a & b). The lowering of the water table can occur by natural spring water drying up, the abstraction of water for irrigation, the lack of rain, or the inefficient management of water resources on the marshes (Jackson & Howlett 1999, Willing 1999). Evidence suggests that a ditch which becomes completely dry or is dry for a large part of the year is unsuitable for any of the RDB molluscs even *S. nitida*. These ephemeral ditches are usually characterised by drought-resistance species such as *Aplexa hypnorum* and *Anisus leucostoma* (Killeen 1999a, 2000, Watson 2000).

The greater control of water on grazing marshes has led to shorter and more intense flooding in the winter months, which does not favour freshwater mollusc communities. Flooding is thought to be essential, allowing the RDB populations to disperse to new ditches. On Pulborough Brooks, the increase in the number of ditches containing *A. vorticulus* has been linked to the prolonged flooding period promoted by the RSPB (Abraham *et al.* 1998, Willing & Killeen 1998, 1999, Temple 1998, Willing 1999, 2000). Lack of dispersal is thought to be a significant factor in preventing re-colonisation of the RDB molluscs (Baker *et al.* 1998, Jackson & Howlett 1999, Willing 1996a & b, Killeen 1999c, 2000).

1.7. Aims & Objectives

The aim of the research described in this thesis was to address the concerns raised in the UK Biodiversity Action Plan over the lack of ecological data for *S. nitida* and *A. vorticulus* and to investigate some of the potential threats facing the species (HMSO 1995). In due course, action plans will be drawn up for *V. macrostoma* and *P. pseudosphaerium* and therefore it was decided to collate ecological information for all four BAP species. The primary objectives were:

1. To assess the distribution of all four Red Data Book species in drainage ditches across several large grazing marshes in south-east England. An associated objective was to examine a range of biotic and abiotic factors to determine which variables correlated with distribution, and which best predicted presence/absence.

2. To assess the distribution of the three gastropods within ditches, thereby gaining an understanding of the associations between abundance and variations in biotic or abiotic factors throughout a given ditch.

3. To assess patterns in gastropod assemblages in drainage ditches from four grazing marshes and relate these to environmental features in the ditches using multivariate statistical methods. Ditches were classified according to their vegetation character and stage of vegetation succession. Variations in snail assemblages and diversity were then assessed between the putative successional stages.

4. To assess the assemblages of bivalve in relation to ditch characteristics. The relationship between the occurrence of bivalves and gastropods was examined to understand the implications for the management of ditches for both gastropods and bivalves.

5. To use an experimental approach to investigate short-term effects of nutrient loading on the water chemistry and mollusc assemblages in ditches.

6. To consider implications of the results of the surveys and field experiment for management of drainage ditches for freshwater molluscs.

1.8. Study sites

The distribution of *S. nitida* and *A. vorticulus* is restricted to the south and east of England, however it was not feasible to include this whole area in this research. The two main regions in which both snails occur respectively are Norfolk/Suffolk and Sussex/Kent. Both regions fall under different authorities of the Environment Agency. For the purpose of this study, only the grazing marshes in Sussex and Kent were surveyed due to the logistical difficulties of fieldwork in two large regions. Four of the largest grazing marshes in south east England were surveyed: the Arun Valley in West Sussex, Lewes Brooks and Pevensey Levels in East Sussex and the Stour Valley in North Kent (Figure 1.3).

1.8.1. Arun Valley

The River Arun flows for 84 kilometres from its source near Horsham, which is fed by springs. It continues southward through the South Downs before joining the sea at Littlehampton on the south coast of England. The largest tributary is the River Rother (a chalk stream) which joins half way along the Arun's length. The Arun runs through countryside and farmland, of which part is situated within the Sussex Downs Area of

Outstanding Natural Beauty (AONB). Much of the Arun and its floodplain was designated Special Protection Area (SPA) under the EC Birds Directive 79/409/EEC (European Commission 1979b) and a Ramsar site (Ramsar Convention Bureau 2002). In the lower valley the grazing marshes contain three SSSIs, internationally important for overwintering birds and aquatic invertebrates (English Nature 2000).

The geology of the floodplain of the Arun between Pulborough and Amberley, consists of alluvial deposits with areas of peat in the northern half of Amberley. Underlying the alluvium there is a complex geology of Upper Greensand, Gault (marly clay), Folkestone Beds (sand and ferruginous rock), Sandgate Beds (sand-rock and clay), Hythe Beds (sand, loam and chert), Atherfield Clay and Weald Clay. South of Amberley, the underlying rock is chalk (Abraham et al. 1998).

Pulborough Brooks comprises 171ha managed by the RSPB and has 15km of internal ditches. The west boundary is along the Arun and along the eastern boundary of the north Brooks are a number of calcareous springs which run off the Downs. Pulborough just falls outside of the Sussex Downs ANOB, but has been designated as SSSI and is part of the Arun SPA (Temple 1998).

Amberley Wildbrooks along the east bank of the Arun is managed by the RSPB, Sussex Wildlife Trust (SWT) and a consortium of private landowners. Covering an area of approximately 300ha, it is a designated SSSI for it botanical interest supporting about 80% of known aquatic plant species in the UK (English Nature 2000). On the opposite bank of the Arun is Waltham Brooks, a small reserve less than 50ha, designated as SSSI and managed by the SWT.

1.8.2. Ouse Valley and Lewes Brooks

The River Ouse flows for approximately 60 kilometres through the High Weald and the Downs before joining the sea at Newhaven. The largest tributary is the River Uck, which joins before the Downs. The river flows through a large proportion of rural area which is included in the High Weald AONB, Sussex Downs AONB and the South Downs Environmentally Sensitive Area (ESA). Downstream from the town of Lewes is Lewes Brooks, a grazing marsh and a SSSI (English Nature 2000). Situated to the west of the Ouse, the former and now drained wetland covers approximately 640ha. It is influenced by the brackish water of the Ouse as well as a number of freshwater springs along the western boundary. The area is served by approximately 8.6km of primary channels managed by the Environment Agency (EA) and over 63km of minor subsidiary channels managed by individual landowners. The soil consists of fertile alluvial deposits overlying a chalk formation (Hicklin 1986).

1.8.3. Pevensey Levels

The Pevensey Levels is one of the largest and least fragmented lowland wet grassland in south east England, lying between Eastbourne and Bexhill-on-Sea. The Levels were originally reclaimed from coastal marshes and today the principle source of surface water flow comes via the Waller's Haven a large drainage channel (Gasca-Tucker & Acreman 1998, 2000). The geology of the Levels is a complex sequence of alluvial clays and peat surrounded by the hills of the Downs and High Wealds (Gasca-Tucker & Acreman 1998). The grazing pastures at Pevensey Levels are intersected by a complex system of ditches supporting a variety of important wetland communities and the site is considered to be one of the most important sites in Britain for freshwater molluscs (Killeen 1994). The Levels have been designated a Ramsar site and parts of the Levels are SSSI and a National Nature Reserve (NNR) (English Nature 2000). EA, EN and SWT have set up the Pevensey Levels Restoration Project. This aims to restore the Levels to the conservation status at the time of the original notification as a SSSI in 1990 under the Countryside and Wildlife Act (HMSO 1981). The Levels cover approximately 3,578ha of which over 3,000ha is SSSI and 314ha is NNR managed by English Nature (EN) and SWT.

1.8.4. Stour Valley

The Great Stour flows approximately for 58 kilometres, in a north-eastly direction from Ashford, through the chalk of the North Downs to Canterbury. Downstream of Canterbury a tributary, the Little Stour (chalk stream), joins the Great Stour and the river then becomes simply known as the River Stour. The Stour flows for about 35 kilometres before joining the sea at Sandwich. The lower Stour Valley runs through floodplains which are important agricultural land, as well as being of conservation interest (NRA 1992). Stodmarsh lies between the Great Stour and Little Stour covering 481ha. Stodmarsh has been designated Ramsar site, SPA, NNR and SSSI managed by English Nature, it is also a proposed candidate for Special Areas of Conservation (SAC) (English Nature 2000). The soil of the Lower Stour valley from

Stodmarsh to Sandwich is mainly marine and river alluvium overlying relative young rocks of Brickearth and Thanet Beds (NRA 1992).

Table 1.1: Conservation status of four scarce wetland molluscs typical of drainage ditches in south-east England.

	S. nitida	*A. vorticulus*	*V. macrostoma*	*P. pseudosphaerium*
Global status				
IUCN Red List (1979-1994) [9, 10]	Vulnerable	none	none	none
IUCN Red List (1996-2000) [7,11]	none	none	none	none
European status				
Berne Convention (1978) [5]	proposed [3]	none	none	none
Habitats directive (1991) [6]	none	none	none	none
European Red List (1991) [13]	Vulnerable	none	none	none
CORINE spp. checklist (1991) [4, 12]	listed	none	none	none
British status				
Wildlife Act (1981) [8]	none	none	none	none
UK RDB (1991) [2]	Endangered	Vulnerable	Vulnerable	Rare
BAP (1995) [1]	priority	priority	listed	listed

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Figure 1.1: Conceptual model of the importance of abiotic and biotic factors in determining the distribution and abundance of freshwater molluscs at two spatial scales (adapted from Lodge *et al.* 1987).

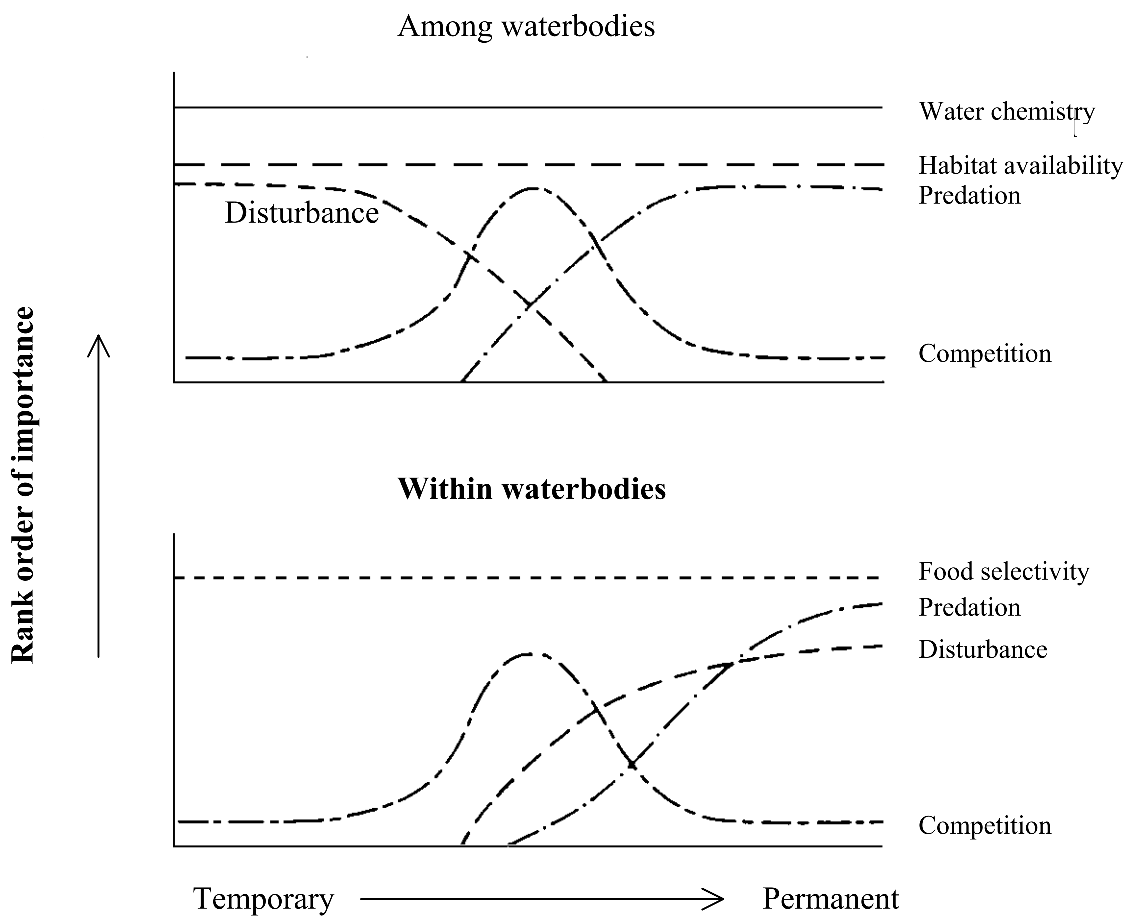
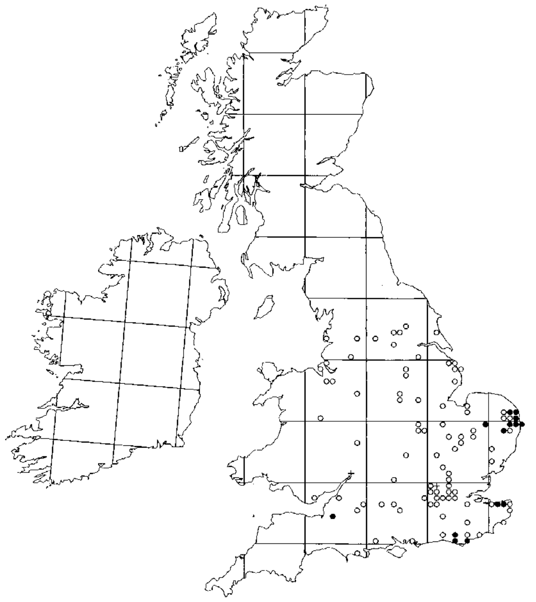
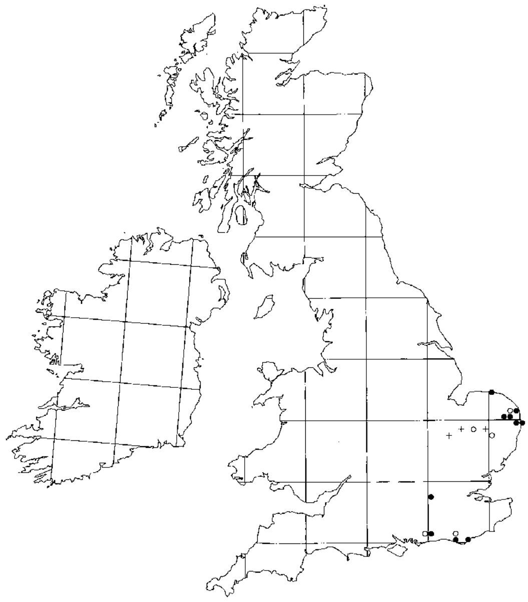


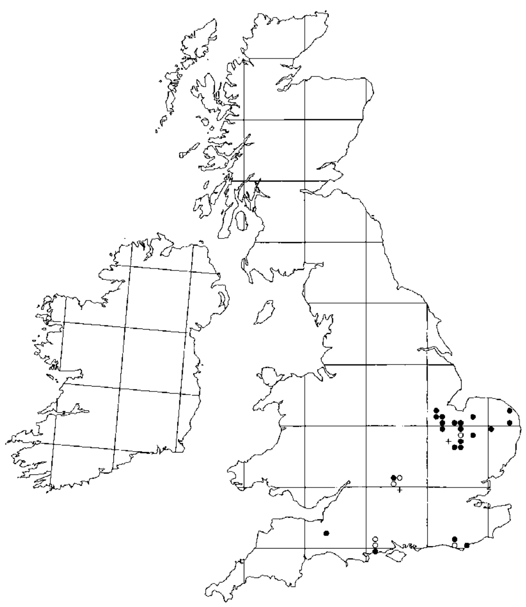
Figure 1.2: Distribution of four British Red Data Book Molluscs in the UK (• = Records made in or after 1965, ○ = Records made prior 1965 only, + = Fossil occurrences, Top of page = North) (maps from Kerney 1999).



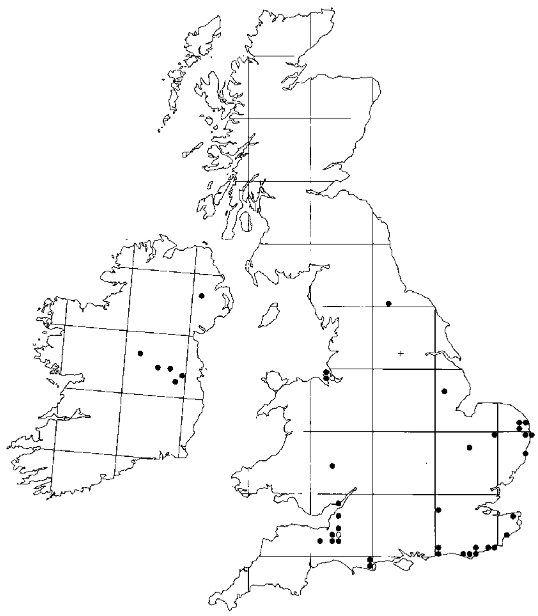
Segmentina nitida



Anisus vorticulus

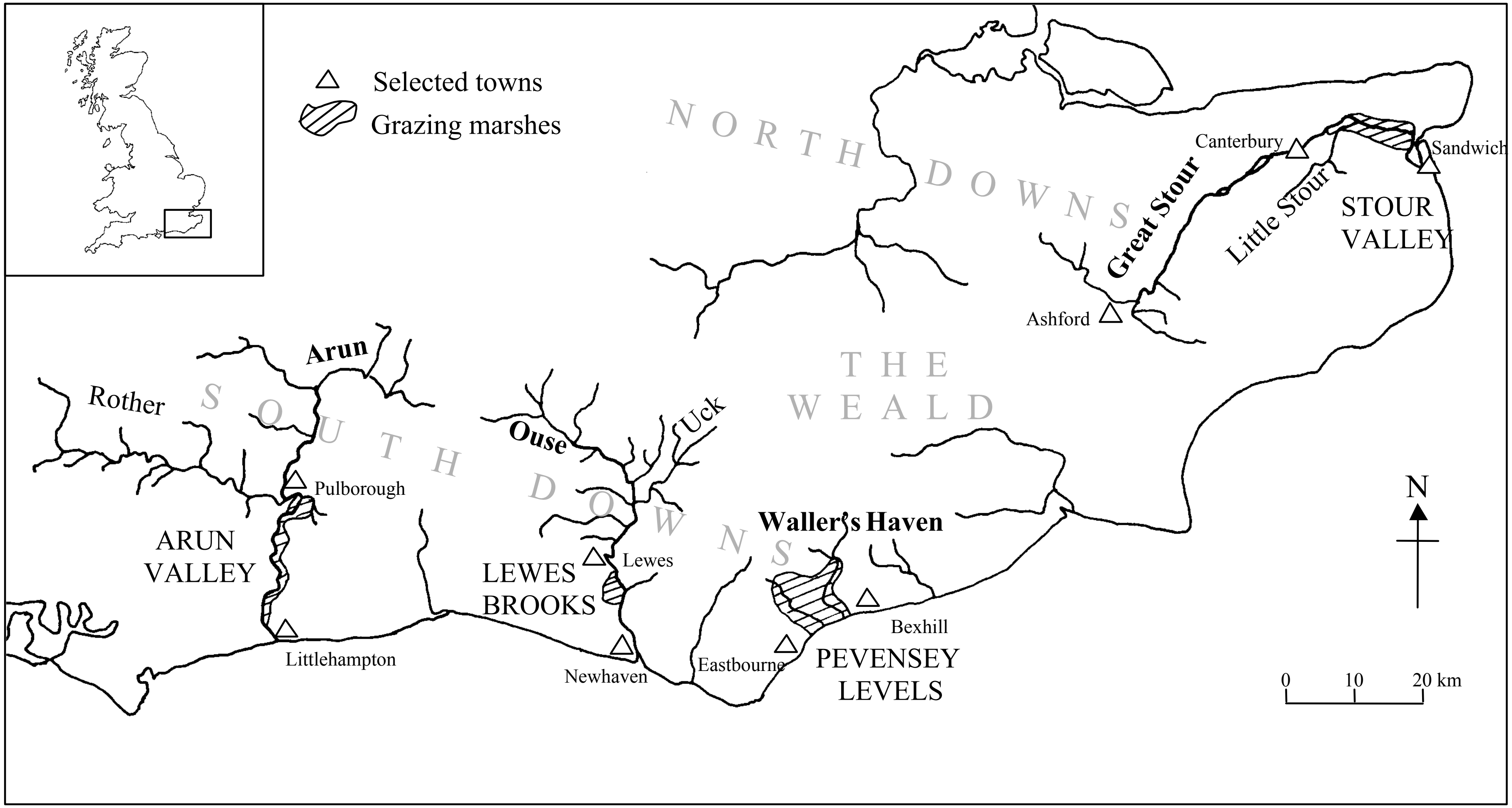


Valvata macrostoma



Pisidium pseudosphaerium

Figure 1.3: South-east England showing the four grazing marshes used for the mollusc surveys, in relation to the adjacent catchment of major rivers.



-Chapter 2-

Factors affecting the distribution of three scarce wetland molluscs of lowland Britain: patterns between drainage ditches

2.0. Abstract

Grazing marshes represent one of the most vulnerable wetland habitats in western Europe, declining in extent in the UK by over 40% between the 1930s and 1980s due to drainage, abstraction and pollution. Their drainage channels (ditches) represent relict habitats of previously extensive marshland but management is now required to maintain and enhance the unique wetland communities that still survive. Three Red Data Book molluscs: *Segmentina nitida*, *Anisus vorticulus* and *Valvata macrostoma* are particularly important on grazing marshes, and their macro-distribution was examined in 106 drainage ditches on four grazing marshes in south-east England in 1999. Data on vegetation, water chemistry and other ditch attributes were collected contemporaneously from each ditch. One-way ANOVA was used for each snail species to assess variations in vegetation structure and water chemistry between occupied and unoccupied ditches. The ranked abundances for each RDB species were related to vegetation character using Spearman's rank correlations against vegetation principal components. Multiple logistic regressions were also carried out to identify which environmental variables best predicted the presence of RDB snails at the ditch-scale, thereby providing vital management information.

S. nitida occurred in shallow calcareous ditches with dense stands of emergent vegetation. Ditches with *V. macrostoma* were dominated by floating plants and had significantly higher concentrations of chloride than unoccupied ditches. *A. vorticulus* was found in comparatively less calcareous ditches with a high diversity of aquatic plants. Multiple logistic models indicated that *S. nitida* and *V. macrostoma* were absent from otherwise suitable ditches, that had significantly higher concentrations of nitrate and nitrite, than occupied ditches. This result is important in indicating potentially negative effects of eutrophication on these scarce wetland species.

To support all three RDB snails at the marsh scale, the management of ditches should offer a range of vegetation types from dense emergent stands to open ditches with submerged and floating plants. Where vegetation conditions in the ditch appear to be ideal for the RDB species, preventing elevated concentrations of nutrients by reducing agro-chemical use on grazing marshes is likely to be of benefit.

2.1. Introduction

Under the Convention of Wetlands of International Importance, wetlands are defined as "areas of marsh, fen, peatland and water. They can be natural or artificial, permanent or temporary with water that is stagnant or flowing, fresh, brackish or salt and which does not exceed 6m at low tide" (Davies 1994, Ramsar Convention Bureau 2002). Wetland types are shaped by their hydrological regimes and in general, regimes characterised by regular flooding and large ranges in water levels will have higher productivity and species richness (Heathwaite 1995, Hughes & Jones 1995, Thompson & Finlayson 2001). However, a range of other factors can influence natural wetland character such as size, location and physico-chemical character (Rodwell 1991, 1995, Heathwaite *et al.* 1993 Hughes & Heathwaite 1995). More importantly and of increasing concern, the attributes, functions and services of wetlands are under threat from human activities such as drainage, abstraction and pollution (Dugan 1990, Gilman 1994). Inevitably, the habitats and the species that depend on these wetlands are affected (Wheeler & Shaw 1995, Newbold & Mountford 1997).

As an important type of lowland wetland in the UK, grazing marshes are dependent on the maintenance of a suitable water-level regime, along with sympathetic management of the wet grasslands and other basin features that contribute to runoff (Driscoll 1985, Mountford *et al.* 1993, Jenman & Kitchin 1998, Jefferson & Grice 1998, Tallowin *et al.* 1998). Grazing marshes are subjected to periodic flooding and high water tables, being characteristically found in river valleys with impeded drainage behind sea defences. Increasingly, intense hydrological management has led to losses in grazing marshes across the whole UK. Between the 1930's and 1980's, they declined in area by 64% in the Greater Thames, 48% in the Romney Marshes and 37% in the East Anglian Broadlands (HMSO 1995, RSPB *et al.* 1997). Important features include the complex networks of drainage ditches which often contain relict wetland systems of species-rich plant and animal communities that were once common to the whole marsh (Marshall *et al.* 1978, Harts 1994, Sutherland & Hill 1995, Jefferson & Grice 1998, Drake 1998b). In recent decades, ditches have become increasingly enriched by nutrients from discharge and runoff (Janse & van Puijenbroek 1998). They have also been either neglected or over-managed (Kirby 1992). As a result, many characteristic species are considered threatened due to the loss of the ditches, the deterioration of water quality and changes in the hydrological cycle on the wetlands. Several species have experienced dramatic declines in recent decades but for many there is a lack of information on their status and ecology. This is particularly true for aquatic invertebrates (Clymo *et al.* 1995, Wells & Chatfield 1995, Koomen & van Helsingen 1996). For example, unique to the drainage ditches of grazing marshes in the UK are three wetland snails, *Segmentina nitida* (Müller 1774), *Anisus vorticulus* (Troschel 1834) and *Valvata macrostoma* (Mörch 1864). All three are in the UK Red Data Book (RDB) (Bratton 1991) and listed as 'Declining but Widespread' in Europe (Wells & Chatfield 1992, 1995). The ditches in which they occur are managed often by conservation agencies, private landowners and water authorities, to create a diverse range of ditch profiles and habitats. However, little is known of the exact habitat requirement of each of the RDB snails and their increasing rarity is still unexplained.

The aim of this survey was to assess the distribution of these three RDB snails between ditches across several grazing marshes in south-east England. A range of biotic and abiotic factors were examined to determine which variables correlated with distribution, which predicted the presence/absence of the snails, and which offered opportunities for management.

2.2. Methods

2.2.1. Study sites

The mollusc assemblages and environmental character of drainage ditches were extensively surveyed during May-September 1999 on four large grazing marshes in south-east England where one or more of the target RDB molluscs had previously been recorded (Chapter 1, Figure 1.3): the Arun Valley in West Sussex (TQ 0314), the Lewes Brooks (TQ 4208) and Pevensey Levels (TQ 6409) both in East Sussex, and the Stour Valley in Kent (SQ 2663) (Killeen & Willing 1997). The marshes vary in area from 3,500 ha on Pevensey Levels to 640ha on Lewes Brooks. All are periodically flooded during the winter months and in the summer months are grazed mainly by cattle. The three largest marshes have been designated as Ramsar sites (Ramsar Convention Bureau 2002): the floodplain of the River Arun, Pevensey Levels and one of the marshes of the Stour Valley (Stodmarsh). The Arun Valley and Stodmarsh have also been designated as Special Protection Areas (SPA) under the EC Birds Directive (79/409/EEC) (European Commission 1979b) and Stodmarsh is a proposed candidate for Special Area of Conservation under the EC Habitats Directive (92/43/EEC) (European Commission 1992). Stodmarsh along with the north-west part of Pevensey Levels are National Nature Reserves (NNR) managed by the statutory agency for nature conservation, English Nature. All the marshes support Sites of Special Scientific Interest (SSSIs) due to their importance for overwintering birds and aquatic communities (Chapter 1).

A total of 106 ditches were individually surveyed, representing 81 randomly selected ditches and 25 targeted ditches where either *A. vorticulus* or *S. nitida* have previously been recorded (Killeen & Willing 1997, Willing & Killeen 1998). The random ditches were selected on the basis of grid numbering across the marshes. An average of 33 ditches were surveyed from the three largest marshes and a smaller selection was surveyed on Lewes Brooks (6 ditches) (Table 2.2). The targeted ditches were vital to ensure a sufficient sample of ditches occupied by the RDB snails for presence/absence analyses while the random ditches provided a true indication of the relative scarcity of *A. vorticulus* and *S. nitida* at the marsh-scale.

2.2.2. Sampling protocol

A 20 m stretch was surveyed along each ditch from which molluscs were collected at four randomly located sampling points along one bank. The sample locations were randomly selected from distances between 0.05 to 1.0 metres from the bank. A sample consisted of a vigorous sweep over 1.0m, parallel to the bank and including the sediment, vegetation and water surface, using a sieve net with 0.18m diameter and 1mm mesh (Killeen 1994). A pilot study comparing this method with more extensive D-net sampling, showed that the sieve adequately detected all snail species and represented relative abundance while also producing a more manageable sample volume (Appendix 1). The samples were preserved on site in 70% Industrial Methylated Spirit (IMS). In the laboratory the samples were washed through a 500µm mesh sieve and RDB snails were removed and identified with a light microscope (x10) using Macan (1977).

Prior to mollusc sampling, a water sample was collected from each ditch at a distance of 1.0m from the bank and 0.15m below the water surface. Samples were analysed within 24 hours for total organic nitrogen (TON), nitrate, nitrite, ammonia, ortho-phosphate and chloride using spectrophotometry. Alkalinity was determined by titration to pH 4.5, calcium was analysed by inductively coupled plasma mass-spectrophotometry and BOD by Winkler's procedure. Chlorophyll-*a* was extracted by acetone from each sample and then determined by spectrophotometry. Conductivity and pH were measured by specific electrodes.

The vegetation in each ditch was assessed by recording macrophyte diversity and by estimating the percentage of the ditch surface covered by all vegetation and individually by amphibious, emergent, floating and submerged plant groups. The 20m ditch section used for sampling molluscs was also used for a contemporaneous vegetation survey adapted from the standard ditch vegetation methodology devised by Alcock & Palmer (1985). An estimate was made of the total percentage of the water surface covered by all vegetation as well as individual cover by submerged, floating, emergent and amphibious plant groups. Cover was defined as the area occupied by each of the above components when the site was viewed from above. Total cover was always 100% or less, whereas the combined percentage of the four plant group was occasionally over 100% due to layering within the vegetation. Submerged plants included species such as *Lemna trisulca* and *Ceratophyllum demersum* that typically grow under a floating layer of vegetation. Floating vegetation consisted of plants with their vegetative parts on the water surface such as *Hydrocharis morsus-ranae*. Examples of emergent plants were *Typha* species and *Phragmites australis* whose root systems are predominantly submerged. Amphibious plants are not aquatic species but are able to tolerate marshy conditions such as *Glyceria* and *Juncus* species.

All the plants in the 20m ditch section were recorded and identified to species using Rose (1981). If plants could not be identified in the field at these levels, they were recorded to genus (e.g. *Callitriche* spp). Nomenclature followed Dony *et al.* (1986) for both common and scientific names. Estimates of cover were allocated for each wetland plant species within the 20m stretch of the ditch using DAFOR scores (Dominant: 71-100%, Abundant: 51-70% , Frequent: 16-50%, Occasional: 6-15% , Rare: 1-5%).

Other ditch attributes were recorded from each ditch at the same time as the molluscs and included the dimensions of individual ditches (width, mid-channel depth, depth of sediment layer, height of bank), the adjacent land-use (grazing, hay, arable, woodland) and a discrete measure of whether the ditch was heavily shaded or had no shade (0: no shade, 1: $<\frac{1}{3}$ of ditch shaded, 2: $\frac{1}{3}$ to $\frac{2}{3}$ of ditch shaded, 3: $>\frac{2}{3}$ shaded).

The depth of the mid-channel was measured using a calibrated pole rested on the substrate. The pole was then pushed into the sediment and the depth of the soft sediment layer calculated. The percentage of the ditch choked by vegetation was estimated by assessing the proportion of the water column that was blocked by macrophytes considered to be impeding water flow. This measure differed from vegetation cover, which only assessed the percentage cover of vegetation on the water surface with no indication that flow was restricted.

2.2.3 Statistical analysis

The objective of the analyses was to determine which environmental factors best described the macro-distribution of the RDB snails, which correlated with abundance, and which predicted the presence/absence of the snails. One-way ANOVA (MINITAB v12 1998) was used separately for each species to assess variations between occupied and unoccupied ditches in the vegetation structure, water chemistry and ditch attributes. Prior to ANOVA, chloride, BOD and chlorophyll-*a* were logarithmically transformed to homogenise the variances, and all protocols followed Fry (1993). Principal Component Analysis (PCA) was used to assess the major variations across all ditches in vegetation composition based on the correlation matrix between plant groups. The ranked abundance for each RDB species was then related to vegetation PCA scores using Spearman's rank correlations.

Stepwise logistic regression (S-PLUS 4.5 1997) was used to identify the best sub-set of variables that optimised the prediction of RDB snails being present in a ditch (MINITAB 1998, Hosmer & Lemeshow 1989, Fielding & Bell 1997, Peeters & Gardeniers 1998, Tabachnick & Fidell 2001). Chemistry data were logarithmically transformed apart from nitrite, which was transformed by inversion, and alkalinity, which required no transformation. The vegetation and habitat features were not transformed with the exception of width, which was logarithmically transformed. Logistic regression uses a linear combination of independent environmental variables to explain the dependent variable coded as 1 or 0, which is the presence and absence of a RDB snail. The logit transformation equation generates a value between 0 and 1 for each ditch which represents the probability of a species being present modelled as a linear function of 22 possible explantory variables:

$$\text{logit}(p) = \frac{p}{1-p} = b_0 + \sum_{i=1}^{22} b_{1i} x_i$$

in which b_0 and b_i are the regression constants. The Kappa statistic (Fielding & Bell 1997) was used to assess which combinations of independent variables best predicted the presence of RDB snails, first on the calibration data set, but also on a smaller set of 20 test ditches which were surveyed the following year (see Chapter 3). Kappa was chosen for its robustness in assessing the extent in which models accurately predict occurrence rather than by chance, in ways that are least affected by low prevalence (Manel *et al.* 2001). The evaluation of performance using Kappa was derived from matrices of confusion that identified true positive, false positive, false negative and true negative predicted by each model (Fielding & Bell 1997, Manel *et al.* 2001). Presence of a species is usually accepted at a threshold probability of 0.5 (Manel *et al.* 1999, Manel *et al.* 2001), however the outcomes for each model were explored across a range of threshold levels from 0.2 to 0.7 to allow for the low prevalence of the RDB species being studied. In medical applications, Kappa values of 0.0-0.4 indicate slight to fair model performance, values of 0.4-0.75 good performance and 0.8-1.0 excellent (after Landis & Koch 1977, Fielding & Bell 1997, Manel *et al.* 2001).

The best logistic models, based on their performances with the calibration and test data-sets, were used to identify ditches that appeared suitable for the RDB snails but for unknown reasons were currently unoccupied. One-way ANOVA was then used to compare variations in the environmental variables between three groups of ditches: those ditches where each RDB snail species was absent, unoccupied ditches where presence was predicted and ditches where the snails were actually present. Where it was not possible through transformation to homogenise the variances of the environmental variables, the Kruskal-Wallis test was used in a similar way.

2.3. Results

2.3.1. Ditch and marsh character

The vegetation structure and plant richness in the ditches were relatively similar across the four grazing marshes used in the study with the exception of Stour Valley where diversity of floating and amphibious plants were significantly lower (Figure 2.1). Also there was significantly less floating cover in the ditches of the Arun compared to Pevensey and Stour (Figure 2.1). Almost 50% of the variations in the ditch character and vegetation structure was described by the first 3 axes of the PCA (Table 2.1). The first PCA axis dominantly described a decrease in ditch size, width and a decrease in open water but increasing cover particularly by emergent species. The second axis described a reduction in both plant diversity and amphibious cover. The third axis described a decrease in floating vegetation as open water increased and depth declined. Most significant in the context of this study, changes in abundance of the three target RDB species correlated respectively with each of these vegetation components (Table 2.1).

Water chemistry varied between the marshes with significantly higher alkalinity and calcium concentrations in the ditches of Lewes Brooks and the Stour Valley compared to Pevensey Levels and the Arun Valley (Figure 2.2). Conductivity and chloride were significantly lower in the Arun ditches compared to the other grazing marshes (Figure 2.2). Nutrient concentrations did not vary significantly across all four grazing marshes although nitrite tended to be higher on the Stour and Arun (Figure 2.3).

2.3.2. Snail distribution

Of the 106 ditches surveyed, *S. nitida* was present in 17%, *A. vorticulus* in 12% and *V. macrostoma* in 18%. When only randomly selected ditches were examined the percentage occurrence was slightly lower for *S. nitida* (13%), *A. vorticulus* (8%) and *V. macrostoma* (16%) (Table 2.2). None of the RDB species were significantly associated with each other (Table 2.3) and so appeared to occur in different ecological conditions.

2.3.3. Segmentina nitida

One-way ANOVA between occupied and unoccupied ditches indicated that *S. nitida* was found at significantly higher concentrations of alkalinity, calcium, chloride and conductivity than where they were absent (Tables 2.4 & 2.5). The snail also apparently preferred ditches with significantly shallower depths, greater percentage cover of emergent plants, less open water and a greater percentage of the ditch choked with vegetation (Tables 2.4 & 2.5). The latter was reflected in increasing abundance of *S. nitida* along vegetation PCA axis 1 representing increasingly species-poor stands of dense emergent and amphibious vegetation (Table 2.1). *S. nitida* thus occurred in shallow, calcareous ditches with dense emergent vegetation and little open water.

2.3.4. Anisus vorticulus

By contrast with *S. nitida*, concentrations of calcium and alkalinity were significantly lower in ditches occupied by *A. vorticulus* compared to ditches without the species (Tables 2.4 & 2.5). Vegetation structure appeared to have little effect on distribution between ditches (Table 2.5). However, of the three snails examined, *A. vorticulus* was most linked to sites with high plant diversity. It occurred in ditches with a range of vegetation structures as seen by its positive correlation with the vegetation PCA axis 2 representing high diversity and increased percentage cover particularly of amphibious plants. *A. vorticulus* declined where ditches became wider and deeper with more open water (Table 2.1).

2.3.5. Valvata macrostoma

One-way ANOVA indicated significantly higher chloride concentrations in ditches occupied by *V. macrostoma* than those that were unoccupied (Tables 2.4 & 2.5). Abundance declined along vegetation PCA axis 3 indicating preference for high percentage cover and diversity particularly of floating vegetation (Table 2.1). Overall *V. macrostoma* was typical of ditches predominately occupied by floating vegetation and little open water (Tables 2.1 & 2.5).

2.3.6. Logistic regression

Multiple logistic regression provided several potential models that could be used to predict the presence and absence of each RDB snail species. According to model performance measures, all three species were best predicted at a probability threshold level of 0.2 (Table 2.6). The model which best predicted the distribution of *S. nitida* consisted of calcium, chloride and percentage cover by emergent vegetation, with Kappa indicating a good fit to both calibration and test data (Table 2.6). *A. vorticulus* was best predicted by calcium, pH, BOD, water depth and percentage of the ditches colonised by amphibious vegetation (Table 2.6). For *V. macrostoma*, the best model consisted of calcium, chloride and percentage cover by floating vegetation (Table 2.6). In the latter two species, Kappa again indicated good model performance (Table 2.6).

The logistic regression models were used to indicate ditches from which each RDB species was currently absent, but which appeared to be suitable for occupancy on the above key predictors. Kruskal-Wallis tests indicated that *S. nitida* was absent from apparently suitable ditches where TON and nitrate concentrations were higher than the occupied ditches (Figure 2.4). Similarly *V. macrostoma* was absent from apparently suitable ditches which had elevated concentrations of nitrite (Figure 2.4). No other factors varied significantly, and there were no patterns for *A. vorticulus*. These results are important in indicating that nutrient concentrations might have eliminated or restricted at least two of the RDB species from ditches where vegetation and other attributes were suitable.

2.4. Discussion

This survey at the ditch scale across a range of protected lowland grazing marshes shows that *Segmentina nitida*, *Anisus vorticulus* and *Valvata macrostoma* occur under distinct but relatively predictable ecological conditions. On the one hand natural variations in chemistry might be important. On the other, human influence on vegetation character and nutrient concentrations appear to be related to the distribution of each of the three species. As always with such correlative studies, separating the causal factors involved presents a challenge.

2.4.1. Co-occurrence and vegetation character

The three scarce wetlands snails examined are all typical of, and restricted, to the ditches of grazing marshes in the UK, and therefore commonly associated together at the marsh scale (HMSO 1995, Willing 1997c, Kerney 1999). However, none of the ditches in this survey of four grazing marshes held all three species and each of the three RDB species appeared to require different ecological conditions with respect to vegetation, chemistry and nutrient status. The vegetation structure in ditches is greatly influenced by the hydroseral succession that follows the dredging of silt from the ditch (Caspers & Heckman 1981, 1982). The vegetation and channel character changes following excavation from being open and deep to being shallow, choked and full of emergent or amphibious vegetation. The cycle requires around 10 to 20 years (Kirby 1992, RSPB *et al.* 1997, Painter 2000). The vegetation cover typical for the three RDB snail species indicated that they all occurred in the middle to later stages of succession. *S. nitida* appeared to favour ditches at the advanced stages with little flowing water. In contrast, *A. vorticulus* and *V. macrostoma* were more likely to occur in the mid-stages where there was flowing water and a diverse plant community of submerged, floating and emergent species (van Strien *et al.* 1991, Best 1993, 1994). These management influences are explored further in Chapter 4.

2.4.2. Ditch chemistry

All three RDB species were classified by Boycott (1936) as calciphile species restricted to aquatic habitats where calcium was over 20mg l^{-1}. Despite *A. vorticulus* being found in ditches that were comparatively less calcareous than for *S. nitida* and *V. macrostoma*, the average concentration of calcium in ditches occupied by *A. vorticulus* was still relatively high at 48mg l^{-1}. Rather than being of direct physiological relevance, the differences in calcium concentrations between the species could be a reflection of the marsh-scale differences. The Arun had the highest frequency of occurrence for *A. vorticulus* and also had the lowest concentrations for calcium and alkalinity. There are no records of *S. nitida* or *V. macrostoma* in the Arun Valley (Kerney 1999). The absence of an RDB species from a marsh could therefore either reflect unsuitable calcium concentrations or the dispersal ability of the snails. *V. macrostoma,* along with *S. nitida,* was found in ditches with significantly higher chloride, a potential indication of influence by sea spray or saline intrusion from the nearby coastline. All the grazing marshes are exposed to tidal intrusions and the mean chloride concentrations for all the ditches in the study was 103mg l^{-1}, comparatively higher than average concentrations for freshwater habitats in the UK at 8.3mg l^{-1} (Wetzel 1975). One possibility is that these species require higher ionic concentrations for osmotic regulations, but incidental effects due to the maritime position of the ditches are likely.

2.4.3. Eutrophication

In the past 10 years the decline of *S. nitida* and the other RDB snails has been attributed to eutrophication, although there are few empirical studies to support this (Bratton 1991, HMSO 1995, Willing 1996a & b, Willing & Killeen 1998). Grazing marshes are under increasing threat from arable farming that has contributed to high loadings of nutrients to drainage ditches (Marshall *et al.* 1978, Palmer 1986, Hicklin 1986). From the analyses presented here, the occurrence of *S. nitida* and *V. macrostoma*, in ditches where vegetation structure and profile were suitable, appears to have been affected by elevated nutrient (N) concentrations. Eutrophication in ditches usually results in an increase in phytoplankton and floating plants such as duckweed. In extreme cases this can cause a decline in aquatic plant diversity as well as a complete loss of all submerged aquatic plants and sometimes the regression of emergent vegetation (Mason & Bryant 1975, Moss 1988, Janse & van Puijenbroek 1998). The effects that changing vegetation structure may have on freshwater snails are not understood. It is believed that most freshwater snails graze on epiphytic algae and organic detritus (Russell-Hunter 1978, Reavell 1980, Brown 1982, Brönmark 1985b, 1989, Underwood *et al.* 1990, Thomas & Kowalczyk 1997) and therefore, eutrophication by increasing the food source, would be expected to be beneficial (Jones *et al.* 1999, 2000). However, results of the present study show that each of the RDB species occurs in high abundance in ditches with specific vegetation characteristics. A subtle change in vegetation structure could therefore result in a decline in snail abundance (Daldorph & Thomas 1991, 1995). This would be particularly important if snail food resources were involved. Additional nutrients might also shift algal species composition or accelerate detrital decomposition, but consequences for snails are not known.

Alternatively, eutrophication, by causing an increase in phytoplankton or floating plant biomass, often leads to higher concentrations of organic matter in the ditches and contributes to an increase in the rate of hypolimnetic deoxygentation in the lower part of the ditch (Veeningen 1982, Marshall 1981, Portielje & Lijklema 1994, Janse & van Puijenbroek 1998). Indeed, eutrophication has been defined by Codd & Bell (1985) as the development of a water body into a state in which the aerobic microbial decomposition of organic matter consumes more oxygen than is introduced into the environment at the substrate layer in which few macroinvertebrates could survive (Moss 1988, Marklund *et al.* 2001). *S. nitida* as a pulmonate species, is able to come to the surface to breathe and therefore would not be expected to be affected by low oxygen concentrations. In contrast, *V. macrostoma* depends on gills for breathing and is potentially vulnerable to reduced oxygen concentrations. A third potential detrimental effect of eutrophication is a direct toxicity effect of elevated concentrations of nitrate, nitrite or more specifically ammonia, and this possibility is examined further in Chapter 5 using an experimental approach.

2.4.4. Management implications

Since the three RDB snails rarely occur in the same ditch, any combined management approach for all three RDB snails should be considered regionally or at the marsh-scale. Despite the paucity of management data on any of the marshes, it was clear that a range of vegetation characteristics at different stages of hydroseral succession will benefit all three RDB snails. This will require continuation or maintenance of a rotational management regime of de-silting and weed clearance of ditches across the marsh (Kirby 1992, RSBP *et al.* 1997). A rotational regime would ensure the availability of ditches with dense emergent stands for *S. nitida* as well a ditches with mixed diverse vegetation of submerged, floating and emergent plants for *V. macrostoma* and *A. vorticulus*. Further work is needed to determine the exact changes that occur in the macrophyte character of drainage ditches after being cleared of vegetation or dredged and to relate these changes to the abundance of the RDB snails. Studies in the Netherlands have indicated that peak species richness of macrophytes was usually achieved in ditches where management was carried out every 3 years, after which plant diversity started to decline (van Strien *et al.* 1991, Best 1993, 1994). It is suggested that increasing abundance of *V. macrostoma* and *A. vorticulus* will occur with increasing diversity of plants. In contrast, as plant richness decreases, and the vegetation structure becomes more homogenous, abundance of *S. nitida* will increase. In order to retain existing populations of scarce snails, however, management at the ditch scale will need to ensure that patches are left untouched as a source of re-colonisation. It is also important to consider the dispersal ability of each species when developing a regime, for example by ensuring inter-connectivity between ditches or ensuring links during flooding. At present, dispersal mechanisms are poorly known in any of the species considered here.

Where vegetation conditions in the ditch appear to be ideal for the RDB species, at least two of the species might potentially be excluded from ditches with elevated concentrations of nutrients. Reduced agro-chemical use on grazing marshes is therefore likely to be of benefit. Current intensive farming methods demand simple monoculture systems with high productivity and the intensive use of agro-chemicals (Stoate *et al.* 2001). Species declines caused by the intensification of agriculture have been well documented for birds (Chamberlain *et al.* 1999, Wilson *et al.* 1997, Mason & MacDonald 1999, Brickle *et al.* 2000, Chamberlain *et al.* 2000, Chamberlain & Fuller 2001) and to a lesser extent for plants (Moreby *et al.* 1994, McCollin *et al*. 1999), mammals (Basquill & Bondrup-Nielsen 1999, Eskens *et al.* 1999) and invertebrates (Tucker 1992, Firbank *et al.* 1994, Euliss & Mushet 1999). The common consensus among authors for reversing species decline on agricultural land, is for agricultural practices to be de-intensified (Ormerod & Watkinson 2000, Stoate *et al.* 2001). Agri-environment schemes such as the Wetland Enhancement Scheme (WES) and Environmentally Sensitive Areas (ESA) which compensate landowners for reducing their consumption of fertilisers on grazing marshes are therefore ideally placed to assist the recovery of the three scarce snails.

Table 2.1: Spearmans' rank correlations between vegetation PCA scores and the vegetation variables from the drainage ditches of south-east England. (Significant correlation coefficents with *** = P <0.001, ** = P <0.010, * = P <0.050, n.s. = not significant).

	PCA 1	**PCA 2**	**PCA 3**
Eigenvalue	4.5618	2.7225	2.0617
Percentage explained	24	14	11
width	-0.482 ***	0.378 ***	n.s.
depth	-0.447 ***	0.253 **	-0.425 ***
% of ditch choked	0.789 ***	-0.326 ***	0.247 *
vegetation cover	0.728 ***	-0.230 *	-0.578 ***
submerged cover	-0.385 ***	-0.219 *	-0.318 ***
floating cover	0.255 **	n.s.	-0.798 ***
emergent cover	0.738 ***	-0.299 **	n.s.
amphibious cover	0.297 **	-0.507 ***	0.226 *
open water	-0.721 ***	0.240 *	0.579 ***
chlorophyll-*a* (mg l^{-1})	0.228 *	n.s.	-0.280 **
wetland plant diversity	-0.550 ***	-0.809 ***	n.s.
submerged diversity	-0.595 ***	-0.293 **	-0.236 *
floating diversity	-0.471 ***	-0.342 ***	-0.253 **
emergent diversity	-0.312 ***	-0.636 ***	n.s.
amphibious diversity	-0.269 **	-0.757 ***	0.225 *
bank diversity	-0.242 *	-0.207 *	n.s.
rank abundance of			
• *S. nitida*	0.319 ***	n.s.	n.s.
• *A. vorticulus*	n.s.	-0.280 **	n.s.
• *V. macrostoma*	n.s.	n.s.	-0.235 *

Table 2.2: Number of drainage ditches containing each of the three scarce wetland snails in the grazing marshes of south-east England.

	All	(Random)	Arun	Pevensey	Lewes	Stour
No. of ditches surveyed	106	(87)	34	35	6	31
No. of ditches containing:						
• *S. nitida*	18	(11)	0	6	3	9
• *A. vorticulus*	13	(7)	10	3	0	0
• *V. macrostoma*	19	(14)	0	19	0	0

Table 2.3: Chi-square values indicating associations in the pairwise frequency of occurrence of RDB snail species in drainage ditches of south-east England (n.s. = not significant).

	S. nitida	*A. vorticulus*
A. vorticulus	3.031 n.s.	
V. macrostoma	0.272 n.s.	0.065 n.s.

Table 2.4: Environmental variables describing drainage ditches in south-east England occupied by each of the three RDB snails. The values are the arithmetic mean (± s.d.) unless denoted * which are geometric mean (×/÷ s.d.) (see Table 2.5 for ANOVA results).

Variables	*Segmentina nitida* absent (N = 88)	*Segmentina nitida* Present (N = 18)	*Anisus vorticulus* absent (N = 93)	*Anisus vorticulus* present (N = 13)	*Valvata macrostoma* Absent (N = 87)	*Valvata macrostoma* present (N = 19)
Physical aspects						
Width (cm)	301 (140)	244 (121)	294 (139)	269 (131)	256 (2)	281(2)
Depth (cm)	77 (32)	59 (35)	73 (34)	85 (24)	74 (34)	74 (32)
Depth and silt (cm)	116 (38)	92 (47)	111 (41)	119 (32)	113 (40)	107 (41)
Choked ditch (%)	30 (39)	57 (40)	34 (40)	32 (43)	35 (41)	29 (38)
Vegetation structure						
Vegetation cover (%)	73 (29)	92 (10)	77 (28)	75 (20)	75 (28)	83 (22)
Submerged cover. (%)	20 (27)	11 (22)	17 (26)	25 (27)	16 (24)	27 (35)
Floating cover (%)	44 (38)	58 (40)	47 (39)	39 (35)	42 (39)	67 (29)
Emergent cover (%)	42 (31)	64 (24)	46 (31)	48 (33)	46 (32)	45 (25)
Amphibious cover (%)	14 (14)	17 (14)	14 (13)	22 (22)	14 (14)	16 (15)
Algae cover (%)	2 (5)	6 (14)	3 (8)	0 (1)	3 (8)	5 (2)
Wetland plant diversity	15 (5)	13 (6)	14 (5)	19 (5)	14 (6)	15 (4)
Submerged diversity	2 (2)	1 (1)	2 (1)	3 (1)	2 (2)	2 (1)
Floating diversity	3 (1)	2 (1)	2 (1)	5 (2)	3 (1)	3 (1)
Emergent diversity	5 (2)	5 (3)	5 (2)	6 (2)	5 (2)	5 (2)
Amphibious diversity	5 (3)	4 (2)	5 (3)	6 (2)	5 (3)	5 (2)
Bank plant diversity	13 (6)	10 (6)	12 (6)	10 (3)	12 (5)	14 (7)
Chlorophyll-*a* (mg l^{-1})*	12.0 (3.1)	23.1 (4.9)	13.6 (3.4)	12.1 (3.9)	12.1 (3.3)	22.1 (4.1)
Water chemistry						
pH	7.4 (0.4)	7.3 (0.2)	7.4 (0.4)	7.5 (0.6)	7.4 (0.4)	7.4 (0.4)
BOD (mg l^{-1})*	3.3 (1.9)	4.3 (2.0)	3.4 (1.8)	4.3 (2.8)	3.3 (2.0)	4.5 (1.8)
Conductivity (μS cm^{-1})	608 (347)	857 (209)	672 (347)	493 (238)	634 (360)	726 (219)
Chloride (mg l^{-1})*	63 (2)	114 (2)	71.24 (2)	59 (2)	64 (2)	104 (2)
Alkalinity (mg l^{-1})	169 (70)	262 (53)	190 (77)	142 (51)	183 (79)	192 (58)
Calcium (mg l^{-1})	66 (31)	99 (26)	75 (32)	48 (18)	74 (34)	61 (18)
TON (mg l^{-1})	0.78 (1.50)	0.31 (0.31)	0.64 (1.29)	1.08 (1.95)	0.80 (1.51)	0.24 (0.18)
Nitrate (mg l^{-1})	0.76 (1.49)	0.30 (0.30)	0.63 (1.28)	1.06 (1.92)	0.78 (1.49)	0.24 (0.18)
Nitrite (mg l^{-1})	0.02 (0.04)	0.01 (0.02)	0.02 (0.03)	0.03 (0.04)	0.03 (0.04)	0.01 (0.02)
Ammonia (mg l^{-1})	0.12 (0.18)	0.11 (0.19)	0.11 (0.17)	0.18 (0.22)	0.12 (0.17)	0.11 (0.22)
Phosphate (mg l^{-1})	0.71 (1.46)	0.80 (1.95)	0.76 (1.64)	0.42 (0.38)	0.55 (1.24)	1.49 (2.40)

Table 2.5: One-way ANOVA comparing environmental features between ditches with and without each of the three RDB snails in drainage ditches of south-east England (with *** = P <0.001, ** = P <0.010, * = P <0.050, n.s. = not significant) (see Table 2.4 for source data).

Variables	*Segmentina nitida* $F_{1, 104}$ (P)	*Anisus vorticulus* $F_{1, 104}$ (P)	*Valvata macrostoma* $F_{1, 104}$ (P)
Physical aspects			
Depth	4.52 *	n.s.	n.s.
Choked ditch	7.23 **	n.s.	n.s.
Vegetation structure			
Vegetation cover	7.33 **	n.s.	n.s.
Emergent cover	8.04 **	n.s.	n.s.
Floating cover	n.s.	n.s.	7.01 **
Wetland plant diversity	n.s.	12.47 ***	
Submerged diversity	n.s.	8.93 **	n.s.
Floating diversity	5.48 *	9.40 **	n.s.
Emergent diversity	n.s.	5.80 *	n.s.
Chlorophyll-*a*	4.26 *	n.s.	3.81 *
Water chemistry			
Conductivity	8.62 **	n.s.	n.s.
Chloride	8.30 ***	n.s.	5.69 *
Alkalinity	32.56 ***	4.90 *	n.s.
Calcium	47.37 ***	8.37 **	n.s.

Table 2.6: The best models predicting presence and absence of each of the three scarce wetland snails on lowland grazing marshes using multiple logistic regression as a function of environmental variables: $P = (\exp(\beta_0 + \beta_1 x ..)) / (1 + \exp(\beta_0 + \beta_1 x…))$. The parameters β_0 and β_1 are regression coefficients with β_0 as the intercept, x is the environmental value and P is the probability of the species being predicted.

Variables	regression coefficients (β_1)	Kappa at probability (P) threshold level of 0.2	
		calibration sites	independent sites
Segmentina nitida	(β_0 = -18.9803)	0.57	0.67
Calcium (mg l^{-1})	5.4112		
Emergent cover (%)	0.0323		
Chloride (mg l^{-1})	2.7064		
Anisus vorticulus	(β_0 = -15.3140)	0.42	0.43
Calcium (mg l^{-1})	-5.0177		
Depth (cm)	0.0180		
Amphibious cover (%)	0.0475		
pH	21.6330		
BOD (mg l^{-1})	1.7458		
Valvata macrostoma	(β_0 = 0.9637)	0.43	0.60
Floating cover (%)	0.0264		
Calcium (mg l^{-1})	-4.9222		
Chloride (mg l^{-1})	2.5447		

Figure 2.1: Vegetation character in drainage ditches on four grazing marshes in south-east England. **a)** Average wetland plant species richness in the ditches (Significant differences are indicated by one-way ANOVA ($F_{3,102}$). Identical letters within vegetation types denotes significant differences indicated by Tukey's pairwise comparison). **b)** Mean percentage cover of the different vegetation types and open water in the ditches. (Kruskal-Wallis tests (H) were used to determine differences between the four marshes as well as pairwise signifcant differences with vegetation types which are denoted with identical letters). (*** = P <0.001, ** = P <0.010, * = P <0.050, n.s. = not significant).

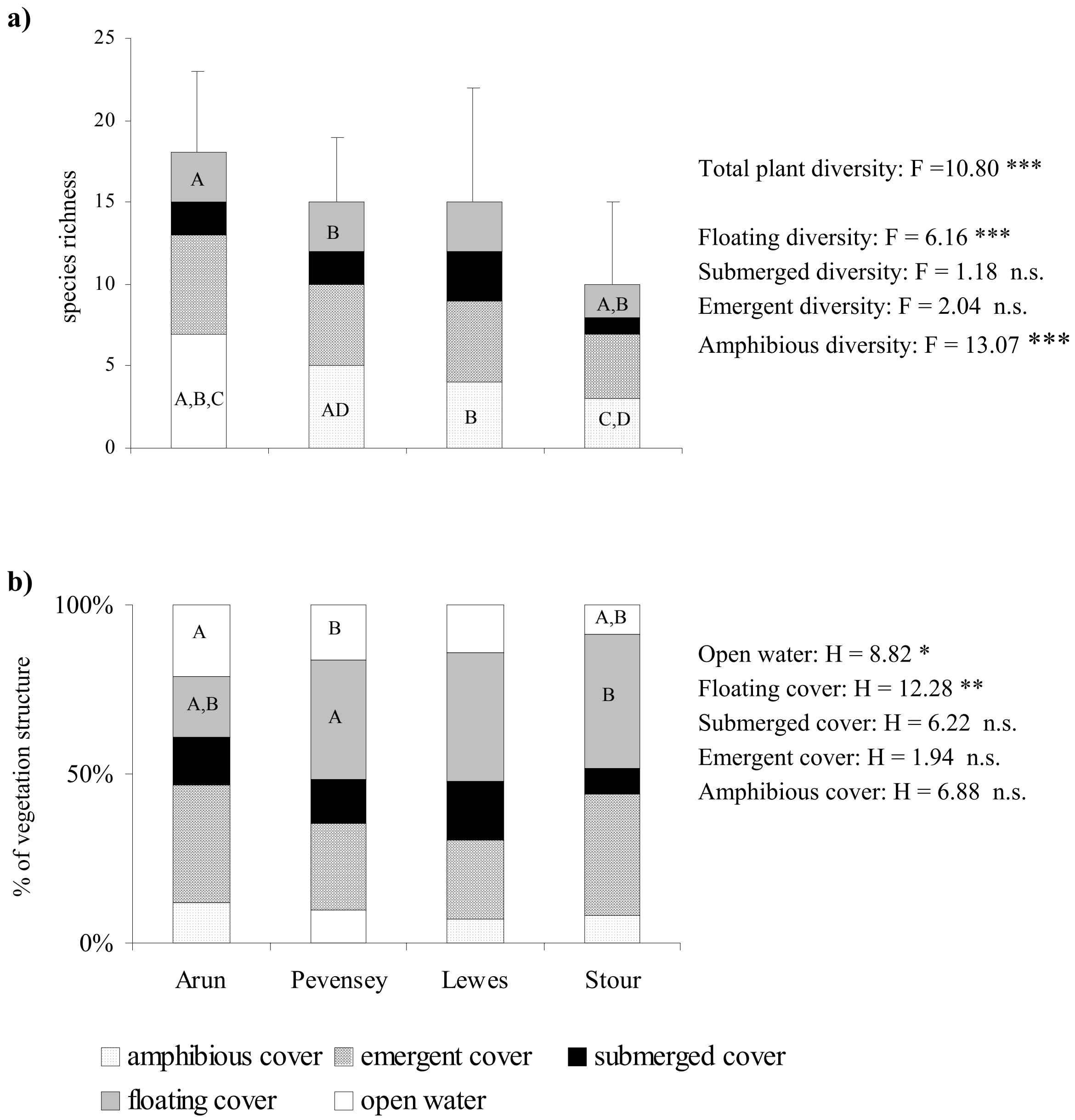


Figure 2.2: Variations in the mean (± s.d.) alkalinity, calcium, conductivity and chloride concentrations between drainage ditches on four different grazing marshes in south-east England. One-way ANOVA was used to determined significant differences, identical letters denote **no** pairwise differences by Tukey's comparison tests.

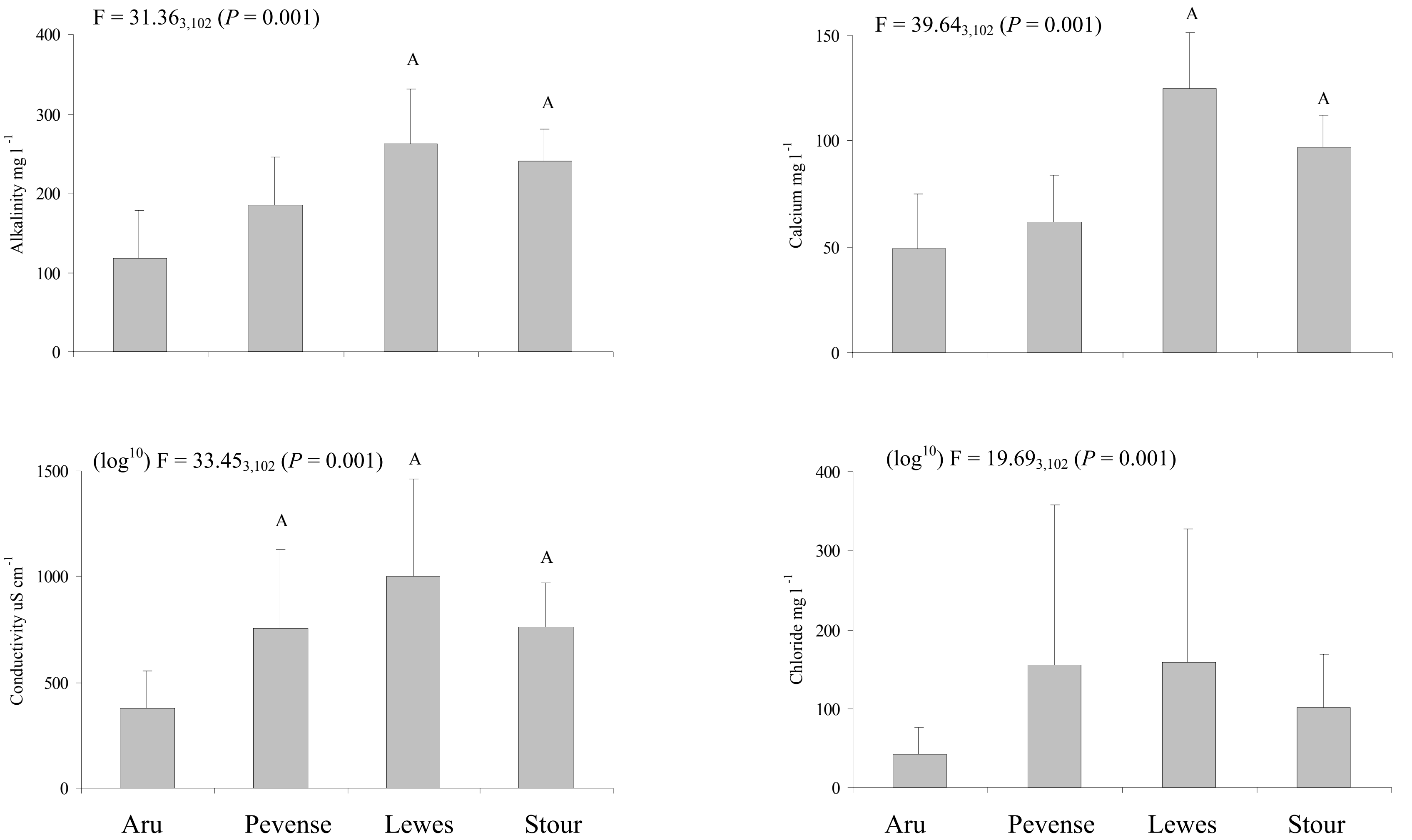


Figure 2.3: Variations in the mean (± s.d.) concentrations of nutrients across the four grazing marshes in south-east England. Kruskal-Wallis tests were used to indicate significant differences between the marshes. Indentical letters denote significant pairwise differences determined by Kruskal-Wallis test.

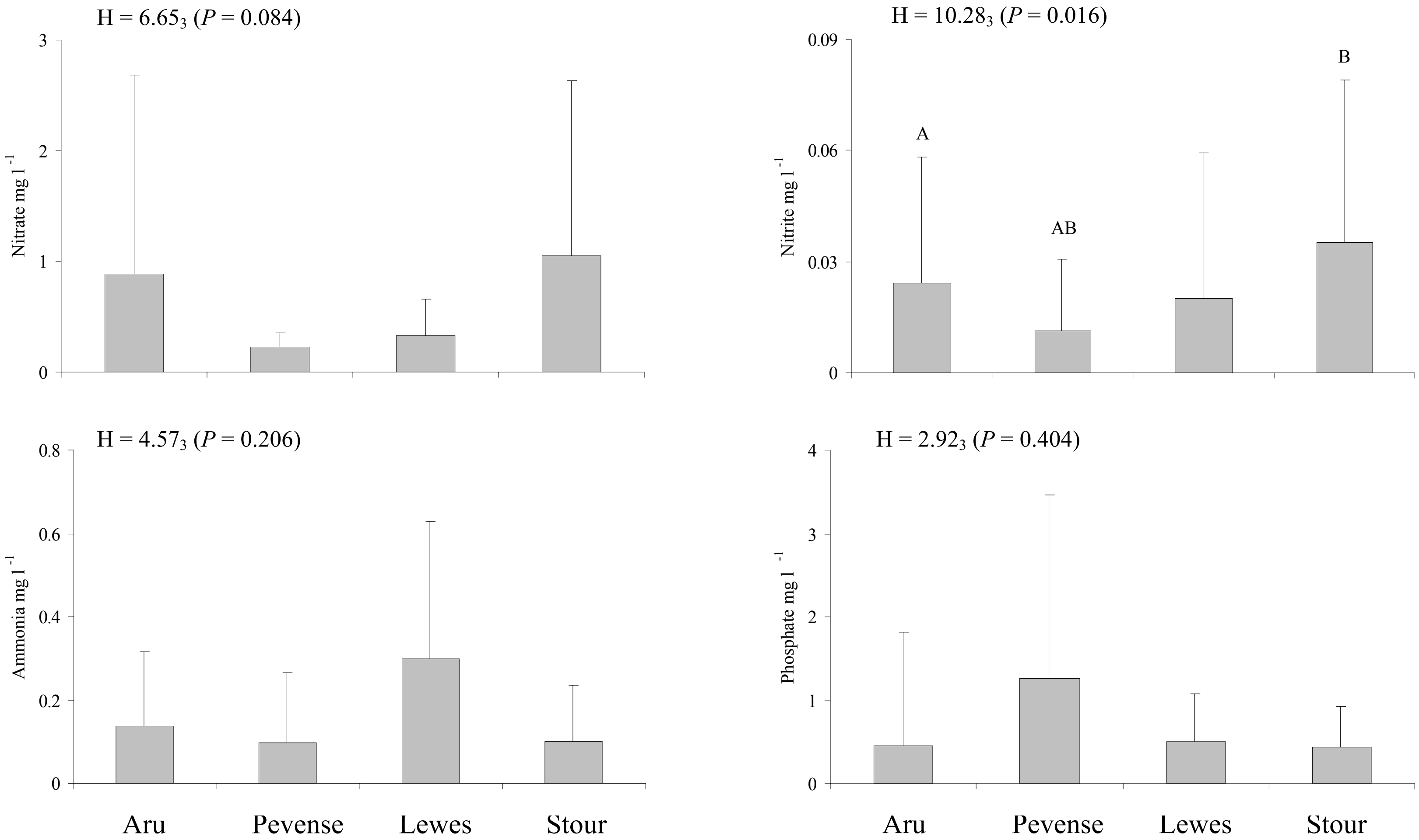
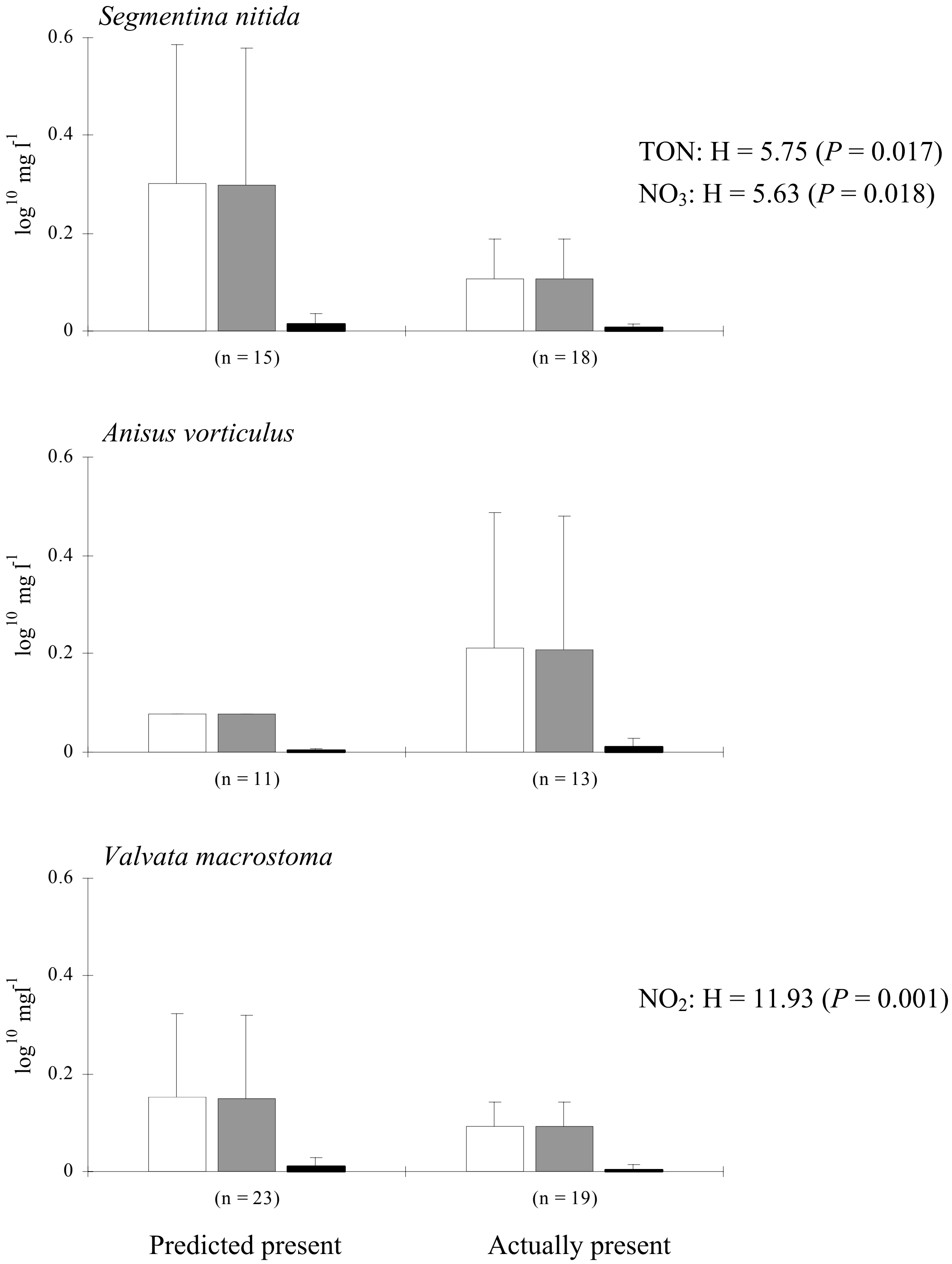


Figure 2.4: Variations in nutrient concentrations between unoccupied ditches where RDB snails were predicted to be present and occupied ditches where they were actually present. (Significant differences were tested using the Kruskal-Wallis test (H) (White bar = TON, Grey bar = NO_3, Black bar = NO_2, n = number of ditches).



- Chapter 3 -

Factors affecting the distribution of three scarce wetland molluscs of lowland Britain: patterns within drainage ditches

3.0. Abstract

Three Red Data Book (RDB) species of wetland snail, *Segmentina nitida, Anisus vorticulus* and *Valvata macrostoma* occur on grazing marshes in drainage ditches under different ecological conditions. However, little is known about factors that affect their micro-distribution. In this chapter, their distributions within the channel were examined across the profile of twenty ditches from grazing marshes in lowland south-east England. This study aimed to improve information available for ditch management at the habitat scale. Snail abundance, vegetation cover and environmental factors were recorded at two depths and various points across the ditch profile. One-way ANOVA and correlations were then used to assess variations in snail abundance within ditches in relation to a range of abiotic and biotic factors.

There were significant variations in abundance between ditch locations for all three RDB snails but only because abundances were significantly greater near the surface than at depth. Depths below 0.6m had significantly lower levels of dissolved oxygen which is likely to reduce abundance particularly of the operculate, *Valvata macrostoma*. In all other respects, the three species occurred throughout the ditch. The survey supported hypotheses suggested from the distribution of these same snail species between ditches: all occurred in ditches with pronounced vegetation cover but each snail species reached higher abundance among certain vegetation structures. For *S. nitida* this was among amphibious vegetation, for *V. macrostoma* among emergent stands and for *A. vorticulus* among floating vegetation.

Management will favour these three species if it provides the correct blend of ditch vegetation character, and oxygen concentrations that are not below 1mg l^{-1}, especially at the surface layer. At the habitat scale, management needs to consider optimising particular vegetation components that support higher abundances of the RDB snails.

3.1. Introduction

It has been suggested that in some taxa, rarity can be a function of habitat specialisation (Gaston 1994, Kunin 1997, rey Benayas *et al.* 1999). A rare organism, which depends on a particular habitat, will be vulnerable to changes in habitat availability or habitat quality at different spatial scales (Lodge *et al.* 1987, Crowl & Schnell 1990, Townsend & Hildrew 1994, Newman 2000). Understanding specific habitat requirements can also help guide positive management to favour threatened organisms (Sutherland & Hill 1995, HMSO 1995). In systems such as rivers or wetlands that are often managed for a range of purposes, modifying management regimes for conservation can offer real benefits (Heathwaite 1995, Thompson & Finlayson 2001). So far, however, little information has been produced that might guide such management for invertebrates, particularly molluscs.

In streams, the micro-distribution of molluscs appears to be influenced mainly by velocity and substrate composition (Cummins & Lauff 1969, Harman 1972, DeKock, *et al.* 1989, Liu & Resh 1997, Crowl & Schnell 1990, Johnson & Brown 1997). For lentic systems, the habitat preference of molluscs appears to be more associated with vegetation character (Dvørak & Best 1982, Brönmark 1985a & b, Lodge 1986, Bailey 1988, Brown & Lodge 1993, Hurley *et al.* 1995, Costil & Clement 1996, Sloey *et al.* 1997, Marklund *et al.* 2001). The micro-distribution of molluscs within drainage ditches is less well understood, but there is a broad consensus that vegetation is a major factor in determining the micro-distribution of macro-invertebrates in general (Wade 1977, Clare 1979, Clare & Edwards 1983, Scheffer *et al.* 1984, Foster *et al.* 1990, Caquet 1990).

This survey focuses on three wetland snails, *Segmentina nitida, Anisus vorticulus* and *Valvata macrostoma* all three being in the British Red Data Book (RDB) (Bratton 1991) and listed as 'Declining but Widespread' in Europe (Wells & Chatfield 1995). In the UK, they are found in drainage ditches of large grazing marshes (Kerney 1999). Ditches of this type are artificial linear water-bodies whose water level and flow are regulated by the use of sluice gates and pumping stations. They are considered to be relict habitats of previously un-drained low-lying marshland and their profile can provide a range of habitats from deep open water to shallow poached margins. Through time, ditches will gradually become less effective in allowing drainage, but conservation interests are usually maintained or enhanced (Kirby 1992, RSPB *et al.*

1997). So far, however little information has been available that might help guide ditch management for any of these three scarce mollusc species.

The distribution between ditches of these same three snails have been discussed elsewhere (Chapter 2). The aim of this chapter is to gain an understanding of the micro-distribution of the snails within ditches and to relate it to habitat conditions.

3.2. Methods

3.2.1 Study sites

A total of twenty drainage ditches were intensively surveyed during June-September 2000 to assess the relationship between environmental character and the distribution of the three target RDB snails at the habitat scale. The survey was restricted to the ditches on four grazing marshes in south-east England: Amberely Wildbrooks (TQ 0314) and Pulborough Brooks (TQ 0617) in West Sussex and Lewes Brooks (TQ 4208) and Pevensey Levels (TQ 6409) in East Sussex (Figure 3.1). The smallest marsh was Pulborough Brooks of 171ha, largely owned and managed by the Royal Society for Protection of Birds (RSBP) since 1989. The other three marshes are managed by a consortium of conservation agencies, private landowners and government agencies, of which Pevensey Levels, covering 3,500ha, was the most complex. The four marshes consist of improved and semi-improved wet grasslands intersected by an extensive network of drainage channels. All the marshes are recognised for their value to nature conservation, with Pevensey Levels and the two marshes Amberley and Pulborough in the Arun Valley designated under the Ramsar Convention (Ramsar Convention Bureau 2002). Also the marshes in the Arun, under the EC Birds Directive 79/409/EEC (European Commission 1979b), are designated as Special Protection Areas (SPA). All marshes contain Sites of Special Scientific Interest (SSSIs) due to their importance for overwintering birds and aquatic communities in the ditches (further information given in chapter 1). The selected ditches were known to contain either *A. vorticulus* or *S. nitida* from previous surveys (Killeen & Willing 1997, Chapter 2), ten ditches being chosen for each species, *V. macrostoma* was included incidentally (Table 3.1).

3.2.2 Sampling protocol

Snail samples were taken along a 100m stretch of each ditch, five replicated samples being taken from five cross-sectional transects selected randomly over this stretch. At each transect, samples were taken from four locations: the marginal zone, which consisted of the first 10% of the ditch from the bank; the intermediate zone, which was between the mid-channel and the margin; the surface and lower zone of the mid-channel (Figure 3.2). The lower zone consisted of the area 0.15m above the sediment and included the top 0.05m of the sediment layer. At each sampling location, the mollusc communities were sampled from an area of 0.2m by 0.2m using a standardised sieve net (see Chapter 2 & Appendix 1). The only exception was the lower mid-channel sampling sites where an Eckman grab was used to sample a 0.2m by 0.2m area at the lower depths. The Eckman grab was used to prevent contamination of the lower samples with gastropods that occupied the surface layer. All the replicated mollusc samples were preserved on site with 70% Industrial Methylated Spirit (IMS). In the laboratory the samples were washed through a 500µm sieve and all the gastropods were removed and identified to species level with a light microscope (x10) using Macan (1977).

The percentage covers of submerged, floating, emergent and amphibious vegetation, were recorded across the ditch (Figure 3.2) (see Chapter 2 for definitions of each vegetation components). Cover was defined at each sampling location as the area (0.2m by 0.2m) occupied by each of the above components when the site was viewed from above. At the centre of each ditch, plants were recorded and identified to species using Rose (1981) from a 20 metre stretch. In the same area, an estimation was made of the overall percentage cover and for each vegetation type as described in Chapters 2 & 4.

Conductivity, pH, dissolved oxygen, temperature, salinity and turbidity were recorded on-site between 0930 and 1130 hours prior to mollusc sampling at each sampling site using a portable meter (GRANT 3800). The sonde was positioned at 0.1-0.2m below the water surface for the upper sampling locations and at 0.1-0.2m above the substrate for the lower sampling locations. From every ditch a water sample was taken 1.0m from the bank, 0.15m below the water surface and analysed within 24 hours for conductivity, pH, biological oxygen demand (BOD), alkalinity, chloride, total organic nitrogen (TON), nitrate, nitrite, ammoniacal-nitrogen, ortho-phosphate and chlorophyll-*a* using methods described in Chapter 2.

Further attributes were collected for each ditch on dimension (width, depth, depth of sediment layer, height of bank), the adjacent landuse (grazing, arable, hay, track, woodland), the percentage extent of trees and shrubs along the ditch, and the percentage of the ditch in shade. The percentage of the ditch channel blocked by vegetation, which prevented a free flow of water, was also estimated (see Chapter 2 for more details).

3.2.3. Statistical analysis

To examine variations in snail abundance within ditches, three data-sets were compiled separately for each RDB snail consisting of only the ditches from where each species was recently recorded (Table 3.2). For each species, abundances were summed within ditches for each specific sampling locations (margin, intermediate, centre surface and centre lower) and logarithimically transformed to homogenise variances. Variations between locations were then assessed using ANOVA with ditches as the replicate sampling units. Pairwise differences were identified using Fisher's pairwise comparison. This approach ensured that true replicates were identified, and all errors between sampling locations were independent at the ditch scale.

A similar approach was used to assess variation in physio-chemical and vegetation composition, again carrying out ANOVA to assess the variation between sampling locations across replicate ditches. Physio-chemical data were represented by the ditch mean values for pH, oxygen and conductivity. This approach ignores error variations between replicate sampling locations within ditches again ensuring independent errors. Vegetation composition was based on the ditch mean values for three vegetation types: submerged, floating and emergent/amphibious.

Additionally, some patterns were assessed for individual sampling locations by analyses using pooled ditch data. Principal component analysis (PCA) analysis was used to assess the major variations in vegetation composition at the surface sampling locations in ditches occupied by each RDB molluscs species, based on the correlation matrix. Rank abundance for each RDB species was then related to the PCA vegetation scores using Spearman's rank correlations. One-way ANOVA was used to assess if there was a significant difference in the PCA vegetation scores between ditches with and without the RDB snails.

3.3. Results

Of the twenty ditches sampled, *S. nitida* and *V. macrostoma* were present respectively in 11 and 12 ditches while *A. vorticulus* was present in 10 ditches (Table 3.2). Only 2 ditches contained all three RDB snails (Table 3.2). A breakdown of the replicate samples indicated *S. nitida* and *A. vorticulus* occurred in less than a quarter of the samples and *V. macrostoma* in 38% (Table 3.2).

Comparison between the ditches requires caution since they were not randomly selected (Table 3.3). However, *S. nitida* occurred in ditches with significantly higher conductivity and higher concentrations of calcium, alkalinity and chloride compared to the ditches from where they were absent (Table 3.3). This species was also more likely to be recorded in ditches choked with emergent plants. *A. vorticulus* tended to be recorded in ditches that were less choked, not dominated by emergent plants and had lower alkalinity and conductivity than where it was absent. *V. macrostoma* was typical of ditches with higher concentrations of conductivity and chloride than elsewhere (Table 3.3).

3.3.1. Water chemistry

One-way ANOVA and Fisher's pairwise comparisons showed that conductivity, dissolved oxygen and pH were similar between the margin, intermediate and surface mid-channel zones occupied by each RDB snail (Figure 3.3). The only significant effects was due to lower dissolved oxygen values in the lower mid-channel compared to the three surface sampling positions in the ditch (Figure 3.3). On water chemistry, therefore drainage ditches were relatively homogeneous between 'locations'.

3.3.2. Vegetation structure

The vegetation cover of ditches occupied by the RDB molluscs approached 100% across the ditch with a slight decrease in percentage cover in the mid-channel zone. The vegetation composition changed across the drainage ditches occupied by each species due to a significant decrease in the percentage cover of emergent and amphibious plant species towards the centre (Figure 3.4).

3.3.3. Segmentina nitida

The abundance of *S. nitida* varied significantly between sampling locations as a result of abundance in the lower mid-channel being less than the three upper level samples irrespective of position across the profile (Figure 3.5). Variations in abundance values were greater between the 11 ditches rather than between the sampling locations. There was, nevertheless, some evidence of variations in abundance between individual sampling points. The abundance of *S. nitida* correlated negatively with axis 3 of the PCA scores of the vegetation components and so declined where there was high percentage of open water and low cover of amphibious vegetation (Table 3.4).

3.3.4. Anisus vorticulus

As with *S. nitida*, the abundance of *A. vorticulus* varied only between the lower mid-channel samples and the three upper samples (Figure 3.5). Also similar to *S. nitida*, the variation in mean abundance was greater between the 10 ditches containing *A. vorticulus* rather than within ditches. Across individual sample points, *A. vorticulus* increased most strongly where there was more floating vegetation compared to submerged vegetation (Table 3.4).

3.3.5. Valvata macrostoma

Similar to the other two RDB snails, the only significant variation in abundance of *V. macrostoma* was between the lower mid-channel samples and the upper three positions. There was greater variation in abundance of *V. macrostoma* between ditches rather than within ditches (Figure 3.5). At individual sampling locations correlations with the vegetation component PCA scores indicated that higher abundance of *V. macrostoma* was more likely in stands of emergent vegetation with low percentage of open water (Table 3.4).

3.4. Discussion

The major variations between ditches supports hypotheses about the large-scale distribution of the snails (Chapter 2). *Anisus vorticulus* was found in ditches that were comparatively less calcareous and had lower chloride concentrations than *Segmentina nitida* and *Valvata macrostoma*. In addition, *A. vorticulus* occurred in more open vegetated ditches compared to *S. nitida*. By contrast, the micro-distributional data from *S. nitida*, *A. vorticulus* and *V. macrostoma* appeared to indicate that the species were unaffected by location within a ditch, with the exception of their scarcity at lower depths. All had similar patterns of occurrence across ditches, were rarely recorded at depth and where they occurred in the lower ditch, they were always found in significantly lower abundance. There were, nevertheless, some significant variations in abundance between all sampling locations that reflected patterns of vegetation. These data suggest that none of the species are confined to particular ditch locations but might be influenced by local vegetation conditions.

3.4.1. Vegetation character

The composition of the vegetation across the ditches was similar for sites occupied by all three RDB species. Emergent and amphibious plants were prominent in the margins but declined significantly towards the centre of the ditch. Floating and submerged vegetation remained constant across the ditch. With no significant variations in abundance in any of the snails across the ditch, it seems likely that small variations in vegetation cover across the ditch profile, at least over the range recorded, were unimportant. Over a wider array of all sites in the survey, however, relationship between abundance and vegetation were clearer (see Table 3.4). Strong correlations between snail distribution and macrophytes have been shown in lentic habitats (Dvørak & Best 1982, Brönmark 1985a, Lodge 1986, Bailey 1988, Brown & Lodge 1993, Hurley *et al.* 1995, Costil & Clement 1996, Sloey *et al.* 1997, Marklund *et al.* 2001). Links to vegetation are well known in aquatic ecology: the snails benefit from plants by having a substrate to oviposit, a source of epiphytic cover and detritus, access to air-water interface and refugia from predation (Brönmark 1988, 1989, Thomas *et al.* 1985, Carpenter & Lodge 1986, Lodge 1985, 1986, 1991, Underwood & Thomas 1990, Økland 1990, Turner 1996).

However, it has been suggested that plant structure and morphology appears to play a greater role in determining snail distribution than specific association between individual species of molluscs and plants (Carlow 1973a, Lodge 1985, Lodge *et al.* 1987). The results from the micro-survey appear to corroborate with this, with greater abundance of each rare snail occurring among particular vegetation types. *S. nitida* was found in higher numbers among amphibious vegetation stands. This supports the idea that the species is typical of ditches that are at the advanced stages of vegetation succession, encroached by plants favouring choked shallow conditions (Chapter 2, Boycott 1936, Kerney 1999). From the previous chapter, *S. nitida* occurred in ditches dominated by emergent vegetation (Chapter 2), however, within these channels the species was most likely to occur among amphibious plants. Despite the absence of significant variations in abundance between the upper sampling locations, there was evidence of increased numbers of *S. nitida* in the margins. The margins are also where encroachment by amphibious vegetation is most likely to occur.

Ditches containing *V. macrostoma* are generally typified by floating cover (Chapter 2), but the species was recorded in higher abundance in stands of emergents. Similar to *S. nitida*, the abundance of *V. macrostoma* was generally greater in the margins where emergent vegetation dominates than in the centre of the channel among the floating vegetation. *A. vorticulus* was recorded in higher numbers among floating vegetation supporting the hypothesis that the species was typical of ditches in a more transitional vegetative state where emergent plants have not yet out-competed floating vegetation (Chapter 2).

3.4.2. Water chemistry

The lower parts of each ditch, as well as being the least favourable area of the ditch for the three RDB snails, also had extremely low concentrations of dissolved oxygen, averaging 0.23mg l^{-1} in ditches with *S. nitida* to 0.6mg l^{-1} in ditches with *A. vorticulus*. These values are equivalent to less than 5% saturation at typical summer water temperature of 15 to 20^{o}C. There was a notable divide between the anoxic conditions in the lower part of the ditch compared with the upper layer where concentrations reached 2mg l^{-1}. Critical levels of dissolved oxygen for macro-invertebrates will vary according to the requirement of specific organisms and have been quoted for more tolerant species at around 1.5mg l^{-1} for lentic environments (Moss 1988, Marklund *et al.* 2001). Members of the Planorbidae are unique in having haemoglobin in their blood, and may not be affected by low oxygen levels due to their ability to utilise atmospheric air for respiration. However *S. nitida* and *A. vorticulus* could possibly rely on cutaneous respiration under water (Chatfield 1998, Costil & Bailey 1998), so that low oxygen concentrations at depth could be limiting. Another factor is the duration planorbids species can remain submerged before coming to the surface to breathe. Organisms occurring at greater depths in a ditch, as well as having less oxygen, are also further away from the water surface. Additionally as an operculate, *V. macrostoma* breathes by use of gills and so is dependent on dissolved oxygen in the water for respiration. From this, it might be expected to have greater abundance in the upper water layers where dissolved oxygen concentrations were higher. Valvatids are regarded as deep water gastropod species but usually only where there is a significant flow of water (Aho *et al.* 1981, Kerney 1999, Dillon 2000).

3.4.3. Management implications

The three RDB snails occurred together at the habitat scale but this was rare, illustrating that as well as occurring in ditches of different ecological conditions (Chapter 2), they also require different local conditions. The snails are efficient colonisers throughout ditches and are not dependent at the micro-habitat scale on a selected location or on particular plant species being available. However, there were associations between the abundance of the snails and individual vegetation components which in turn, reflected local vegetation structure. Management therefore should consider maximising these vegetation types at the habitat scale to optimise the abundance values for each of the rare snails. *S. nitida* was found in greatest abundance among amphibious vegetation, of ditches at the advanced stages of vegetation succession typically dominated by emergent plants (Chapter 2). Alternatively, management could aim for ditches with large margins colonised by amphibious plants such as *Glyceria maxima*.

Similarly, *V. macrostoma* would also benefit from ditches with dense margins but where emergent plants dominate instead of amphibious species. Ditches containing *V. macrostoma* have a high percentage cover of floating plants (Chapter 2), suggesting that the species does not favour channels completely choked by emergents. Therefore, a mixture of vegetation components of floating and emergent plants across the channel appears to be an important criteria for *V. macrostoma*. In contrast, *A.*

vorticulus requires more open ditches in which floating vegetation can flourish (Chapter 2).

The types of vegetation that can establish in a drainage ditch are often determined by water depth (Hawke & José 1996, Newbold & Moutford 1997). Ditches with deeper water will be inhospitable to emergent and amphibious plants and this could adversely affect the abundance of *S. nitida*. In contrast, where the ditch is shallow, allowing domination of emergent and amphibious plants, it is likely to have a detrimental effects on the abundance of *A. vorticulus*. A rotational de-silting regime offering ditches at different stages of succession, depths and vegetation composition would provide the ecological conditions required by each of the RDB snails as well as between ditches (Kirby 1992, RSPB *et al.* 1997, Chapter 2). The one location in which all three snails were rarely found was the lower depth, which had significantly lower concentrations of dissolved oxygen and was usually devoid of vegetation. Managing ditches for the scarce snails needs to ensure sufficient access to water/air interfaces to aid the respiration requirements of the snails, in particular for the planorbids. A high vegetation cover across the ditch will offer sufficient access for the snails to the water surface, especially in the near anoxic conditions typical of drainage ditches.

Table 3.1: A summary of the three RDB mollusc populations in each ditch (^{S} denotes ditches selected for *S. nitida* and ^{A} denotes ditches selected for *A. vorticulus*). (Number of samples are from a total of 20 samples per ditch).

Ditch no.	Total abundance of *S. nitida*	No. of samples containing *S. nitida*	Total abundance of *A. vorticulus*	No. of samples containing *A. vorticulus*	Total abundance of *V. macrostoma*	No. of samples containing *V. macrostoma*
2^S	23	8	0	0	38	17
3^S	14	7	0	0	0	0
5^S	0	0	0	0	850	15
6^S	448	17	0	0	0	0
8^S	675	17	0	0	231	17
9^S	121	10	0	0	898	15
10^S	23	11	0	0	1999	17
17^S	12	3	0	0	1612	20
18^S	45	8	0	0	138	10
20^S	26	6	0	0	177	12
4^A	0	0	1	1	0	0
7^A	0	0	267	14	29	9
11^A	2	2	120	13	25	10
12^A	0	0	1	1	0	0
13^A	0	0	39	11	0	0
14^A	0	0	3	2	16	7
15^A	0	0	108	14	0	0
16^A	0	0	3	2	0	0
19^A	14	3	1369	17	2	1
21^A	0	0	49	9	0	0

Table 3.2: The environmental variables for drainage ditches in south-east England occupied by each of the three RDB snails. The values are the means (± s.d.). (see Table 3.3 for ANOVA results).

Variables	*Segmentina nitida*		*Anisus vorticulus*		*Valvata macrostoma*	
	absent (N = 9)	present (N = 11)	absent (N = 10)	present (N = 10)	absent (N = 8)	present (N = 12)
Physical aspects						
Width (cm)	372 (83)	348 (119)	328 (89)	390 (110)	331 (96)	378 (107)
Depth (cm)	82 (13)	80 (19)	78 (18)	84 (13)	76 (11)	83 (19)
Depth and silt (cm)	103 (16)	97 (37)	93 (36)	107 (19)	99 (20)	100 (35)
Choked ditch (%)	32 (31)	71 (36)	77 (32)	30 (30)	52 (34)	55 (43)
Vegetation structure						
Vegetation cover (%)	61 (33)	89 (18)	88 (22)	65 (31)	65 (33)	84 (24)
Submerged cover (%)	34 (29)	43 (27)	38 (27)	41 (30)	34 (24)	42 (31)
Floating cover (%)	49 (28)	54 (23)	55 (24)	49 (26)	49 (29)	54 (23)
Emergent cover (%)	44 (25)	76 (28)	81 (24)	43 (24)	63 (27)	61 (34)
Amphibious cover (%)	15 (14)	17 (14)	18 (14)	15 (13)	16 (13)	17 (14)
Algae cover (%)	6 (11)	5 (10)	2 (3)	9 (14)	5 (9)	6 (12)
Plant diversity	36 (8)	32 (5)	32 (5)	36 (7)	35 (8)	33 (6)
Submerged diversity.	3 (1)	2 (1)	2 (1)	3 (1)	3 (1)	2 (1)
Floating diversity	4 (1)	3 (1)	3 (1)	4 (1)	4 (0)	3 (1)
Emergent diversity	8 (2)	7 (3)	7 (3)	8 (2)	8 (2)	7 (3)
Amphibious diversity	9 (3)	8 (2)	7 (2)	9 (3)	9 (3)	8 (2)
Bank plant diversity	12 (3)	12 (3)	13 (3)	12 (3)	11 (4)	13 (3)
Chlorophyll-*a* (mg l^{-1})	46 (45)	39 (47)	40 (50)	45 (43)	48 (46)	39 (46)
Water chemistry						
pH	7.2 (0.3)	7.2 (0.4)	7.2 (0.4)	7.2 (0.3)	7.1 (0.2)	7.2 (0.4)
BOD (mg l^{-1})	4.8 (2.1)	5.9 (4.4)	5.4 (4.7)	5.4 (1.9)	5.2 (1.9)	5.5 (4.3)
Conductivity (µS cm^{-1})	372 (102)	613 (163)	599 (177)	410 (140)	397 (152)	576 (171)
Chloride (mg l^{-1})	46 (28)	88 (48)	85 (49)	54 (35)	34 (5)	93 (45)
Alkalinity (mg l^{-1})	120 (29)	204 (62)	199 (70)	132 (40)	149 (83)	174 (49)
Calcium (mg l^{-1})	43 (12)	67 (26)	68 (27)	44 (13)	56 (34)	56 (15)
TON (mg l^{-1})	0.3 (0.3)	0.3 (0.2)	0.3 (0.3)	0.3 (0.3)	0.3 (0.3)	0.3 (0.2)
Nitrate (mg l^{-1})	0.3 (0.2)	0.3 (0.2)	0.3 (0.2)	0.3 (0.2)	0.3 (0.3)	0.3 (0.2)
Nitrite (mg l^{-1})	0.02 (0.03)	0.01 (0.03)	0.02 (0.03)	0.02 (0.03)	0.02 (0.03)	0.01 (0.03)
Ammonia (mg l^{-1})	0.1 (0.1)	0.1 (0.2)	0.1 (0.1)	0.1 (0.1)	0.1 (0.2)	0.1 (0.1)
Phosphate (mg l^{-1})	0.2 (0.2)	0.7 (1.6)	0.8 (1.7)	0.2 (0.2)	0.2 (0.3)	0.7 (1.5)

Table 3.3: One-way ANOVA comparing environmental features between ditches with and without each of three RDB snails in drainage ditches in south-east England (*** = *P* <0.001, ** = *P* <0.010, * = *P* < 0.050, n.s.= not significant) (see Table 3.2 for source data).

Variables	*S. nitida* $F_{1,18}$ (*P*)	*A. vorticulus* $F_{1,18}$ (*P*)	*V. macrostoma* $F_{1,18}$ (*P*)
Physical aspects			
Choked ditch	6.76 **	11.40 **	n.s.
Vegetation structure			
Vegetation cover	5.68 *	n.s.	n.s.
Emergent cover	6.94 **	11.96 **	n.s.
Water chemistry			
Conductivity	14.76 ***	6.95 *	5.74 *
Chloride	5.57 *	n.s.	13.71 **
Alkalinity	13.64 **	6.79 *	n.s.
Calcium	6.93 *	6.35 *	n.s.

Table 3.4: The PCA scores of variations in vegetation across sampling locations within the ditches for three RDB snails. (Significant correlations with ranked species abundance are denoted by ** = P <0.010).

	Axis 1	Axis 2	Axis 3	Axis 4
Segmentina nitida			**** (-)**	
Eigenvalues	1.5976	1.3899	1.1064	0.7455
Variations explained	32%	28%	22%	15%
Floating vegetation	-0.494	0.316	-0.244	-0.727
Submerged vegetation	-0.487	0.440	-0.047	0.664
Emergent vegetation	-0.269	-0.767	0.115	0.015
Amphibious vegetation	0.599	0.115	-0.570	0.030
Open water	0.296	0.324	0.775	-0.169
Anisus vorticulus				**** (+)**
Eigenvalues	1.8128	1.4136	1.1316	0.5082
Variations explained	36%	28%	23%	10%
Floating vegetation	0.627	-0.055	-0.007	0.735
Submerged vegetation	0.534	-0.410	-0.175	-0.615
Emergent vegetation	0.104	0.687	0.479	-0.204
Amphibious vegetation	-0.252	0.300	-0.802	0.078
Open water	-0.497	-0.517	0.310	0.184
Valvata macrostoma		**** (-)**		
Eigenvalues	1.7008	1.4251	1.0953	0.6029
Variations explained	34%	29%	22%	12%
Floating vegetation	0.611	-0.041	-0.144	-0.740
Submerged vegetation	0.620	0.197	0.199	0.598
Emergent vegetation	-0.224	-0.764	0.140	0.020
Amphibious vegetation	-0.130	0.124	-0.914	0.168
Open water	-0.419	0.600	0.292	-0.257

Figure 3.1: South-east England showing the three grazing marshes used for the micro-distribution survey in relation to the adjacent catchments of the major rivers. Pulborough Brooks and Amberley Wildbrooks are indicated on the Arun Valley.

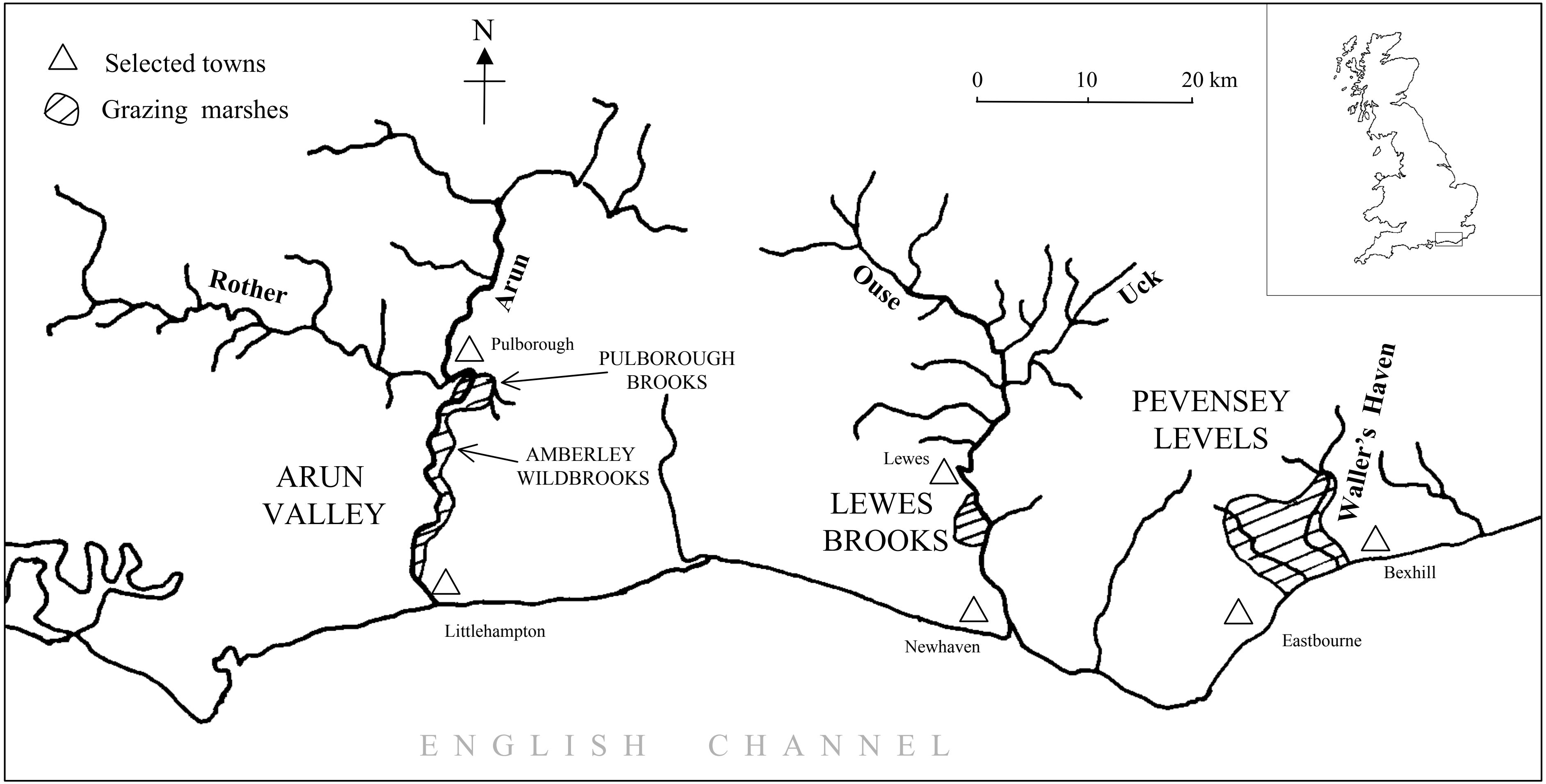
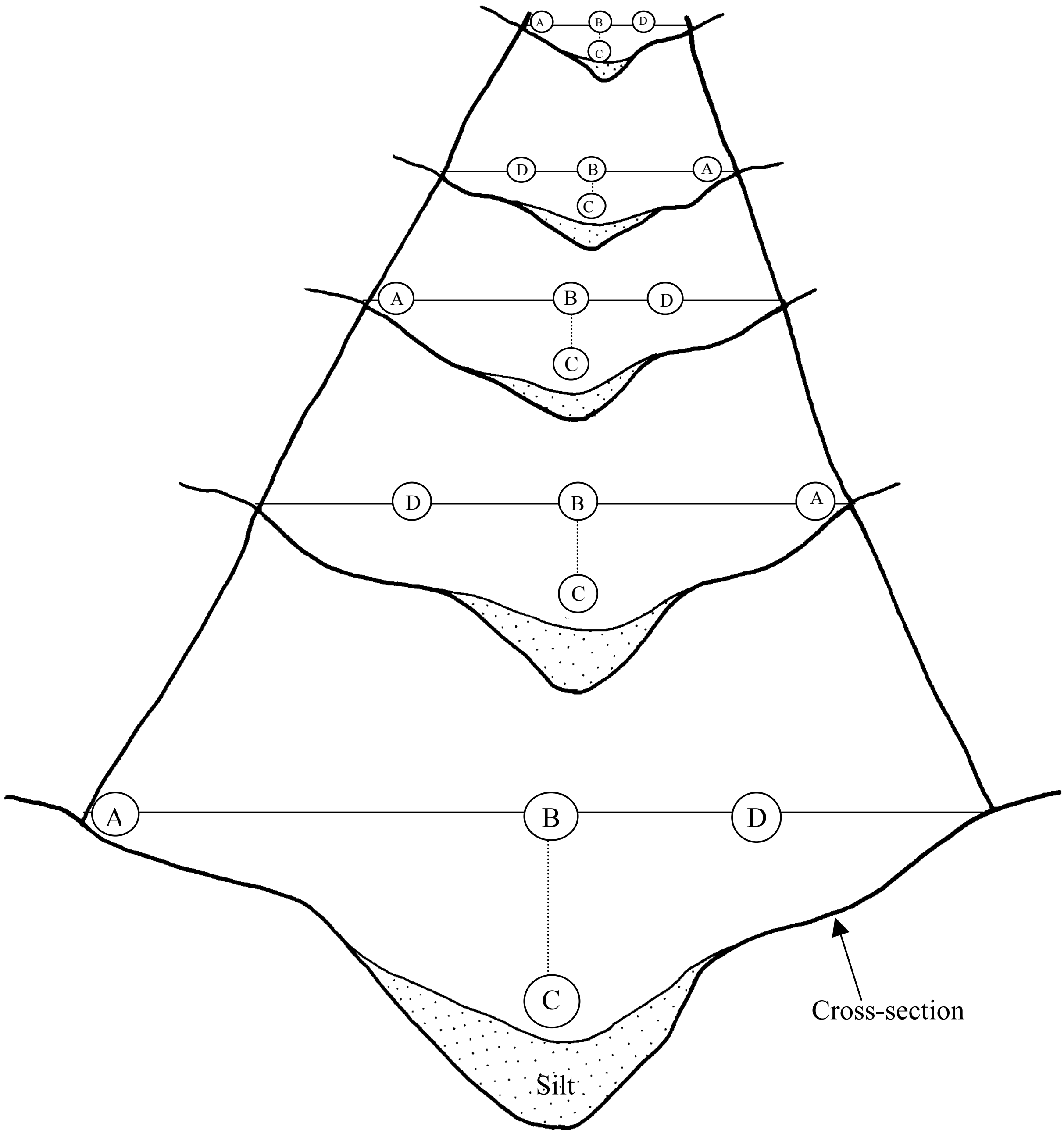


Figure 3.2: Cross-section of a ditch showing the positions of the transects and sampling locations.



(A) Marginal samples

(B) Surface mid-channel samples

(C) Lower mid-channel samples

(D) Intermediate samples

Figure 3.3: Variations in water chemistry between four different loactions in drainage ditches of south-east England occupied by each of the three RDB snail species. The values are means (± s.d.). Significant differences were tested with one-way ANOVA, and pairwise differences with Fisher's pairwise comparison tests which is denoted by identical letters.

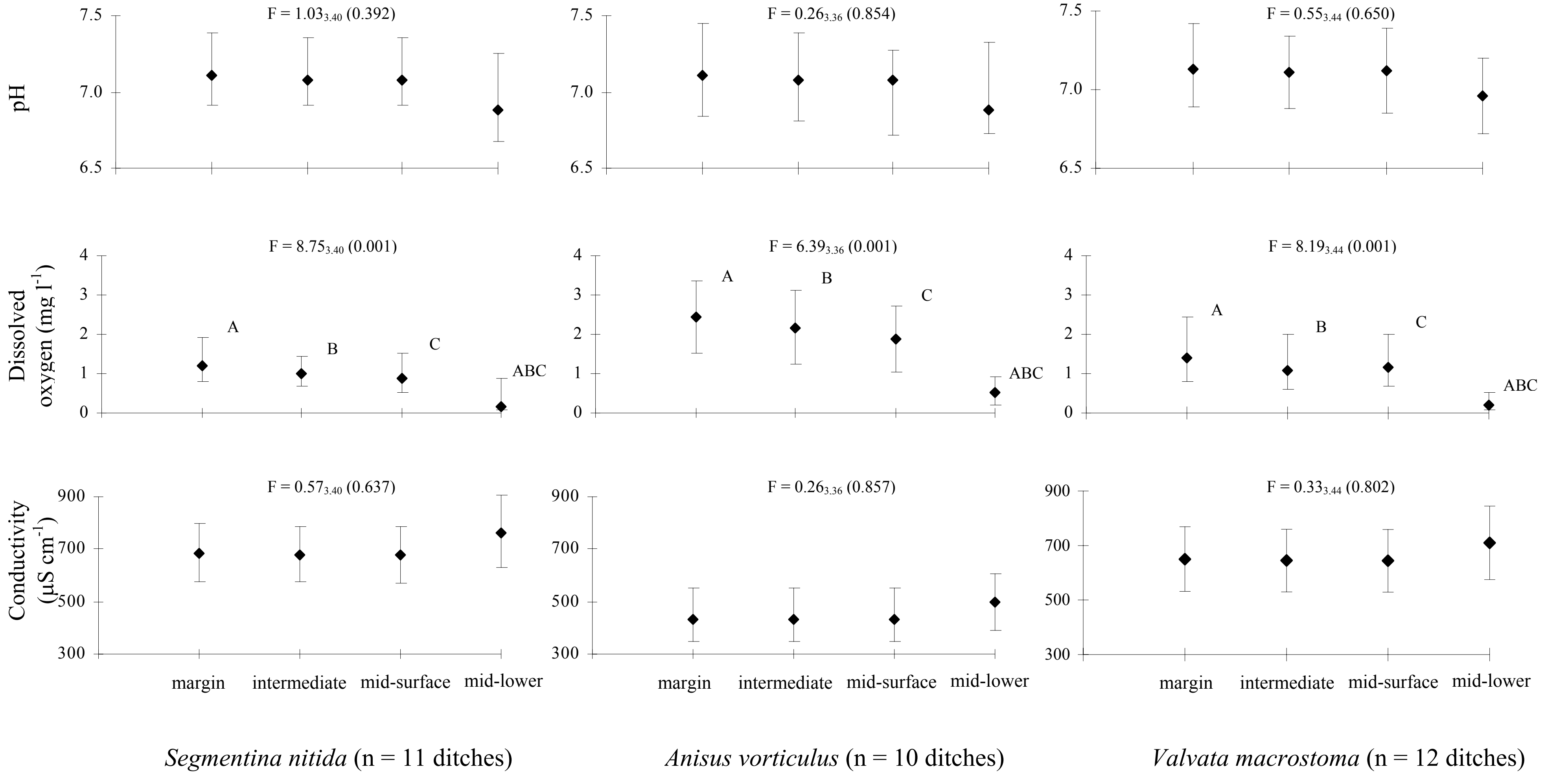


Figure 3.4: Variations in the cover of 3 major vegetation components between different locations within drainage ditches in south east England occupied by three RDB snails. The values are means (± s.d). Significant differences were determined by one-way ANOVA (F), identical letters denote significant pairwise differences indicated by Fisher's pairwise comparison. (Black bar = submerged vegetation, Grey bar = floating vegetation, White bar = emergent/amphibious vegetation).

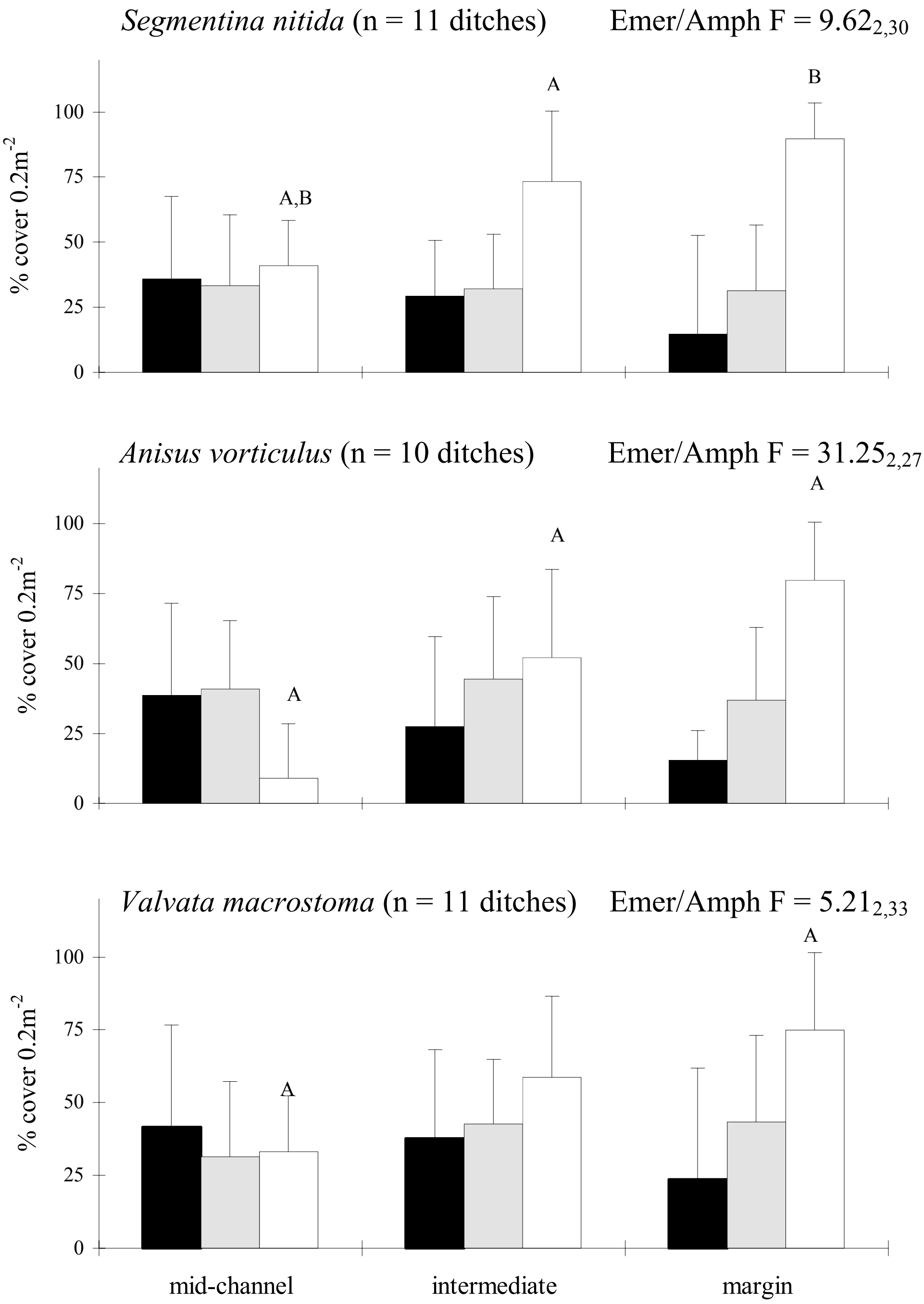
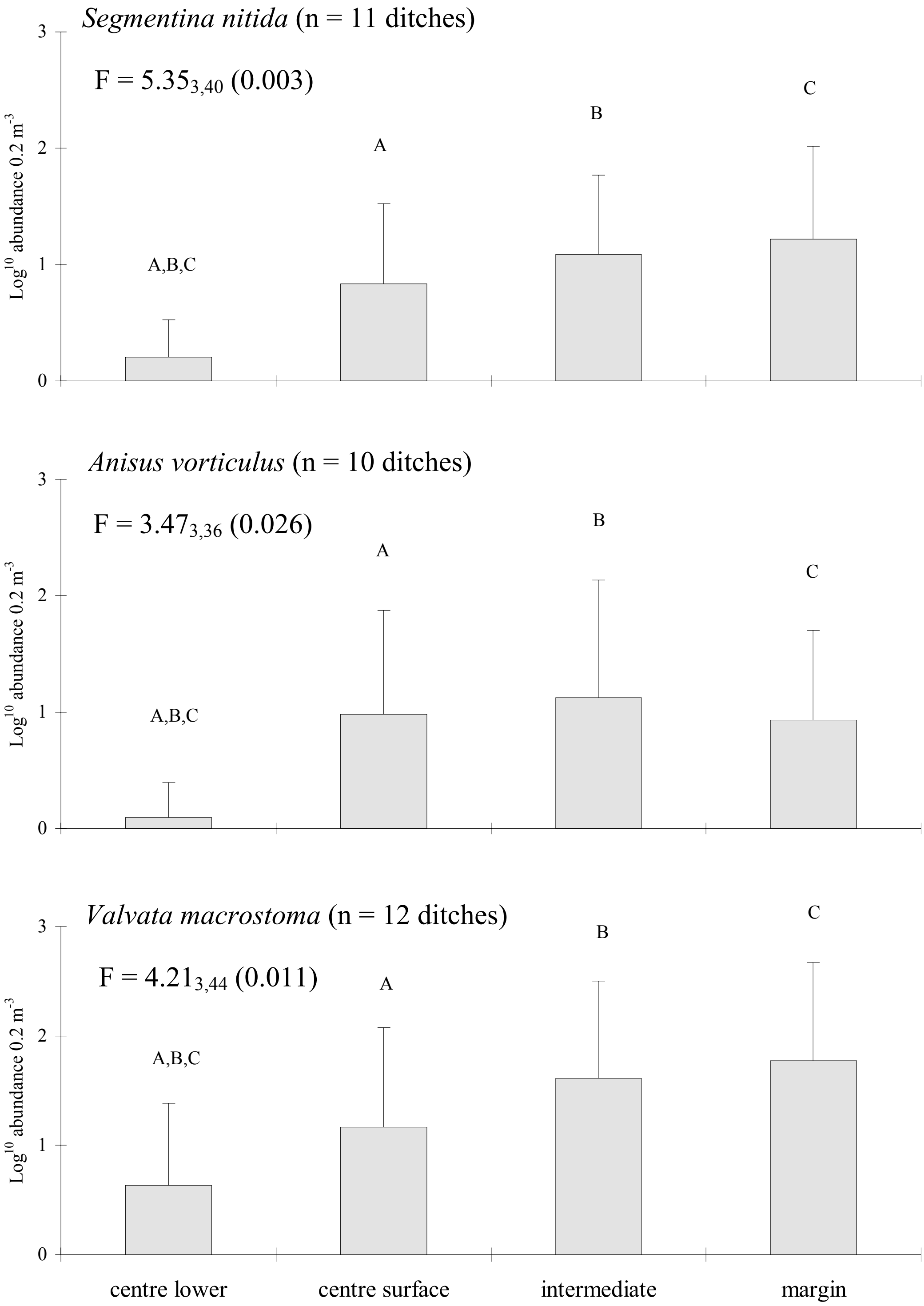


Figure 3.5: Variations in the abundance of three RDB snail species across replicate drainage ditches in south-east England. The values are log means (± s.d.). Significant differences were determined by one-way ANOVA (F), identical letters denote significant pairwise differences indicated by Fisher's pairwise comparison.



- Chapter 4 -

Assemblages of aquatic gastropods on grazing marshes of south-east England in relation to the ecological character and successional stages of drainage ditches.

4.0. Abstract

Assemblages of aquatic snails were examined in 106 ditches on four grazing marshes in lowland south-east England. These artificial habitats contain relict features from formerly large wetlands and are now managed rotationally but often haphazardly, through a de-silting and vegetation clearance process, which maintains a diversity of ecological successional stages. This study assessed whether snail assemblages were associated with particular ditch characteristics and the implications for management. Snail abundance, vegetation cover and environmental factors were recorded from each ditch. Classification by TWINPSAN and ordination by canonical correspondence analysis were used to assess how pattern in the major species assemblages related to vegetation and water chemistry. Kruskal-Wallis tests were used to assess differences in species abundance, diversity/conservation indices, water chemistry and vegetation between contrasting groups of ditches indicated by TWINSPAN. Putative successional stages were derived from the vegetation data using principal component analysis and differences in snail abundance between stages were assessed using Kruskal-Wallis tests.

Three snail assemblages indicated by TWINSPAN were respectively characterised by the presence of each of three Red Data Book (RDB) species. Assemblages differed between sites varying in conductivity, chloride, alkalinity and calcium concentrations. *Anisus vorticulus* (RDB, Vulnerable) and associated species were found in deeper less calcareous ditches with open water, high cover of submerged vegetation and with the greatest diversity of aquatic plants. *Valvata macrostoma* (RDB, Vulnerable) was found with the highest diversity of snails, in ditches that had a mixture of submerged, floating and emergent vegetation. Mixed vegetated ditches occupied by this diverse assemblage also supported high abundances of several species that were borderline between assemblages, including *Segmentina nitida*. However, *S. nitida* (RDB, Endangered) and associated snail species mostly characterised shallow, densely vegetated and calcareous ditches with homogenous stands of emergent vegetation. The three assemblages, respectively, characterised different stages of ditch succession and their contrasting structure of ‘open’ (*A. vorticulus*), ‘mixed’ (*V.macrostoma*) and ‘dense’ vegetation (*S. nitida*).

A management regime that maintains ditches at all stages of ecological succession across a given marsh is most likely to provide a mosaic of conditions suitable to

support each respective gastropod assemblage and their associated RDB species. This strategy will depend also on maintaining suitable water quality with low nitrogen, and flood management that allows mollusc dispersal between ditches. These data reveal how RDB molluscs can act as ‘umbrella’ species in conservation by typifying distinct ecological conditions and wider species assemblages.

4.1. Introduction

Shallow, slow flowing or lentic waterbodies are prone to sedimentation and encroachment by macrophytes (Sutherland & Hill 1995, Thompson & Finlayson 2001). The diversity of habitats in lakes, ponds, ditches, lagoons and backwaters of rivers are often the result of this hydroseral succession and the resulting variation in macrophyte assemblages (Castella *et al.* 1984, Hingley 1979, Sutherland & Hill 1995, Ray *et al.* 2001). Succession, in turn, causes a gradation in communities of plants and animals. Unless the ecological succession is interrupted or reset by some form of intervention or disturbance, the assemblages of macrophytes and macroinvertebrates will continue to change until they reach climax stages which are often terrestrial in character (MacKenzie *et al.*1999).

One example of wetland environments characterised by succession, are the drainage ditches which form complex artificial networks across many of the large grazing marshes in south-east England. These shallow ditches (depth c1.5m) are often dominated by macrophytes, and can support high diversity of aquatic macro-invertebrates. Ditches of this type are considered to represent relict habitats that once occurred widely on previously un-drained, low-lying marshland. They are interesting also in that succession in ditches depends strongly on management intervention. Through time, ditches become less effective in allowing drainage and if left undisturbed revert to terrestrial habitat (Caspers & Heckman 1981, 1982, Kirby 1992, Painter 1999). To fulfil their requirements in providing drainage, the ditches have to be managed by a combination of weed clearance and silt dredging, often by mechanical means. This major disturbance halts the natural process of ditch succession and prevents competitive plant species from becoming established. Other minor disturbances include annual flooding, intrusion of saline water, intermittent flows and encroachment by cattle and other livestock (Clare & Edwards 1983, RSPB *et al.* 1997). In addition, the diversity of ditches is further enhanced by natural variations in water chemistry, geology and anthropogenic characteristics across the grazing marshes.

There is a lack of quantitative data, and few guidelines on how ecological succession and ditch management might affect relict communities of wetland organisms that still survive in many drainage ditches. This is particularly true for macro-invertebrates among which freshwater snails constitute a significant part of the community. Among

Britain's 36 freshwater species, over 78% occur in drainage ditches. This includes several scarce Red Data Book (RDB) snails: *Segmentina nitida*, *Anisus vorticulus* and *Valvata macrostoma* (Killeen 1994). Currently, ditch management for drainage purposes is carried out with little cognisance of how it might be optimised for these scarce wetlands snails or indeed other gastropods. Snail assemblages in ditches will inevitably be influenced by management and in turn, the resulting vegetation structure. However, ditches are artificial habitats and the need for frequent management can mask other factors that may affect assemblage composition. Variations have been recorded in snail abundance, for example, with increasing water depth (Økland 1964, Caquet 1990), with persistence of the habitat (Caquet 1990, Costil *et al.* 2001) and with increasing salinity (Costil *et al.* 2001). The range of factors that can affect mollusc assemblages are often difficult to clarify, making it a challenge to determine the actual causal effects on assemblage composition.

In this chapter, patterns in snail assemblages in drainage ditches from four grazing marshes were assessed and related to environmental features in the ditches using multivariate methods. Sites were also classified according to their vegetation character and stage of vegetation succession. Variations in snail assemblages and diversity were then assessed between the putative successional stages.

4.2. Methods

4.2.1. Study sites

Four grazing marshes in south-east England were used in the study: the Arun Valley in West Sussex (TQ 0314), Lewes Brooks (TQ 4208) and Pevensey Levels (TQ 6409) both in East Sussex, and the Stour Valley in Kent (SQ 2663) (Chapter 1, Figure 1.3). The largest of the grazing marshes is Pevensey Levels, at 3,500ha, whilst the smallest at 640 ha is Lewes Brooks. All are periodically flooded during the winter and in the summer are grazed mainly by cattle. All are recognised for their value to nature conservation. In 1999 the floodplain of the Arun Valley and Pevensey Levels were added to the UK list of sites notified under the Ramsar Convention which already included Stodmarsh, one of the marshes of the Stour Valley (Ramsar Convention Bureau 2002). The Arun Valley and Stodmarsh have also been designated as Special Protection Areas (SPA) under the EC Birds Directive (79/409/EEC) (European Commission 1979b), and Stodmarsh is a proposed candidate for Special Areas of

Conservation (SAC) under the EC Habitats Directive (92/43/EEC) (European Commission 1992). All the marshes contain Sites of Special Scientific Interest (SSSIs) due to their importance for over-wintering birds and aquatic plant/invertebrate communities. Stodmarsh and the north-west part of Pevensey Levels are National Nature Reserves (NNR) managed by the statutory agency for nature conservation, English Nature (Chapter 1).

4.2.2. Sampling protocol

Between May and September 1999, a total of 106 ditches on all four study marshes were individually surveyed representing 81 randomly selected ditches and 25 targeted ditches known to be occupied by two rare snails: *Segmentina nitida* and *Anisus vorticulus*. The targeted ditches were used to ensure that a sufficient number of ditches contained these Red Data Book (RDB) snails for the presence/absence analyses discussed in Chapter 2. The random ditches provided a true indication of the relative coverage and occupancy by each mollusc assemblage. Molluscs were sampled in each ditch using a standardised sieve net (Chapter 2 & Appendix 1). Four mollusc samples taken from a 20m stretch of each ditch were pooled and preserved on site with 70% Industrial Methylated Spirit (IMS). In the laboratory, the samples were washed through a 500µm sieve and all gastropods were removed and identified to species with a light microscope (x10) using Macan (1977).

The 20m ditch section used for sampling molluscs was also used for a contemporaneous vegetation survey adapted from the standard ditch vegetation methodology devised by Alcock & Palmer (1985). An estimate was made of the total percentage of the water surface covered by all vegetation as well as individual cover by submerged, floating, emergent and amphibious plant groups. Cover was defined as the area occupied by each of the above components when the site was viewed from above. Total cover was always 100% or less, whereas the combined percentages of the four plant group was occasionally over 100% due to layering within the vegetation. Submerged plants included species such as *Lemna trisulca* and *Ceratophyllum demersum* that typically grow under a floating layer of vegetation. Floating vegetation consisted of plants with their vegetative parts on the water surface such as *Hydrocharis morsus-ranae*. Examples of emergent plants were *Typha* species and *Phragmites australis* whose root systems are predominantly submerged.

Amphibious plants are not aquatic species but are able to tolerate marshy conditions such as *Glyceria* and *Juncus* species.

All the plants in the 20m ditch section were recorded and identified to species using Rose (1981). If plants could not be identified consistently in the field at these levels, they were recorded to genus (e.g. *Callitriche* spp). Nomenclature followed Dony *et al.* (1986) for both common and scientific names. Estimates of cover were allocated for each wetland plant species within the 20m stretch of the ditch using DAFOR scores (Dominant: 71-100%, Abundant: 51-70% , Frequent: 16-50%, Occasional: 6-15% , Rare: 1-5%).

Habitat features were recorded from each ditch at the same time as the molluscs and included the dimensions of individual ditches (width, mid-channel depth, depth of sediment layer, height of bank), the adjacent land-use (grazing, hay, arable, woodland), the percentage extent of trees and shrubs along the ditch and the percentage of the ditch in shade. The percentage of the ditch choked by vegetation was estimated by assessing the proportion of the water column that was blocked by macrophytes considered to be impeding water flow (Chapter 2).

Water samples from each ditch were analysed for conductivity, pH, biological oxygen demand (BOD), alkalinity, chloride, calcium, total organic nitrogen (TON), nitrate, nitrite, ammoniacal-nitrogen, ortho-phosphate and chlorophyll-*a* using methods described in Chapter 2.

4.2.3. Statistical analysis

Prior to statistical analysis, each ditch in the survey was assigned a Conservation Score (CS), a Molluscan Conservation Index (MCI) and an abundance-adjusted Molluscan Conservation Index (AMCI) based on the whole mollusc community (Appendix 2). The conservation indices were calculated using individual scores for each species devised by Killeen (1998) based on how local they are to ditch habitats and their status in the British Red Data Book (RDB) list (Table 4.1 & Appendix 2). The CS represents a simple presence/absence index but also increased weighting due to the presence of rare species. Ditches with low species diversity but containing species of conservation interest sometimes have a low CS, so the MCI provides more weighting determined by the highest conservation scoring species present in these ditches. The AMCI is similar to the MCI but the average score per taxon is calculated making it more sensitive to low abundance of rare species (see Appendix 2 for equations). Two diversity indices for all molluscs were also calculated, Simpson's Index (D) (Simpson 1949) and Shannon's Index (H) (Shannon & Weaver 1949). Species-richness and abundances for gastropods and bivalves were calculated separately (Chapter 5). Principal component analysis (PCA) (MINITAB v12 1998) was used to assess the major variations across all the ditches in their diversity of mollusc species based on the correlation matrix of the diversity measure. Contributions to the principal components were judged from loading values and from Spearman's rank correlation between individual diversity/conservation indices scores on the first three axes of the mollusc PCA .

Ordination by CANOCO (ter Braak & Smilauer 1998) and classification by TWINSPAN (Hill 1979) were used to assess the major species assemblages among the gastropods. Ordination arranges sites and assemblages into an objective order based on species associations on both their co-occurrence and abundances. Classification by TWINSPAN performs a similar function but hierarchically clusters groups of ditches based on their gastropods assemblages. The assemblages of species are also simultaneously classified on the basis of their co-occurrence in the ditches. Before carrying out analyses using TWINSPAN and CANOCO, species which occurred in less than 10% of the ditches were removed, to prevent chance association masking the assemblage patterns.

For TWINSPAN, species abundances are represented as pseudo-species for which a range of cut-levels were explored but found to have negligible effect on the end-groups created. The final cut-levels chosen corresponded with the ACFOR scale, which placed emphasis on the species occurring at lower frequency, of particular relevance to the RDB species (Rare: 1-5, Occasional: 6-10, Frequent: 11-50, Common: 51-100 and Abundant: over 100). The TWINSPAN division of both species and ditches was halted at the second level of classification beyond which groups were too small for meaningful analysis. Non-parametric Kruskal-Wallis tests were used to assess any significant differences in the abundance of each snail species between TWINSPAN groups and to assess inter-group variations in water quality, vegetation structure and mollusc indices.

For ordination, the species abundances were logarithmically transformed and ordinated with individual environmental variables and the scores from the first axis of the mollusc diversity PCA using Canonical Correspondence Analysis (CCA). Monte-Carlo permutation tests were used to evaluate the significance of each variable in the ordination using a stepwise forward selection criteria in CANOCO (ter Braak & Smilauer 1998). CCA uses multiple regressions to create a series of environmental gradients, otherwise known as axes, that reflect trends in assemblage composition in relation to environmental character. The relative strengths and importance of each axis were given by eigenvalues and by the percentages of the total variance in the data-set explained.

Trends in vegetation structure between all ditches were assessed by PCA on the correlation matrix between percentage cover and diversity for all vegetation types. This analysis was described in Chapter 2, but here was used to indicate vegetation succession. The ditches were then separated into three equal-sized vegetational groups taken to represent categories of ditch succession. Variations in vegetation data, diversity/conservation indices and the abundance of snails between the different stages of vegetation types were assessed using one-way analysis of variance (ANOVA) or where the variance could not be normalised, Kruskal-Wallis tests.

4.3. Results

Twenty-four freshwater gastropod species were recorded across the drainage ditches including, *S. nitida* (RDB, Endangered), *A. vorticulus* (RDB, Vulnerable) and *Valvata macrostoma* (RDB, Vulnerable). The four most widespread snails, appearing in over 70% of the ditches, were *Lymnaea peregra, Bithynia tentaculata, Anisus vortex* and *Planorbis planorbis* (Figure 4.1). The least widespread were *Anisus leucostoma, Aplexa hypnorum, Potamopyrgus antipodarum* and *Physa acuta*, all four being found in six ditches or less (Figure 4.1). The latter two are non-native species while the former two are species typical of ditches with little standing water. Since these species all occurred in less than 6% of the ditches, they were removed from further analyses. Mollusc diversity and conservation interest was strongly represented by just one PCA axis which captured 50% of the variation among the diversity measures (Table 4.2). This axis reflected a gradient from sites with high mollusc diversity and high conservation interest to sites with poor mollusc diversity and no RDB species.

4.3.1. Species assemblages

TWINSPAN classification indicated three gastropod assemblages that were also clearly recognisable on the ordination biplot (Figure 4.2). Interestingly, the three RDB species were characteristic of different assemblages that were respectively *A. vorticulus* in assemblage 1, *V. macrostoma* in assemblage 2 and *S. nitida* in assemblage 3 (Figure 4.2). Based on the same TWINSPAN analysis, three site groups were apparent comprising of group 1 with 28 ditches, group 2 with 33 ditches and group 3 with 43 ditches. Ditches in TWINSPAN group 1 were typically deeper than both groups 2 and 3 with more open water, a higher diversity of aquatic plants, and a higher percentage of submerged vegetation (Table 4.3). In group 2, the ditches were choked with a mixture of submerged, floating and emergent vegetation from a diverse plant community and there were higher concentrations of chlorophyll-*a* (Table 4.3). Ditches in group 3 were shallower and choked particularly by emergent vegetation (Table 4.3). For water chemistry, the TWINSPAN group 1 ditches had significantly lower levels of conductivity, alkalinity and calcium than groups 2 and 3 (Table 4.3). The latter two groups of calcareous ditches were separated by significantly higher levels of chloride and BOD in group 2 (Table 4.3).

Although all twenty snails species were represented in at least one site in each of the three groups of ditches, there were significant differences in their abundance values between the groups (Table 4.4). Thus, ditches in group 1 had the highest abundances for *A. vorticulus, Planorbis carinatus, Gyraulus albus* and *Valvata piscinalis* that were all representatives of snail assemblage 1 (Table 4.4). Group 2 ditches had the highest abundances for eleven snail species mostly typical of assemblage 2 but also including *S. nitida* (Table 4.4). The least favourable ditches for snails were in group 3 where the abundant species included *P. planorbis* and *Planorbarius corneus* from assemblage 3 (Table 4.4). The frequency of occurrence of *S. nitida* was greatest among the ditches of group 3, signifying it as a characteristic species of assemblage 3 rather than assemblage 2.

4.3.2. Ordination

Axes 1 and 2 of the CCA represented 64% of the variation in the relationship between mollusc species and the environmental variables (Figure 4.2, Table 4.5), this value falling by only 2% when the mollusc diversity PCA 1 was omitted as an explanatory variable. The diversity and conservation indices correlated strongly with scores of CCA axis 2, and hence the mollusc diversity PCA was retained as an explanatory variable since it illustrated this major trend. Variations in snail assemblages on axis 2 of the CCA biplot were related to mollusc diversity and conservation interest (Figure 4.2 & Table 4.2). Species such as *V. macrostoma, S. nitida, Bithynia leachii, Acroloxus lacustris* and *A. vorticulus* all had low scores on this axis and were indicators of mollusc-rich assemblages (Figure 4.2). In contrast, species with high scores on CCA axis 2, *P. planorbis* and *L. peregra,* were generally found in species-poor ditches, reflecting their wide tolerance and appearance where no other species occurred (Figure 4.2).

In general, axis 1 separated calcareous, densely vegetated ditches with pronounced emergent vegetation but low plant diversity from deeper, more open ditches with more diverse plant assemblages. Species such *as A. vorticulus, V. piscinalis* and *G. albus* from assemblage 1 all had high positive scores along this axis, further indicating preference for less calcareous ditches with deeper open water. By contrast, the species in assemblage 3, including *S. nitida* and *B. contortus* had low scores along axis 1 indicating a preference for calcareous ditches that were shallow and choked with emergent vegetation (Figure 4.2).

4.3.3. Vegetation succession

The PCA on the vegetation data indicated one dominant principal component reflecting a trend from open water sites with high diversity of mostly submerged plants to shallow ditches choked with mostly emergent plants of low diversity (Chapter 2, Table 2.1). When divided into three equal sized groups of ditches, this axis appeared to separate early, mid and late successional ditches characterised respectively by ‘open’, ‘mixed’ and ‘dense’ vegetation (Table 4.6). As expected from the division, the first group represented deep, wide ditches with an open vegetation structure of submerged vegetation and open water. The second group had mixed vegetation dominated by submerged, floating and emergents. The last group consisted of shallow ditches at the advanced stages of vegetation succession choked with emergent and amphibious vegetation (Table 4.6). *G. albus*, *B. tentaculata* and *Physa fontinalis* were all recorded in greater abundance in the open vegetated ditches than in the densely vegetated ditches (Table 4.7). In contrast, the choked ditches with dense vegetation had higher abundance of all the species in TWINSPAN assemblage 3 compared to the open vegetated ditches (Table 4.7). However, there were no significant differences between successional groups in the mollusc diversity or conservation indices, indicating that high conservation interest could occur at any stage of ditch succession. This reflects the varying preferences of the respective RDB molluscs and their associated assemblages for different stages of ditch succession.

4.4. Discussion

A ditch considered to be of high conservation value for freshwater snails will usually support ten species or at least one of the species listed in the RDB (Hingley 1979). Ditches in this survey ranged from no snails to a maximum of 16 species indicating the range of ditches surveyed. All three RDB snails typical of drainage ditches were recorded: *S. nitida*, *A. vorticulus* and *V. macrostoma*. Most interestingly of all, each occurred with a different gastropod assemblages and under distinct ecological conditions.

4.4.1. Water chemistry

The main water chemistry variations between the TWINSPAN assemblages were in calcium, alkalinity, conductivity and chloride. Distribution of molluscs have long been regarded as governed by calcium concentrations and water hardness (Boycott 1936, Macan 1950, Aho 1966, Dussart 1976, Aho *et al.* 1981, Lodge *et al.* 1987, Økland 1983, 1990, Lewis & Magnuson 2000). The absence of snails from waterbodies with low calcium concentrations can be attributed to their inability to obtain sufficient calcium for shell construction at low concentrations (e.g. Boycott 1936). Later research has indicated that calcium may just be an indication of a range of other associated variables that can restrict the distribution of molluscs (Dussart 1976, Dillon 2000). Low calcium concentrations in waterbodies have been associated with poor productivity, a reduction in detrital decomposition, less effective osmotic regulation and a lower buffering capacity against fluctuations in pH (Dussart 1976, Dillon & Benfield 1982, Webster & Benfield 1986, Dillon 2000). There are also strong inter-correlations between calcium and other physio-chemical factors such as alkalinity, water hardness, pH, total solids and conductivity (Dillon & Benfield 1982, Dillon 2000). However many physio-chemical factors, only limit snail distribution at extreme levels such as in non-calcareous areas (Macan 1950, Økland & Økland 1997). Calcium and other physio-chemical factors rarely explains differences in abundance across a small geographical distance or between waterbodies which are naturally eutrophic (Lassen 1975, Aho 1978a,b & c, Russell-Hunter 1978, Aho *et al.* 1981, Dillon & Benfield 1982, Økland 1983, Lodge *et al.* 1987). The TWINSPAN assemblage 1 was typical of less calcareous ditches compared to the other two TWINSPAN assemblages. However, the ditches containing the highest abundances of assemblage 1 species had an average calcium concentrations of 50mg l^{-1} exceeding the suggested critical concentrations for the majority of freshwater snails at 5mg l^{-1} (Lodge *et al.* 1987).

4.4.2. Vegetation character

Where physio-chemical factors are not limiting, the distribution and diversity of molluscs appears to be influenced by area size and associated habitat diversity (Lassen 1975, Lodge *et al.* 1987, Dillon 2000). In lotic environments, the habitats, and in turn, mollusc distribution appears to be greatly influenced by velocity and substrate composition (Cummins & Lauff 1969, Harman 1972, Carlow 1973b, Mason & Bryant 1975, DeKock *et al.* 1989, Crowl & Schnell 1990). By contrast, in lentic habitats, variations in mollusc assemblages are associated with vegetation distribution and character (Aho 1966, Pip & Stewart 1976, Clare & Edwards 1983, Scheffer *et al.* 1984, Lodge 1986, Caquet 1990, Økland 1990). Freshwater snails and macrophytes can have a strongly mutualistic relationship, snails assisting the plants with the removal of epiphytic cover from their surfaces (Thomas 1990). Macrophytes are rarely eaten directly by snails but enter the food web as detritus after decomposition or act as surface for epiphytic cover (Reavell 1980, Brönmark 1989, Thomas & Kowalczyk 1997). Specific associations between snails and individual plant species are infrequent, instead plant structure and morphology playing a greater role in determining snail distribution (Carlow 1973a, Lodge 1985, Lodge *et al.* 1987, Caquet 1990). Snails also benefit from plants as substrata for oviposition, as a means to gain access to air-water interface, for refugia and also because macrophytes detoxify the water by removing ammonia (Brönmark 1989, Thomas *et al.* 1985, Carpenter & Lodge 1986, Lodge 1986, Underwood & Thomas 1990, Økland 1990, Turner 1996). All of these factors could be involved in mediating interactions between the snail assemblage composition and vegetation character in this study. However, exact details and linkage are poorly known for most individual species.

Previous studies have shown that snail diversity increases with habitat diversity, which in turn is determined by plant richness, physical structure and substrate types (Harman 1972, Crowder & Cooper 1982, Brönmark 1985a, Costil & Clement 1996). The high snail diversity found in ditches with mixed vegetation structure of submerged, floating and emergent would be consistent with this pattern. Ditches which are frequently or have recently been managed either by de-silting or weed clearance will offer an homogenous vegetation structure in the first two years (van Strien *et al.* 1991, Best 1993, 1994). Snails typical of deeper water with less vegetation such as *V. piscinalis*, *G. albus* and *P. carinatus,* could be regarded as pioneer species of these recently managed ditches. Without management, ditches often become increasingly choked with emergent and amphibious plants forming a uniform vegetation composition throughout the ditch (van Strien *et al.* 1991, Best 1993, 1994) and snail species such as *P. planorbis* and *L. palustris* usually start to dominate (Boycott 1936, Kerney 1999).

4.4.3. Management implications

The strong relationship between vegetation structure and freshwater snail assemblages has implications for ditch management. Freshwater snails of grazing marshes appear to be adapted to the periodic disturbance caused by a traditional management regime involving rotational clearance of the silt and plants on a 15-20 years basis (Hingley 1979, Clare & Edwards 1983). In the past, clearance was carried out using hand tools but since the 1970s has largely been carried out by mechanical means (Marshall *et al.* 1978). The rotational regime across a marsh allows a range of vegetation structures to occur simultaneously as a result of hydroseral progression (Kirby 1992, RSPB *et al.* 1997, Painter 2000). Length of rotation can vary from annual light maintenance of all the ditches to a radical cleaning of 10-20% of the drainage channels every year. Because the three RDB snails occur in different vegetation structures, a rotational regime of a certain percentage of the ditches should ensure that there always ditches at the appropriate stage for each. In addition, the RDB snails are each indicators of a distinct mollusc assemblage so that management for all three should ensure the conservation of both a diverse array of species and a distinct array of assemblages. In this way, the RDB species appear to be wider indicators or ‘umbrella species’ (Caro & O’Doherty 1999, Simberloff 1997) for which active management would benefit gastropod conservation as a whole.

For the rotational management system to succeed, however, either the persistence of snail populations must be maintained within ditches or dispersal should be facilitated between ditches. The intensive drainage management of grazing marshes has led to infrequent and shorter flooding periods as well as the infilling or underdrainage of ditches (Marshall *et al.* 1978, Hughes & Rood 2001). This has lead to isolation of snail populations across the marsh and hence a higher risk of local extinction in particular species with poor colonising abilities (MacArthur & Wilson 1967, Lassen 1975, Jokinen 1987). Possible methods to assist the colonisation between ditches include artificial intervention and introduction to ditches which have suitable vegetation structure and water quality, but methods are poorly developed and nor would the populations be self-sustaining at the marsh scale. Moreover, the transport and introduction of scarce organisms is governed by strict legislative criteria, re-introduction should only occur within the historical range of the species. (IUCN 1987, 1998). More preferable, would be water level management that encouraged flooding to occur on a regular basis. Annual flooding on Pulborough Brooks, a nature reserve in the Arun Valley which was previously intensive farmland, has possibly contributed to an increase in the distribution of *A. vorticulus* across the reserve (Willing 2000). Alternatively, to maintain persistence in occupied ditches, remnants of previous vegetation structure should be preserved as refuges when clearing a ditch (Kirby 1992, RSBP *et al.* 1997). A final management option is to ensure that sequences of ditch succession and management occurs among a cluster of adjoining ditches, thereby maintaining connectivity between ditches of different successional stages.

Table 4.1: Conservation values for freshwater snails typical of drainage ditches on lowland grazing marshes in south-east England (adapted from Killeen 1998).

Species	Common name	Status in UK	Conservation values
Gastropod species:			
Anisus vorticulus	Little whirlpool ram's-horn snail	RDB2	10
Segmentina nitida	Shining ram's-horn snail	RDB1	9
Valvata macrostoma	Large mouthed valve snail	RDB2	8
Bithynia leachii	Leach's Bithynia	Local	5
Acroloxus lacustris	Lake limpet	Common	4
Hippeutis complanatus	Flat ram's-horn snail	Local	4
Planorbarius corneus	Great ram's-horn snail	Common	4
Valvata piscinalis	Common valve snail	Local	3
Valvata cristata	Flat valve snail	Local	3
Bathyomphalus contortus	Twisted ram's-horn snail	Local	3
Bithynia tentaculata	Common Bithynia	Common	3
Lymnaea palustris	Marsh pond snail	Common	3
Lymnaea stagnalis	Great pond snail	Common	3
Planorbis planorbis	Margined ram's-horn snail	Common	3
Planorbis carinatus	Keeled ram's-horn snail	Common	3
Anisus vortex	Whirlpool ram's-horn snail	Common	3
Armiger crista	Nautilus ram's-horn snail	Common	3
Gyralus albus	White ram's-horn snail	Local	3
Anisus leucostoma	Button ram's-horn snail	Common	2
Aplexa hypnorum	Moss bladder snail	Local	2
Physa fontinalis	Common bladder snail	Common	2
Lymnaea peregra	Common pond snail	Common	1
Physa actua	American bladder snail	Naturalised	0
Potamopyrgus antipodarium	Jenkins' spire snail	Naturalised	0

RDB = Red Data Book, 1 = endangered, 2 = vulnerable, 3 = rare

Table 4.2: Spearman's rank correlations between the first three axes of the molluscs PCA scores and the molluscs diversity and conservation indices (*** = P <0.001, ** = p <0.010, n.s. = not significant).

Variables	Axis 1	Axis 2	Axis 3
Eigenvalue	4.5275	1.4818	1.1329
Percentage explained	50%	17%	13%
Gastropod diversity	0.875 ***	n.s.	-0.304 **
Gastropod abundance	0.462 ***	0.673 ***	-0.452 ***
Bivalve diversity	0.875 ***	n.s.	0.780 ***
Bivalve abundance	0.480 ***	0.421 ***	0.203 ***
Shannon diversity index	0.793 ***	-0.519 ***	n.s.
Simpson diversity index	0.648 ***	-0.627 ***	n.s
Mollusc conservation index (MCI)	0.739 ***	n.s	0.291 **
Conservation score (CS)	0.952 ***	n.s	n.s
Abundance-adjusted MCI (AMCI)	0.781 ***	0.409 ***	n.s

Table 4.3: Mean (± s.d.) environmental variables for each TWINSPAN group. Significant differences between groups were indicated by Kruskal-Wallis tests (H) (*** = P <0.001, ** = P <0.010, * = P <0.050).

(Pairwise differences were established with Kruskal-Wallis tests ⬤ = significantly higher values than the other TWINSPAN groups, ● = significantly lower values than one TWINSPAN group but higher than the other group, • = significantly lower values than the other TWINSPAN groups. Equal size symbols indicate no significant differences between the two groups except where ♦ was used to indicate no significant differences with either of the other two TWINSPAN groups).

Variables	Group 1 (N=28)	Group 2 (N=33)	Group 3 (N=43)	H value
Vegetation structure				
Floating vegetation cover (%)	• 23 (26)	⬤ 74 (26)	• 41 (42)	24.44 ***
Chlorophyll a (mg l^{-1})	• 17 (19)	⬤ 58 (95)	• 19 (27)	12.63 **
Ditch choked by vegetation (%)	• 14 (32)	⬤ 34 (38)	⬤ 45 (42)	9.49 **
Vegetation cover (%)	• 58 (30)	⬤ 87 (16)	⬤ 81 (28)	15.66 ***
Emergent vegetation cover (%)	• 33 (29)	⬤ 49 (22)	⬤ 52 (36)	8.22 **
Submerged vegetation cover (%)	⬤ 31 (31)	⬤ 22 (29)	• 8 (16)	15.98 ***
Wetland plant species diversity	⬤ 17 (6)	⬤ 15 (4)	• 12 (6)	13.62 ***
Depth (m)	⬤ 0.9 (0.3)	♦ 0.7 (0.3)	• 0.7 (0.4)	6.27 *
Open water (%)	⬤ 41 (30)	• 13 (16)	• 20 (27)	13.28 ***
Water chemistry				
BOD (mg l^{-1})	• 4 (4)	⬤ 6 (4)	• 4 (3)	12.47 **
Chloride (mg l^{-1})	•59 (52)	⬤ 127 (76)	• 115 (196)	21.82 ***
Conductivity (µS cm^{-1})	•459 (231)	⬤ 781 (226)	● 688 (414)	24.47 ***
Alkalinity (mg l^{-1})	•128 (50)	⬤ 215 (50)	⬤ 203 (84)	26.08 ***
Calcium (mg l^{-1})	• 50 (21)	⬤ 77 (26)	⬤ 84 (34)	21.70 ***
Mollusc community				
Gastropod species diversity	• 9 (3)	⬤ 13 (2)	• 8 (3)	52.68 ***
Gastropod abundance	• 228 (219)	⬤ 679 (512)	• 256 (313)	28.44 ***
Mollusc Shannon diversity index.	• 1.5 (0.5)	⬤ 1.9 (0.3)	• 1.3 (0.5)	25.78 ***
Mollusc conservation scores	● 39 (15)	⬤ 58 (11)	• 30 (10)	53.52 ***
Bivalve species diversity	⬤ 3 (2)	⬤ 3 (1)	• 2 (1)	19.89 ***
Bivalve abundance	⬤ 42 (69)	⬤ 70 (90)	• 9 (10)	33.36 ***

Table 4.4: Mean (± s.d.) abundances of gastropod species for each TWINSPAN group. Significant differences between groups were indicated by Kruskal-Wallis tests (H) (*** = *P* <0.001, ** = *P* <0.010, * = *P* <0.050).

(Pairwise differences were established with Kruskal-Wallis tests ● = significantly higher abundance than the other TWINSPAN groups, ● = significantly lower abundance than one TWINSPAN group but higher than the other group, • = significantly lower abundance than the other TWINSPAN groups. Equal size symbols indicate no significant differences between the groups except where ♦ was used to indicate no significant differences in abundance with either of the other two TWINSPAN groups).

Species (Twinspan species assemblage)	**Group 1** (N=28)	**Group 2** (N=33)	**Group 3** (N=43)	H value
V. macrostoma (2)	• 6 (29)	● 65 (157)	• 1 (6)	28.93 ***
B. leachii (2)	• 11 (28)	● 21 (91)	• 4 (12)	28.61 ***
L. stagnalis (2)	• 1 (1)	● 5 (13)	• 1 (1)	12.61 **
V. crisata (2)	• 6 (8)	● 36 (55)	• 4 (9)	30.61 ***
A. vortex (2)	• 14 (22)	● 61 (71)	• 13 (25)	30.87 ***
H. complanatus (2)	• 5 (12)	● 38 (65)	• 1 (2)	45.43 ***
A. crista (2)	• 3 (14)	● 3 (8)	• 1 (5)	9.59 **
P. corneus (3)	• 1 (2)	● 4 (7)	● 1 (2)	11.23 **
P. planorbis (3)	• 3 (10)	● 62 (112)	● 54 (94)	36.47 ***
S. nitida (3)	• 0 (0)	● 15 (33)	● 3 (13)	15.52 ***
L. palustris (3)	• 1 (2)	● 17 (35)	● 7 (13)	27.56 ***
B. contortus (3)	• 6 (30)	● 85 (214)	● 62 (184)	28.45 ***
L. peregra (2)	• 16 (17)	● 60 (73)	♦ 66 (109)	4.46
A. lacustris (2)	● 2 (3)	● 18 (68)	• 0 (0)	26.55 ***
B. tentaculata (1)	● 61 (96)	● 84 (114)	• 25 (89)	21.80 ***
P. fontinalis (1)	● 12 (18)	● 25 (48)	• 6 (16)	12.48 **
A. vorticulus (1)	● 17 (47)	♦ 10 (47)	• 0 (1)	6.73 *
P. carinatus (1)	● 20 (38)	• 9 (28)	• 1 (4)	36.70 ***
G. albus (1)	● 13 (27)	• 1 (4)	• 0 (1)	15.22 ***
V. piscinalis (1)	● 7 (16)	• 2 (8)	• 0 (0)	22.45 ***

Table 4.5: Eigenvalues and cumulative percentage variance explained for the first four axes of the CCA biplot (see Figure 4.2 for the biplot of the first two axes).

	Axis 1	Axis2	Axis 3	Axis 4
Eigenvalues	0.149	0.087	0.037	0.034
Species-environmental correlations	0.771	0.781	0.593	0.551
Cumulative percentage variance of:				
-species data	10	16	18	21
-species-environmental relation	40	64	73	83

Table 4.6: Kruskal-Wallis tests (H) were used to indicate significant difference between three groups of ditches based on their vegetation structure (*** = $P < 0.001$, ** = $P < 0.010$). Values are means (± s.d.) of ditch dimensions and vegetation covers for each group of ditches.

(Pairwise differences were established with Kruskal-Wallis tests ⬤ = significantly higher values than the other TWINSPAN groups, ● = significantly lower values than one TWINSPAN group but higher than the other group, • = significantly lower values than the other TWINSPAN groups. Equal size symbols indicate no significant differences between two groups except where ♦ was used to indicate no significant differences with either of the other two TWINSPAN groups).

Variables	**Open vegetation** (N = 35)	**Mixed vegetation** (N = 35)	**Dense vegetation** (N =36)	H value
Width (metres)	⬤ 3.8 (1.4)	• 2.6 (1.1)	• 2.3 (1.1)	23.73 ***
Depth (metres)	⬤ 0.9 (0.3)	⬤ 0.8 (0.3)	• 0.5 (0.3)	25.82 ***
Wetland plant diversity	⬤ 17 (4)	⬤ 15 (6)	• 11 (4)	24.83 ***
Open water (%)	⬤ 50 (25)	● 15 (19)	• 5 (10)	52.27 ***
Submerged cover (%)	⬤ 29 (30)	⬤ 21 (27)	• 5 (15)	18.78 ***
Floating cover (%)	• 27 (26)	⬤ 57 (39)	⬤ 54 (42)	10.58 **
Emergent cover (%)	• 23 (14)	● 42 (29)	⬤ 73 (24)	46.70 ***
Amphibious cover (%)	• 9 (6)	♦ 14 (14)	⬤ 21 (18)	9.20 **
Vegetation cover (%)	• 49 (26)	● 85 (19)	⬤ 95 (9)	53.33 ***
Ditch choked (%)	• 1 (3)	● 26 (32)	⬤ 74 (33)	59.80 ***

Table 4.7: Significant differences in abundances indicated by Kruskal-Wallis tests (H) of gastropod species between three stages of vegetation structure (*** p < 0.002, ** p <0.020, * < 0.050).

(Pairwise differences were established with Kruskal-Wallis tests ● = significantly higher abundance than the other TWINSPAN groups, • = significantly lower abundance than the other TWINSPAN groups. Equal size symbols indicate no significant differences between the groups except where ♦ was used to indicate no significant differences in abundance with either of the other two TWINSPAN groups).

Species (TWINSPAN species assemblage)	**Open vegetation** (N = 35)	**Mixed vegetation** (N = 35)	**Dense vegetation** (N =36)	H value
G. albus (1)	● 11 (25)	• 0 (1)	• 0 (0)	18.91 ***
B. tentaculata (1)	● 67 (109)	● 60 (93)	• 31 (100)	13.14 ***
P. fontinalis (1)	● 9 (10)	● 22 (48)	• 8 (20)	7.87 **
P. carinatus (1)	♦ 8 (18)	♦ 11 (33)	♦ 7 (25)	2.60
A. vorticulus (1)	♦ 12 (42)	♦ 10 (45)	♦ 2 (9)	2.41
A. crista (2)	♦ 4 (15)	♦ 1 (2)	♦ 2 (6)	0.93
A. lacustris (2)	♦ 2 (5)	♦ 14 (66)	♦ 1 (6)	3.47
L. peregra (2)	♦ 45 (73)	♦ 53 (77)	♦ 51 (100)	2.35
L. stagnalis (2)	♦ 1 (3)	♦ 4 (13)	♦ 1 (1)	1.75
H. complanatus (2)	♦ 4 (7)	♦ 7 (16)	♦ 29 (64)	0.39
A. vortex (2)	♦ 19 (41)	♦ 41 (65)	♦ 24 (34)	2.32
B. leachii (2)	♦ 23 (48)	♦ 35 (69)	♦ 31 (71)	0.59
V. macrostoma (2)	♦ 11 (34)	♦ 14 (78)	♦ 41 (134)	3.51
V. cristata (2)	• 12 (36)	• 8 (16)	● 24 (44)	6.48 *
B. contortus (3)	• 22 (54)	♦ 31 (54)	● 106 (276)	5.81 *
P .corneus (3)	• 1 (2)	♦ 1 (2)	● 3 (6)	5.73 *
S. nitida (3)	• 0 (2)	♦ 6 (22)	● 11 (28)	7.92 **
P. planorbis (3)	• 30 (81)	● 34 (49)	● 62 (122)	7.56 **
L. palustris (3)	• 3 (6)	● 6 (9)	● 16 (34)	16.44 ***

Figure 4.1: The frequency of occurrence of each freshwater gastropod in the drainage ditches from four grazing marshes in south-east England (see Table 4.1 for full name of gastropods).

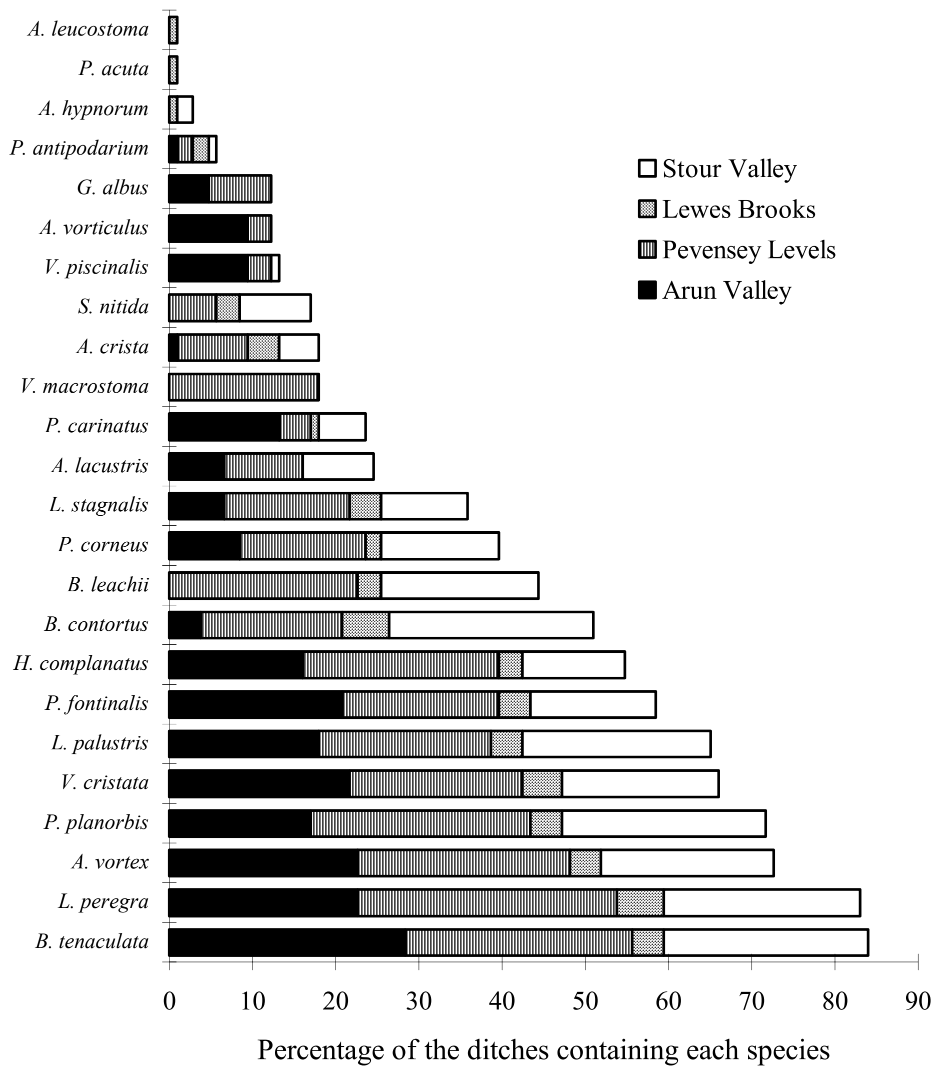
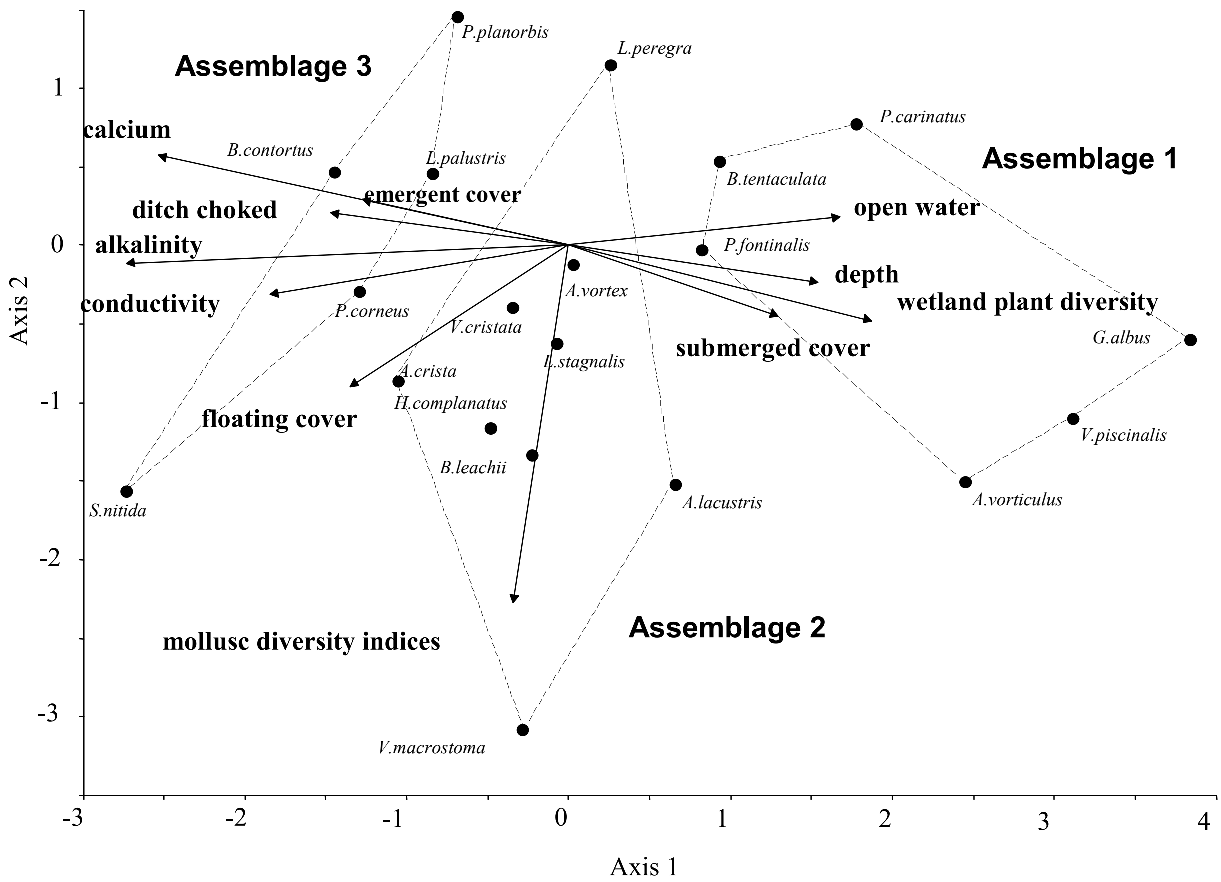


Figure 4.2: Two-dimension species ordination plot derived from the canonical correspondence analysis (CCA) of the species data and environmental variables. The species assemblages were determined by TWINSPAN analysis which are indicated by the polygons (dashed line). Increasing length of arrow indicates greater significant correlation of environmental variable with the axes.



- Chapter 5 -

Factors influencing the distribution of *Pisidium pseudosphaerium* and associate bivalves species between drainage ditches

5.0. Abstract

Despite an increasing body of work describing possible influences on the distribution of scarce wetland gastropods and large bivalves, rather less is known of the distribution and ecology of small bivalves. Among them, *Pisidium pseudosphaerium* is a rare pea mussel listed in the British Red Data Book (RDB Rare) and the UK Biodiversity Action Plan. It appears to have a relict distribution in the UK restricted to lowland grazing marshes and might be threatened by intensive drainage, nutrient enrichment and insensitive management of the drainage ditches in which it occurs. The macro-distribution of *P. pseudosphaerium* and the associated bivalve community was examined across 106 drainage ditches on 4 grazing marshes in south east England. Kruskal-Wallis tests were used to assess significant differences in the vegetation structure and water chemistry between the ditches with and without *P. pseudosphaerium*. The bivalve assemblages were examined using multivariate techniques of classification (TWINSPAN) and ordination (CANOCO) to indicate which species and environmental characters were inter-related. Kruskal-Wallis tests were also used to assess any significant differences in abundance values, mollusc diversity/conservation indices, water chemistry and vegetation between the sites occupied by two contrasting bivalve assemblages indicated by TWINSPAN.

P. pseudosphaerium occurred in over half of the ditches sampled, generally being found in ditches with slightly elevated BOD (6 ±7 mg l^{-1}) and relatively low concentrations of calcium (64 ± 31 mg l^{-1}), nitrate (0.5 ±1.2 mg l^{-1}) and nitrite (0.02 ±0.03 mg l^{-1}). This RDB species occurred where bivalve richness was locally elevated but was associated with a species poor assemblage (= Assemblage 1) comprising *Sphaerium corneum, Musculium lacustre* and *Pisidium obtusale*, typical of ditches with a high percentage cover of floating vegetation. Ditches occupied by this assemblage also had a high diversity and abundance of gastropod species, especially those of conservation interest. The second bivalve assemblage (= Assemblage 2) represented a more diverse group of bivalves including *P. milium*, *P. subtruncatum*, P. *personatum* and *P. nitidum* commonly found in the wider, deeper ditches with a greater percentage of open water.

Marked co-occurrence between *P. pseudosphaerium* and two RDB snail species - *Valvata macrostoma* (RDB Vulnerable) and *Anisus vorticulus* (RDB Vulnerable) suggests all three of theses RDB molluscs share overlapping habitat requirements.

Like *V. macrostoma* and *Segmentina nitida* (RDB Endangered), *P. pseudosphaerium* also appears to be affected negatively by elevated concentrations of nutrients. All the RDB species will therefore benefit from similar management of runoff quality, while *P. pseudosphaerium* would also benefit from the latter stages of the rotational management regimes as these other species. In contrast, the majority of the other Sphaeriidae species in assemblage 2 did not appear to favour the shallower ditches of denser vegetation required by the RDB molluscs. Therefore to ensure their peristence at the marsh-scale, any management regime need to ensure the availability of deeper ditches with open water.

5.1. Introduction

In Britain there are 28 recognised species of freshwater bivalves in three families. In turn, three bivalve species are listed in the British Red Data Book (RDB), but all are members of just one family, the Sphaeriidae or pea mussels (Bratton 1991). Hitherto, the main effort of freshwater bivalve conservation in the UK has been focused on the bivalve family with the largest individuals, the Unionidae (Willing 1997b Young & Williams 1983a & b, Young 1995, Oliver & Killeen 1996, Drake 1998a, Gittings *et al.* 1998, Hastie *et al.* 2000, Aldridge 2000, Cosgrove & Hastie 2001). In contrast, there have been very few studies of the smaller pea mussels and their habitat requirements (Boycott 1936, ∅kland & Kuiper 1982, Ham & Bass 1982, Willing 1997a). This contrasts with an increasing body of knowledge on the macro- and micro-distribution of scarce gastropods (Chapters 2, 3 and 4).

As a widespread family of freshwater bivalves, the Sphaeriidae includes species such as *Pisidium personatum* and *P. obtusale* that are adapted to temporary habitats (Boycott 1936, Kerney 1999) as well as species such as *P. subtruncatum* and *P. conventus* that are characteristic of the profoundal zones of lakes (Bagge & Jumppanen 1968, Harman 1972, Dudgeon 1983, Dillion 2000). In general, however, the habitat choices of the Sphaeriidae are poorly understood. Often the Sphaeriidae are the only molluscs to be found in the lower depths of large waterbodies with sparse plant growth which has led to a broad generalisation that they are typical of open waterbodies with some flowing water (Aho 1966, Bagge & Jumppanen 1968, Harman 1972, Mouthon 1992, Bechara 1996, Dillion 2000, Hamburger *et al.* 2000, Mouthon & Dubois 2001). Their macro-distributions are considered to be limited by excessively low pH values, low calcium concentrations and high humic contents (Aho 1966, Dussart 1976, ∅kland & Kuiper 1982, ∅kland 1990, Mouthon 1992, ∅kland & ∅kland 1997).

Contrasts and similarities between the distribution of bivalves and gastropods in freshwater environments are relatively unknown. It has been suggested that bivalves have different food requirements to the aquatic gastropod species (Boycott 1936). Bivalves are considered to be sediment dwelling species, which filter water from within sediments (Boycott 1936, Janus 1965, Kerney 1999, Dillion 2000). By contrast, gastropods are more likely to occur as epiphytic grazers among vegetation nearer the water surface (Aho 1966, Mouthon 1992, ∅kland & ∅kland 1997, Dillion 2000).

In lowland areas, drainage ditches are considered as an ideal habitat supporting many gastropod species and also at least 60% of the known Sphaeriidae in the UK. Here, the water is generally free of suspended silt and mud, but the flow is slow enough to prevent molluscs being dislodged (Boycott 1936, Kerney 1999). In conservation terms, drainage ditches are considered to be relict habitats of previously un-drained low-lying marshland, forming an extensive inter-connecting network across the grazing marshes. They are managed by conservation agencies, private landowners and water authorities for drainage on a rotational basis, thus creating a diverse range of ditch profiles and habitats (Chapters 1,2 and 4). Many such ditches are the last surviving refuge in the UK for a unique wetland community consisting of several Red Data Book (RDB) molluscs, including one member of the Sphaeriidae, *Pisidium pseudosphaerium*.

P. pseudosphaerium has been identified for conservation action under the UK Biodiversity Action Plan (BAP) due to the relative scarcity of information on its ecology and habitat requirements (HMSO 1995). To date, no species action plan has been drawn up for *P. pseudosphaerium* but the perceived threats to the species are intensive drainage of grazing marshes, dredging of the ditches and eutrophication caused by nitrate or phosphate enrichment (Bratton 1991, Kerney 1999). The aim of this chapter was therefore to assess which biotic and abiotic factors correlated with the distribution of *P. pseudosphaerium* and associated bivalve communities across several grazing marshes in south-east England. In addition, the relationship between the occurrence of bivalve and gastropod communities was examined with a view to understanding the implications for the management of drainage ditches to support scarce gastropod and bivalve species.

5.2. Methods

5.2.1. Study sites

The mollusc assemblage and the environmental character of the drainage ditches were extensively surveyed between May and September 1999 on four large grazing marshes of south-east England where *P. pseudosphaerium* had previously been recorded: the Arun Valley in West Sussex (TQ 0314), the Lewes Brooks (TQ 4208) and Pevensey Levels (TQ 6409) both in East Sussex, and the Stour Valley in Kent (SQ 2663) (Killeen & Willing 1997) (Chapter 1, Figure 1.3). The marshes vary in area from 3,500ha on Pevensey Levels to Lewes Brooks of 640ha, consisting of improved and semi-improved wet grassland are periodically flooded during the winter months and typically grazed by cattle in the summer months. All are recognised for their value to nature conservation. In 1999 the floodplain of the Arun Valley and Pevensey Levels were added to the UK list of sites notified under the Ramsar Convention which already included Stodmarsh, one of the marshes of the Stour Valley (Ramsar Convention Bureau 2002). The Arun Valley and Stodmarsh have also been designated as Special Protection Areas (SPA) under the EC Birds Directive 79/409/EEC (European Commission 1979b), and Stodmarsh is a proposed candidate for Special Areas of Conservation (SAC) under the EC Habitats Directive 92/43/EEC (European Commission 1992). All the marshes contain Sites of Special Scientific Interest (SSSIs) due to their importance for over-wintering birds and aquatic communities in the ditches. Stodmarsh along with the north-west part of Pevensey Levels are National Nature Reserves (NNR) managed by the statutory agency for nature conservation, English Nature (Chapter 1).

5.2.2. Sampling protocol

A total of 106 ditches were individually surveyed, an average of 33 ditches from the three largest marshes and a smaller selection from Lewes Brooks (n = 6) (Chapter 2, Table 2.2). A mixture of 81 ditches were randomly selected and 25 ditches were targeted based on previous occupancy by two rare snails: *Segmentina nitida* and *Anisus vorticulus*. The targeted ditches were vital to ensure a sufficient number of ditches contained these RDB snails for the presence/absence analyses discussed in chapter 2. The random ditches provided a true indication of the relative coverage and occupancy by the mollusc assemblage. A 20m stretch was surveyed along each ditch, four mollusc samples were collected randomly at distances between 0.05m to 1.0m from one of the banks. A sample consisted of a vigorous sweep over 1m, parallel to the bank and including the sediment, vegetation and water surface layer, using a sieve net of 0.18m diameter and a 1mm mesh (Appendix 1 and Chapter 2). The four samples were pooled and preserved on site in 70% Industrial Methylated Spirit (IMS). In the laboratory, samples were washed through a 500µm mesh sieve and all molluscs were removed. A light microscope was used to identify the gastropods using Macan

(1977) and the bivalves were sent to an expert on Sphaeriidae identification who identified all individuals with the exception of a few juvenile *Pisidium*.

Prior to mollusc sampling, a water sample was collected from each ditch 1.0m from the bank at 0.15m below the water surface. Samples were analysed within 24 hours for conductivity, pH, biological oxygen demand (BOD), alkalinity, chloride, calcium, total organic nitrogen (TON), nitrate, nitrite, ammoniacal-nitrogen, ortho-phosphate and chlorophyll-*a* using methods described in Chapter 2.

The vegetation in each ditch was assessed by estimating percentage coverage and recording macrophyte diversity. An estimate of the percentage of the ditch surface covered by all vegetation was made along with individual coverage by amphibious, emergent, floating and submerged plant groups. A plant species list was recorded for each ditch (see Chapters 2 & 4 for definition of different plant components).

The dimensions of the ditch (width, depth, depth of sediment layer, height of bank), adjacent land-use (grazing, arable, hay, track, woodland), percentage extent of trees and shrubs along the ditch, and the percentage of ditch in shade were all recorded. The percentage of the ditch channel blocked by vegetation, which prevented a free flow of water, was also estimated (Chapters 2 & 4).

5.2.3. Statistical analysis

Shannon's Diversity Index (H) was calculated for the whole mollusc community in each ditch (Shannon 1949), while species richness and total abundances for gastropods and bivalves were determined separately. Each ditch in the survey was also assigned a conservation score (CS) for the bivalves assemblage and also for the gastropod assemblage. The CS were calculated using individual scores for each species devised by Killeen (1998) based on how local they were to ditch habitats and the Red Data Book list (Table 5.1 & Appendix 2). The CS represents a simple presence/absence index but with increased weighting due to the presence of rare species. Kruskal-Wallis tests (MINITAB v12 1998) were used to compare the mollusc diversity/conservation indices and the environmental characters between the ditches occupied and unoccupied ditches by *P. pseudosphaerium*. Significant associations between *P. pseudosphaerium* and other RDB molluscs were tested used Chi-square.

Ordination by CANOCO (ter Braak & Smilaner 1998) and classification by TWINSPAN (Hill 1979) were used to assess the major species assemblages among the bivalves. Ordination arranges the bivalves into an objective order across ditches based on their association with each other in terms of their distribution and abundances, such that sites with similar bivalve assemblages occurred near to each other on the ordination axes. The relationship between vegetation and water chemistry and the assemblage of bivalves in the ditches were also evaluated by using canonical correspondence analysis (CCA) (ter Braak & Smilaner 1998).

Classification by TWINSPAN hierarchically clustered groups of ditches occupied by similar assemblages of bivalves (Hill 1979). The assemblages of bivalves were also simultaneously classified on the basis of their co-occurrence in the ditches. In TWINSPAN, species abundances are represented as pseudo-species for which a range of cut-levels were explored. The final cut-levels chosen corresponded with the ACFOR scale, which placed emphasis on the species occurring at lower frequency applying to the majority of the Sphaeriidae (Rare: 1-5, Occasional: 6-10, Frequent: 11-50, Common: 51-100 and Abundant: over 100). The TWINSPAN division of both species and ditches was halted at the first level of classification beyond which groups became too small for meaningful analysis. One species *Pisidium pulchellum* only occurred in a single ditch and was removed from further analyses. Kruskal-Wallis was used to test for significant differences in the environmental character and the abundances of individual bivalve and gastropod species between the groups of ditches.

5.3. Results

The survey of 106 ditches recorded eleven species of Sphaeriidae representing 50% of all known species from this family in the UK, including *P. pseudosphaerium* (Figure 5.1). However, only two bivalve species were recorded from over half of the ditches: *Sphaerium corneum* and *P. pseudosphaerium*. The majority of bivalve species were found in less than 20% of the ditches (Figure 5.1).

5.3.1. Pisidium pseudosphaerium

P. pseudosphaerium occurred on all four grazing marshes but was only widespread in the ditches of Arun Valley and Pevensey Levels (Figure 5.1). Kruskal-Wallis tests between the occupied and unoccupied ditches indicated significant differences in the diversity of aquatic plants and the concentrations of BOD, calcium, TON, nitrate and nitrite (Table 5.2). *P. pseudosphaerium* occurred in ditches that were comparatively less calcareous with a high diversity of submerged, floating and emergent plant species and with low concentrations of nutrients and a high BOD (Table 5.1). Ditches containing *P. pseudosphaerium,* had higher abundances of other bivalves species and locally elevated bivalve diversity (Table 5.2). The occurrence of *P. pseudosphaerium* was significantly associated with the occurrence of *V. macrostoma* and *A. vorticulus* (Table 5.3) as well as occurring in ditches with high abundance and diversity of gastropod species (Table 5.2).

5.3.2. Bivalve assemblages

The first TWINSPAN assemblage contained *P. pseudosphaerium*, *Sphaerium corneum*, *Musculium lacustre* and *P. obtusale* (Assemblage 1, Figure 5.2). The second assemblage contained *P. nitidium*, *P. subtruncatum*, *P. milium*, *P. hibernicum, P. henslowanum* and *P. personatum* (Assemblage 2, Figure 5.2). On CCA, the first two axes explained 66% of the variations in the species and environmental data (Table 5.4), and the two TWINSPAN assemblages were clearly visible. Species in assemblage 1 were generally found in shallower, narrower ditches with a greater percentage cover of floating and emergent vegetation (Figure 5.2). However, the species in assemblage 1 occurred close to the ordinal of the CCA plot indicating negligible influence by any of the variables measured in the survey. By contrast, species in assemblage 2 were generally found in wider, deeper, less calcareous ditches with the greatest percentage of open water, lower BOD and lower chlorophyll-*a* concentrations (Figure 5.2). Of the two assemblages, assemblage 2 had greatest bivalve diversity whereas assemblage 1 was typical of ditches with higher gastropod diversity (Figure 5.2).

5.3.3. Drainage ditch groups

Two groups of ditches were apparent from TWINSPAN, group 1 holding 69 ditches and group 2, 27 ditches. The ditches in group 1 had the highest abundances of *P. pseudosphaerium*, *S. corneum* and *P. obtusale,* all typical of assemblage 1 (Table 5.5). The ditches with the best representation of bivalves were in group 2 and had the highest abundances of five bivalves all included in assemblage 2 (Table 5.5). The ditches in group 1 had significantly greater alkalinity and had a higher percentage cover of floating vegetation compared to the ditches in group 2 (Table 5.5). The two groups of ditches occupied by different bivalve assemblages did not differ significantly in their general conservation status for bivalves (Table 5.5). However, the ditches in group 1 had a higher abundance of the RDB bivalve, *P. pseudosphaerium* whereas the ditches in group 2 supported higher abundances for a more diverse group of bivalves species (Table 5.5). The highest abundances for nine gastropod species, including two RDB species, *Segmentina nitida* and *Valvata macrostoma,* occurred in the ditches in bivalve group 1 (Table 5.5). Only one snail species, *Gyraulus albus* had significantly higher numbers in the group 2 ditches (Table 5.5).

5.4. Discussion

The majority of the individual Sphaeriidae species in the survey occurred in less than 20% of the ditches. The lower prevalence of bivalves compared to gastropods (Chapter 4) could be explained by bivalves having a more localised distribution within the ditches that were not effectively sampled by the sieve net as seen in the pilot sampling study between pond net and sieve net (Appendix 1). Despite this drawback, variations in ditch character appeared to be related to the assemblage of bivalves. In addition, variations in nutrient concentrations could also be a significant influence on the distribution of *P. pseudosphaerium*. As with all correlative studies, caution is needed when attempting to separate the causal factors from chance occurrence in the data-set.

5.4.1. Pisidium pseudosphaerium and ditch character

The RDB bivalve *P. pseudosphaerium* occurred in over half of the ditches sampled and was the second most widespread sphaeriid in these ditches. In the light of this high prevalence, its current status as rare in the British Red Data Book and inclusion in the UK BAP could be considered as overly cautious. However, the distribution of *P. pseudosphaerium* is rarely recorded beyond the confines of grazing marshes, with the Somerset Levels, East Anglian Broadlands, Arun Valley and Pevensey Levels being the major strongholds (Kerney 1999). These marshes are increasingly threatened with intensive drainage (Hicklin 1986, Williams & Hall 1987, Palmer 1986), nutrient enrichment of ditches (Hicklin 1986, Palmer 1986, De Groot *et al.* 1987, Janse & van Puijenbroek 1998, Thomas & Daldorph 1994) and insensitive management of the ditches (Newbold *et al.* 1989, RSPB *et al.* 1997). Therefore, action is needed to ensure that the current range of *P. pseudosphaerium* is not markedly reduced.

There were significant co-occurrences between *P. pseudosphaerium* and two RDB snail species, *Valvata macrostoma* (RDB Vulnerable) and *Anisus vorticulus* (RDB Vulnerable) suggesting that the three species share similar habitat requirements (Chapter 2). *P. pseudosphaerium* occurred in ditches with high macrophyte diversity of submerged, floating, emergent and amphibious plants. Ditches supporting this complex structure of vegetation are more likely to be at the mid-stages of vegetational succession where emergent and amphibious plants have yet to dominate the centre of the channel. Ditches with high macrophyte diversity are indicators of ditches that are not intensively managed allowing the recolonisation of more locally-demanding species in between dredging operations (Newbold *et al.* 1989, RSPB *et al.* 1997, Best 1993, 1994, van Strien *et al.* 1991).

In addition to vegetation character, *P. pseudosphaerium* along with *V. macrostoma* and *Segmentina nitida* (RDB Endangered) also appeared to be negatively affected by elevated concentrations of nutrients (Chapter 2). Excessive use of nutrients on the marshes over the last 30 years has contributed to increasing eutrophication in the drainage ditches (Palmer 1986, Hicklin 1986). Eutrophication in ditches usually results in an increase in phytoplankton and floating 'nuisance' plants such as duckweed. In extreme cases this can cause a decline in aquatic plant diversity as well as a complete loss of all submerged aquatic plants and sometimes the regression of emergent vegetation (Mason & Bryant 1975, Moss 1988, Janse & van Puijenbroek 1998). The effect of elevated nutrients on *P. pseudosphaerium* could be due to direct toxicity on the mussel. Alternatively, eutrophication by causing an increase in phytoplankton or floating plant biomass often leads to higher concentrations of organic matter in the ditches and contributes to an increase in the rate of hypolimnetic deoxygenation in the lower part of the ditch (Veeningen 1982, Marshall 1981, 1984 Codd & Bell 1985, Portielje & Lijklema 1994, Janse & van Puijenbroek 1998). The resulting oxygen deficit in the water would contribute to an anoxic environment especially at the substrate layer in which few macroinvertebrates could survive (Moss 1988, Marklund *et al.* 2001). All Sphaeriidae *including P. pseudosphaerium* depend on gills for breathing and are therefore potentially vulnerable to reduced oxygen concentrations, particularly if they live in the sediment (Dillion 2000). This is highly relevant given the extremely low oxygen concentration apparent in the profoundal zone (Chapter 3).

5.4.2. Bivalve assemblage and ditch character

The two bivalve assemblages indicated by TWINSPAN occurred in ditches of different ecological conditions. Assemblage 2 with the greatest diversity appeared to be the most-demanding in their requirement of ditch character. They occurred in deeper less calcareous ditches with the highest percentage of open water and appeared to be adversely affected by increasing cover of floating and emergent vegetation. This group supported the notion that Sphaeriidae are typical of open waterbodies with some flowing water (Aho 1966, Bagge & Jumppanen 1968, Harman 1972, Mouthon 1992, Bechara 1996, Dillion 2000, Hamburger *et al.* 2000). Earlier descriptive studies of the ecology of the individual bivalves in assemblage 2, suggest that they all avoid waterbodies that are stagnant and liable to dry up, with the exception *of P. personatum* (Boycott 1936, Kerney 1999). *P. personatum* is known from stagnant waters such as ditches at the advanced stages of vegetation succession (Boycott 1936, Kerney 1999). However, it has also been recorded in the profoundal zones of lakes (Bagge & Jumppanen 1968, Harman 1972, Dudgeon 1983) and therefore could be expected to occur in ditches at all stages of succession. The species-poor assemblage 1, containing *P. pseudosphaerium* and the larger Sphaeriidae such as *S. corneum* and *M. lacustre* occurred in ditches that were comparatively shallower than those occupied by assemblage 2 with denser vegetation. The two larger sphaeriids are frequently known to inhabit the vegetation instead of the benthos, thus enabling them to colonise more anoxic ditches than other bivalves (Boycott 1936, Kerney 1999). Likewise, *P. pseudosphaerium* and *P. obtusale* have been described occurring in ditches that are stagnant with dense vegetation (Kerney 1999).

The only significant difference in water chemistry between the two groups of sphaeriids was alkalinity. Higher concentrations of calcium bicarbonate in the water may be an essential requirement of assemblage 1, which contained the largest species, for shell construction (Dillion 1999). Alternatively, vegetation growth is often greater and richer in areas with higher calcium and alkalinity (Riis *et al.* 2000, Vestergaard & Sand-Jensenk 2000a & b), which could indirectly affect the distribution of bivalve species dependent on the access to free flowing water, supplying oxygen to the substrate layer. Unless a sphaeriid species has the ability to attach itself to vegetation, they will be disadvantaged in ditches with dense vegetation in particular where dissolved oxygen is significantly reduced. The oxygen layer in the lower depths of ditches are significantly lower than the water surface (see Chapter 3). Moreover, dissolved oxygen was significantly lower (<8mg l^{-1}) where vegetation cover was 100% compared to > 20mg l^{-1} where vegetation cover was less than 50%.

In contrast to the majority of the bivalves, the diversity and abundance of gastropod species significantly increased with vegetation cover and diversity (Chapter 4, Crowder & Cooper 1982, Brönmark 1985a, Costil & Clement 1996). Therefore, it is unsurprising that the bivalve species in assemblage 1 are associated with ditches with the greater diversity, abundance and conservation interest for gastropods.

5.4.3. Management implications

All Sphaeriidae are considered to be sediment-dwelling with the exception *of P. pseudosphaerium* and some of the larger species which have been found among dense vegetation (Boycott 1936, Janus 1965, Kerney 1999, Dillion 2000). An intensive de-silting regime which removes silt from the channel is not likely to benefit the general bivalve communities in drainage ditches, as had been the case with larger bivalves from the Unionidae family in rivers and canals (Young & Williams 1983a & 1983b, Young 1995, Oliver & Killeen 1996, Drake 1998a, Gittings *et al.* 1998, Hastie *et al.* 2000, 2001, Alridge 2000, Cosgrove & Hastie 2001). However, regular clearance of the vegetation in the ditches will optimise the ditch characteristics that support the greatest diversity of bivalves. Species such as *P. milium*, *P. henslowanum* and *P.*

hibernicum all occur in ditches with a high percentage of open water. Vegetation clearance varies from a complete removal of the macrophytes to just keeping the centre of the channel free of emergents such as *Phragmites*, *Sparganium* and *Glyceria* species, thereby allowing a flow of water through the ditch (Kirby 1992, RSPB *et al.* 1997). In contrast, this is likely to be detrimental for *P. pseudosphaerium* and the majority of the gastropod species which occur in ditches with high vegetation cover and hence demand a less frequent vegetation clearance regime (Chapters 2 & 4).

Management of the ditches for the rare snails which were all associated with high vegetation cover (Chapter 2 & 3) will probably also benefit *P. pseudosphaerium*, the only RDB pea mussel found on grazing marshes. A rotational regime of weed clearance and de-silting across a marsh, as well as within ditches, will allow a range of vegetation structures to occur simultaneously as a result of hydroseral progression (Caspers & Heckman 1981, 1982, van Strien *et al.* 1991, Kirby 1992). This will provide ditches with reduced vegetation cover for high diversity of bivalves as well as ditches at the later stages of succession for *P. pseudosphaerium* and other RDB molluscs. Similar to the other RDB molluscs, *P. pseudosphaerium* was potentially excluded from ditches with elevated concentrations of nutrients and therefore reduced agro-chemical use on grazing marshes is likely to be of benefit. Agri-environmental schemes such as Wetland Enhancement Scheme (WES) and Environmentally Sensitive Areas (ESA) which compensate landowners for reducing their consumption of fertilisers on grazing marshes are ideally placed to assist the recovery of this local sphaeriid.

Table 5.1: Conservation values for freshwater bivalves typical of drainage ditches on lowland grazing marshes in south-east England (adapted from Killeen 1999).

Species	Common name	Status in UK	Conservation values
Bivalve species:			
Pisidium pseudosphaerium	Fasle orb pea mussel	RDB 3	8
Pisidium pulchellum	Iridescent pea mussel	Local	7
Pisidium obtusale	Porous-shelled pea mussel	Common	6
Pisidium milium	Quandrangular pea mussel	Common	3
Spaherium corneum	Horny orb mussel	Common	3
Musculium lacustre	Capped orb mussel	Common	3
Pisidium subtruncatum	Short-ended pea mussel	Common	3
Pisidium nitidum	Shining pea mussel	Common	3
Pisidium henslowanum	Henslow's pea mussel	Common	3
Pisidium hibernicum	Globular pea mussel	Common	3
Pisidium personatum	Red-crusted pea mussel	Common	3

RDB = Red Data Book, 1 = endangered, 2 = vulnerable, 3 = rare

Table 5.2: Variations in the mean (± s.d.) environmental variables between ditches occupied by *P. pseudosphaerium* and unoccupied ditches in south-east England. Kruskal-Wallis (H) tests were used to indicate significant differences between the means (*** = P <0.001, ** = P <0.010, * = P <0.050, n.s = not significant).

Variables	Present (N = 58)	Absent (N = 48)	H value (P)
Physical aspects			
Width (cm)	280 (130)	300 (150)	n.s.
Depth (cm)	72 (30)	77 (37)	n.s.
Silt layer (cm)	39 (21)	36 (24)	n.s.
Choked ditch (%)	32 (39)	37 (42)	n.s.
Vegetation structure			
Vegetation cover (%)	78 (27)	75 (28)	n.s.
Submerged cover (%)	23 (30)	12 (20)	n.s.
Floating cover (%)	52 (36)	40 (41)	n.s.
Emergent cover (%)	46 (29)	46 (33)	n.s.
Amphibious cover (%)	15 (13)	14 (16)	n.s.
Open water (%)	22 (26)	25 (28)	n.s.
Wetland plant diversity	17 (5)	12 (5)	23.13 ***
Submerged plant diversity	2 (1)	2 (2)	4.96 *
Floating plant diversity	3 (1)	2 (1)	18.32 ***
Emergent plant diversity	6 (2)	4 (2)	16.81 ***
Amphibious plant diversity	6 (3)	4 (2)	7.10 **
Bank plant diversity	12 (6)	12 (5)	n.s.
Chlorophyll-*a* (mg l^{-1})	32 (48)	29 (70)	n.s.
Water chemistry			
pH	7.4 (0.4)	7.5 (0.5)	n.s.
BOD (mg l^{-1})	6 (7)	4 (5)	6.72 **
Conductivity (μS cm^{-1})	597 (261)	715 (409)	n.s.
Chloride (mg l^{-1})	67 (2)	73 (2)	n.s.
Alkalinity (mg l^{-1})	176 (77)	195 (74)	n.s.
Calcium (mg l^{-1})	64 (31)	81 (32)	8.80 **
Ammonia (mg l^{-1})	0.1 (0.1)	0.2 (0.2)	n.s.
TON (mg l^{-1})	0.5 (1.2)	0.9 (1.6)	9.48 **
Nitrate (mg l^{-1})	0.5 (1.2)	0.9 (1.6)	5.94 *
Nitrite (mg l^{-1})	0.02 (0.03)	0.03 (0.04)	7.95 **
Phosphate (mg l^{-1})	0.8 (1.6)	0.7 (1.5)	n.s.
Mollusc community			
Gastropod species diversity	10 (3)	7 (3)	21.39 ***
Gastropod abundance	422 (433)	319 (396)	4.63 *
Gastropod’s conservation scores	35 (13)	22 (11)	24.03 ***
Bivalve species diversity	3 (1)	2 (1)	36.92 ***
Bivalve abundance	52 (73)	17 (53)	36.00 ***
Molluscs’ Shannon diversity index	1.69 (0.38)	1.30 (0.53)	14.26 ***

Table 5.3: Chi-square values indicating significant associations in the pairwise frequency of occurrence of RDB snails with *P.pseudosphaerium* in drainage ditches of south-east England (*** = *P* <0.001, * = *P* <0.050, n.s.= not significant).

	P. pseudosphaerium
S. nitida	2.681 n.s.
A. vorticulus	5.346 *
V. macrostoma	11.287 ***

Table 5.4: Eigenvalues and cumulative percentage variances explained for each CCA axis (see Figure 5.2 for the biplot of the first two axes).

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.199	0.064	0.057	0.035
Species-environmental correlations	0.656	0.499	0.443	0.454
Cumulative percentage variance of:				
-species data	10	14	17	19
-species-environmental relation	50	66	81	90

Table 5.5: Significant differences in mollusc abundance and environmental variables between the TWINSPAN groups indicated by Kruskal-Wallis tests (H) (● = significantly higher abundance or values, • = significantly lower abundance or values) (*** = P <0.001, ** = P <0.010, * = P <0.050).

	Group 1 (N = 69)	Group 2 (N = 27)	H value
Bivalve abundance			
S. corneum	● 16 (45)	• 2 (6)	16.34 ***
P. pseudosphaerium	● 23 (51)	• 3 (6)	17.67 ***
P. obtusale	● 4 (9)	• 1 (2)	5.31 *
P. personatum	• 0 (0)	● 1 (7)	9.24 **
P. milium	• 1 (4)	● 4 (4)	18.00 ***
P. subtruncatum	• 1 (3)	● 8 (14)	25.31 ***
P. nitidium	• 0 (0)	● 1 (2)	23.21 ***
P. hibernicum	• 0 (0)	● 1 (2)	5.17 *
Ditch character			
Open water (%)	• 19 (25)	● 34 (28)	6.86 **
Vegetation cover (%)	● 81 (25)	• 66 (28)	6.41 **
Floating vegetation cover (%)	● 52 (39)	• 29 (34)	6.53 **
Alkalinity (mg l^{-1})	● 188 (73)	• 152 (79)	4.90 *
Mollusc community			
Bivalve abundance	● 48 (78)	• 20 (27)	4.81 *
Gastropod species diversity	● 10 (3)	• 7 (3)	15.18 ***
Gastropod's conservation scores	● 33 (13)	• 20 (11)	18.21 ***
Gastropod abundance	● 403 (425)	• 218 (246)	5.82 *
Shannon diversity index	● 1.7 (0.4)	• 1.2 (0.5)	13.90 ***
Molluscs' conservation score	● 46 (17)	• 32 (14)	13.73 ***
Gastropod abundance			
V. crisata	● 17 (34)	• 3 (8)	14.67 ***
H. complanatus	● 19 (48)	• 2 (6)	14.36 ***
L. palustris	● 11 (25)	• 2 (5)	11.48 ***
S. nitida	● 8 (26)	• 0 (0)	7.90 **
B. contortus	● 43 (152)	• 41 (187)	6.96 **
P. corneus	● 3 (5)	• 0 (1)	6.36 **
A. vortex	● 31 (50)	• 15 (27)	5.37 *
V. macrostoma	● 34 (113)	• 1 (2)	3.97 *
L. peregra	● 48 (74)	• 35 (77)	3.85 *
G. albus	• 2 (7)	● 10 (27)	8.08 **

Figure 5.1: The frequency of occurrence of freshwater bivalves in the drainage ditches from four grazing marshes in south-east England (see Table 5.1 for full name of bivalves).

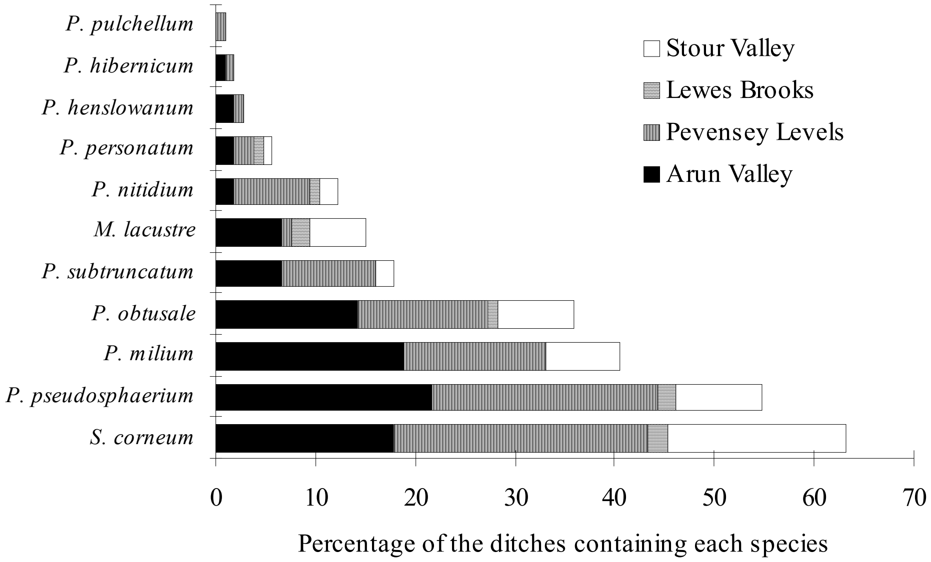
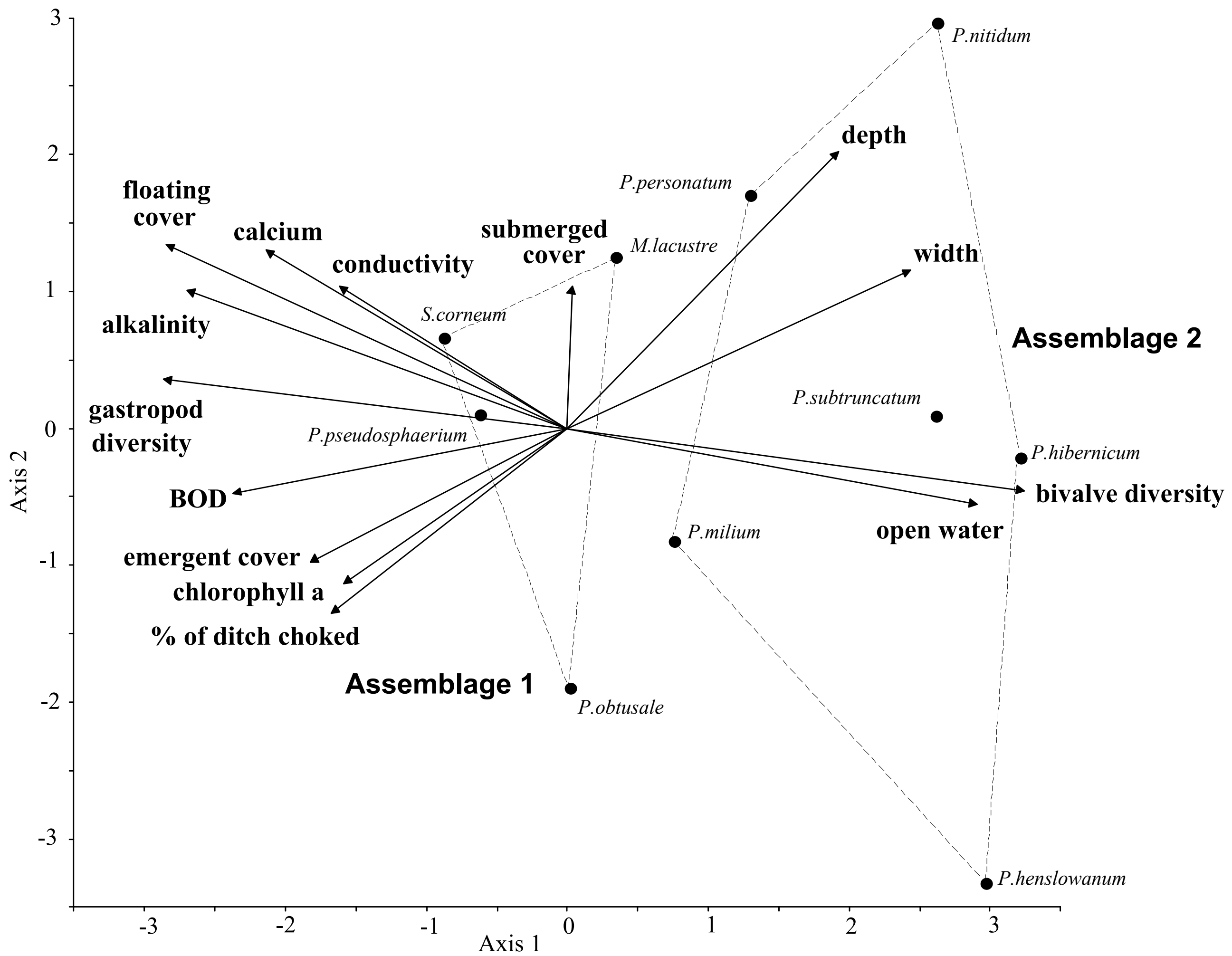


Figure 5.2: Two-dimension species ordination plot derived from the canonical correspondence analysis (CCA) of the bivalve data and environmental variables. The bivalve assemblages were determined by TWINSPAN analysis which are indicated by the polygons (dashed line). Increasing length of arrow indicates greater significant correlation of environmental variable with the axes.



- Chapter 6 -

Using experimental enclosures to assess the effects of elevated nutrient concentrations on gastropods in a drainage ditch

6.0. Abstract

Eutrophication is often cited as one of the main causes of a decline in the distribution and abundance of threatened species in aquatic systems, including several scarce wetland molluscs. Recent evidence from surveys has shown that some scarce molluscs might be affected. However, despite a considerable history of mesocosm experiments and other approaches, few studies have investigated the direct or indirect in-situ effects of nutrient enrichment on aquatic mollusc species of conservation concern. An experimental approach was therefore designed to assess the direct short-term effects of elevated nutrients on populations of *Segmentina nitida* (Red Data Book, Endangered) and other freshwater snails. Thirty-five large enclosures (0.4m diameter) were placed into a ditch on Pevensey Levels, which had no previous records of *S. nitida*. The existing biotic community was retained and populations of *S. nitida* were introduced into each enclosure. Five different treatments involving nitrogen and phosphorous additions were applied weekly to the enclosures over 6 weeks. Respectively, the treatments were: (H) high nitrate and phosphate; (L) low nitrate and phosphate; (N) high nitrate and low phosphate; (P) low nitrate and high phosphate enclosures; (R) reference enclosures with no additions. Maximum nominal concentrations added regularly were 10mg l^{-1} of total nitrogen and 1mg l^{-1} of phosphate. Water chemistry was monitored over the 6 weeks and at the end of the experiment the molluscs were sampled and weighed.

The only significant increase indicated by one-way ANOVA in nutrient concentrations, was in ammoniacal-nitrogen in the H and N enclosures; concentrations reached approximately 5mg l^{-1}, probably caused by low oxygen concentration and ammonification in the enclosures. Repeated measure analysis using the non-parametric Scheirer-Ray-Hare test also indicated significantly lower pH and higher conductivity in the N enclosures.

Despite chemical variations between treatments, there were no significant variations in the weight or abundance of *S. nitida*, nor among other snail species after 6 weeks when the experiment ended. Further work is required on the longer-term effects of both nitrogen and phosphorus additions on scarce molluscs such as *S. nitida*, and on the effects of elevated ammoniacal-nitrogen.

6.1. Introduction

Despite over four decades of research into eutrophication, the impact on groups of organisms or species of conservation concern are surprisingly poorly described. In shallow lentic systems, eutrophication is accompanied by profound changes among phytoplankton, attached algae, submerged macrophytes and floating macrophytes (Moss 1976, 1983, 1988, Phillips *et al.* 1978, Veeningen 1982, Barko & Smart 1983, Istvánovics *et al.* 1986, De Groot *et al.* 1987, Fairchild *et al.* 1989, Balls *et al.* 1989, Daldorph & Thomas 1991, 1995, Thomas & Daldorph 1994, Portielje & Roijackers 1995, Portielje *et al.* 1996, Janse 1998, Janse & van Puijenbroek 1998) leading to a reduction in the diversity of invertebrates and fish (Mason & Bryant 1975, Moss 1983, Cartwright *et al.* 1993, Thomas & Daldorph 1994, Marneffe *et al.* 1997, Lemly & King 2000, Miranda *et al.* 2001). Areas of high conservation or amenity value in an agricultural landscape can be particularly vulnerable.

Changes in the water chemistry and macrophyte communities in drainage ditches caused by eutrophication have been investigated extensively in the Netherlands (Veeningen 1982, Drent & Kersting 1993, Portielje & Roijackers 1995, Portielje & Lijklema 1994, 1995, Portielje *et al.* 1996, Janse 1998, Janse & van Puijenbroek 1998). These small linear water bodies are also common on the grazing marshes of southern England and many lowland areas throughout Europe, their main purpose being to drain excess water. The shallow ditches (1.5m) are often dominated by macrophytes and can support high diversity of aquatic molluscs including several British Red Data Book (RDB) species such as *Segmentina nitida* (RDB Endangered), *Anisus vorticulus* (RDB Vulnerable), *Valvata macrostoma* (RDB Vulnerable) and *Pisidium pseudosphaerium* (RDB Rare) (Bratton 1991). However, many such drainage ditches are affected by eutrophication due to agricultural nutrient losses (Janse 1998). At high nutrient loading, their macrophytes can be affected by increased algal growth until the ditches become dominated by a surface layer of filamentous algae or by floating species such as duckweed which can contribute to the demise of submerged plants (Portielje & Roijackers 1995, Janse & van Puijenbroek 1998). Subtle effects of nutrient addition on mollusc assemblages are still poorly understood, with only a few mescosm experiments having been conducted (Daldorph & Thomas 1991, 1995, Jones *et al.* 1999). A mesocosm experiment over 8 weeks with a common snail *Physa fontinalis*, showed that improved nutritional quality by nutrient loading contributed to increased growth and reproduction (Jones *et al.* 1999). However, elsewhere in a longer experiment over 5 months, *P. fontinalis* declined in response to enhanced nutrient loading and was attributed to a decreased epiphytic cover due to the demise of the macrophytes (Daldorph & Thomas 1991, 1995). While effects of increased nutrient concentrations in particular on common molluscs may still be poorly understood (Daldorph & Thomas 1991, 1995, Jones *et al.* 1999, 2000, 2002), even less is known specifically about the scarce species.

In 1999, an extensive survey of the mollusc communities in the ditches on several large grazing marshes in south-east England revealed that *S. nitida*, *V. macrostoma* and *P. pseudosphaerium* were notably absent from ditches with significantly higher concentrations of nitrogen than elsewhere (Chapters 2 & 5). It was suggested that where ecological attributes within ditches otherwise suitable for the RDB species, elevated nutrient concentrations may have eliminated or restricted them (HMSO 1995, Kerney 1999). The reasons for this pattern remain poorly understood. Here, as a first step, this chapter investigates whether there are any short term effects of excess nutrients. An experimental approach was designed to examine the effects of nutrient loading on the water chemistry and mollusc assemblages in drainage ditches. The experiment involved increasing the allochthonous loading of nitrate and phosphate in enclosures, which contained populations of *S. nitida* and other gastropod species. In addition, changes in water chemistry were monitored during the 6 weeks of the experiment to determine the effects of excess nutrients on dissolved oxygen, pH, conductivity and productivity in the ditch, which may indirectly affect the gastropods.

6.2. Methods

6.2.1. Experimental ditch

The experiment was conducted in a single drainage ditch (TQ 635054) on Pevensey Levels (East Sussex), a large grazing marsh of 3,500ha area. The marsh has been designated under the Ramsar Convention due to its extremely rich macrophyte and mollusc communities. The experimental ditch ran through an organic farm south of Pevensey Levels on Manxey Level. The adjacent land was used for sheep and cattle grazing, with several fields also mown for hay. The ditch was approximately 3 metres wide and depth of water varied from 0.5 to 1.0m, controlled by means of sluice gates. Pre-treatment chemical data indicated that the ditch was ion rich (conductivity 538-572 $\mu S\ cm^{-2}$) but nutrient concentrations were relatively low (PO4 0.2 mg l^{-1}, TON

0.2 mg l^{-1}) (Table 6.1). A mix of emergent and floating plants contributed to a densely choked ditch that had a diverse mollusc assemblage, but there had been no records of *S. nitida* (Table 6.1).

6.2.2. Sampling protocol

Thirty-five enclosures were placed in the experimental ditch on the August 15th 2000. Approximately 0.5m from the margins, 17 enclosures were placed along one bank and 18 along the opposite bank (Figure 6.1). The experimental enclosures were adapted from similar enclosures designed by Daldorph and Thomas (1991), consisting of plastic cylinders (clear PET-G plastic) of 1.5m height and 0.4m diameter, pushed into the clay substrate of the drainage ditch so that the existing biotic community was retained (Figure 6.2). Approximately two thousand live specimens of *S. nitida* were collected from two ditches elsewhere on Manxey Level and, within 24 hours, populations with a ratio of 5 adults to 50 juveniles were introduced to each enclosure on 25th August 2000. The juveniles were all approximately 1.0mm in diameter whereas the adults were 2.5mm and over.

Five different treatments involving nitrogen (N) and phosphorous (P) addition were applied to the enclosures from 30th August to 9th October 2000, aiming to produce a N:P ratio of 16:1, which is known to stimulate excessive algae growth (Table 6.2) (Cartwright *et al.* 1993, Horne & Goldman 1994). Respectively the dosages were: (H) high nitrate and phosphate, (L) low nitrate and phosphate, (N) high nitrate and low phosphate, (P) low nitrate and high phosphate, (R) reference enclosures with no addition; each treatment replicated seven times arranged in a randomised block design (Figure 6.1). Nutrient additions were applied weekly as ammonium nitrate (NH_4NO_3) and sodium di-hydrogen orthophosphate (NaH_2PO_4). Targeted nominal concentrations of nitrogen were 10mg l^{-1} in the H and N enclosures and around 1mg l^{-1} in the L and P enclosures. For phosphate, it was aimed to attain nominal concentrations of 1mg l^{-1} in the H and P enclosures and 0.1mg l^{-1} in the L and P enclosures.

Conductivity, pH, dissolved oxygen and turbidity were measured weekly in each enclosure using a portable meter (GRANT 3800) between 1100 and 1400 hours. Replicated measurements were made near the surface (20cm depth) and the benthos (20cm from substrate). Two litres of water from four of the seven randomised blocks of enclosures were sampled on three occasions at the start, middle and end of the experiment in order to measure nutrient concentrations and other determinands, resource availability prevented sampling of all seven. The samples were analysed within 24 hours for ammoniacal-nitrogen, nitrate, nitrite, total oxidised nitrogen (TON), ortho-phosphate and chloride using spectrophotometry. Alkalinity was determined by titration to pH 4.5 and chlorophyll-*a* was extracted from each sample by acetone and then determined by spectrophotometry.

Water depth and percentage vegetation cover were monitored every 2 weeks to assess physical changes within the enclosures over the 6 weeks of treatment. When the experiment ended, the whole biotic content and the upper 5cm layer of the sediment were removed by pond net (mesh size: 1mm) from each enclosure, transported to the laboratory and preserved in 70% Industrial Methylated Spirit (IMS). The samples were then washed through a series of sieves with the smallest mesh size of 500μm. All molluscs were removed and the gastropods identified under a light microscope (x10.5) using Macan (1977). For each enclosure, the weight of individual gastropod species of both shell and soft parts was determined after drying to a constant weight at 50^{o}C for 48 hours.

6.2.3. Statistical analysis

Data on the water volume, chlorophyll-*a*, vegetation cover and turbidity from all thirty-five enclosures were pooled to provide a quantitative indication of the changes occurring inside all enclosures over the six weeks of the experiment. One-way analysis of variance (ANOVA) (MINITAB v12 1998) was used to assess any treatment effects in chlorophyll-*a*, vegetation cover and turbidity.

The mean expected concentrations of total nitrogen and phosphate for each treatment were calculated from the mass of nutrient added and the changes in volume of water in the enclosures. These were compared with actual nutrient data from four replicate enclosures sampled from each treatment. Differences between sampling periods for each treatment were compared using one-way ANOVA. Where it was not possible to homogenise variance after transformation (e.g. TON and nitrate) a non-parametric Kruskal-Wallis test was used.

Differences in chemistry and physical characteristics between treatments were analysed using two-way repeated measures ANOVA with treatments and sampling days as factors. Variables for which the variance could not be normalised or homogenised were tested using the non-parametric equivalent of two-way ANOVA, the Scheirer-Ray-Hare test based on ranked data (MINITAB v12 1998, Dytham 1999).

One-way ANOVA was used to assess significant differences between treatments in the abundance and dry weight of *S. nitida* and other gastropod species that were present at the end of the experiment. For *S. nitida*, initial densities were known to be the same in all enclosures so that any differences at the end of the experiment could be ascribed to treatment effects. For all other species, initial densities were not known so ascribing any differences to treatment effects depends on the initial randomisation of treatments.

6.3. Results

Water volume in the enclosures increased by an average of c.50 litres in the six weeks of the experiment reflecting patterns of rainfall and discharge over the marsh. Vegetation cover and chlorophyll-*a* in the enclosures declined probably due to seasonal trends (Figure 6.3, Table 6.3). However, only one of of these patterns reflected variations between treatments (Table 6.3), the one exception was vegetation cover, which was significantly greater in the N treatment compared to the other treatments at the end of the experiment (One-way ANOVA: $F = 8.13_{4,30}$, $P < 0.001$). For turbidity, there were no differences between the treatments and trend over the 6 weeks of the experiment (Figure 6.3, Table 6.3).

6.3.1. Nutrient concentrations

The weekly nominal concentrations of nitrogen added to the N and H enclosures were approximately ten times the concentrations recorded in ditches containing *S. nitida* (Chapter 2). Phosphate dosages should yield P concentrations 20 % higher in the P and L enclosures compared to the measurements taken from *S. nitida* ditches (Chapter 2).

Despite the weekly dosage into the enclosures, no significant changes in phosphate concentrations were recorded through time for any of the treatments (Figure 6.4), nor any significant treatment effects (Table 6.3). By contrast nitrogen addition was accompanied by an increase in ammoniacal-nitrogen in the H and N enclosures although not to the expected nominal concentrations (Figure 6.5). Two-way ANOVA indicated significant differences between the treatments only in ammoniacal-nitrogen, which was higher in the H and N enclosures (One-way ANOVA: $F = 13.04_{4,15}$, P <0.001) (Table 6.3). Although there was some evidence of increased nitrite following N additions, in no case were the variations in TON, nitrate or nitrite concentrations significant between time or treatment (Figure 6.6 & Table 6.3).

6.3.2. Other chemical determinands

Alkalinity and chloride generally declined in all the enclosures over the experiment (Figure 6.6), although there were significant differences between treatments (Table 6.3). However, Fisher's pairwise comparison tests indicated that alkalinity and chloride were significantly higher in the H enclosures than some of the other treatments even before nutrients were added (alkalinity: $F = 3.41_{4,30,}$ P >0.021, chloride: $F = 2.30_{4,30}$, P >0.05).

Overall, the trends throughout the experiment in pH, conductivity and dissolved oxygen were very similar between treatments with the exception of conductivity in the lower mesocosm depths (Figures 6.7 & 6.8). However, there were some significant differences between treatments (Table 6.3). In particular, conductivity was higher in the H and N enclosures compared to the references enclosures (Figures 6.7 & 6.8). In both upper and lower depths of the enclosures, pH was significantly lower on several occasions in the N enclosures compared to the R enclosures (Figures 6.7 & 6.8). For dissolved oxygen in the upper layer, significantly lower concentrations were recorded in the H and L enclosures at the beginning of the experiment (Table 6.3).

6.3.3. Gastropod assemblage

Over 9 000 gastropods were removed at the end of the experiment from the thirty-five enclosures. Of these, *S. nitida* represented 4% of the total abundance whereas the most dominant species *Bithynia leachii,* accounted for 71% of the total abundance. Nine other gastropod species were also collected from the enclosures; three prosobranch species and six pulmonate species (number of species = 11, see Table 6.4). The average survival rate for *S. nitida* across all the enclosures was 17% (range: 0-53%), all the surviving specimens being over 2.5mm in diameter. There were no significant differences in the survival nor the dry weight of *S. nitida* between treatments (Figures 6.9 & 6.10). There were no differences between treatments ($F = 0.50_{4,30}$, $P = 0.739$) in gastropod richness, in total dry weight (Table 6.4), nor in the abundances or dry weight of any individual species (Table 6.4). In other words, variations in chemistry between experimental treatments were not accompanied by any significant effect on gastropods.

6.4. Discussion

Despite substantial dosing into the experimental enclosures, no variations in phosphate concentrations were detectable between treatments. It is likely that the dosage was not sufficiently high to induce higher concentrations of orthophosphate in the P and H enclosures. By contrast, there were clear variations in ammoniacal-nitrogen, which was elevated in both treatments receiving additional nitrogen. Other significant treatment effects were apparent, for example in pH, conductivity and vegetation cover (see Table 6.3, Figures 6.7 & 6.8). However, none of these changes affected *S. nitida* or any other gastropod species. There were nevertheless indications of changes that might be important over the longer term, which are discussed below.

6.4.1. Nutrient dynamics

In general, orthophosphate concentrations, even following addition to the enclosures, were within the range observed during marsh surveys (Chapter 2, Table 2.4), with no treatment effect apparent. In other wetland systems, and providing that oxygen is present, phosphate can be rapidly removed from solution either through assimilation by plants, sorption onto organic matter or as insoluble complexes formed with a range of metals such as iron (Gachter & Meyer 1993, Smolder *et al.* 1995). Any of these processes might have removed phosphate additions during the experiment. Longer-term effects would be dependent either on subsequent release from the sediment or on any additional plant biomass resulting from uptake (Marsden 1989, Auer *et al.* 1993, Nohener & Gachter 1994, Smolder *et al.* 1995). Such effects were recorded by Jones *et al.* (1999) over durations similar for this experiment, but they were not assessed here.

In some contrast to phosphate, nitrogen dynamics in wetland systems are far more complex, involving a range of chemical transformations, plant uptake and mediation by microbial processes. In well-oxygenated water overlying anoxic sediments, reduced nitrogen compounds will be oxidised to nitrate, while nitrate or ammoniacal-nitrogen are readily used as plant nutrients. By contrast, in anoxic, carbon-rich sediment typical of drainage ditches, nitrate will be converted to nitrogen gas through the denitrification process (Roelofs 1983, Roelofs *et al.* 1984). In this experiment, however, nitrogen additions to both H and N enclosures resulted in ammoniacal-nitrogen concentrations higher than those normally found in drainage ditches (Chapter 2, Table 2.4). Nitrate concentrations, by contrast, were similar between treatments and within the range typical for drainage ditches elsewhere on the same marshes. Nitrite concentrations were moderately elevated in the excess nitrogen-treated enclosures, reflecting either transformations of ammoniacal-nitrogen or reducing conditions. At low oxygen concentrations typical of those in the experimental ditch (<2-3mg l^{-1}), and for example in other wetlands or lake hypolimnion, ammoniacal-nitrogen can be stable even at relatively high concentrations (Soltero *et al.* 1994, Prepas & Burke 1997, Beutel 2001). Such conditions, coupled with dissociation of added fertiliser into nitrate and ammoniacal-nitrogen, would therefore explain the observed chemical responses to treatment in this experiment. Fluxes of ammoniacal-nitrogen can also occur from anoxic sediments (Veeningen 1982, van Luijn *et al.* 1998a & b) following organic nitrogen mineralisation, although this process would not explain variations observed across treatments. It is unknown whether fertiliser additions elsewhere have led to similarly elevated ammoniacal-nitrogen concentrations in drainage ditches, nor what any prolonged ecological effects might be.

6.4.2. Other chemical processes

Concentrations of dissolved oxygen near the substrata were extremely low in all the enclosures (c.0.2-mg l^{-1}), reflecting high sediment oxygen demands (SOD) typical of ditches (Di Toro *et al.* 1990, van Luijn *et al.* 1998a & b). The SOD can be attributed to the nitrification of ammonia and methane (Roelofs 1983, Roelofs *et al.* 1984, Di Toro *et al.* 1990, van Luijn *et al.* 1998a & b). The oxidation of methane (CH_4) leads to the production of carbon dioxide (equation 1), and furthermore, the oxidation of ammoniacal-nitrogen (NH_4) contributes hydrogen ions (equation 2) (Sweerts *et al.* 1991, van Luijn *et al.* 1998a).

(1) $CH_4 + 2O_2 \rightarrow CO_2 + 2H_2O$

(2) $NH_4^+ + 2O_2 \rightarrow NO_3^- + H_2O + 2H^+$

In addition, another hydrogen-ion generating process includes the precipitation of sulphate with iron and other metals to form insoluble sulphide, in both oxidising and reducing environments (e.g. equation 3) (Smolder *et al.* 1995).

(3) $H_2S^- + Fe^{2+} \rightarrow FeS + 2H^+$

Sulphate is usually sequestered by the sediment in large quantities, as hydrogen sulphide, which is the main cause of the typical odour of ditch sediment (Dojlido & Best 1993). Hydrogen sulphide is formed as a result of bacterial breakdown of organic matter and the reduction of sulphate (O'Neill 1993, Dojlido & Best 1993, Portnoy 1999).

Both carbon dioxide and hydrogen ions produced by these processes will cause pH to decrease (Roelofs 1983, Roelofs *et al.*1984, Smolder *et al.* 1995). Methane and sulphate concentrations were not recorded during the experiment and would have affected all enclosures. By contrast, a drainage ditch with high SOD and high concentrations of ammoniacal-nitrogen will likely experience a decrease in pH, if mixing occurs in the water supplying oxygen to the lower depths. The significantly lower pH in the N enclosures in the first 4 weeks may be a reflection of this nitrogen dynamic.

Another factor to consider with ammoniacal-nitrogen (NH^4) is the undissociated form ammonia ions (NH^3). Ammonia ions are toxic to aquatic organisms but only at high pH of above 8-9 (Roelofs 1983, Dojlido & Best 1993, Horne & Goldman 1994). Throughout the experiment, pH measurements during the day remained below 7.2, and therefore ammonia poisoning in the enclosures was unlikely.

6.4.3. Potential implications for the mollusc community

Eutrophication is known to influence the plant community in drainage ditches (e.g. De Groot *et al.* 1987, Ball *et al.* 1989, Janse & van Puijenbroek 1998) but its effect on molluscs is still poorly understood. Increased growth in snails has been shown from altered nutritional quality but also declining snail abundance from the demise of aquatic plants and their epiphytic cover (Dorgelo 1988, Daldorph & Thomas 1991, Jones *et al.* 1999). Over the six weeks of the experiment, there was clearly no short-term direct effect on *S. nitida* nor any other snail species present in the enclosures. Mortality rates of *S. nitida* were equal in all enclosures and may reflect natural juveniles loss to predation by sticklebacks and other macro-invertebrates that were not removed from the enclosures prior to dosing. Snails from eutrophic waters have been shown to have faster growth than species from less productive waters due to a better supply of epiphytic algae (Brown & DeVries 1985, Dorgelo 1988, Jones *et al.* 1999). There was an increase in shell size for *S. nitida* with remaining juveniles at least doubling in size but this was the same for all enclosures.

The experiment was carried out at the end of the summer, and therefore the decline of chlorophyll-*a* and plant cover through the experiment was expected in all the enclosures. Excessive nutrient enrichment over several months can cause decline in vegetation, in particular of submerged plants in ditches (Veeningen 1982, Drent & Kersting 1993, Portielje & Roijackers 1995, Portielje & Lijklema 1995, Portielje *et al.* 1996, Janse 1998, Janse & van Puijenbroek 1998). However, in the experimental ditch, natural vegetation dieback of the main plant species *Hydrocharis morsus-ranae, Lemna triscula* and *Sparganium erectum* was occurring in the whole ditch as well as in all the enclosures. Consequently, the demand for carbon dioxide would have declined with the natural dieback of the vegetation in the enclosures. This would have reduced pH to levels in which elevated ammoniacal-nitrogen was relatively harmless to the mollusc community in the H and N enclosures. It would be interesting to examine the effect of elevated ammoniacal-nitrogen in late spring when the ditches are at their most productive and the diurnal fluctuations of dissolved oxygen and pH are at their greatest (Veeningen 1982).

All three of the Red Data Book snails typical of drainage ditches *S. nitida, Anisus vorticulus* and *Valvata macrostoma* rarely occur in the lower depths where dissolved oxygen is significantly lower (Chapter 3). The three species are most likely found at their minimum threshold concentrations of acceptable dissolved oxygen. The loading of nitrate into ditches especially at the substrate layer will increase the rate of denitrification, thereby increasing SOD, and thus place an increasing demand on a limited oxygen supply. The implications of nitrogen loadings on molluscs may be more pronounced at other times of the year and on the more vulnerable stages of the mollusc's life cycle such as the neonates (Boycott 1936). Further experimental work is therefore required to assess the long-term effect of eutrophication on scarce molluscs in drainage ditches in relation to changes in the water chemistry and also changes in the vegetation structure.

Table 6.1: Overview and description of an experimental ditch on Pevensey Levels, south-east England used to assess short-term nutrient effects on gastropods. Local water chemistry was measured from two locations within the ditch: surface layer and lower depth. Abundance of gastropod species was estimated using AFCOR scale (Abundant >101, Frequent 51-100, Common 16-50, Occasional 6-15, Rare 1-5) (NTU = Nephelometric Turbidity Units)

Variable	Experimental ditch	
Mid-channel depth (metres)	0.70m	
Average width (metres)	2.00m	
Ditch choked with vegetation	95 %	
Vegetation cover	100 %	
Floating	80 %	
Submerged	50 %	
Emergent	90 %	
Amphibious	10 %	
Wetland plant richness	20	
Submerged plants	2	
Floating plants	4	
Emergent plants	8	
Amphibious plants	6	
Ammoniacal-nitrogen (mg l^{-1})	0.07	
TON (mg l^{-1})	0.2	
Nitrate (mg l^{-1})	0.2	
Nitrite (mg l^{-1})	0.01	
Phosphate (mg l^{-1})	0.2	
Alkalinity (mg l^{-1})	227	
Chloride (mg l^{-1})	96	
Hardness (mg l^{-1})	267	
	<0.2m from water surface	<0.2m from substrate layer
Depth of sonde (metres)	0.1m	0.65m
pH	7.3	7.0
Dissolved oxygen (mg l^{-1})	2.61	0.11
Conductivity (µS cm^{-1})	538	574
Salinity (%)	0.3	0.3
Turbidity (NTU)	4	15
Gastropod species richness	11	
Valvata macrostoma	O	
Valvata cristata	R	
Bithynia leachii	O	
Bithynia tentaculata	F	
Lymnaea peregra	A	
Lymnaea stagnalis	F	
Lymnaea palustis	O	
Physa fontinalis	-	
Planorbis planorbis	F	
Planorbarius corneus	O	
Anisus vortex	R	
Hippeutis complanatus	R	
Sphaerium cornum	F	
Pisidium species	R	

Table 6.2: Five different treatments of total nitrogen (N) and total phosphate (PO_4) applied to experimental enclosures, with 7 replicated enclosures per treatment. Weekly amounts of N and P are in grams m^{-2} of the water surface in the enclosure.

Treatment		Total Nitrogen		Total Phosphate	
H	High dosage	High	5	High	0.5
L	Low dosage	Low	0.5	Low	0.05
N	High nitrate dosage	High	5	Low	0.05
P	High phosphate dosage	Low	0.5	High	0.5
R	Reference	None	0	None	0

Table 6.3: Variations in water quality between experimental mesocosms used to assess the effects of nutrients on gastropods during Aug-Sept 2000. The non-parametric equivalent of repeated-measure ANOVA was used to test for significant differences in water chemistry with treatments, using the Sheirer-Ray-Hare test. Where variables (#) could be normalised or homogenised, they were tested using two-way ANOVA (*** = p <0.001, ** = p <0.010, * = p <0.050, n.s. = not significant).

Variables	Treatments		Time	
Phosphate #	$2.18_{4,59}$	n.s.	$2.92_{2,59}$	n.s.
Ammoniacal-nitrogen	$23.17_{4,59}$	***	$4.22_{2,59}$	n.s.
TON	$5.34_{4,59}$	n.s.	$6.14_{2,59}$	*
Nitrate	$5.34_{4,59}$	n.s.	$6.14_{2,59}$	*
Nitrite	$9.46_{4,59}$	*	$5.68_{2,59}$	n.s.
Alkalinity #	$8.72_{4,59}$	***	$30.57_{2,59}$	***
Chloride #	$3.59_{4,59}$	*	$6.61_{2,59}$	**
Upper pH	$9.71_{4,279}$	*	$138.18_{7,279}$	***
Lower pH #	$5.30_{4,174}$	***	$8.73_{4,174}$	***
Upper conductivity	$94.71_{4,279}$	***	$55.23_{7,279}$	***
Lower conductivity	$65.62_{4,174}$	***	$12.41_{4,174}$	*
Upper DO	$10.97_{4,279}$	*	$83.90_{7,279}$	***
Lower DO	$5.18_{4,174}$	n.s.	$45.36_{4,174}$	***
Upper turbidity	$7.32_{4,279}$	n.s.	$9.95_{7,279}$	n.s.
Lower turbidity	$2.48_{4,174}$	n.s.	$5.90_{4,174}$	n.s.
Chlorophyll-*a*	$7.11_{4,59}$	n.s.	$14.02_{2,59}$	***
Vegetation cover	$9.52_{4,104}$	*	$54.32_{2,104}$	***
Volume	$4.37_{4,279}$	n.s.	$202_{7,279}$	***

Table 6.4: Mean (± 1 s.d.) abundance (n) and total dry weight of individual species per enclosure, for each treatment at the end of an experimental period of nutrient loading. One-way ANOVA was used to indicate significant differences in abundance and biomass between treatment. (For definition of treatments H, L, N, P, R: see Table 6.2).

	H	L	N	P	R	$F_{4,30}$
S. nitida (n)	12 (7)	8 (5)	7 (5)	11 (9)	11 (8)	0.94 n.s.
dry weight mg	68 (28)	44 (33)	30 (23)	64 (51)	67 (49)	1.36 n.s.
V. macrostoma (n)	13 (8)	12 (12)	18 (19)	13 (11)	19 (17)	0.41 n.s.
dry weight mg	56 (37)	55 (59)	56 (61)	57 (46)	82 (65)	0.31 n.s.
V. cristata (n)	6 (4)	9 (15)	5 (4)	6 (7)	9 (16)	0.24 n.s.
dry weight mg	10 (5)	15 (20)	8 (5)	5 (11)	16 (16)	0.35 n.s.
B. tentaculata (n)	15 (8)	23 (22)	23 (18)	14 (16)	21 (22)	0.42 n.s.
dry weight mg	465 (197)	1195 (1178)	986 (1146)	504 (495)	618 (516)	1.14 n..s
B. leachii (n)	147 (63)	204 (211)	225 (165)	163 (140)	187 (165)	0.28 n.s.
dry weight mg	960 (396)	1802 (1859)	1711 (1688)	1688 (1212)	1189 (961)	0.54 n.s.
L. peregra (n)	18 (17)	16 (9)	15 (6)	9 (7)	13 (9)	0.75 n.s.
dry weight mg	465 (445)	442 (292)	426 (186)	206 (146)	328 (254)	1.00 n.s.
L. stagnalis (n)	3 (3)	2 (2)	3 (2)	2 (2)	3 (2)	0.35 n.s.
dry weight mg	157 (226)	349 (276)	360 (282)	95 (204)	374 (349)	1.62 n.s.
L. palustris (n)	0.3 (0.5)	0.3 (0.5)	0.4 (1)	1 (1)	1 (1)	0.91 n.s.
dry weight mg	3 (8)	8 (21)	1 (3)	2 (3)	1 (1)	0.72 n.s.
P. fontinalis (n)	0.3 (0.5)	1 (1)	1 (1)	1 (1)	1 (1)	0.84 n.s.
dry weight mg	2 (5)	17 (14)	14 (20)	15 (12)	10 (10)	1.29 n.s.
P. planorbis (n)	2 (2)	1 (2)	2 (2)	4 (4)	1 (1)	1.73 n.s.
dry weight mg	176 (145)	194 (363)	250 (280)	351 (315)	102 (120)	0.88 n.s.
A. vortex (n)	3 (2)	1 (1)	2 (1)	1 (1)	2 (3)	0.68 n.s.
dry weight mg	43 (30)	21 (15)	30 (24)	24 (25)	38 (55)	0.55 n.s.
Total number	224 (83)	278 (251)	304 (198)	228 (173)	269 (225)	0.21 n.s.
Total biomass (grams)	2.4 (1.1)	4.1 (3.2)	3.9 (3.0)	2.5 (1.6)	2.8 (1.9)	0.85 n.s.

Figure 6.1: Positioning of the enclosures in the experimental ditch on Pevensey Levels, south-east England (shaded/unshaded enclosures: alternating blocks of randomised treatments).

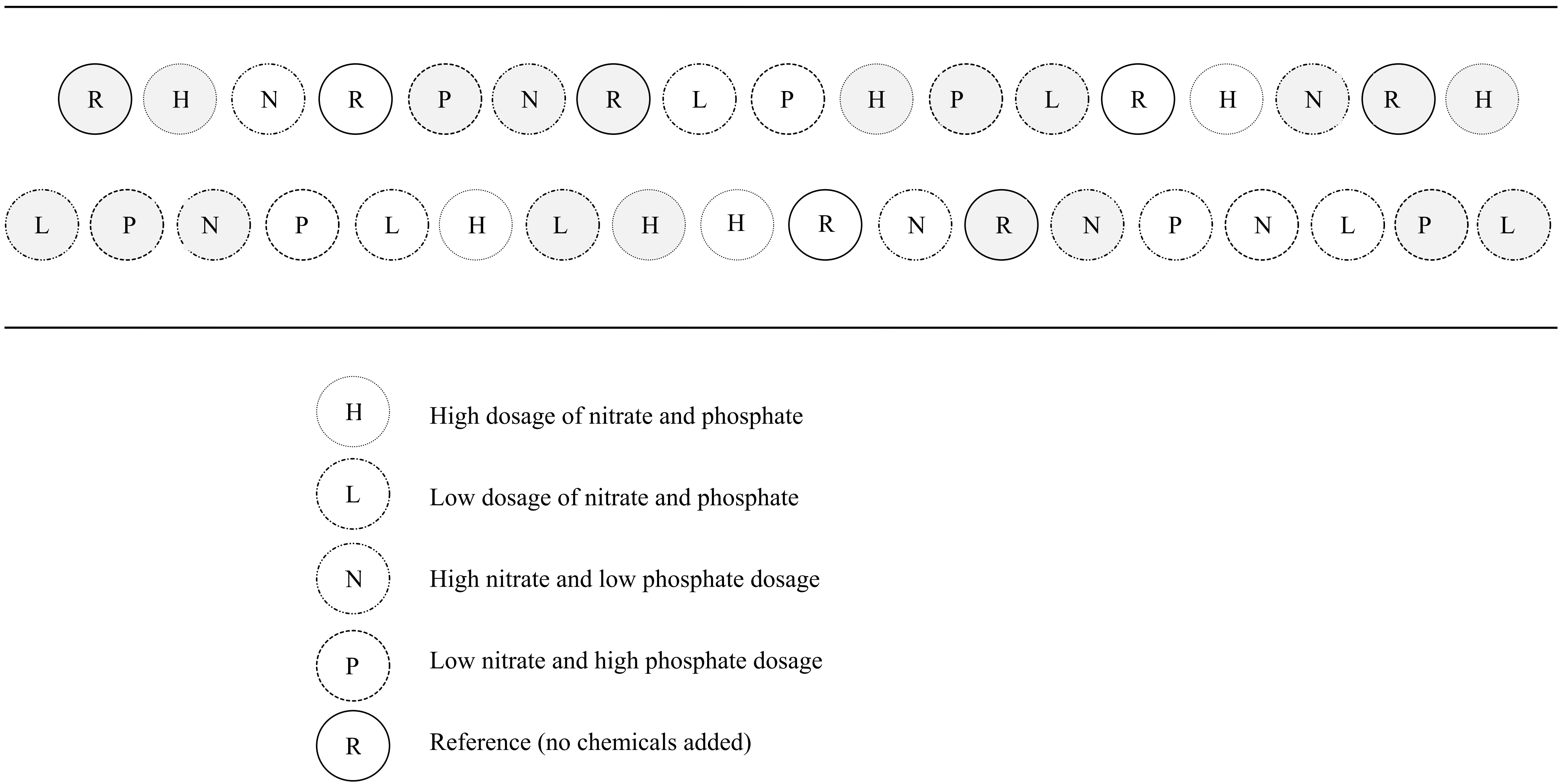


Figure 6.2: Diagram of the experimental enclosures (not to scale)

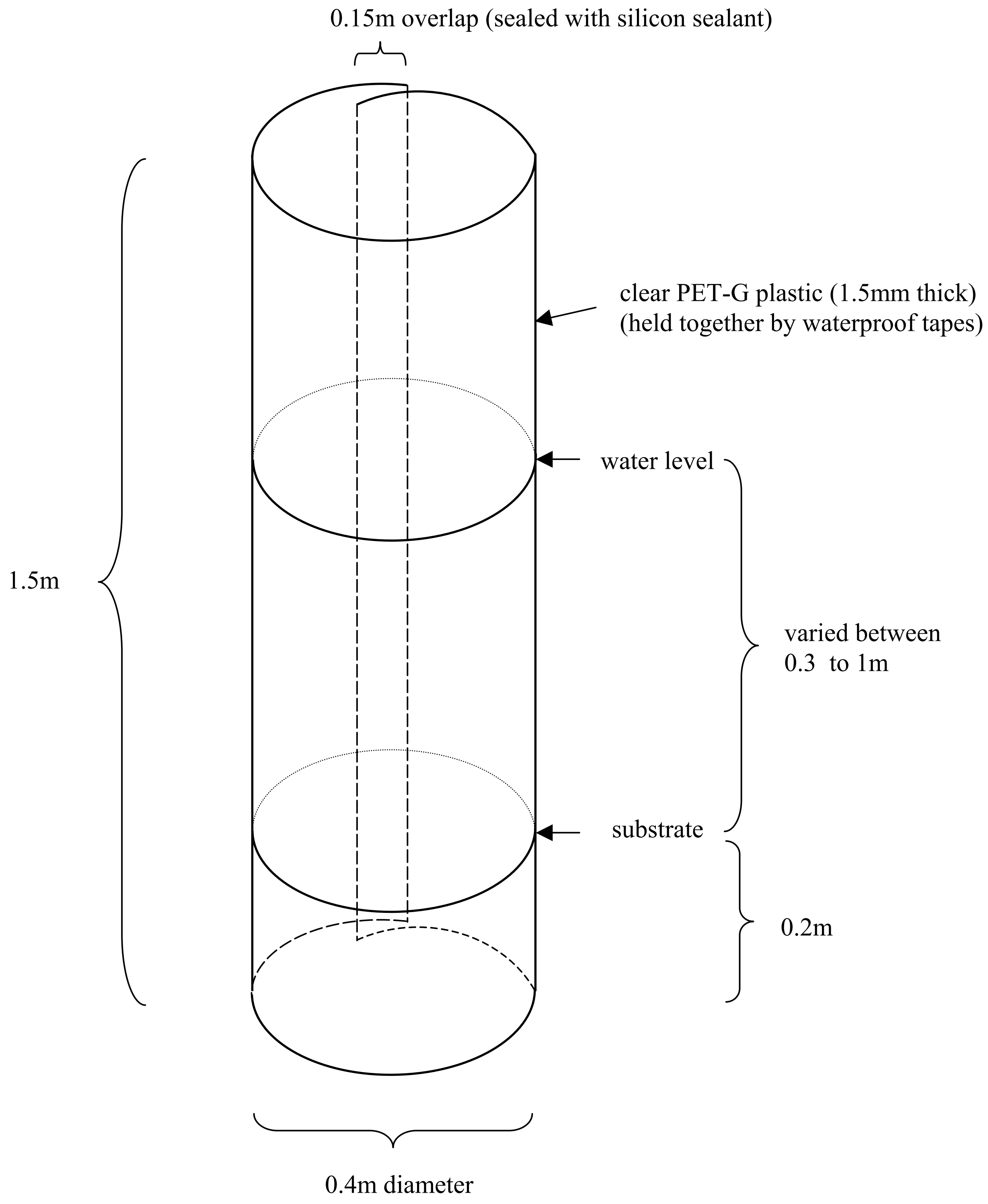
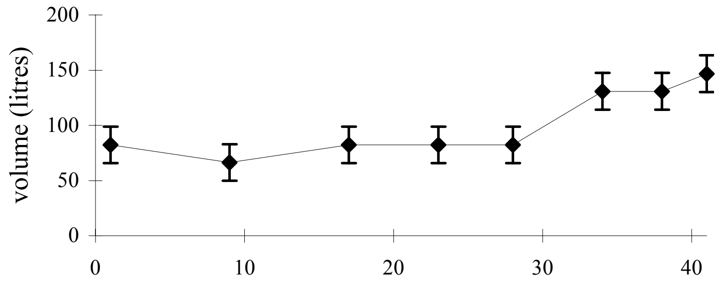
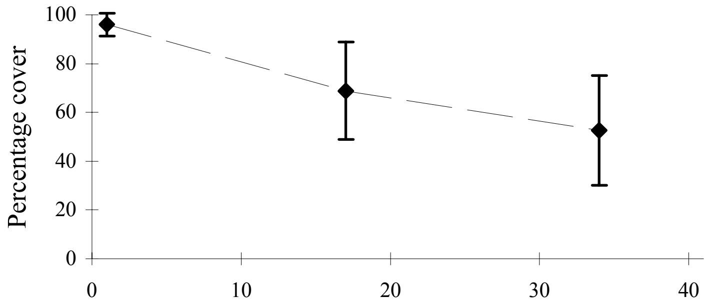


Figure 6.3: Changes in the experimental enclosures in the mean (± s.d.) water volume, vegetation cover, chlorophyll-a and turbidity over the 6 weeks of the experiment. Data have been pooled across all treatments.

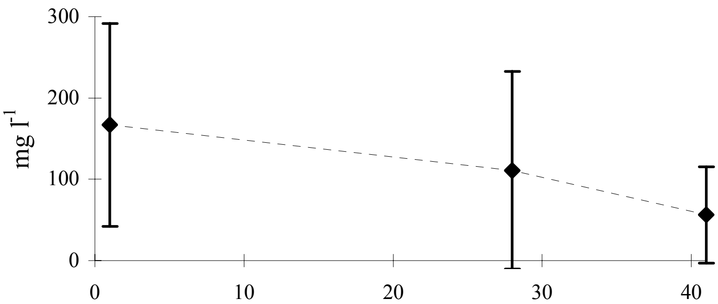
a) average volume of water in enclosures



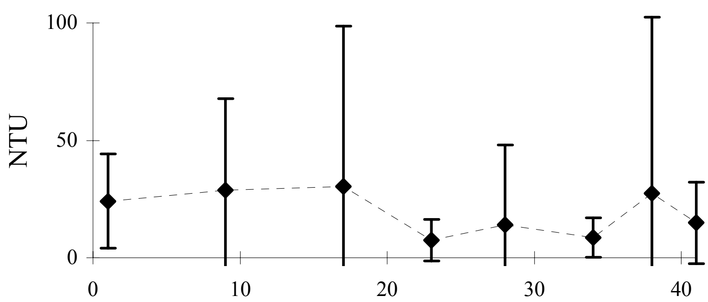
b) average percentage cover of vegetation in enclosures



c) average concentrations of chlorophyll-*a* in enclosures



d) average turbidity in the enclosures



Number of days

Figure 6.4: Mean (± 1 s.d.) concentrations of orthophosphate recorded on three occasions for each treatment (4 replicates) (• = expected concentration based on quantity of phosphate added as sodium dihydrogen orthophosphate on a weekly basis; points joined for ease of interpretation). One-way ANOVA (F) are shown between recorded PO_4 concentrations at different times (n.s. = not significant). Identical letters denote significant Fisher pairwise differences.

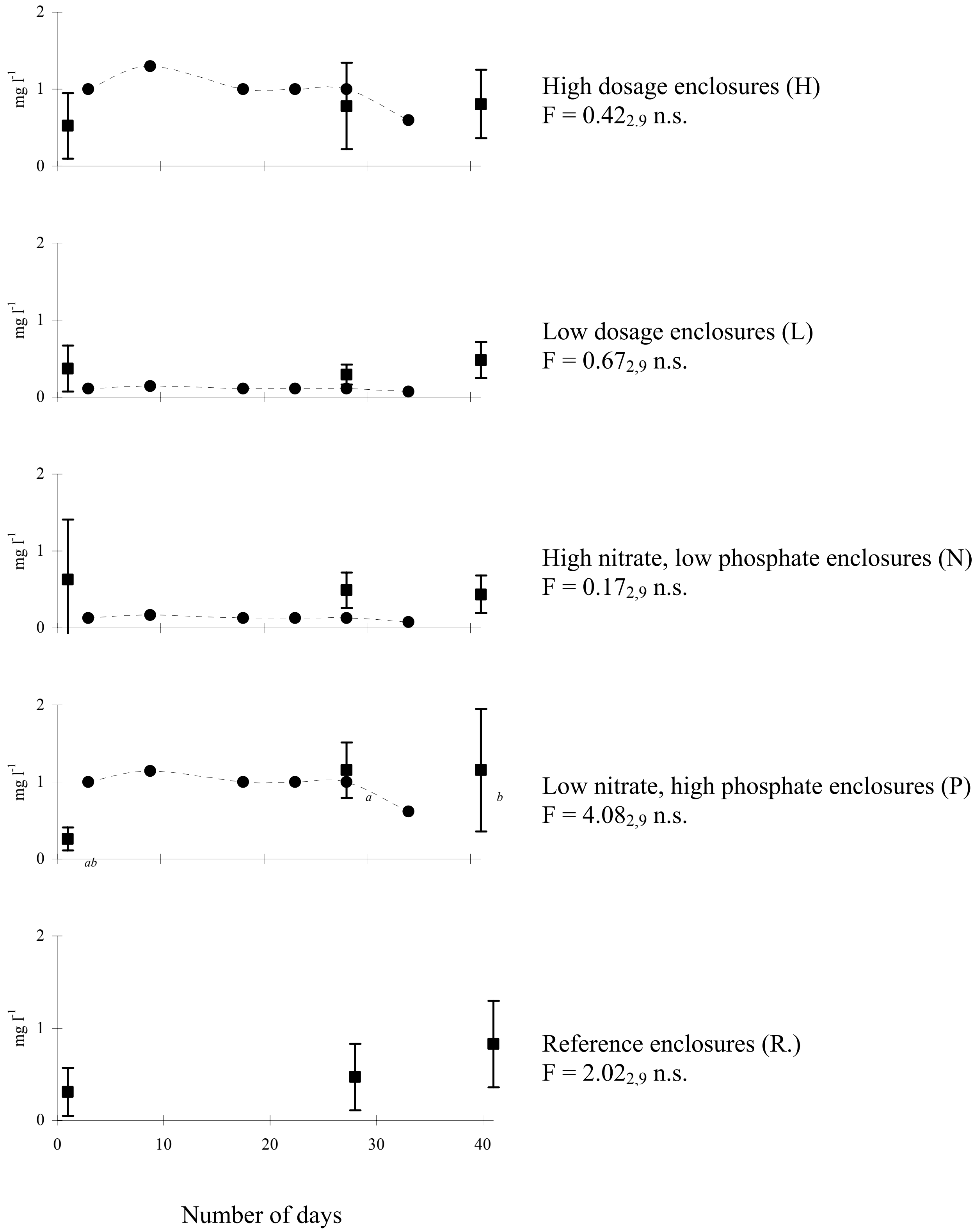


Figure 6.5: Mean (± 1 s.d.) concentrations of ammoniacal-nitrogen recorded on three occasions for each treatment (4 replicates) (• = quantity of total nitrogen added as ammonium nitrate on a weekly basis; points joined for ease of interpretation). One-way ANOVA (F) are shown between recorded NH_4 concentrations at different times (** = P <0.010, * = P <0.050, n.s. = not significant). Identical letters denote significant Fisher pairwise differences.

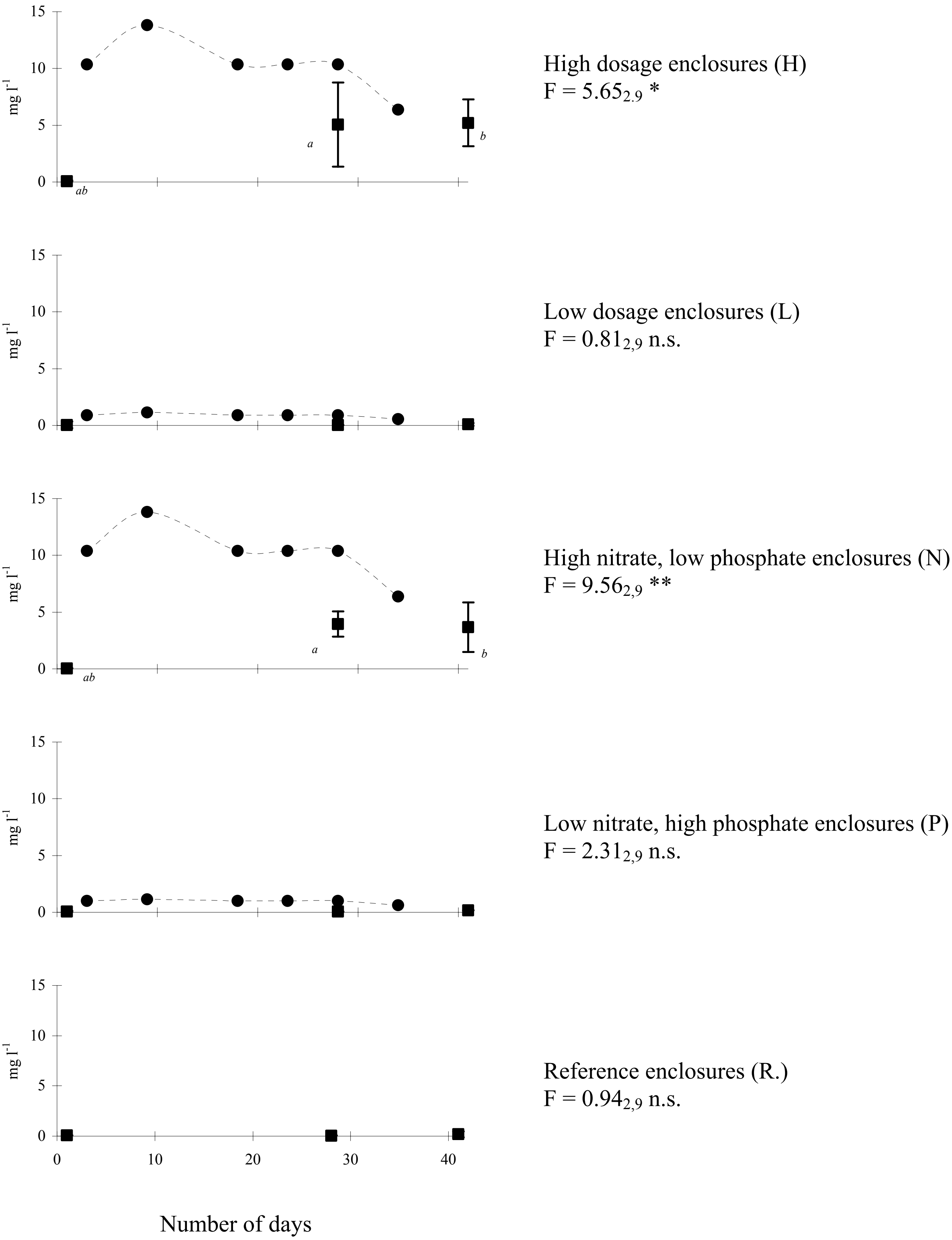
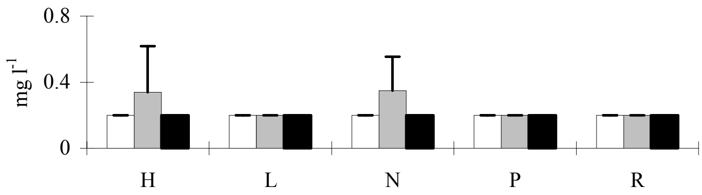


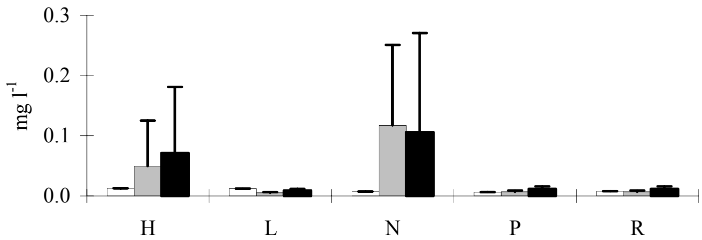
Figure 6.6: Mean nitrate, nitrite, alkalinity and chloride concentrations for each treatment on three occasions over 6 weeks (4 replicates). (White bar = day 1, Grey bar = day 28, Black bar = day 41). One-way ANOVA ($F_{2,9}$) or Kruskal Wallis test (H_2) were used to determine significant differences between the three sample occasions (*** = P <0.001, * = P <0.010, n.s. = not significant). Pairwise differences indicated by Tukey comparison tests, are denoted by identical letters. (For definition of treatment type H,L,N,P,R: see Table 6.2).

a) nitrate



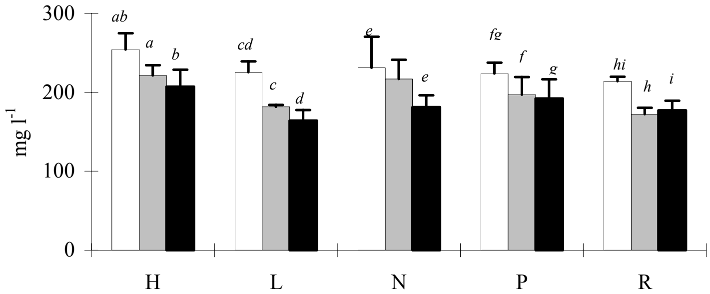
H: H = 2.00 n.s.
L: H = 0.00 n.s.
N: H = 4.36 n.s.
P: H = 0.00 n.s.
R: H = 0.00 n.s.

b) nitrite



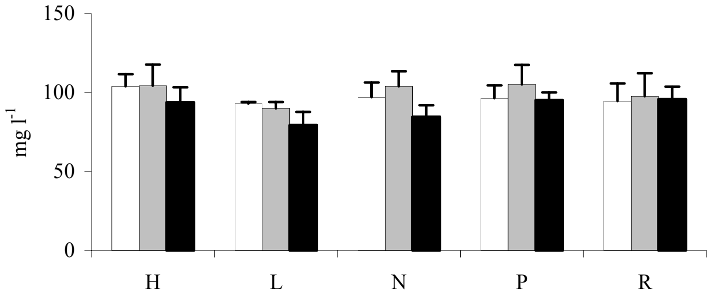
H: F = 0.59 n.s.
L: F = 1.35 n.s.
N: F = 0.96 n.s.
P: F = 0.89 n.s.
R: F = 1.56 n.s.

c) alkalinity



H: F = 6.68 *
L: F = 31.76 ***
N: F = 3.32 n.s.
P: F = 2.70 n.s.
R: F = 26.09 ***

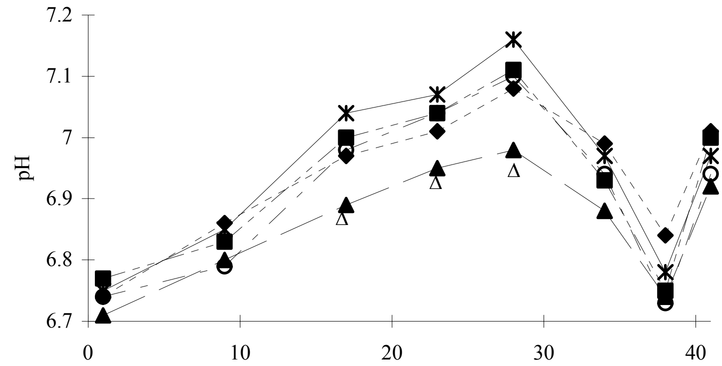
d) chloride



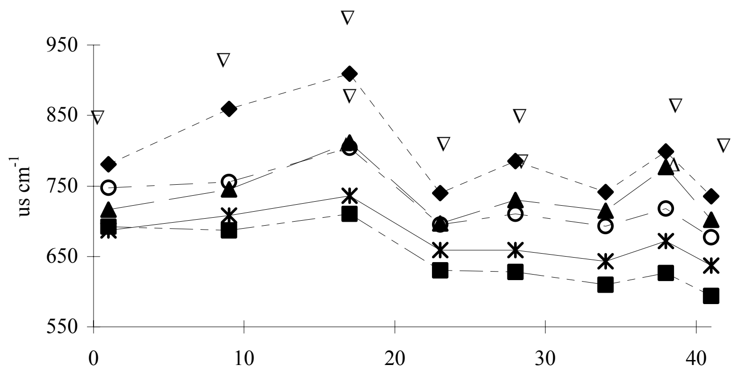
H: F = 1.29 n.s.
L: F = 7.12 *
N: F = 5.01 *
P: F = 1.41 n.s.
R: F = 0.07 n.s.

Figure 6.7: Weekly trends in pH, conductivity and dissolved oxygen in the upper layer of water in the enclosures for each treatment (20cm from water surface) (*= R enclosures, ♦ = H enclosures, ■ = L enclosures, ▲ = N enclosures, O = P enclosures). Measurements were taken between 1100 and 1400 hours (7 replicates per enclosure, per treatment). Kruskal Wallis tests indicated significant differences between the treatments and the reference enclosures (significant differences denoted by Δ).

a) pH



b) conductivity



c) dissolved oxygen

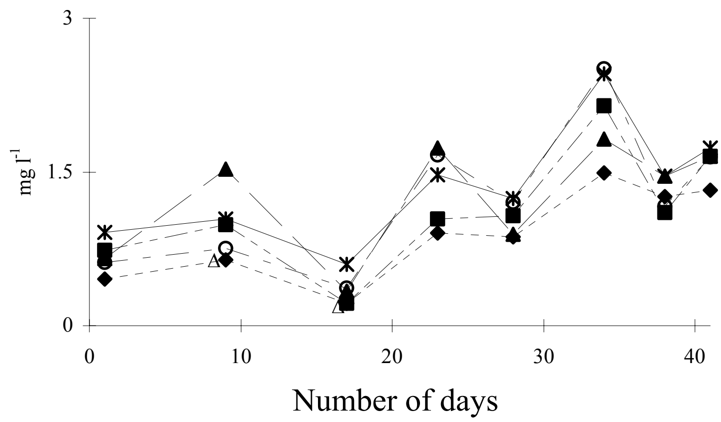
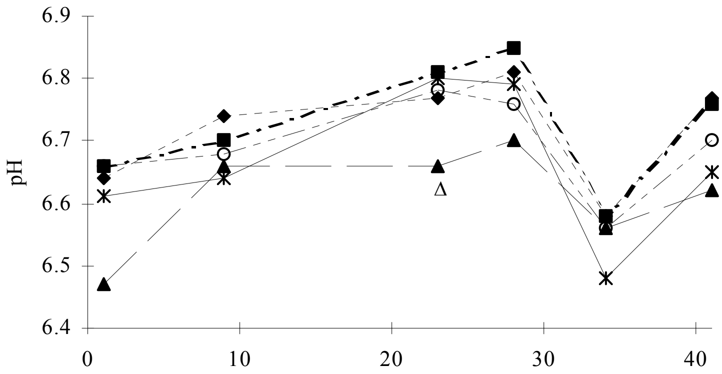
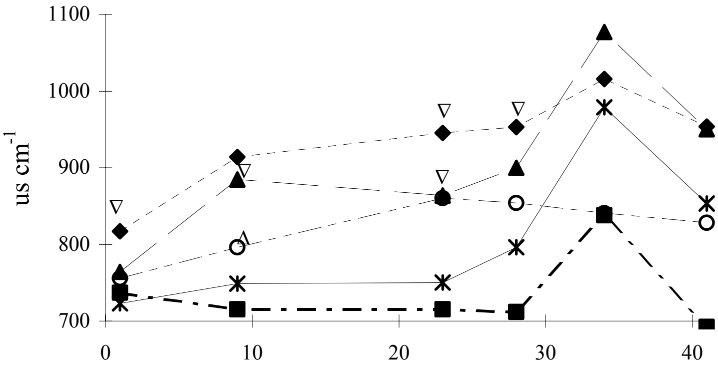


Figure 6.8: Weekly trend of pH, conductivity and dissolved oxygen in the lower layer of water in the enclosures for each treatment (20cm from substrate) (*= R enclosures, ♦ = H enclosures, ■ = L enclosures, ▲ = N enclosures, O = P enclosures). Measurements were taken between 1100 and 1400 hours (7 replicates per treatment). Kruskal Wallis tests indicated significant differences between the treatments and the reference enclosures (significant differences denoted by Δ).

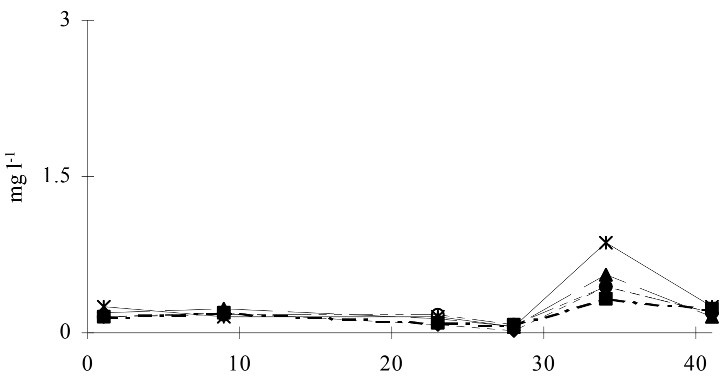
a) pH



b) conductivity



c) dissolved oxygen



Number of days

Figure 6.9: Number of live and empty shells of *Segmentina nitida* retrieved from the enclosures after 6 weeks of treatment. (grey = live animals, white = empty shells). One-way ANOVA between the different treatments indicated no significant differences in number of shells retrieved F = $0.46_{4,30}$ (0.767) nor in number of *S. nitida* surviving F = $0.94_{4,30}$ (0.453). (For treatment types H, L, N, P, R: see Table 6.2).

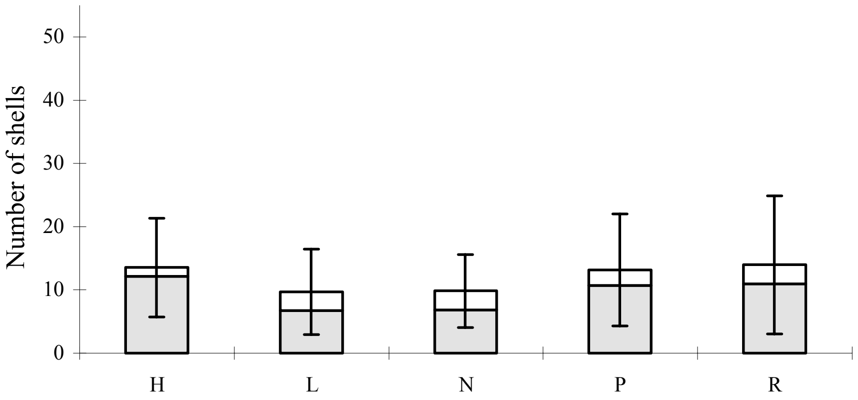
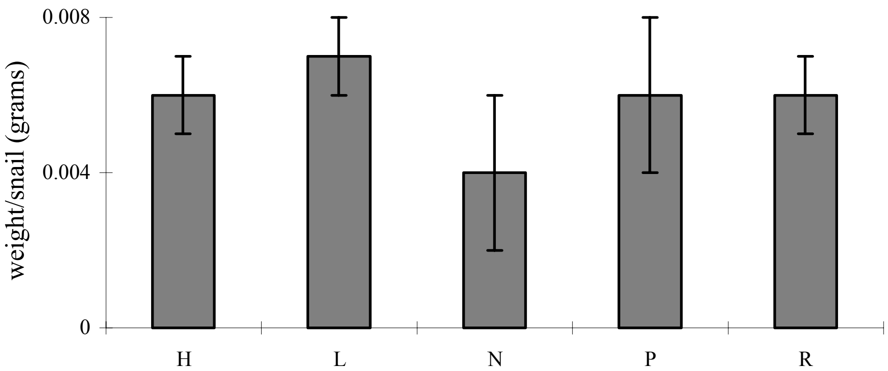


Figure 6.10: The mean biomass of *Segmentina nitida* from each treatment type after 6 weeks. All retrieved specimens were over 2.5mm in shell diameter. One-way ANOVA between treatment types indicated no significant differences F = $1.62_{4,30}$ (0.195). (For treatment types H, L, N, P, R: see Table 6.2).



- Chapter 7 -

General Discussion

7.1. Introduction

Drainage ditches, a characteristic feature of grazing marshes in the UK, were first created over 300 years ago to drain large lowland marshes that were previously inaccessible to people (Sutherland & Hill 1995, Harts 1994). The surveys in this thesis of the grazing marshes of south-east England have confirmed the status of the drainage ditches as one of richest molluscs habitats in the UK, supporting over 55% of its freshwater molluscs including several Red Data Book (RDB) species (Chapters 4 & 5, Bratton 1991). Between the 1960s and 1980s, however, there has been an estimated 40% decline in the area of grazing marsh and their associated ditches in the UK (RSPB *et al.* 1997). The driving force behind this decline has largely been the UK and European agricultural policies which offer economic incentive to reclaim grazing marshes for intensive agricultural production (Armstrong *et al.* 1995, MAFF 1975). Improved drainage infrastructure and efficiency on marshlands has facilitated the conversion of grazing land to arable land. In addition, fertiliser applications have led to increasing eutrophication. Also, the lowering of water levels has led to the fragmentation of ditches at the marsh-scale with consequences for the dispersal of wetland plants and animals, including the four RDB molluscs. As a result of these intensive agricultural improvements, local extinctions have occurred.

The survival of rare molluscs and other wetland organisms is therefore totally dependent on appropriate and responsible management by landowners and drainage authorities. The three RDB snails, *Segmentina nitida, Anisus vorticulus* and *Valvata macrostoma* were all scarce, occurring in 16% or less of the ditches surveyed (Chapter 2). However, the single RDB bivalve *Pisidium pseudosphaerium* was found in at least half of the ditches and was the second most common bivalve occurring on the grazing marshes (Chapter 5). The threats to the molluscs by the loss of grazing marshes, ditch degradation, eutrophication and intensive drainage, is further compounded by the lack of knowledge of the conservation and ecology of each mollusc species. This thesis has attempted to improve understanding of the ecological requirements of each of the four molluscs, which are summarised in this chapter. Moreover, the conservation status of the molluscs is reviewed along with implications for management of grazing marshes and the drainage ditches.

7.2. Ecological implications

One of the current conservation targets outlined for *S. nitida* and *A. vorticulus*, both priority species under the UK Biodiversity Action Plan (BAP), is to collate ecological data to try and explain why these species are in decline. A greater understanding of the ditch characteristics in which each species thrive will inform management.

S. nitida occurred in shallow calcareous ditches with dense stands of emergent vegetation (Chapter 2). However, within the ditches, its greatest abundance was recorded among amphibious vegetation (Chapter 3). *S. nitida* appeared to thrive in low dissolved oxygen concentrations of less than 1mg l^{-1} but was possibly restricted by the near anoxic conditions of the lower depths (Chapter 3). The description of its occurrence in dense vegetation was consistent with suggestions by other authors (Killeen 1994, Killeen & Willing 1997, Willing & Killeen 1998, Jackson & Howlett 1998). On many occasions, *S. nitida* was recorded in large numbers in ditches with dense floating vegetation mats of *Glyceria maxima,* an amphibious plant (Killeen 1994, Jackson & Howlett 1998). The shallow depth and the domination by emergent and amphibious plants typified ditches at the advanced stages of vegetation succession (Kirby 1992, RSPB *et al.* 1997). Furthermore, *S. nitida* was associated with other species such as *Lymnaea palustris*, *Planorbis planorbis, Bathyomphalus contortus* that were typical of water-bodies prone to desiccation, a characteristic feature of ditches at the late successional stages (Chapter 4, Boycott 1936, Kerney 1999).

In contrast, *A. vorticulus* was associated with other gastropod species such as *Valvata piscinalis*, *Gyraulus albus* and *Planorbis carinatus,* all typical of deeper water rarely subjected to desiccation (Chapter 4, Boycott 1936, Kerney 1999). *A. vorticulus* also avoided the anoxic substrate layer, typical of most drainage ditches (Marshall 1981), and instead concentrated at the surface layer where average dissolved oxygen concentrations were around 2mg l^{-1} (Chapter 3). The species was recorded in comparatively less calcareous ditches than *S. nitida.* It typically occurred in ditches with high diversity of aquatic plants, and consequently was found in greatest number among floating vegetation (Chapters 2 & 3). Other surveys have also found *A. vorticulus* among diverse vegetation (Willing & Killeen 1998) in particular with high percentage cover of floating plants such as *Lemna trisulca* and *Hydrocharis morsus-ranae* (Willing & Killeen 1998, Jackson & Howlett 1998). In comparison to *S. nitida,* *A. vorticulus* occurred in deeper and wider ditches with a lower vegetation cover, reflecting a preference for ditches that are not at the advanced stages of vegetation succession (Chapter 4, Jackson & Howlett 1998).

Similarly to *A. vorticulus*, *V. macrostoma* occurred in ditches that were not densely choked with emergent and amphibious vegetation across the channel (Chapters 2 & 4). However, the highest abundance of *V. macrostoma* occurred among emergent vegetation (Chapter 3) typifying ditches at later stages of vegetation succession compared to *A. vorticulus*. Along with *S. nitida*, *V. macrostoma* was associated with ditches with significantly higher chloride concentrations, possibly an incidental effect due to the maritime positions of the ditches (Chapter 2). As was the case with *S. nitida* and *A. vorticulus*, the valvatid was rarely recorded in the lower depths and was generally found throughout the upper layer of the ditch (Chapter 3). All valvatid species are regarded as typical of deeper flowing water, however this assumption is mainly based on observations on the more common and larger *Valvata piscinalis* (Boycott 1936, Dillion 2000). *V. macrostoma* and *V. piscinalis* use their gills in gas exchange and are likely to be affected by the hypolimnetic deoxygentation in the lower part of the ditch. By definition, dense vegetation, especially of emergent and amphibious plants, will reduce water flow and, in turn, the concentrations of dissolved oxygen (Marshall 1981). *V. macrostoma* can tolerate low dissolved oxygen averaging around 1mg l^{-1} but at advanced stages of vegetation succession, increasingly anoxic conditions may be problematic.

The same scenario would be expected with *P. pseudosphaerium*, another gill breathing mollusc, however no data for its distribution within the ditch was collected. This RDB sphaeriid was typical of ditches with high vegetation diversity of submerged, floating and emergent plants similar to *A. vorticulus* and *V. macrostoma* (Chapter 5). *P. pseudosphaerium* was associated with a species-poor bivalve assemblage, including *Pisidium obstusale* and *Sphaerium corneum,* characterised by an ability to colonise densely vegetated ditches (Chapter 5, Abraham *et al.* 1998, Jackson & Howlett 1998). In contrast, the more diverse assemblage of bivalves occurred in deeper channels with a higher percentage of open water indicating a preference for ditches at an earlier stage of vegetation succession than observed for *P. pseudosphaerium* or any of the RDB snails (Chapter 5).

Where ditch ecological characteristics were suitable for *S. nitida*, *V. macrostoma and P. pseudosphaerium*, they appeared to have been eliminated or restricted by elevated concentrations of nitrogen compounds (Chapters 2 & 5). Direct toxicity to the RDB molluscs was investigated by a field experimental approach, through which *S. nitida* and *V. macrostoma* were exposed to excess loading of ammonium nitrate fertiliser (Chapter 6). However, over the six weeks of the experiment, there were no short-term toxic effects on either of these two snails or any other snail species present in the experimental enclosures. This suggests that any effect of elevated nitrogen concentrations on the RDB species occurs over a longer time-scale or at other stages of the life cycle. Excess nutrients in ditches can cause substantial changes to the wetland vegetation structure (Mason & Bryant 1975, Moss 1988, Janse & van Puijenbroek 1998), contribute to further deoxygentation of the hypolimnetic layer (Veeningen 1982, Miranda *et al.* 2001), can lead to the dissociation of ammoniacal-nitrogen to toxic ammonia ions (Roelofs 1983, Dojlido & Best 1993, Horne & Goldman 1994), and can also affect the nitrogen dynamics in the ditches (Sweerts *et al.* 1991, van Luijn *et al.* 1998a & b). To assess the influence of these potential changes caused by eutrophication on the RDB molluscs, appropriately long term studies and experiments are required, especially on the more vulnerable neonates (Boycott 1936). The rare molluscs all occur in exacting ecological conditions and a slight change in the ditch characteristics could result in a decline in their abundance and distribution. Future studies should therefore focus on the effects of excess nutrients on macrophytic and algal vegetation, and on the diurnal and seasonal changes in temperature, pH, oxygen and ammonia in drainage ditches

7.3. Conservation implications

It is generally assumed that the four RDB molluscs, because they are confined to grazing marshes, occur in ditches of similar characteristics and that management for one species will assist the others (Bratton 1991, Kerney 1999). However, as discussed above, the ecological requirements at the marsh scale of the three snails appear to be very different. This is supported by the scarcity of occassions in which all three snail species occur in the same ditch (Chapters 2,3,4). The three snails appeared to be ‘umbrella species’ representing and indicating the presence of different assemblages of freshwater snails (Chapter 4). Such umbrella species are usually those which require large tracts of habitat, and whose preservation will consequently conserve other species (Simberloff 1997). By encompassing the habitat requirements for all three RDB snails, an array of freshwater snails in contrasting assemblages is likely to be supported across grazing marshes.

In addition, *P. pseudosphaerium* has indicator value since it occurs in ditches with high conservation interests of gastropods, in particular *A. vorticulus* and *V. macrostoma* (Chapter 5). However, it did not indicate the most diverse bivalve assemblage, which occurred instead in open vegetated ditches compared to the majority of the gastropods (Chapter 5). To cater for the conservation interest of bivalve species and the three distinct assemblages of gastropods, ditch management needs to be considered at the marsh scale. Appropriate rotational management should offer a wide range of ecological conditions from open ditches suitable for bivalves to densely choked ditches where *S. nitida* thrives.

The low prevalence of the three snails, even at the established stronghold sites in this survey, justifies their British RDB status and inclusion in the UK BAP (Bratton 1991, HMSO 1995). In contrast, with *P. pseudosphaerium* occurring in over half of the ditches surveyed and being the second most abundant bivalve, its current RDB status and BAP listing is questionable. However, the distribution map of this bivalve in Britain indicates that the species is generally confined to large areas of grazing marshes (Kerney 1999). The current range, and the association with occurrence of *V. macrostoma* and *A. vorticulus* suggests that *P. pseudosphaerium* has a relict distribution. Threats faced by grazing marshes, the major habitat of *P. pseudosphaerium,* as well as the three RDB snails, place all the Red Data Book species in a vulnerable position.

S. nitida was originally listed on the global Red List (IUCN 1979, 1988, 1990, 1994a) but was removed when new criteria of rarity were adopted by The World Conservation Union (IUCN 1994b). The reinstating of *S. nitida* and the inclusion of the other three RDB molluscs onto the Global Red List (Hilton-Taylor 2000), and in turn the European Red List (UNECE 1991) will depend on future ecological surveys being implemented in other European countries. The patchy nature of information on distribution from large areas of Europe and parts of Asia makes it difficult to clarify whether the species are truly threatened (Table 7.1).

Despite listings in the British Red Data Book (Bratton 1991) and the UK BAP (HMSO 1995), there is little legal protection for the four species considered in this thesis. Current legislation that affords protection to UK wildlife, the Countryside and Wildlife Act (as amended) (HMSO 1981) and the Habitats Directive 92/43/EEC (European Commission 1992) only lists a few wetland mollusc species: *Margaritifera margaritifera*, *Myxas glutinosa* and several *Vertigo* species (Drake 1998a, Fowles 1998, Stebbings & Killeen 1998). There is a lack of ecological data for the majority of mollusc species in the UK. Licences are required to handle and kill protected species listed by the CRoW Act and Habitats Directive. Therefore any proposed designation for protection of rare molluscs such as those discussed in this thesis can potentially thwart efforts in improving understanding of their habitat requirements (HMSO 1998). An additional means of protection is to improve the designation of their habitats as Sites of Special Scientific Interest (SSSI) or as Special Areas of Conservation (SAC) under the Habitats and Species Directive. However, a more proactive protection would be the encouragement of sympathetic agriculture across marshland by the use of positive management agreements and enhancement schemes, which are discussed below under management implications.

7.4. Management implications

With regards to nature conservation, the intensification of drainage and agriculture on grazing marshes has led to inappropriate ditch management regimes, decreasing connectivity between water bodies and increasing eutrophication (e.g. Palmer 1986, Jefferson & Grice 1998, Abraham *et al.* 1998).

Drainage ditches on grazing marshes have traditionally been managed by the dredging of accumulated silt and vegetation on a 10-30 years cycle. This was previously carried out by hand but since the 1970's has increasingly been carried out by mechanical means (Marshall *et al.* 1978). Between de-silting operations, the ditches are often cleared of vegetation in an attempt to reduce sediment accumulation. After de-silting or weed clearance, the ditches are usually devoid of vegetation and have maximum efficiency for drainage. Generally, with time, the vegetation community will gradually recover, and depending on the rate of vegetation succession, will be completely choked in 10-30 years (RSPB *et al.* 1997). Vegetation succession, in turn, is accompanied by changes in the assemblages of macrophytes and macoinvertebrates until they reach a climax stage that is usually terrestrial (MacKenzie *et al.* 1999, Caspers & Heckman 1981, 1982). However, there is usually a risk that species with poor dispersal or colonising abilities may not return (Kirby 1992, RSPB *et al.* 1997)

Despite the paucity of management data from any of the marshes, it was clear that a range of vegetation characteristics at different stages of the hydroseral succession at the marsh-scale would accommodate the whole array of freshwater molluscs (Chapters 2,4 and 5). Any de-silting operation might initially be harmful for the majority of the molluscs unless refuge areas were left undistributed. Sphaeriidae are generally sediment dwelling organisms, and, as has been observed with larger bivalves, the removal of the sediment is likely to be detrimental (Young & Williams 1983a & b, Young 1995, Drake 1998a, Hastie *et al.* 2000, Aldridge 2000). In addition, the removal of vegetation is unlikely to benefit gastropod assemblages. Snails depend on plants for access to the air-water interface, refugia, a substrata for oviposition, and also as a food source of epiphytic algae and detritus (Carlow 1973a, Reavell 1980, Lodge 1985, Lodge *et al.* 1987, Caquet 1990, Thomas & Kowalczyk 1997).

With time, the ditch and the vegetation will recover and when the appropriate ecological conditions are attained, it will be re-colonised by a particular group of mollusc species. By definition, rich macrophyte compositions are characteristic of ditches where emergent and amphibious plants have not yet colonised the centre of the channel, thereby allowing floating and in particular submerged vegetation to flourish (Caspers & Heckman 1981, 1982, van Strien *et al.* 1991). A high diversity of molluscs is therefore expected in these same ditches due to the greater range of microhabitats available (Chapter 4, Southwood 1977, Townsend & Hildrew 1994). Eventually, emergent and amphibious plants will successfully dominate the centre of the channel and as the vegetation structure becomes more homogenous, and conditions become more exacting, with lower concentrations of dissolved oxygen, the freshwater community will be replaced by terrestrial molluscs (Chapter 4, van Strien *et al.* 1991, Miranda *et al.* 2001).

A rotational ditch management regime across a marsh will enable a range of vegetation structures to occur simultaneously as a result of the hydroseral progression described above (Kirby 1992, RSPB *et al.* 1997, Painter 2000). Length of rotation can vary from annual light maintenance of all the ditches to a radical cleaning of only 10-20% of the ditches every year. In addition, rotation can also refer to a percentage of a ditch that is managed every year. A few studies have examined the recovery of the vegetation and macro-invertebrate assemblages in a ditch after de-silting but these have rarely been monitored continuously over 10-20 years (Hingley 1979, Palmer 1986, van Strien *et al.* 1991, Best 1993, 1994). Moreover, comparisons between types of de-silting and weed clearance techniques are still lacking and therefore current recommendations for aquatic invertebrates have little scientific basis (Newbold *et al.* 1989, van Strien *et al.* 1991, Kirby 1992, RSPB *et al.* 1997, Jefferson & Grice 1998).

However, for management regimes to succeed, the persistence of mollusc populations must be maintained within ditches or dispersal facilitated between ditches. Persistence can be encouraged by retaining remnants of vegetation during de-silting or clearance to act as refuges. A variety of management has been suggested from leaving one bank of the channel untouched, to a scallop formation creating a meander (Newbold *et al.* 1989, Kirby 1992, RSPB *et al.* 1994, 1997). The dispersal of molluscs, particularly in a freshwater environment, is poorly understood. Explanations for the dispersal of mollusc species range from ‘hitching a ride’ on waterfowl or accidental introduction by people. However, the most likely explanation is that molluscs are dependent on hydraulic connectivity between water bodies (Boycott 1936, Dillon 2000). On a grazing marsh, this would either be via the network of drainage ditches or overland during periods of flooding (Abraham *et al.* 1998). The extensive rainfall in the south-east England in the autumn of 2000 was the heaviest on record (Environment Agency 2001), and it would be interesting to monitor the progress of ditches from where RDB molluscs were recorded absent during the survey of 1999 (Chapters 2, 4 and 5).

Where there are no restrictions in the facilitation of dispersal or persistence of molluscs and the ecological characteristics in the ditches are apparently suitable, it appears that three RDB molluscs are potentially excluded from ditches with elevated concentrations of nitrogen compounds (Chapters 2 and 5). As already discussed, no direct toxicity effect of elevated nutrients was observed on the abundance and weight of the RDB snails (Chapter 6). However, longer-term effects on scarce molluscs are possible and therefore remedial actions should be taken to mediate any effect that eutrophication may cause in drainage ditches. The increasing use of fertiliser on agricultural land such as the grazing marshes needs to be reduced, and even reversed. Agricultural schemes such as Wetland Enhancement Scheme (WES), Countryside Stewardship Scheme (CSS) and Environmentally Sensitive Areas (ESA) which all compensate landowners for reducing their consumption of fertiliser on grazing marshes, are ideally placed for this extensification of agriculture on the marshes (Jefferson & Grice 1998, Stoate *et al.* 2001).

7.5. Conclusion

The distribution of the four scarce wetland molluscs: *S. nitida*, *A. vorticulus*, *V. macrostoma* and *P. pseudosphaerium* and their corresponding assemblages suggests that the mollusc communities are mainly affected by the vegetation structure within the drainage channels and water quality. Detailed autecology of each of the four scarce molluscs indicates that they require different vegetation structure and characteristics. These characteristics are potentially influenced by hydroseral succession that occurs in these ditches and can be manipulated by the management regime of grazing marshes. The two main reasons for the decline of the rare molluscs in the last 60 years appears to be the long term effects of eutrophication and ditch management not aimed at the conservation of molluscs populations. A third contributing factor was suggested, the lack of connectivity between ditches which does not facilitate the dispersal of the scarce molluscs.

Table 7.1: Conservation status of the RDB molluscs in other European countries (data source: shaded rows from the Red Lists of threatened species of individual countries, remaining data are cited in Wells & Chatfield 1992) (✓ = species present, ? = unknown).

	S. nitida	*A. vorticulus*	*V. macrostoma* (* *V. pulchella*)	*P. pseudosphaerium*
Albania	?	?	?	?
Austria	endangered	endangered	vulnerable*	endangered
Belgium	rare	rare	rare	?
Belorussia	?	?	?	?
Bosnia-Herzegovina	?	?	?	?
Bulgaria	?	?	?	?
Croatia	?	?	?	?
Czech Republic	✓	rare	vulnerable*	concerned
Denmark	not threatened	✓	?	✓
Estonia	?	?	?	?
Finland	not threatened	?	not threatened	rare
France	vulnerable	rare	?	vulnerable
Germany	vulnerable	rare	vulnerable	endangered
Greece	?	?	?	?
Hungary	not threatened	not threatened	✓*	rare
Ireland	absent	absent	?	vulnerable
Italy	rare	?	?	rare
Latvia	?	?	?	?
Liechtenstein	✓	?	?	?
Lithuania	?	?	?	?
Moldavia	?	?	?	?
Netherlands	not threatened	rare	endangered*	rare
Norway	endangered	absent	not threatened	endangered
Poland	not threatened	rare	vulnerable*	endangered
Portugal	?	?	?	?
Romania	✓	✓	✓*	?
Russia	not threatened	not threatened	✓*	✓
Slovakia	✓	✓	?	?
Slovenia	?	?	?	?
Spain	✓	?	?	?
Sweden	rare	endangered	rare	not threatened
Switzerland	vulnerable	rare	endangered	vulnerable
Ukraine	?	?	?	?
Yugoslavia	?	✓	?	?

- Chapter 8 -
References

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- Chapter 9 -

Appendices

Appendix 1: Comparison of two sampling techniques for freshwater molluscs

A pilot study was carried out in May 1999 to assess the efficiency of two different nets for sampling the freshwater molluscs in drainage ditches. The first net was a standard pond net with a mesh size of 1mm (0.25m x 0.27m D-net). The second net was a sieve net (0.15m diameter kitchen stainless steel sieve) also with a mesh size of 1mm, developed and standardised in previous surveys on freshwater molluscs (Killeen 1994, Killeen & Willing 1997). Two drainage ditches, where the Red Data Book (RDB) *Anisus vorticulus* previously been recorded from Amberley Wildbrooks, (Arun Valley, West Sussex) were sampled (Willing & Killeen 1998). The first ditch (TQ 030142) was dredged in 1998 and was sparsely vegetated. The other ditch (TQ 029144) was densely choked and no management had been carried out for at least 10 years.

Method

Four mollusc samples were taken from four randomly located sampling points in each ditch using the pond net and then again with the sieve net. Each sample was taken by a vigorous sweep over 1m parallel to the bank and included the sediment, vegetation and water surface, the sweep of the net took approximately 15 seconds. The samples were preserved on site in 70% Industrial Methylated Spirit (IMS). In the laboratory, the samples were washed through a 500µm mesh sieve and all gastropod species were removed and identified to species level with a light microscope (x10) using Macan (1977). Bivalves were only identified to genus level (Fitter & Manuel 1994).

Significant differences in abundance of species between the two net types were indicated by one-way analysis of the variance (ANOVA) for each ditch. For both ditches, the abundance data from 4 replicated samples for each net type was pooled and the mean log abundance of each snail was then calculated per ditch. The mean log abundance was then plotted against the probability of capture for each species, which was calculated as a proportion of the samples in which it occurred.

Results

Overall, eleven gastropod species were found in both ditches (Tables A1.1 & A1.2). *Bathyomphalus contortus* and *Lymnaea stagnalis* were only recorded in ditch 1, and ditch 2 had the only records for *A. vorticulus* and *Lymnaea palustris*. One-way ANOVA did not indicate any significant differences in abundances of gastropod species between the two net types. Higher abundances for both *Sphaerium* and *Pisidium* species were recorded when the pond net was used, but only in ditch 2 (*Pisidium*: $F = 15.65_{1,6}$ (0.007) and *Sphaerium*: $F = 6.15_{1,6}$ (0.048)).

Figures A1.1 and A1.2 shows the probability of capturing each species at any level of abundance and indicates that the probability was very similar between the pond net and the sieve net. However both methods share a problem in that there was markedly reduced probability of capturing less abundant snails, for example the RDB snail *A. vorticulus*.

Conclusion

The only difference between the two net types appears to be among the bivalve species in the densely vegetated ditch, where greater abundance of bivalves was captured using the pond net. The area of the pond net was much greater and can cover a larger area of the sediment where the bivalves typically live. The disadvantage of the pond net was the quantity of the material collected for analysis. At least double the time was required in the laboratory to sort out the pond net samples compared to the samples collected by the sieve net. As the main drawback of the sieve appears to be the reduced efficiency in sampling the sediment, it was suggested that a larger sieve should be used (0.18m diameter).

With the exception of the bivalves, there appears to be no benefit in using the pond net, which effectively creates more work but no significant increase in the gastropod richness or abundance. With both nets there appeared to be a risk of under-recording the occurrence of rare gastropod species and may require a greater sampling effort than the current four replicated samples per ditch.

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Table A1.1: Molluscs abundances in ditch 1 caught by the sieve net and the pond net in two drainage ditches on Amberley Wildbrooks in West Sussex.

species	sieve net				pond net			
	1	**2**	**3**	**4**	**1**	**2**	**3**	**4**
Valvata cristata	1	-	-	-	-	-	-	-
Bithynia tentaculata	-	-	-	-	-	-	-	1
Lymnaea peregra	5	5	10	5	6	30	8	15
Lymnaea stagnalis	-	-	-	-	-	-	-	-
Lymnaea palustris	1	-	-	-	-	-	-	-
Physa fontinalis	1	-	-	-	1	-	-	-
Bathyomphalus contortus	-	2	-	-	1	3	-	3
Planorbarius corneus	-	1	-	-	-	-	-	-
Planorbis planorbis	21	6	15	6	7	45	13	15
Anisus vortex	3	5	3	-	-	13	-	9
Anisus vorticulus	-	-	-	-	-	-	-	-
Sphaerium species	-	-	-	-	-	-	1	-
Pisidium species	-	2	1	7	-	-	1	2

Table A1.2: Molluscs abundances in ditch 2 caught by the sieve net and the pond net in two drainage ditches on Amberley Wildbrooks in West Sussex.

species	sieve net				pond net			
	1	**2**	**3**	**4**	**1**	**2**	**3**	**4**
Valvata cristata	2	-	-	2	1	1	-	-
Bithynia tentaculata	7	3	-	1	9	2	-	6
Lymnaea peregra	36	34	13	10	46	76	25	103
Lymnaea stagnalis	4	-	1	-	-	-	1	2
Lymnaea palustris	-	-	-	-	-	-	-	-
Physa fontinalis	3	3	-	-	9	4	1	6
Bathyomphalus contortus	-	-	-	-	-	-	-	-
Planorbarius corneus	2	-	-	-	1	-	-	-
Planorbis planorbis	13	44	2	18	52	40	10	89
Anisus vortex	7	2	8	10	20	17	10	7
Anisus vorticulus	-	1	-	-	-	1	-	-
Sphaerium species	-	-	-	-	5	4	-	2
Pisidium species	5	4	3	2	23	15	9	24

Figure A1.1: The probability of capture at any level of abundance in ditch 1, using the sieve net and pond net. (• = pond net, Δ = sieve net).

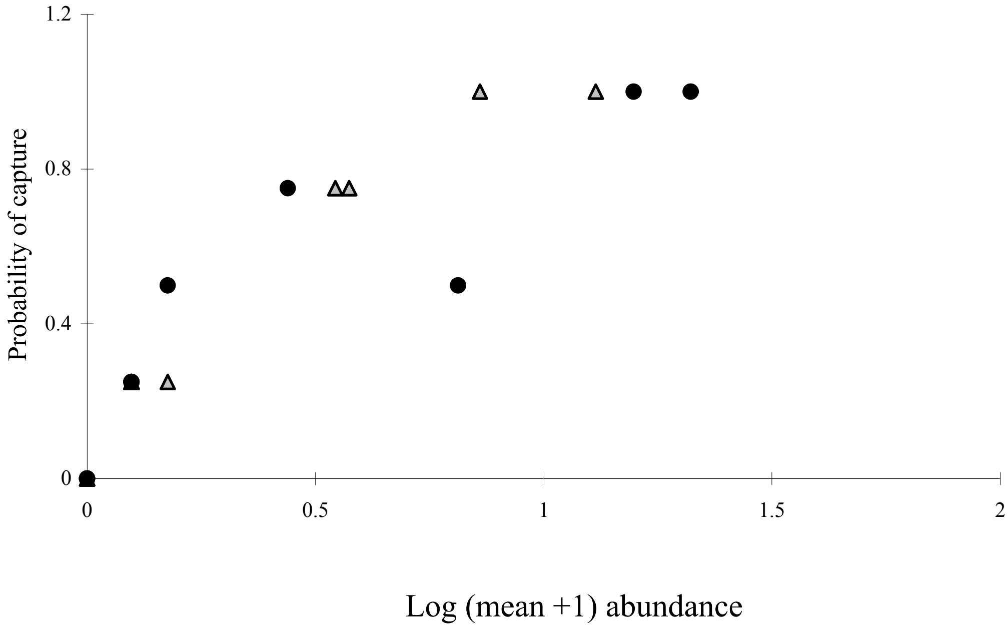
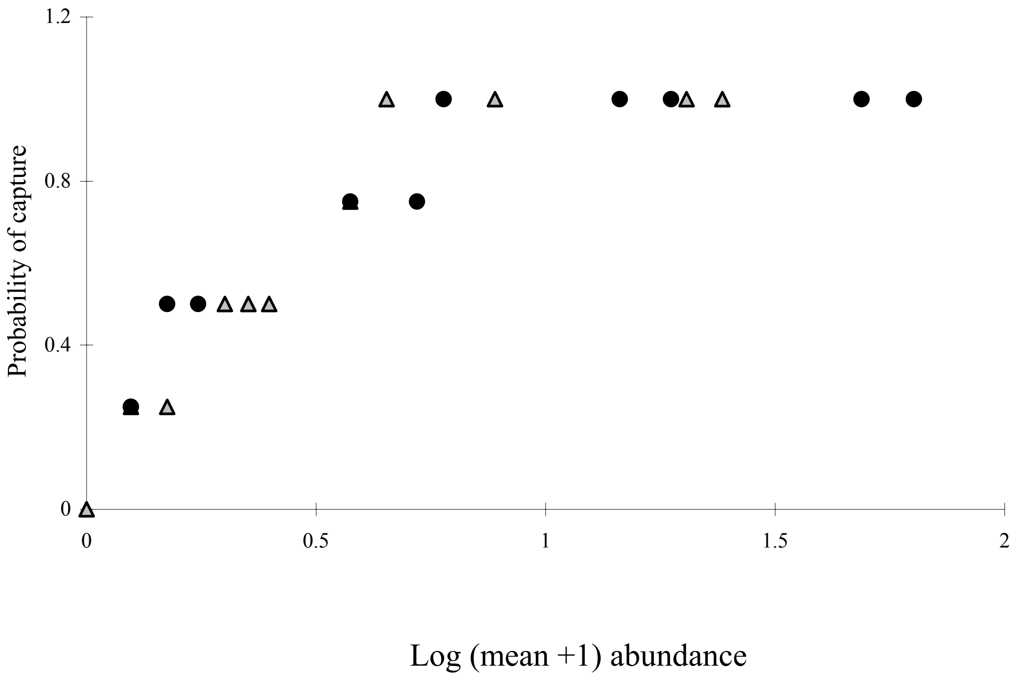


Figure A1.2: The probability of capture at any level of abundance in ditch 2, using the sieve net and pond net. (• = pond net, Δ = sieve net).



Appendix 2: Conservation Indices using data on the freshwater mollusc assemblages in drainage ditches.

Three numerical indices have been developed using freshwater molluscs to assess the conservation interests of drainage ditches (Killeen 1998). The following conservation indices: Conservation Score, Molluscan Conservation Index and Abundance-adjusted Molluscan Conservation Index were adapted from earlier indices developed by Extence & Ferguson (1989) and Extence & Cadd (1996). The indices are based on the conservation values (Table A2.1) and the ACFOR abundance scale (Table A2.2). In all cases the higher the conservation indices, the higher the molluscan importance of a ditch. Conservation priority for freshwater molluscs can therefore be given to the ditches, which have a high index value (Table A2.3).

Killeen (1998) has given each mollusc species a conservation value from 1 to 10 according to its rarity and ecological significance in a grazing marsh ditch habitat. The Red Data Book (RDB) lists four molluscs species typical of drainage ditches: *Segmentina nitida* (Müller 1774), *Anisus vorticulus* (Troschel 1834), *Valvata macrostoma* (Mörch 1864) and *Pisidium pseudosphaerium* (Schlesch 1947) (Bratton 1991). These four rare species were all assigned a high conservation value. However the conservation values in Table A2.1 were also designed to reflect the wider molluscs assemblages in ditches. High conservation values were therefore assigned to locally occurring species such as *Bithynia leachii and Pisidium pulchellum* both indicators of high quality ditches. *Pisidium obtusale* was rated a high conservation value as it often occurs in ditches at the advanced stages of vegetational succession, which is favoured by many of the rarer, and local species mentioned above. The abundance of the molluscs species were categorised into 5 levels according to the ACFOR scale (Table A2.2). The scale was designed to give greater emphasis on species occurring at lower frequency.

Conservation Indices:

1. Conservation score (CS): $= \sum CV$

2. Molluscan Conservation Index (MCI): $= \left(\frac{CS}{N}\right)$ x HCV

3. Abundance-adjusted MCI (AMCI): $= \left(\frac{\sum CVxAV}{N}\right)$x HCV

Conservation value **(CV):** the conservation value of each species present in a ditch (Table A2.1)

Highest conservation value **(HCV):** the highest conservation value in a ditch (Table A2.1)

Species richness **(N):** total number of mollusc species present in the ditch

Abundance value **(AV):** abundance value of each species present in the ditch (Table A2.2)

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Table A2.1: Conservation values for freshwater molluscs typical of drainage ditches on lowland grazing marshes in south-east England.

Species	Common name	Status in UK	Conservation values
Gastropod species:			
Anisus vorticulus	Little whirlpool ram's-horn snail	RDB2	10
Segmentina nitida	Shining ram's-horn snail	RDB1	9
Valvata macrostoma	Large mouthed valve snail	RDB2	8
Bithynia leachii	Leach's Bithynia	Local	5
Acroloxus lacustris	Lake limpet	Common	4
Hippeutis complanatus	Flat ram's-horn snail	Local	4
Planorbarius corneus	Great ram's-horn snail	Common	4
Valvata piscinalis	Common valve snail	Local	3
Valvata cristata	Flat valve snail	Local	3
Bathyomphalus contortus	Twisted ram's-horn snail	Local	3
Bithynia tentaculata	Common Bithynia	Common	3
Lymnaea palustris	Marsh pond snail	Common	3
Lymnaea stagnalis	Great pond snail	Common	3
Planorbis planorbis	Margined ram's-horn snail	Common	3
Planorbis carinatus	Keeled ram's-horn snail	Common	3
Anisus vortex	Whirlpool ram's-horn snail	Common	3
Armiger crista	Nautilus ram's-horn snail	Common	3
Gyralus albus	White ram's-horn snail	Local	3
Anisus leucostoma	Button ram's-horn snail	Common	2
Aplexa hypnorum	Moss bladder snail	Local	2
Physa fontinalis	Common bladder snail	Common	2
Lymnaea peregra	Common pond snail	Common	1
Physa actua	American bladder snail	Naturalised	0
Potamopyrgus antipodarium	Jenkins' spire snail	Naturalised	0
Bivalve species:			
Pisidium pseudosphaerium	False orb pea mussel	RDB3	8
Pisidium pulchellum	Iridescent pea mussel	Local	7
Pisidium obtusale	Porous-shelled pea mussel	Common	6
Pisidium milium	Quadrangular pea mussel	Common	3
Sphaerium corneum	Horny orb mussel	Common	3
Musculium lacustre	Capped orb mussel	Common	3
Pisidium subtruncatum	Short-ended pea mussel	Common	3
Pisidium nitidum	Shining pea mussel	Common	3
Pisidium henslowanum	Henslow's pea mussel	Common	3
Pisidium hibernicum	Globular pea mussel	Common	3
Pisidium casertanum	Caserta pea mussel	Common	2
Pisidium personatum	Red-crusted pea mussel	Common	1

RDB = Red Data Book, 1 = vulnerable, 2 = endangered, 3 = rare

Table A2.2: ACFOR abundance scale for ditch molluscs.

Abundance scale		**Abundance value**	Number of species
A	Abundant	**5**	> 101
C	Common	**4**	51 - 100
F	Frequent	**3**	16 - 50
O	Occasional	**2**	6 - 15
R	Rare	**1**	1 - 5

Table A2.3: Suggested baselines recommended by Killeen (1998) to determine the conservation priority of drainage ditches according to the freshwater mollusc community.

	Low conservation priority	Medium conservation priority	High conservation priority
CS	< 30	30-50	> 50
MCI	< 20	20-30	> 30
AMCI	< 50	50-150	> 150

Appendix 3: Photographical documentation of fieldwork and types of ditches

Above: Using the sieve net in a ditch on Amberley Wildbrooks, W. Sussex

Above left: Using an Eckman grab on a rope, it was decided to use a pole-mounted Eckmand grab which provided greater control of collection. **Above right**: The GRANT 3800 meter was used to record pH, conductivity and dissolved oxygen in situ.

 

Above left: Densely vegetated ditch on Pevensey Levels with mainly emergent and amphibious vegetation, an excellent ditch for *S. nitida*. **Above right**: A ditch on Pulborough Brooks, W. Sussex, with a population of *A. vorticulus*, densely vegetated margins with an open centre channel.

 

Above left: An intensively mantained ditch, primarily for drainage purpose on Gwent Levels, S. Wales. **Above right**: A ditch on Pevensey Levels NNR with extensive flooding on the adjacent land during autumn 2000.

Above left: A ditch on Pevensey Levels, E. Sussex, sympathetically dredged for conservation with gentle slopes and retention of vegetation. **Above right**: A recently dredged ditch on Gwent Levels, S. Wales, steeply sloped for maximum drainage effiency.

Above: Without active management, ditches will gradually silt up and revert back to terrestrial landscape, West Dean, Seven Sisters Country Park, E. Sussex.

Above: A plastic enclosure (0.4m diameter and 1.5 m long). **Right**: The experimental ditch surrounded by grazing land on Pevensey Levels, E. Sussex, with 35 enclosures. **Below**: Looking inside one of the enclosures, the existing biotic community was retained within each enclosure.

Appendix 4: Grid References for all the ditches surveyed in 1999 and 2000

Ditch	Grid Reference	Ditch	Grid Reference	Ditch	Grid Reference
	(1999)	**P9**	Tq 6822 1108	**S11**	TR 2273 6218
A1	TQ 0301 1423	**P10**	Tq 6805 1146	**S12**	TR 2311 6215
A2	TQ 0289 1437	**P11**	TQ 6704 0921	**S13**	TR 2342 6242
A3	TQ 0255 1480	**P12**	TQ 6538 0714	**S14**	TR 2346 6223
A4	TQ 0233 1485	**P13**	TQ 6571 0718	**S15**	TR 2318 6235
A5	TQ 0409 1424	**P14**	TQ 6761 1057	**S16**	TR 2250 6217
A6	TQ 0441 1427	**P15**	TQ 6741 1010	**S17**	TR 2308 6196
A7	TQ 0443 1443	**P16**	TQ 6166 0671	**S18**	TR 2346 6090
A8	TQ 0546 1776	**P17**	TQ 6139 0679	**S19**	TR 2340 6067
A9	TQ 0589 1796	**P18**	TQ 6160 0690	**S20**	TR 2324 6055
A10	TQ 0525 1720	**P19**	TQ 6899 0683	**S21**	TR 2777 6354
A11	TQ 0538 1716	**P20**	TQ 6922 0659	**S22**	TR 2750 6385
A12	TQ 0527 1693	**P21**	TQ 6577 0709	**S23**	TR 2306 6177
A13	TQ 0558 1785	**P22**	TQ 6235 0815	**S24**	TR 3290 6199
A14	TQ 0561 1802	**P23**	TQ 6222 0832	**S25**	TR 3307 6171
A15	TQ 0443 1482	**P24**	TQ 6822 0679	**S26**	TR 3153 6275
A16	TQ 0418 1478	**P25**	TQ 6840 0622	**S27**	TR 3211 6206
A17	TQ 0226 1575	**P26**	TQ 6660 0742	**S28**	TR 2940 6279
A18	TQ 0216 1551	**P27**	TQ 6062 1054	**S29**	TR 2767 6191
A19	TQ 0390 1424	**P28**	TQ 6091 1057	**S30**	TR 2422 6190
A20	TQ 0345 1459	**P29**	TQ 6096 0909	**S31**	TR 2422 6165
A21	TQ 0306 1345	**P30**	TQ 6145 0876		(2000)
A22	TQ 0585 1725	**P31**	TQ 6659 1065	**1**	TQ 654 072
A23	TQ 0572 1727	**P32**	TQ 6677 0618	**2**	TQ 612 072
A24	TQ 0416 1446	**P33**	TQ 6284 0938	**3**	TQ 412 088
A25	TQ 0415 1405	**P34**	TQ 6294 0850	**4**	TQ 028 144
A26	TQ 0316 1467	**P35**	TQ 6316 0695	**5**	TQ 665 053
A27	TQ 0193 1026	**L1**	TQ 4117 0896	**6**	TQ 412 092
A28	TQ 0199 1057	**L2**	TQ 4112 0868	**7**	TQ 665 055
A29	TQ 0283 1369	**L3**	TQ 4237 0550	**8**	TQ 669 057
A30	TQ 0585 1782	**L4**	TQ 4252 0695	**9**	TQ 652 067
A31	TQ 0286 1458	**L5**	TQ 4116 0879	**10**	TQ 654 067
A32	TQ 0305 1443	**L6**	TQ 4152 0922	**11**	TQ 666 065
A33	TQ 0246 1168	**S1**	TR 2963 6223	**12**	TQ 026 145
A34	TQ 0222 1196	**S2**	TR 2984 6188	**13**	TQ 056 180
P1	TQ 6330 0757	**S3**	TR 3035 6225	**14**	TQ 609 091
P2	TQ 6379 0737	**S4**	TR 3028 6198	**15**	TQ 060 178
P3	TQ 6359 0659	**S5**	TR 2960 6265	**16**	TQ 026 145
P4	TQ 6387 0669	**S6**	TR 3010 6282	**17**	TQ 657 072
P5	TQ 6158 0975	**S7**	TR 2996 6271	**18**	TQ 625 082
P6	TQ 6087 0991	**S8**	TR 2525 6322	**19**	TQ 612 072
P7	TQ 6113 0713	**S9**	TR 2487 6324	**20**	TQ 628 094
P8	TQ 6112 0730	**S10**	TR 2273 6201	**21**	TQ 053 173