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Interactions between coot (*Fulica atra*) and submerged macrophytes: the role of birds in the restoration process

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Key words: herbivory, bird grazing, bird diet, macrophyte colonisation, macrophyte growth, seasonal population trends, shallow lakes

Abstract

Grazing by herbivorous birds is often cited as an important factor in suppressing macrophyte development in shallow lakes undergoing restoration, thus delaying the attainment of the stable clear water state. Development and succession of macrophyte communities and size, diet and grazing pressure of coot (*Fulica atra*) populations upon macrophytes, were monitored over the seasonal cycle at ten shallow lakes of varying nutrient status, in the Norfolk Broads in eastern England. In spring, territorial breeding birds were at relatively low density and included only a small proportion of macrophytes in their diet, resulting in low grazing pressure on macrophytes. In summer, there was a significant relationship between macrophyte cover and bird density, illustrating the importance of macrophytes in the dispersion phase for birds following breeding. Macrophytes comprised the bulk of bird diet where they were available and the consumption of macrophytes was up to 76 fold higher than in spring. However, losses to grazing in both periods were negligible when compared to potential growth rates documented in the literature. Grazing experiments at two biomanipulated lakes confirmed that birds were not responsible for limiting macrophytes during the spring colonisation phase or in the summer growth period. During the period of autumnal senescence and over the winter months where some macrophyte species remain available, e.g. as developed individuals or dormant buds, grazing by birds may conceivably have an impact on the development and structure of macrophyte populations in subsequent growing seasons.

The relative importance of bird grazing compared to other factors limiting the development of macrophytes in shallow lakes is discussed in the light of other experimental studies.

Introduction

Much scientific and technical effort has recently been directed at the restoration of shallow lakes in temperate Europe and North America as a consequence of their huge ecological and sociological importance (National Research Council, US, 1992; Broads Authority, 1994; National Environmental Research Institute, Denmark, 1994). In most cases, the reversal of anthropogenic eutrophication is the target of this investment (Ryd-

ing & Rast, 1990). In simple terms, clear water dominated by submerged macrophytes is preferred over turbid, phytoplankton-dominated water (Moss, 1990). Further, the simple reduction of nutrient loading has rarely been successful as a single measure (Sas, 1989). It is widely accepted that restructuring the biological community of shallow lakes, usually through biomanipulation of the fish community (Lammens et al., 1990) is important in counteracting buffering mechanisms tending to preserve algal domination even where

the nutrient concentration is suitable for stable macrophyte populations (Irvine et al., 1989; Scheffer et al., 1993).

Once clear water, the essential prerequisite for a submerged macrophyte community, is attained, there are two scenarios. The first is the spontaneous development of an extensive and dense macrophyte community (Meijer et al., 1994). However, even where this has occurred, it may prove to be unstable in the long term (Blindlow et al., 1993; Perrow et al., 1994) with a concurrent increase in algal populations. Alternatively, macrophytes may be slow to colonise (Lauridsen et al., 1994; Moss et al., 1996; Strand, unpubl. data).

The impact of grazing birds, principally coot (*Fulica atra*) and swans (especially Mute swan *Cygnus olor*) has been widely discussed as the limiting factor in the colonisation, development and subsequent stability of macrophytes (Jupp & Spence, 1977; Lauridsen et al., 1993, 1994; Perrow et al., 1994; Moss et al., 1996; Søndergaard et al., in press). However, information relating to the impact of grazing by birds frequently relies on experiments using macrophytes transplanted into the site (Lauridsen et al., 1993; Moss et al., 1996; Søndergaard et al., in press), rather than the impact on naturally occurring macrophytes (Anderson & Low, 1976; Esler, 1989). Alternatively, a measure of macrophyte production is compared with losses due to grazing often derived by multiplying the number of bird days against some estimate of dietary input derived from the literature (Kiørboe, 1980; Schutten et al., 1994). In addition, there is often little attempt to determine macrophyte/bird interactions in relation to population parameters, including seasonal fluctuation, macrophyte phenology or actual bird diet.

This paper reports on a two-pronged study of macrophyte/bird interactions. First, detailed monitoring over the seasonal cycle was undertaken on macrophyte and coot populations, including dietary selection and consumption of macrophytes, at a range of sites in an attempt to assess likely grazing effects according to seasonal patterns of macrophyte development and bird populations and dietary intake. Second, short-term enclosure experiments were conducted at two biomanipulated sites, both of which had shown a lag in the development of macrophyte populations under apparently suitable conditions. These tested hypotheses developed during the monitoring phase.

Background information and site descriptions

The Norfolk Broads in eastern England, is an internationally important wetland complex of around 50 shallow (<2 m) lakes (broads) many of which are connected by rivers and interspersed by areas of fen and marsh. As a result of intense anthropogenic eutrophication, principally through P-rich sewage effluent, many of the lakes are now classed as hypertrophic and only 4 retain their original macrophyte populations (Broads Authority, 1994). Restoration attempts have been undertaken involving (a) reduction of external nutrient supply through installation of works at sewage treatment plants, (b) isolation (Moss et al., 1986, 1990; Perrow et al., 1994), (c) control of internal loading primarily through suction dredging (Moss et al., 1986, 1996) and (d) biomanipulation (Perrow, 1990; Phillips et al., 1996; Moss et al., 1996). Clear water conditions have been attained in many cases. Development of stable macrophyte populations in lakes with a suitable light climate has been retarded however, and grazing by birds, particularly coot, has been cited as a possible negative factor (Moss et al., 1986; Perrow et al., 1994; Moss et al., 1996). Experiences in attempting to establish macrophyte inocula over the last ten years by the water managers, the Broads Authority, also implicated bird grazing (unpubl. data). The management need to understand the role of bird grazing led the Broads Authority to commission the current project.

Coots are a common, widespread species in the UK with the resident population being supplemented by continental birds on autumnal passage (e.g. in 1990/91 peak numbers of over 85 000 birds were recorded in September, Ferns & Kirby, 1992) and throughout winter (Cramp & Simmons, 1980). The Norfolk Broads are known to harbour considerable populations e.g. the wintering population in the 1960's at Hickling Broad alone was estimated at 2500 birds (Seago, 1967). Coots occurred at all broads studied in all seasons (Howes & Perrow, 1994) and frequently outnumbered other waterfowl (Perrow, Howes & Holzer, unpubl. data), particularly during the breeding season. With a known high dietary intake of macrophytes (see Cramp & Simmons, 1980, for review), coots were considered to be the principal herbivorous bird in the Broads.

Coots exhibit considerable flexibility in their foraging behaviour (Cramp & Simmons, 1980; Draulans & Vanherck, 1987; Howes & Perrow, 1994); upending in shallow water or diving in deeper water (generally 1–2 m but to 6.5 m) to forage on macrophytes, algae, detritus and benthic invertebrates; cropping emergent

Table 1. Characteristics of the study sites.

Lake	Area (ha)	Direct Riverine connection	Management	Submerged macrophytes '92
Alderfen	5.1	None	Isolated 1979 Suction-dredged 1992/93 Biomanipulated 1993-	2 species 50% <i>C. demersum</i>
Belaugh	1.9	River Bure	Dredged 1987	4 species <5% <i>C. demersum</i>
Cockshoot	5.5	None	Isolated 1981 Suction-dredged 1981 Biomanipulated 1989-	9 species 25% <i>C. demersum</i>
Cromes	2.0	None	Suction-dredged 1988 Isolated 1992	1 species 50% <i>C. demersum</i>
Hickling	129.8	None	None	11 species 75% <i>M. spicatum</i>
Hoveton Great	36.2	River Bure	1 ha Exclosure Biomanipulated 1992-	5 species 25% <i>P. crispus</i>
Martham North	6.7	River Thurne	None	16 species 75% <i>N. marina</i>
Ormesby	56.4	None	None	10 species <5% <i>C. globularis</i>
Pound End	5.5	River Bure via Hoveton Little	Suction-dredged 1990 Biomanipulated 1990-	5 species <5% <i>C. demersum</i>
Upton	5.6	None	None	3 species 75% <i>N. marina</i>

Macrophyte data is taken from Kennison (1993). The number of species and maximum % cover of the dominant species are shown.

or bankside vegetation from on the water or on land; gleaning insects, seeds and fruits from the water surface or vegetation; or taking handouts or leftovers from human visitors. Such behavioural plasticity and ability to take a wide range of plant and animal material enabled coots to persist at all broads studied, even where macrophytes were absent. The continuous presence of coots was thought to restrict the colonisation and establishment of macrophytes at low density (Howes & Perrow, 1994).

The primary monitoring phase of the study was undertaken at ten sites, which ranged from phytoplankton to macrophyte dominated and encompassed those lakes subjected to recent restoration measures. Characteristics of the study lakes are shown in Table 1. During the subsequent experimental phase, two small bioma-

nipulated sites, Pound End and Cockshoot Broad were selected (Table 1).

Methods and materials

Monitoring study

Bird monitoring

Coot populations were monitored monthly at all sites from July 1993–June 1994. The preliminary study of Howes & Perrow (1994) recorded foraging activity throughout the hours of daylight with birds feeding in bouts interspersed by preening and resting (Brown, unpubl. data). Birds then roosted at night (Draulans & Vanherck, 1987; Brown, unpubl. data). Observations

Table 2. Mean (+ 1 S.E.) wet weight (g) per coot bill length of the submerged plant taxa consumed.

Taxon	Wet weight (g)
<i>Callitriche</i> spp.	0.37 ± 0.02
<i>Ceratophyllum demersum</i>	1.14 ± 0.19
<i>Ceratophyllum submersum</i>	0.13 ± 0.01
<i>Chara</i> spp.	0.57 ± 0.06
<i>Elodea canadensis</i>	0.40 ± 0.03
<i>Hippurus vulgaris</i>	1.00 ± 0.03
<i>Myriophyllum spicatum</i>	0.23 ± 0.03
<i>Najas marina</i>	0.85 ± 0.03
<i>Nitellopsis obtusa</i>	0.50 ± 0.03
<i>Potamogeton pectinatus</i>	0.26 ± 0.02
<i>Potamogeton crispus</i>	0.80 ± 0.03
<i>Zannichellia palustris</i>	0.25 ± 0.01
Filamentous algae	1.44 ± 0.12

conducted at any time of day were thus thought to be representative of foraging activity and grazing pressure on macrophytes at the site, particularly as bird numbers fluctuated little over the course of the day. Two sites a day were monitored and observations were made over the entire lake, except at Ormesby and Hoveton Great Broad, where observations were restricted to a 12 ha section and the 1 ha fish enclosure respectively. Bird numbers in the latter area could not be related directly to macrophyte abundance in the main broad and this site was therefore excluded from that part of the analysis.

Observations were made from land (usually bird hides) or from a boat using a 30 magnification × 80 mm Optolyth telescope or 8 × 20 Leica binoculars. If birds were disturbed by the observers taking position, monitoring was delayed for at least twenty minutes until birds had repositioned and resumed natural activity. Birds were counted at intervals to determine peak numbers. Food intake and selection was determined through continuous observation for fifteen minutes each on a minimum of four randomly selected individual birds. When foraging underwater, coots bring items to the surface to handle and swallow. This allowed the majority of dietary items to be identified and their size to be estimated relative to bill length before they were consumed.

Daily consumption of each dietary item at each site was calculated by extrapolating the consumption in fifteen minutes to one hour and then multiplying by the number of daylight hours and the number of birds present.

For macrophytes and filamentous algae, the mean wet weight (g) per bill length was measured by taking ten replicate one bill-length equivalent samples of each species and weighing them to the nearest 0.1 g (Table 2). The consumption per occasion in bill lengths at each location of known size was then converted to wet weight (g m^{-2}) for each species.

Macrophyte monitoring

Macrophyte densities were monitored at all sites at bimonthly intervals from April to October 1993. At each site, 3 permanent transects (25–50 m in length) were sampled by a snorkel diver. The vertical projected sediment coverage of each macrophyte species (all vascular plants and *Chara* spp.) and filamentous algae as well as total community cover along the line and in the area up to 2 m (depending on visibility) on either side of the line were estimated using an adapted Tansley scale (see Schutten et al. (1994) for details).

Grazing experiments

The impact of coot grazing on a natural communities of macrophytes and filamentous algae at Cockshoot and Pound End was tested using ten replicate pairs of cylindrical exclosures (1 m height, 113 cm diameter enclosing a total surface area of 1 m^2) made of black, plastic 'Netlon Tensar SS3' mesh (71 × 51 mm). Lids of the same mesh were fitted to exclude birds from the treatment exclosures, whereas controls had no lids. Each exclosure was pushed into the sediment, leaving 75 cm above the sediment surface, but still under water, and anchored in place with a 2.5 m wooden stake.

The ten pairs, one treatment and its control, were placed within the known territory of a pair of coots at each of the sites, in early May 1994, the season after the monitoring study. The members of each pair of exclosures were within 2 m of each other, whilst pairs were at least 7 m apart. Macrophytes were monitored every 2–3 weeks from late June to mid September. The % cover of each macrophyte species and/or filamentous algae was estimated visually through a perspex-bottomed bucket from a stationary boat. In late September, the plants in five randomly-selected pairs were harvested using a long-handled rake. Species were separated and wet weighed to the nearest 0.5 g.

Differences between treatments and controls on each occasion (total cover and cover of common plant species, were tested using Wilcoxon signed ranks tests.

At each broad, coot diet and macrophyte intake were monitored using the methods described above, within a few days of the macrophyte sampling.

Results

Monitoring study

Macrophyte populations

The seasonal changes in macrophyte and filamentous algae density are variable (Figure 1). Turbid lakes known to be dominated by phytoplankton (Broads Authority, 1994), including Hoveton Great, Ormesby and Belaugh Broads, were characterised by low cover of macrophytes (<5%) with representation of only a few species, typically *Zannichellia palustris* L. and several *Potamogeton* species in spring to summer, and *Ceratophyllum demersum* L. in late summer and autumn. Filamentous algal cover was typically an early season phenomenon, with densities up to 25%.

The clear-water biomanipulated sites, Alderfen and Pound End (Table 1) had very few macrophytes with the same pattern as above. In contrast, Cockshoot had more macrophyte species with a combined cover of up to 30%, and some seasonal succession from *Zannichellia/Potamogeton* spp. to *C. demersum* and *Lemna trisulca* L. Filamentous algal cover was high (to 45%) at both Cockshoot and Pound End with a peak in mid-summer.

Cromes, Upton and Hickling and Martham North were all dominated by macrophytes. The former three were characterised by slow spring development, with a peak in macrophyte cover (>50%) in late summer and autumn by only a few species; *C. demersum* at Cromes, *Chara* spp. and *Myriophyllum spicatum* L. at Hickling and *Najas marina* L. at Upton. Martham North, on the other hand, had a large number of species/genera of macrophytes (12), with pronounced seasonal shifts in abundance, starting with *Hippuris vulgaris* L. and *M. spicatum*, to *Chara* spp. and finally to *N. marina* in late season. Macrophyte cover was always high, increasing from 40% in spring to 80% in late summer.

Bird populations

In general, birds were at relatively low density in spring (mean + S.E. density in April = 1.58 ± 0.30 individuals ha^{-1}) (Figure 2), as a result of the intense territoriality of breeding pairs (Cramp & Simmons, 1980). At Broads with little plant cover, such as Alderfen,

Belaugh and Hoveton Great Broad, the population consisted almost solely of breeding pairs and their offspring resulting, although with some decline over winter, in relatively stable densities. In contrast, bird density fluctuated markedly (the pattern is damped at Hickling on account of its large size) at broads with significant plant cover (with the exception of Ormesby), with the incursion of juvenile and non-breeding/post-breeding birds to supplement the resident population. The timing of this immigration was usually between July and September possibly related to the attainment of peak abundance of the dominant plant(s). For example, high densities of birds corresponded to the peak occurrence of *Z. palustris/Potamogeton* spp. in Ormesby in July, maximum cover of *N. marina* and *Chara* spp. in Martham North in August and high coverage of filamentous algae in Pound End in August and Cockshoot in September. Only Cromes and Upton received an incursion of birds in winter, where the late developing *C. demersum* and *N. marina* dominated respectively. In the increase phase, bird numbers peaked between 8 ha^{-1} (Cromes) and 18 ha^{-1} (Martham North). Breeding densities were resumed between January and March.

Bird diet

The diet of birds varied considerably between site and season, although several general trends were identified (Figure 3). In spring (March to May) the diet was dominated by invertebrates and filamentous algae. This is explained by these 'soft' foods being fed to chicks (Howes & Perrow, 1994). Consequently, macrophytes made up a low proportion of the diet at this time, even where they were present. In contrast, in summer (June–August) and autumn (September–November) where present, macrophytes formed the bulk of the diet, although filamentous algae was often also important. In autumn and especially winter (December–February) the diet of birds was generally more variable with invertebrates, emergent plants, detritus and filamentous algae all dominant at different sites. However, in lakes with a peak macrophyte cover of >50%, macrophytes were still the major dietary item.

Interactions between birds and macrophytes

If all sites on all occasions are included, there is no relationship between coot density (birds ha^{-1}) and % total plant cover (Spearman rank correlation, $r_s = 0.04$, $n = 23$, $p = 0.87$). However, if this is teased apart in separate analyses, coot density is not related to %

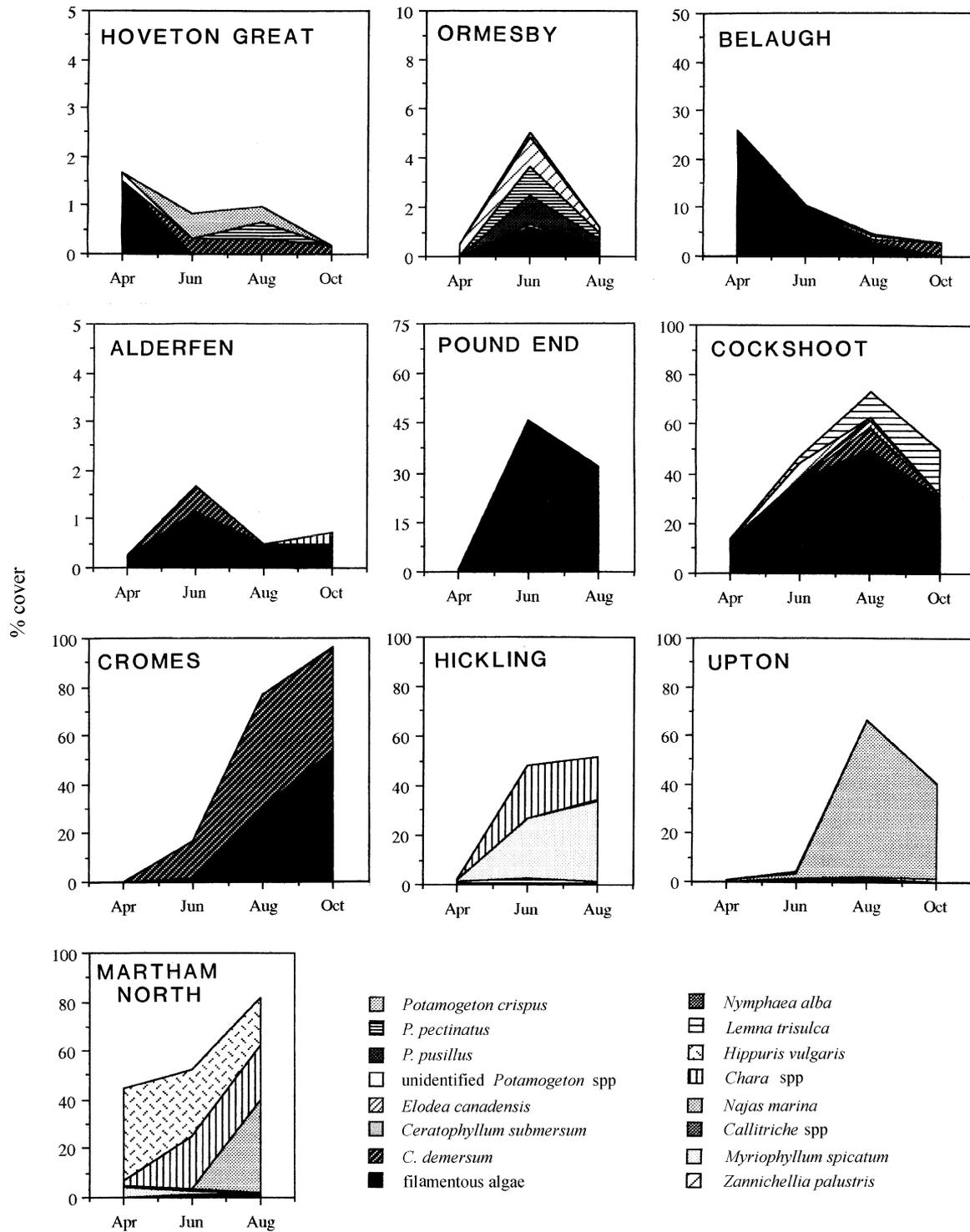


Figure 1. Seasonal changes in the cover (%) of macrophytes and filamentous algae during 1993, in the ten study sites.

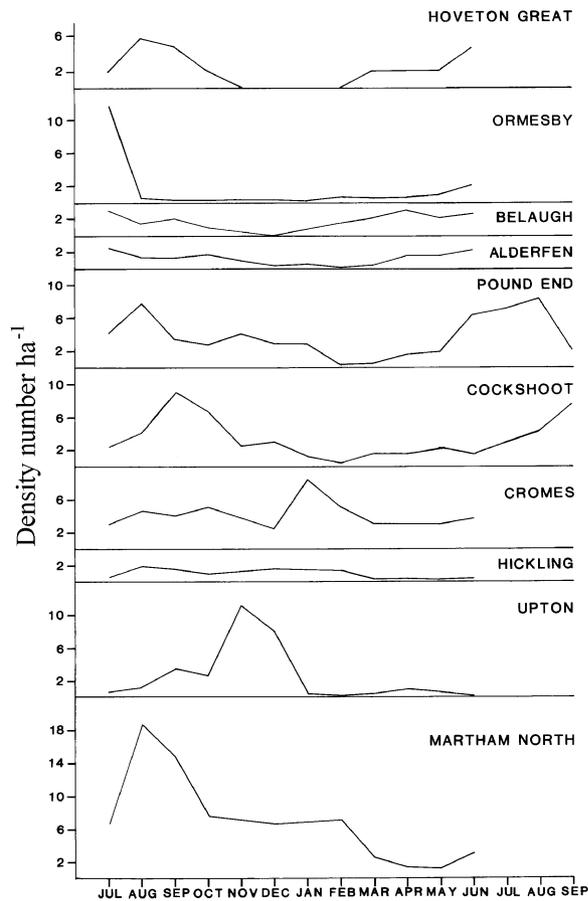


Figure 2. Seasonal changes in density (birds ha^{-1}) of coot populations during 1993/1994 in the ten study sites.

macrophyte cover ($r_s = 0.19$, $n = 23$, $p = 0.38$) but is significantly positively related to % cover of filamentous algae ($r_s = 0.58$, $n = 23$, $p < 0.01$).

Taking the population fluctuations in late summer and autumn into account, by expressing the densities in August and October as a % of the breeding density in June, the relationships between bird density and plant cover change markedly. There was a significant positive relationship between % total cover and birds ($r_s = 0.55$, $n = 14$, $p < 0.05$), and it is macrophyte cover ($r_s = 0.67$, $n = 14$, $p < 0.01$) and not algae ($r_s = 0.08$, $n = 14$, $p = 0.79$) that is the important factor.

Furthermore, there were significant positive relationships between the proportion of macrophytes or filamentous algae in the diet of birds and % cover ($r_s = 0.73$, $n = 23$, $p < 0.001$ and $r_s = 0.72$, $n = 23$, $p < 0.001$ respectively). In lakes with macrophytes, an

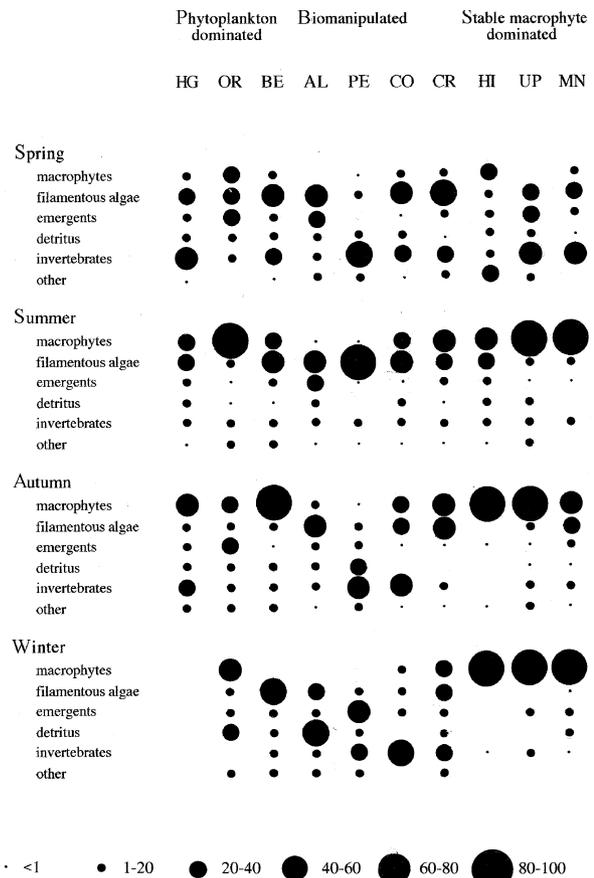


Figure 3. Seasonal dietary composition of coot populations at all study sites where: HG = Hoveton Great, OR = Ormesby, BE = Belaugh, AL = Alderfen, PE = Pound End, CO = Cockshoot, CR = Cromes, HI = Hickling, UP = Upton, MN = Martham North. The size of circle is proportional to the contribution (%) made by each group to the total bill lengths consumed in each season (spring March–May, summer June–August, autumn September–November, winter December–February).

increase in the number of birds with an increasing proportion of macrophytes in the diet, results in an increase in grazing pressure ($\text{g m}^{-2} \text{day}^{-1}$ consumed) ($r_s = 0.34$, $n = 80$, $p < 0.01$).

Grazing experiments

Cockshoot

The total plant cover and cover of the seven different species in both protected treatments and grazed controls over the experimental period are illustrated in Figure 4. *P. berchtoldii* & *Z. palustris* made an important contribution to early season cover, whereas *C. demersum* tended to dominate later in the summer and into

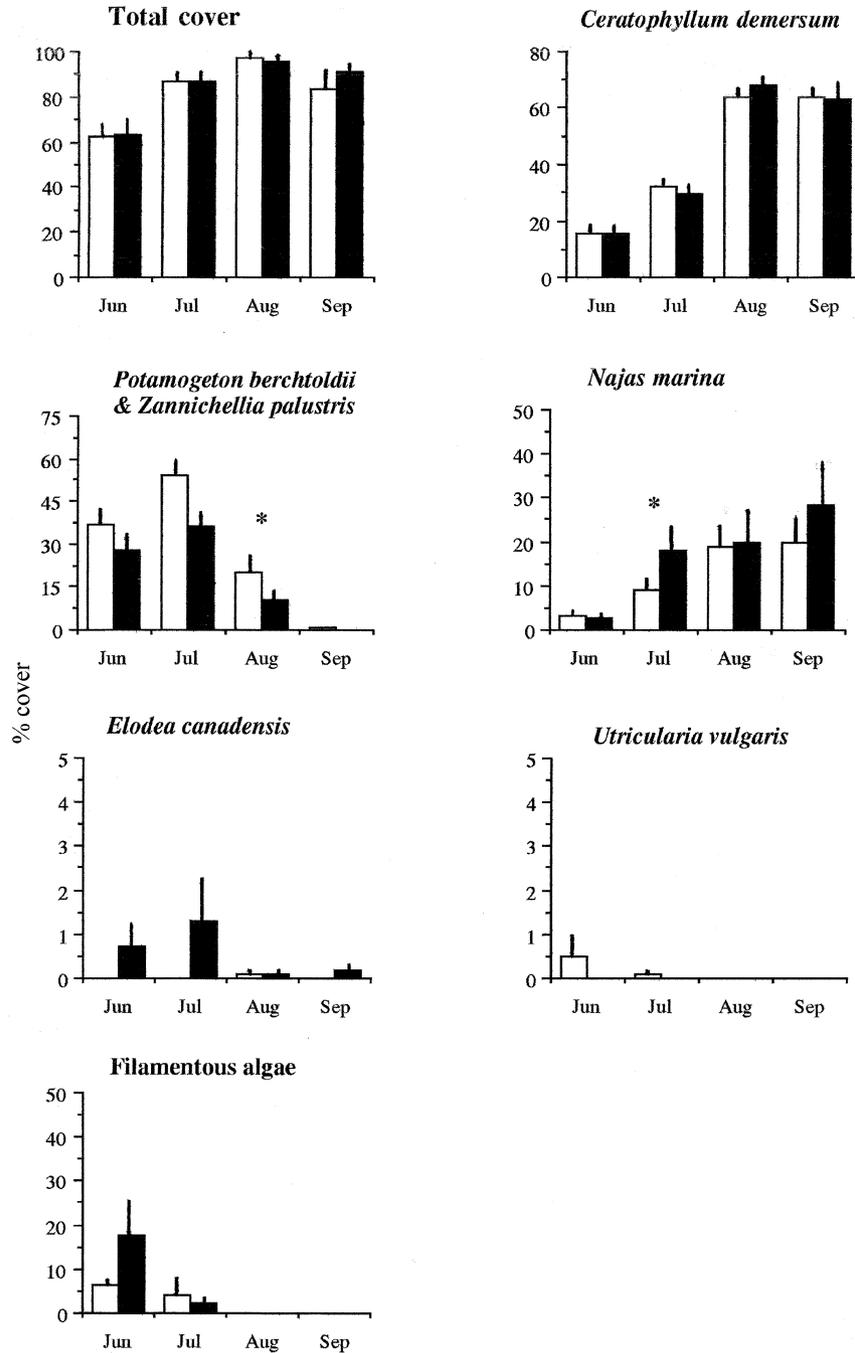


Figure 4. Mean (\pm 1 S.E, $n=10$) total plant cover and cover of different plant species in both grazed controls (open bars) and protected treatments (shaded bars) over the experimental period at Cockshoat Broad. Statistical tests were only conducted on total cover, *C. demersum*, *P. berchtoldii/Z. palustris* & *N. marina*. Significant differences at the $p < 0.05$ level are indicated (*).

autumn. At peak, macrophyte cover (with some filamentous algae) approached 100%.

Overall, there were few significant differences between treatments and controls illustrating potential positive and negative effects of bird grazing. Any differences were only apparent after at least two months of the experiment had elapsed and never occurred in a consistent fashion. That no differences occurred in the early stages of the experiment is consistent with the negligible consumption of macrophytes by the coot population in this period (Figure 5). Even though consumption by coots increased markedly during the experimental period, this did not lead to any significant differences in the biomass of any macrophyte taxon at the end of the experiment (Table 3).

Pound End

In contrast to Cockshoot, Pound End was dominated by filamentous algae, particularly *Enteromorpha* spp. This gradually declined over the course of the experiment (Figure 6) until only a small biomass was present in early October (Table 3). Only two macrophyte species were found, *Elodea canadensis* Michaux and *C. demersum*, in two separate treatment exclosures and *C. demersum* in one control on one occasion (Figure 6). There were no significant differences in the cover of algae or macrophytes on any occasion.

Discussion

To critically evaluate the potential impact of grazing coots upon submerged macrophyte populations it is necessary to divide the cycle of seasons into distinct phases according to macrophyte ecology and coot behaviour and ecology. In simple terms, these are the spring germination or initial growth phase for macrophytes and the nesting season for birds; the summer growing and reproduction (for sexually reproducing species such as *Potamogeton* spp.) phase for macrophytes and the recruitment and dispersal phase for birds; the autumn period of senescence for most species of macrophytes and the peak passage of birds at many sites; and the winter period in which macrophytes are either unavailable, coinciding with the lowest bird populations, or occur either as senescent material or as overwintering stages (most notably in the case of a few asexually reproducing species such as *Ceratophyllum* and *Elodea*) where high coot populations are maintained.

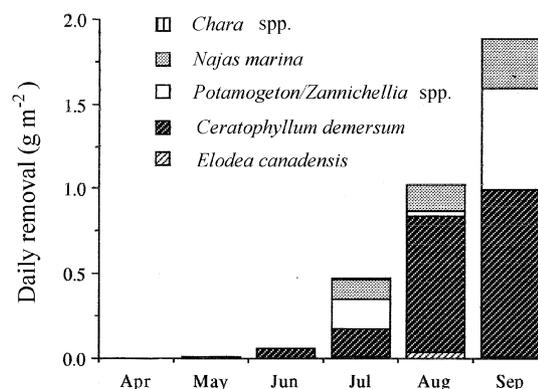


Figure 5. The relative daily consumption (g m^{-2} WW) of different macrophyte species by coot at Cockshoot Broad from April–September 1994, covering the period of the grazing experiment.

Is colonisation of macrophytes in spring affected by bird grazing?

Germination of macrophyte seedlings from seed or overwintering buds/turions takes place in spring. Limitation during this establishment phase (sensu Harper, 1977) determines successful colonisation. A number of factors are prerequisites for the establishment of macrophytes, prior to any possible limiting effect of bird grazing. These include the presence of a viable seed bank; suitable conditions for germination e.g. the presence of reducing sediments and consequent high production of sulphides and ammonia may inhibit seeds germinating (Perrow et al., 1994); and suitable conditions for subsequent growth and survival e.g. Jupp & Spence (1977) and Lauridsen et al. (1993) illustrated the importance of sediment structure and organic content.

What of the impact of birds? Sandsten (1995), in Lake Krankesjon, showed that were there was a viable seed bank, under suitable conditions for germination and growth, macrophytes colonised successfully in the presence of birds. In contrast, Lauridsen et al. (1993), Søndergaard et al. (in press) and Moss et al. (1996) concluded that bird grazing was responsible for limiting colonisation and establishment. These studies used transplanted macrophytes and therefore we suggest it is inappropriate to draw conclusions from these studies on the response of naturally occurring macrophyte populations. In addition, transplants represent unusual concentrations of food which may attract birds and induce unnaturally high estimates of grazing pressure.

In the current study, the density of breeding birds was considerably lower than peak populations. Birds

Table 3. The mean (± 1 S.E.) plant biomass (g m^{-2} WW) in exclosures in Cockshoot and Pound End at the end of the experimental period. No significant differences were recorded between ungrazed treatments and grazed controls (each $n=5$) for any taxon.

Taxon	Cockshoot		Pound End	
	– Grazing	+ Grazing	– Grazing	+ Grazing
Total macrophytes	600.6 \pm 88.7	461.5 \pm 74.7	0.3 \pm 0.2	0.0 \pm 0.0
<i>C. demersum</i>	371.0 \pm 97.0	348.0 \pm 71.9	0.2 \pm 0.2	0.0 \pm 0.0
<i>E. canadensis</i>	0.1 \pm 0.1	1.2 \pm 1.0	0.1 \pm 0.1	0.0 \pm 0.0
<i>L. trisulca</i>	1.2 \pm 0.8	0.5 \pm 0.3		
<i>N. marina</i>	222.3 \pm 128.8	101.4 \pm 6.8		
<i>P. berchtoldii</i>	6.0 \pm 4.5	10.4 \pm 6.8		
<i>Z. palustris</i>				
Filamentous algae	103.6 \pm 52.2	138.4 \pm 76.0	0.8 \pm 0.5	0.2 \pm 0.1

are strictly territorial, with factors such as shoreline length (as habitat for nesting) and food resource availability determining territory size and consequently the density of breeding pairs at a site (Cramp & Simmons, 1980). The diet of birds at this time, even where macrophytes are available, was dominated by invertebrates and filamentous algae. This seems largely due to the requirements of chicks for such foods, invertebrates in particular, dominating in the first ten days of life (Cramp & Simmons, 1980). The presence of filamentous algae in the diet in spring, as well as throughout the summer may explain the overall relationship between coot density and filamentous algal cover.

A combination of a low number of birds, with a low proportion of macrophytes in the diet resulted in a low consumption of macrophytes. When compared to the published growth rates of selected macrophyte species, it is clear that consumption by birds was typically only a fraction of the potential growth rate during spring (Table 4). The negligible impact of birds upon colonisation by macrophytes is also supported by the virtual lack of macrophyte consumption by the coot population in Cockshoot in the spring (April/May) period (Figure 5). Moreover, in Pound End, few macrophytes colonised even where they were protected from birds (Figure 6). Here, as in some other biomanipulated sites, filamentous algae was prevalent. Phillips et al. (1978) suggested that mats of benthic and epiphytic algae were the principal cause of the decline of macrophyte populations in the Broad.

In the current study, there was a significant negative relationship between the abundance of macrophytes (expressed as % cover) and filamentous algae (Spear-

man rank correlation, $r_s = 0.57$, $n = 18$ —those occasions and sites $>10\%$ cover, $p = 0.01$). However, the extent to which this is the result of an interaction between the two groups or simply the tendency of filamentous algae to colonise clear water sites before macrophytes (re: Cockshoot between 1993 and 1994) is unknown.

The effects of bird grazing in summer and autumn

Macrophytes are clearly important to coots in late summer and autumn, as populations increased dramatically at sites with significant macrophyte cover. The proportion of macrophytes in the diet was also high, including that of young birds which switch to an adult diet within 5 weeks of birth (Cramp & Simmons, 1980; Howes & Perrow, 1994). The apparent preference for macrophytes late in the season may be linked to improved nutritional content (e.g. carbohydrates) at this time (Best & Dassen, 1987; Best & Visser, 1987). But does bird grazing have an impact?

As above, the potential growth rate of macrophytes should typically easily outstrip any losses to grazing birds during the summer period (Table 4). The only exception to this being *Potamogeton* spp./*Z. palustris* in Ormesby in July when up to 30% of potential net growth was consumed.

The lack of impact was confirmed by the experiments at Cockshoot, where macrophyte cover or biomass were not greatly influenced by bird grazing, effects being species-specific and creating positive and negative consequences perhaps as a result of changing interspecific competitive interactions (Lodge, 1991). Similar results were reported by Sandsten (1995), with *Chara* spp. apparently benefiting from an impact of

Table 4. Removal ($\text{g m}^{-2} \text{d}^{-1}$ WW) by birds of selected macrophyte species expressed as a % of published growth rates from similar water bodies in north-western Europe.

Species		March	April	May	June	July
<i>C. demersum</i> ¹	mean	0.51	0.10	0.48	0.83	0.37
	max.	3.02	0.51	2.77	2.91	0.99
	min.	0.00	0.00	0.00	0.00	0.00
	n	6	6	6	6	8
<i>C. demersum</i> ²	mean	0.29	0.05	0.25	1.03	0.41
	max.	1.53	0.26	1.40	3.23	1.10
	min.	0.00	0.00	0.00	0.00	0.00
	n	6	6	6	6	8
<i>C. demersum</i> ³	mean	0.29	0.05	0.25	0.38	0.17
	max.	1.53	0.26	1.40	1.32	1.32
	min.	0.00	0.00	0.00	0.00	0.00
	n	6	6	6	6	8
<i>E. canadensis</i> ⁴	mean	0.00	0.09	0.01	0.06	0.13
	max.	0.00	0.47	0.06	0.29	0.56
	min.	0.00	0.00	0.00	0.00	0.00
	n	5	5	5	5	7
<i>N. marina</i> ⁵	mean	–	–	–	0.00	0.07
	max.	–	–	–	0.00	0.35
	min.	–	–	–	0.00	0.00
	n	–	–	–	4	5
<i>Potamogeton</i> spp. <i>/Z. palustris</i> ⁶	mean	<0.01	<0.01	<0.01	0.03	0.92
	max.	0.03	0.04	0.05	0.22	6.50
	min.	0.00	0.00	0.00	0.00	0.00
	n	8	8	8	8	9
<i>Potamogeton</i> spp. <i>/Z. palustris</i> ⁷	mean	0.02	0.03	0.04	0.13	4.29
	max.	0.17	0.26	0.33	1.03	30.33
	min.	0.00	0.00	0.00	0.00	<0.01
	n	8	8	8	8	9
<i>Potamogeton</i> spp. <i>/Z. palustris</i> ⁸	mean	0.11	0.16	0.20	0.10	3.06
	max.	0.85	1.30	0.73	0.73	21.66
	min.	0.00	0.00	0.00	0.00	0.00
	n	8	8	8	8	9
<i>P. crispus</i> ³	mean	0.00	0.00	0.00	0.00	0.20
	max.	0.00	0.00	0.00	0.00	0.41
	min.	0.00	0.00	0.00	0.00	0.00
	n	2	2	2	2	2
<i>P. pectinatus</i> ^{10,11,12}	mean	0.00	0.00	0.00	0.00	0.01
	max.	0.00	0.00	0.00	0.00	<0.01
	min.	0.00	0.00	0.00	0.00	0.00
	n	5	5	5	5	5

References: ^{1,2} Best & Visser (1987); ^{3,5} Phillips (1976); ^{4,9} Lauridsen et al. (1994); ^{6,10} Schutten et al. (1994); ^{7,8,11,12} Doef et al. (1994).

grazing on *Potamogeton* spp. and Kiørboe (1980) who found no statistical differences in the biomass of several species including *Chara* spp. and *Potamogeton* spp.

In contrast, many authors (e.g. Anderson & Low, 1976; Jupp & Spence, 1977; Esler, 1989; Lauridsen et al., 1993, 1994; Moss et al., 1996); Søndergaard et al., in press) have described effects on growth and/or

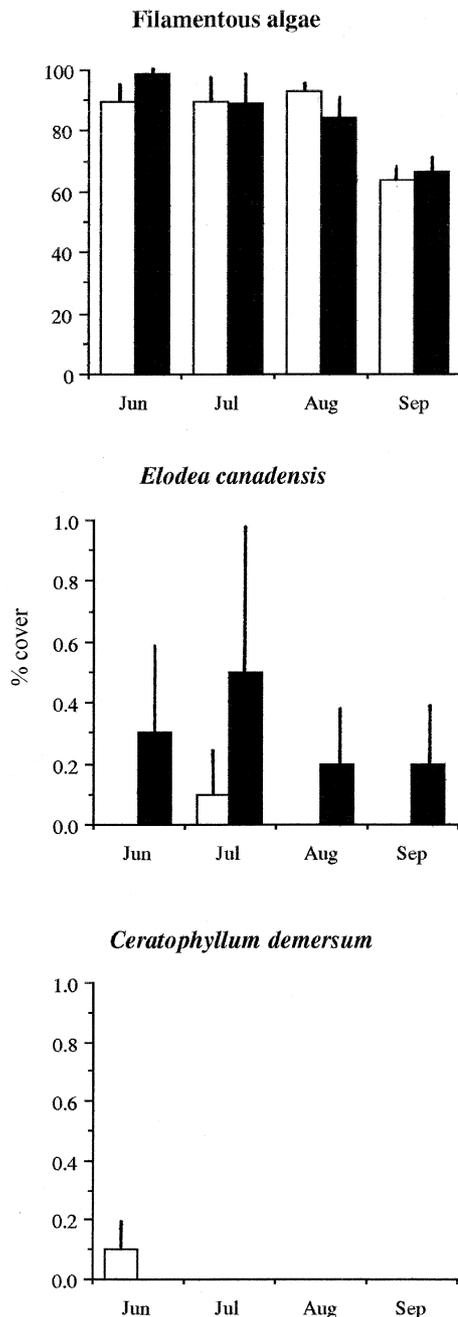


Figure 6. Mean (\pm S.E., $n=10$) cover of filamentous algae and macrophyte species in both grazed controls (open bars) and protected treatments (shaded bars) over the experimental period at Pound End.

biomass of macrophytes in protected enclosures versus unprotected controls. There were many differences in experimental technique between the studies; such as the use of transplanted inocula (see above), variable numbers of replicates, comparison of treatments with true controls or adjacent areas, measurements of different variables including cover, biomass, growth (e.g. shoot length) and shoot number; but also in the abundance and type of herbivorous birds and macrophytes.

One element was relatively consistent. That is, any effect on macrophytes was only apparent from summer onwards when macrophytes reached a maximum standing crop or began to senesce, i.e. Lauridsen et al. (1993); mid July onwards; Søndergaard et al. (in press) early July and late July onwards; Moss et al. (1996) August; Anderson & Low (1976) August and September; Esler (1989) beginning in November with a consistent pattern by December.

The timing of any effect is likely to be critical. For example, for sexually reproducing flowering species, if grazing removes whole plants or sexual parts (seeds, fruits) before reproduction is complete, then grazing may be a limiting factor. Although this must be tempered against the fact that some species have shown improved seed germination after consumption by birds (Agami & Waisel, 1986).

In the Broads, as in other temperate European and North American shallow lakes *Potamogeton* spp. are widespread and common and an important component of macrophyte communities. They tend to dominate in early season, flower followed by vegetative reproduction and tuber formation in July/August and senesce in autumn. In Cockshoot at least, the peak in grazing pressure coincided with the decay of the above sediment biomass (Figure 5), birds never inducing a negative impact throughout the growing and flowering period (Figure 4, Table 3). In support of Kjørboe (1980), we suggest that significant removal of macrophytes tends to occur in autumn during the period of senescence of many species, during the peak passage period for waterfowl on migration and therefore any impacts on growth, biomass etc. are of little consequence for many of the macrophyte populations concerned. Rather, it is the abundance of birds that is controlled by the abundance/biomass of macrophytes (Mitchell et al., 1988; Giles, 1992; Hargeby et al. 1994; Lillie & Evrard, 1994; McKinnon & Mitchell, 1994).

Table 5. Maximum summer (August) standing crop (g DW m⁻²) of *Ceratophyllum demersum* in waterbodies in the Norfolk Broads, compared with the maximum recorded consumption by a coot population (0.114 g DW m⁻² d⁻¹ in Cromes Broad), expressed as % of standing crop consumed/day.

Site	g DW m ⁻²	Source	% day ⁻¹
Alderfen Broad (1982)	60.0	Perrow et al. (1994)	0.19
Alderfen Broad (1983)	38.0	Perrow et al. (1994)	0.30
Alderfen Broad (1984)	25.0	Perrow et al. (1994)	0.46
Alderfen Broad (1985)	1.5	Perrow et al. (1994)	7.60
Alderfen Broad (1987)	2.1	Perrow et al. (1994)	5.43
Alderfen Broad (1988)	16.5	Perrow et al. (1994)	0.69
Alderfen Broad (1989)	22.5	Perrow et al. (1994)	0.51
Alderfen Broad (1990)	54.0	Perrow et al. (1994)	0.21
Alderfen Broad (1991)	24.0	Perrow et al. (1994)	0.48
Belaugh Broad (1993)	1.4	Stansfield (1994)	8.14
Cockshoot Broad (1993)	12.1	Stansfield (1994)	0.94
Cockshoot Dyke (1993)	2.9	Stansfield (1994)	3.93
Pound End-bird enclosure (1993)	2.5	Stansfield (1994)	4.56
Woodbastwick Fen Dyke (1972)	248.0	Phillips (1976)	0.05
Woodbastwick Fen Dyke (1974)	338.0	Phillips (1976)	0.03

The effects on subsequent macrophyte development

There is a lack of compelling evidence to show that bird grazing limits macrophyte populations within a season, but it is possible that any impact is only manifested in subsequent seasons (Lodge, 1991). This is relevant for species such as *Elodea* or *Ceratophyllum* that may overwinter as developed plants or buds respectively (Van Donk et al., 1994) and perhaps even for tuber-forming species such as *P. pectinatus* (Anderson & Low, 1976), all of which may be available throughout the autumn and winter months.

Elodea and *Ceratophyllum* are an important component of the flora in restored lakes (Lauridsen et al., 1994; Perrow et al., 1994, Van Donk et al., 1994, Moss et al., 1996). This is probably a consequence of their rapid colonising ability, aided by dispersion from fragmentation (Best & Dassen, 1987; Best & Visser, 1987) and their tolerance to relatively eutrophic conditions (Palmer, 1992). However, they are also prone to rapid die-back (Krzyżanek, et al., 1986; Perrow et al., 1994; Moss et al., 1996) with bird grazing being implicated in some studies (Perrow et al., 1994; Moss et al., 1996). In support of this, Van Donk et al. (1994) demonstrated that herbivory by birds in the winter months was partly responsible for the decline of the *Elodea* population and restructuring of the macrophyte community in favour of *Ceratophyllum*.

Any impact of birds is obviously determined by the size of the initial standing crop. For example, the

standing crop of *C. demersum* recorded in the broads is highly variable between sites and years (Table 5). Using the maximum recorded grazing pressure by a coot population, simple calculations reveal that the time taken for a coot population to remove the standing crop of *C. demersum* may be as little as 12 days or as long as the equivalent of 9 years. For sites with a low standing crops at the end of the growing season, it is conceivable that birds may quickly remove the entire overwintering stock, thereby having a major impact on the population in subsequent seasons.

The reliance on monocultures of potentially vulnerable species such as *Elodea* and *Ceratophyllum* in lake restoration programmes, underlines the need to establish a diverse macrophyte community, which may buffer any effect from bird grazing or other factors. This may only be possible where nutrient levels are reduced significantly, aiding stability (Hosper & Jagtman, 1990).

Conclusions

There is little evidence that grazing by coots birds limits colonisation and establishment of macrophytes in spring in the shallow lakes of the Norfolk Broads. This is related to the low grazing pressure from a low density of territorial breeding birds and the low prevalence of macrophytes in their diet. There is little conclusive

experimental evidence in the literature to support the hypothesis that birds directly influence colonisation and establishment of naturally occurring macrophytes. Indeed, in shallow lakes undergoing restoration, any lag in the response of macrophytes is likely to be caused by a number of factors other than bird grazing. However, losses to birds may contribute to a low abundance of macrophytes.

In general, grazing by birds tends to peak in late summer and autumn after the principal growing season and after reproduction, i.e. flowering and setting of seed has occurred. Any impact of grazing may therefore be considered to be unimportant for many existing macrophyte populations. However, grazing at this time and into the winter months, where some species of macrophytes remain available as developed plants, dormant buds or even tubers, may be important in determining macrophyte abundance and community structure in subsequent growing seasons.

Overall, it is clear that further long-term replicated enclosure experiments are required in a variety of circumstances (e.g. with different start-up inocula of macrophytes and different species of macrophytes and herbivorous birds) to reach a consensus of opinion on the impact of bird grazing. If limiting, additional measures controlling bird grazing (e.g. through supplementary feeding, scaring or culling) or enhancing macrophyte populations (e.g. transplantation and initial protection) may be needed to accelerate macrophyte colonisation and development in lakes undergoing restoration.

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