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RH: Impact of swan grazing • Porteus et al.

The impact of grazing by mute swans (*Cygnus olor*) on the biomass of chalkstream macrophytes

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SUMMARY

1. In the U.K. the population of Mute swans (*Cygnus olor*) has doubled since the early 1980s. Swans feed mainly on submerged aquatic macrophytes, especially water crowfoots (*Ranunculus* spp. subgenus *Batrachium*). The River Avon (a chalk-stream in southern England) is designated a Special Area of Conservation, in which *Ranunculus*-dominated habitat is required to be protected. This study focused on the River Wylye (part of the Avon catchment) to quantify the impact of grazing by swans on the biomass of chalkstream macrophytes.

2. In spring 2004 the resident swan population in the Wylye valley comprised 21 pairs and approximately 65 non-breeders. 17 nest sites were found, of which only 3 fledged a total of 14 cygnets. Swan presence was monitored at 46, 100 m sample sites along the river, from January to September 2004.

3. *Ranunculus* biomass was estimated at the same sites using a low-impact destructive sampling technique, on 3 occasions (roughly May, July and September). Mean biomass estimates (with ranges) for sample 1, 2 and 3 respectively were 544 (0-2,752), 818 (0-3,328) and 781 (25-4,388) kg fresh weight per 100 m of river.

4. Using a regression model, swan numbers at each site were found to be a significant influence on change in *Ranunculus* biomass between May and July, accounting for at least 15% of the variation in growth rate. No significant relationship was found between swan numbers and *Ranunculus* growth during July to September.

5. *Ranunculus* is important both as a habitat in its own right, and because of its influence on hydrological processes. The scale of *Ranunculus* biomass loss due to swan grazing is presented in terms of fresh weight and volume to allow these ecosystem consequences to be considered.

Introduction

The Mute swan (*Cygnus olor,* Gmelin, 1789) is indigenous to Eurasia and has been introduced widely elsewhere as a decorative waterfowl. In North America, where mute swans were introduced from the late 1800s (Bellrose, 1980), they are considered an undesirable invasive species (e.g. Conover & Kania, 1994; Petrie & Francis, 2003), and management aims to reduce mute swan populations to mitigate negative ecological impacts on wetland habitats (Atlantic Flyway Council, 2003). In the United Kingdom, the breeding population of swans underwent a rapid increase from the mid-1980s to 2000, attributed to reduced lead poisoning following a ban of lead fishing weights in wetland habitats (Kirby *et al.,* 1994; Rowell & Spray 2004), and to milder winters increasing juvenile first-winter survival. During 2000-2005 numbers have remained level in Great Britain, but there has been a sharp decline in Northern Ireland. A census in spring 2002 estimated a total UK population of 6,150 breeding pairs and 19,400 non-breeding individuals, totalling 31,700 birds (Banks *et al.*, 2006).

Mute swans can cause economic loss through grazing of arable and pastoral crops, especially oilseed rape (Eltringham, 1963; Birkhead & Perrins, 1986; Rees *et al.,*1997; Parrott & McKay, 2001). However, swans mainly feed on aquatic vegetation (Rees *et al.,* 1997) and may have an adverse effect on brown trout (*Salmo trutta* L.) and Atlantic salmon (*Salmo salar* L.) fisheries in southern England through their impact on macrophytes, especially water crowfoots (*Ranunculus*, subgenus *Batrachium*) (Birkhead & Perrins, 1986; Trump *et al.,* 1994; O'Grady, 1993) . The loss of submerged and emergent vegetation reduces structural and biological habitat diversity, affecting macroinvertebrates, shellfish and fish using the habitat as food and shelter (e.g. Krull, 1970; Hurley, 1991; Harrison & Harris, 2002).

Swans consume a large amount of vegetation. In Chesapeake Bay on the East Coast of the United States, Fenwick (1983) calculated that mute swans could consume up to 43% (females) and 35% (males) of their body weight daily. Given that adult swans in the UK weigh between 10-12 kg (Reynolds, 1972; Cramp *et al.,* 1977), this implies that they may consume 4.5-5.5 kg of vegetation (fresh weight) per day. Mathiasson (1973) calculated that mute swans in Sweden consumed an average of 4.9 kg of sea lettuce (*Ulva lactuca*) per swan per day. Swan weight depends on the local availability of food, and therefore in areas of high availability even larger amounts of vegetation may be consumed. In Chesapeake Bay, Tatu *et al.,* (2007) compared grazed sites against exclosures to demonstrate a substantial impact of swan grazing on submerged aquatic vegetation, with an average 79% reduction in percentage cover after 2 years. Shallow-water sites (< 0.75 m) were predominantly occupied by flocks rather than breeding pairs, and here submerged vegetation was reduced by 75-100%. Within their native range, large flocks of non-breeding or moulting swans have been shown to severely reduce and in some areas remove beds of vegetation before moving on from the area (Mathiasson, 1973).

The River Avon in southern England (the ‘Hampshire Avon’) has been designated as a Special Area of Conservation (SAC) under Article 3 of the European Union (EU) Habitats Directive (German & Sear, 2003). SAC designation requires the establishment of conservation measures to protect internationally rare or threatened habitats and species. The River Avon is a chalk-stream characterised by the abundance of *Ranunculus* spp., a habitat type listed on Annex I of the Directive. The productivity of *Ranunculus* is highly variable throughout the river Avon (German & Sear, 2003). The Habitats Directive proposes that in any 100 m stretch at least 25% of *Ranunculus* should be allowed to flower. The percentage cover by *Ranunculus* in ideal conditions has been suggested to be between 25% (German & Sear, 2003) and 40% (Grieves *et a*l., 1999) of the in-channel area. Other species supported by the Avon catchment and listed on Annex II of the Habitats Directive include Atlantic salmon (*S. salar*), Bullhead (*Cottus gobio* L.), Brook lamprey (*Lampetra planeri*, Bloch 1784), Sea lamprey (*Petromyzon marinus* L.) and Desmoulin's whorl snail (*Vertigo moulinsiana*, Dupuy, 1849) (McLeod *et al.,* 2005).

The River Avon SAC Conservation Strategy regards swans as a 'problem' or 'nuisance' species. Where feeding activity is concentrated, flocks of non-breeding swans can deplete the *Ranunculus* community and reduce the availability of refuges for fish, including salmon parr and bullhead (Wheeldon, 2003). Grieve *et al.* (1999, 2000) estimated that swan grazing affected 30% of the overall SAC length. On the River Wylye (a tributary of the Avon) and elsewhere, the issue of swans grazing has been controversial since the early 1980s (Trump *et al.,* 1994), and in 2004 it became the focus of national media attention (Elliott, 2004; Fort, 2004).

Angling clubs and fishing syndicates on the Wylye, especially those with brown trout interests, insist that swan grazing is having a highly detrimental effect on macrophytes in the river (Wiltshire Fisheries Association, pers. comm.). They claim that where large flocks of non-breeding swans concentrate their feeding, they not only strip *Ranunculus* from sections of river, but through persistent grazing pressure prevent its recovery

(Wheeldon, 2003). Apart from the loss of brown trout habitat that the *Ranunculus* provides (including shelter from predators such as cormorants), they claim that the loss of large quantities of macrophytes (which increase flow resistance, helping to “back up” water and maintain water depth - Dawson, 1989) creates sections of river that are unattractive to brown trout and consequently to anglers. Low water reserves in the aquifer, caused by low rainfall years and possible over-abstraction of water for domestic and industrial use, are generally accepted to exacerbate the problem of swan grazing on the Wylye, because lower river depth allows swans easier access to *Ranunculus* (Solomon, 1997, unpublished data).

Previous swan research in the Wylye Valley has sought to clarify aspects of swan habitat use and swan population dynamics (Harrison, 1985, unpublished data; Trump *et al.,* 1994). Watola *et al.* (2003) modelled the effect of clutch reduction on the breeding and non-breeding swan population and assessed the limitations of clutch reduction as a means of population management. The aim of the study reported here was to quantify the impact of swan grazing on *Ranunculus* by relating macrophyte biomass to grazing pressure.

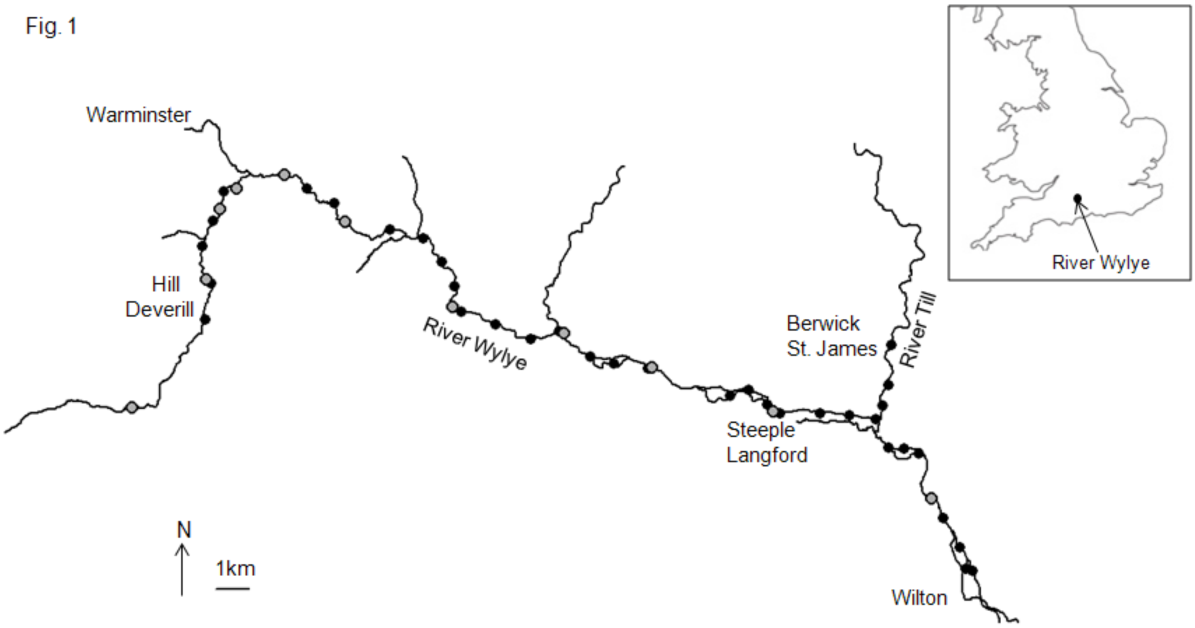
Methods

Study area

The study focused on the River Wylye and its main tributary, the Till, which form part of the Hampshire Avon catchment in central Southern England. On the Wylye the study area included the main river and its carriers from headwaters at Hill Deverill (National Grid Reference ST868397) to Wilton (SU096323) including the flooded gravel pits at

Steeple Langford (SU043369), and the Till from Berwick St James (SU071390) downstream to the Wylye confluence (Fig. 1). Both rivers drain the chalk uplands of

Fig. 1



Salisbury Plain and the South Wiltshire Downs and are characteristic of lowland chalk streams. The Wylye Valley is approximately 44 km long with a floodplain up to 2 km wide in places. From the 17th century until the 1930s it was managed as water meadows by means of sluices, but most of the land is now agriculturally ‘improved’ to create higher quality grazing, silage grass and cereals (Trump *et al.,* 1994).

The *Ranunculus* community on the Wylye is dominated by stream water crowfoot *Ranunculus penicillatus* ssp. *pseudofluitans* (Syme) S. D. Webster. Headwater reaches fed by seasonally active springs (‘winterbournes’) are characterised by pond water-crowfoot *R. peltatus* Schrank, with river water-crowfoot *R. fluitans* Lam common in downstream reaches. These *Ranunculus* species are associated with other aquatic plants, such as water-cress *Rorippa nasturtium-aquaticum* (L.) Hayek, water-starworts

Callitriche spp., water-parsnips *Sium latifolium* (L.) and *Berula erecta* (Huds.) Coville, fools' watercress *Apium nodiflorum* (L.) Lag., water-milfoils *Myriophyllum* spp. and water forget-me-not *Myosotis scorpioides* (L.) (Grieve *et al.*, 1999; McLeod *et al.*, 2005). The Wylye is a substantially altered drainage (German & Sear, 2003), and the in-stream vegetation has been subject to a series of influences from changing land-use over at least four centuries. During the 20th century, deliberate management of the in-stream vegetation to benefit fishing interests has taken the form of selective 'weed-cutting'. Formerly this took place at least twice a year to reduce water depth and hence the risk of summer flooding, and to provide better access to the river for fishermen. Latterly, given the shortage of *Ranunculus*, weed-cutting has been much more limited. By agreement among river keepers, there are narrow seasonal weed-cutting 'windows' of about 10 days in April, May and July, and 3 days in August.

Swan Monitoring

Swan presence was monitored at 46 sites (Fig. 1). Thirty five of these were already selected as sites for mink (*Mustela vison,* Schreber, 1777) rafts as part of a long-term mink control project (Porteus *et al.,* unpublished data). These were more or less regularly spaced at intervals of ~1 km, and were therefore assumed to be randomly located relative to swan presence. Sites were visited at two-week intervals, and the numbers of swans seen at each visit were recorded from January to September 2004. The 11 remaining sites were selected by Wessex Water (WW) for aquatic macrophyte and invertebrate monitoring concomitant with the present work. Here too swans were monitored at two-week intervals subsequent to the first macrophyte sampling visit (May 2004). Swans were also recorded when sites were visited for macrophyte sampling (see below).

The location of each site was marked by a wooden post in the river margin. In addition to searching the 100 m reach around the site, any swan visible upstream or downstream within the river valley during a site visit was recorded. The numbers of swans present (adults, juveniles or cygnets), their distance from the site, their location (river, bank, pasture or arable) and their behaviour (resting, grazing or incubating) were recorded. The numbers of swans seen per site visit were then averaged over three periods: A) prior to the first macrophyte sample, B) between the first and second sample, and C) between the second and third sample, and were log-transformed. During April and May the full length of the river was searched for pairs of swans and for nests. All nest locations were logged with a GPS unit, and adult leg ring codes (if present) and clutch size were recorded. Nests were then monitored at two-weekly intervals until cygnets fledged or the nest was abandoned.

Visits to raft sites happened at different times of day, determined by logistics. To establish the extent to which the size, movements and feeding activity of non-breeding herds might fluctuate within a 24-hour period, a herd of swans feeding primarily on silage grass in a field adjacent to a river channel at Little Langford (National Grid Reference SU057368) was monitored from daybreak (04:30 hrs) to nightfall (21:30 hrs) on 14 May 2004. The number of swans in the herd and their behaviour (resting or feeding) were recorded at 30 minute intervals from a natural view-point 0.5 km from the herd. It was clear that feeding took place only during daylight hours, and continued throughout the day without any obvious peak. Individual swans left the herd and entered the river intermittently throughout the day, typically for periods of 10-30 min.

Macrophyte sampling

Aquatic macrophytes are frequently measured by estimating percentage cover visually (Murray-Bligh, 1999; Flynn *et al.,* 2002). However, this lacks precision, there are inconsistencies between observers and - important in the context of this research - it ignores macrophyte volume. There is no standardised methodology to measure macrophyte biomass. Several different sampling methods have been used previously (Dawson, 1976; Conover & Kania, 1994; Flynn *et al.,* 2002), all of them destructive and labour-intensive. As we wanted to measure growth in biomass, repeated visits to the same sites would be necessary. In the context, repeated destructive sampling within what were often sparse stands of vegetation could have had an unacceptable impact, so we devised a low-impact destructive sampling technique.

At each site, both 2-dimensional cover and biomass of aquatic macrophytes were measured. We used a 'skeletal' sampling grid which combined presence/absence scores in two dimensions, with destructive sampling at a small random subset of grid nodes where *Ranunculus* was recorded as present in more than trace quantities. This led to estimates of biomass for a 100 m stretch of river centred on each site. Sampling took place at each site on 3 occasions approximately 60 days apart, in May, July and September 2004. The order in which the sites were sampled remained the same for each session.

Stage 1: Longitudinal sampling

Presence/absence of each macrophyte species was recorded at intervals along a 100 m stretch of river centred at each sample site. A temporary anchor stake was knocked into the river bed in the middle of the river at the site. A 50 m buoyant polypropylene rope, knotted at 5 m intervals was fastened to the stake and allowed to extend downstream, forming a floating longitudinal transect line that followed the line of strongest current. The 5 m interval was chosen to avoid the risk of counting individual plants more than once.

At each knot, presence/absence of a species along an imagined transect at right angles to the rope was recorded. Very small quantities of a species (individual stands < 7.5 cm in width) were recorded as a 'trace', allowing these instances to be included or excluded in analysis. All marginal bank-side species were recorded in a single category to save time identifying them. The presence of silt deposits was also recorded. The knotted rope was then removed and tethered to a second anchor stake 50 m upstream of the original anchor point and the sampling procedure repeated. This provided a 100 m transect sample of macrophyte cover, centred at the sample site.

Stage 2: Transverse sampling

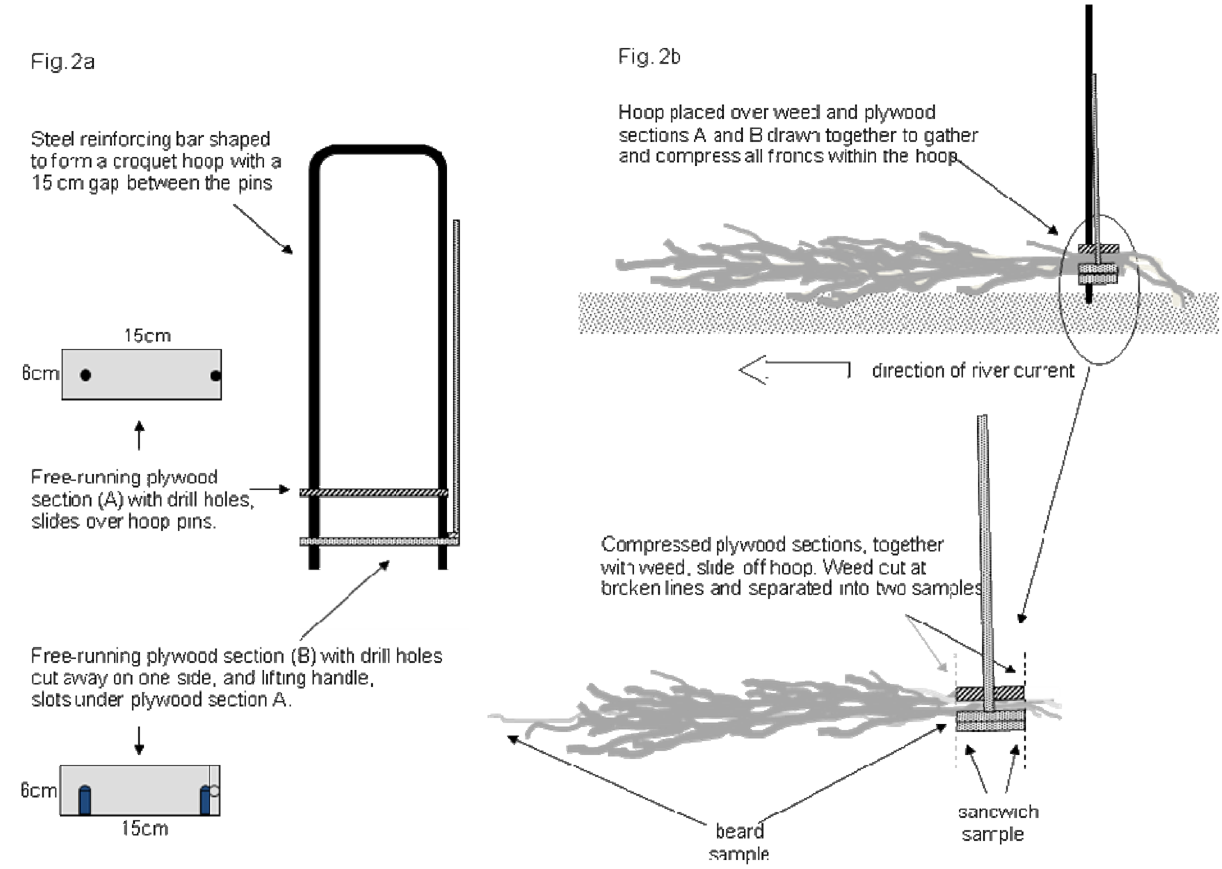
If Stage 1 indicated that *Ranunculus* spp. was present at a site in more than trace quantity, presence/absence was scored across the second (transverse) dimension. One transect point was selected at random from among those at which *Ranunculus* had been recorded in Stage 1. A transverse transect was defined at this point by suspending a rope - knotted at 15 cm intervals - across the river from bank to bank, just above the surface of the water. As in Stage 1, a species was recorded as present if there was a continuous stand greater than 7.5 cm in width or 'trace' presence if less. Five 15 cm sections were randomly selected for biomass sampling (below) from all sections positive for *Ranunculus*. If there were only five or fewer positive *Ranunculus* sections, all positive sections were sampled. Percentage cover was calculated for each macrophyte species, by multiplying the proportion of longitudinal sections by the proportion of transverse sections in which a given species was present.

Details of the general morphology of each transverse transect were recorded: the width of river at the site, the depth at quarter distances across the river, the geographical orientation of the transect line, and the degree of shading on either bank at the site.

Stage 3: Biomass sampling

Destructive biomass sampling took place only at raft sites to avoid biasing the WW invertebrate study. To avoid pseudo-replication, biomass data from sampled sections were averaged to give a single figure for each site and sample occasion. Previously sampled transverse sections were avoided on subsequent sampling occasions, so that the effect of previous sampling was never an issue. Biomass sampling could not be undertaken where water depth was greater than 1.0 m.

We devised a simple tool to sample *Ranunculus* fronds lying across any 15 x 6 cm area of the river bed. This consisted of a 1.5 m length of 12 mm steel bar, bent into a straight-sided hoop, with an internal width of 15 cm between the sides. A 6 cm x 22 cm piece of 10 mm plywood with two 16 mm diameter holes was fitted over the ends of the hoop so that it could slide up and down the sides (Part A in Fig. 2).



In use, the plywood slider was raised, the hoop pins were aligned with the rope knots of a section and pushed down vertically until they touched the river bed. A second piece of plywood 6 cm x 24 cm (Part B in Fig. 2) was then fitted from upstream, beneath the first piece and as close to the river bed as possible. This had cut-outs to locate it on the hoop, and a wooden dowel fixed vertically at one end to serve as a lifting handle. When the two pieces of plywood were brought together the fronds of weed passing through a column of water of base 6 x 15 cm (0.009 m^2) were trapped. The sample was cut on the upstream side of the holding device with wallpaper scissors and brought out of the water for easier manipulation. A cleaner cut, flush with the edge of the ply, was then made on the upstream side of the ply 'sandwich'.

The length of the longest *Ranunculus* frond within each sample was measured to the nearest cm. The sample was then divided into two components to give two alternative biomass measures. First, fronds hanging from the downstream side of the tool were cut off flush with the plywood boards, and dropped into a freezer bag – this formed a sample of variable length, referred to as the 'beard'. The fronds trapped between the two boards, referred to as the 'sandwich', were placed in a separate freezer bag. If necessary, samples were stored frozen prior to processing.

In the laboratory, samples were oven-dried at 50°C until a constant weight (to the nearest 0.1 g) was achieved. An attempt was made to remove all material other than *Ranunculus* from the sample before it was weighed, but this was not possible with samples that were coated in algae.

For each site and sample occasion, the following were calculated:

- proportion of grid sections positive for *Ranunculus* (percentage cover; p) = number of positive longitudinal sections x number of positive transverse sections / (21 x total number of transverse sections)
- area of river in the 100 m section (a; m^2) = 100 x river width (m)
- average sandwich biomass (b; kg) = total dry weight of sandwich samples / number of sandwich samples
- section biomass (kg dry weight per 100 m river section) = p x a x b / 0.009

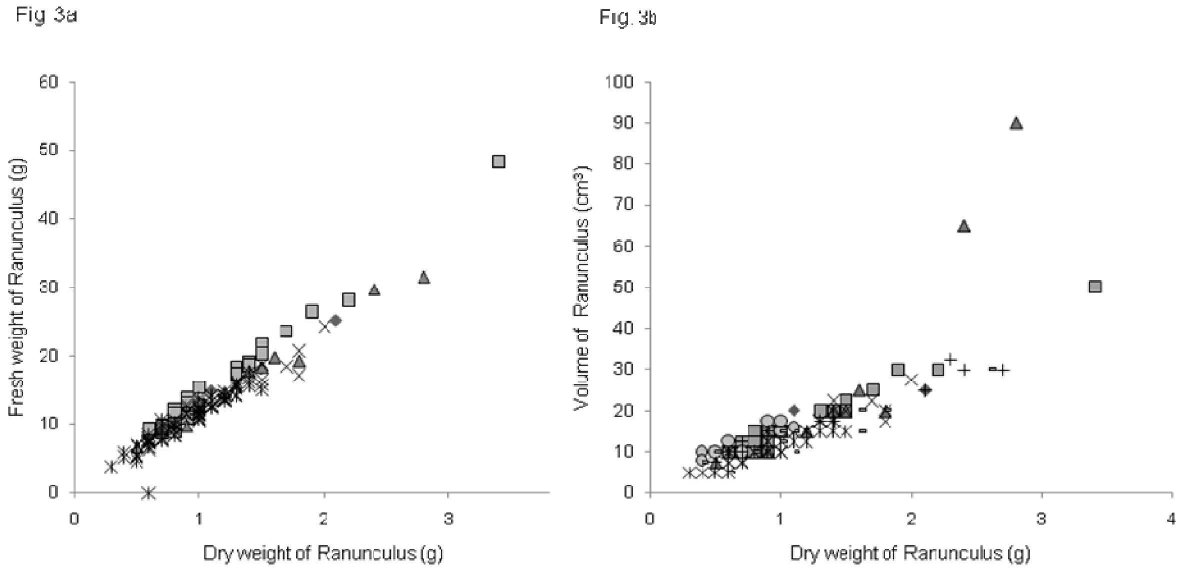
Stage 4: Relating dry weight to fresh weight and fresh volume

In September 2005, samples of *Ranunculus* were collected to determine the relationship between volume of the fresh plant and dry weight, in order to begin to predict the hydrological consequences of changes in *Ranunculus* biomass. The relationship between fresh weight and dry weight was also estimated, but mainly as an aid to visualising the impact of swans. *Ranunculus* plants vary somewhat in growth form, depending on grazing or cutting history and sub-species. To allow for this, samples (average 23 per site, ±S.E. 8) were collected from 8 sites (fresh weight was estimated for 5 of these sites). Clumps of fronds were cut off from the roots and placed into bags. In the laboratory, samples were carefully separated into individual fronds and washed to remove any debris.

Individual fronds of *Ranunculus* were measured from the tip back to the root end, and grouped into 200, 300 or 400 mm lengths. (This allowed for possible differences in structure between short and long fronds.) A sample was defined as ten individual fronds of the same length. Excess water was removed either by blotting on paper towels (early samples), or using a plastic salad spinner (Tontarelli S.P.A., Castelfidardo, Italy). Fresh weight was then measured to the nearest 0.1 gram. Each sample was then pushed into a measured volume of water in a measuring cylinder. The change in volume of water plus sample represented the volume of water displaced. Samples were then oven-dried and weighed as in Stage 3.

The relationships of fresh weight and fresh volume with dry weight were examined by general linear models with site included as a factor. Although site had a significant effect on both fresh weight ($F_{4,147} = 16.42$, $P < 0.001$) and fresh volume ($F_{7,181} = 5.01$, $P < 0.001$), site explained only 2% of the variation in fresh weight and 4% of the variation in fresh volume, therefore for the purposes of this paper simpler models were adopted:

fresh weight (g) = (12.297 ± 0.109) x *dry weight* (g); $F_{1,148} = 12622.51$, $P < 0.001$; Fig. 3a)



fresh volume (cm^3) = (14.064 ± 0.320) x *dry weight* (g); $F_{1,182}$= 1930.36, P < 0.001; Fig. 3b).

The estimated biomass of *Ranunculus* per 100 m was converted into fresh volume per 100 m stretch. The volume of a 100 m length of river (including the in-stream macrophytes) at each site was also calculated using the depth and width measurements averaged across all sample occasions at the site.

Statistical analyses

A recognised problem in analysing river processes is that where variables must be measured at stations along the river length, they are often highly correlated because they relate to the maturation of the river. This ‘multi-collinearity’ can lead to spurious relationships being suggested by statistical models. Thus river width, depth, volume per unit length, and flow all reflect the size of the river channel and are correlated with position along the river, and with each other. Because the size of the river channel also sets an upper limit to the size of *Ranunculus* stands, *Ranunculus* biomass per unit length of river is also correlated with these variables.

We therefore began analysis with careful examination of correlations amongst measured variables. Correlations among all macrophyte species recorded were examined, but there were no strong correlations to explore further, other than obvious associations of certain species with slow deep water, or with shading.

For *Ranunculus*, sandwich biomass and beard biomass (averaged for each site and sample) were highly correlated ($R^2_{81} = 0.656$, $P < 0.001$), the correlation being stronger at short "beard" lengths. Sandwich biomass was felt to be the more dependable measure of biomass per square metre; hence beard biomass was not used in statistical models.

The influence of swan grazing pressure on change in *Ranunculus* biomass was examined by General Linear Modelling. All analyses were performed in Genstat release 10.2. Initially, the dependent variable used was the difference in log-transformed section biomass between start and end of the period in question (B or C), divided by the number of days between samples, to give daily growth rates on a log scale. Distance from river source, forming a deliberate surrogate for many correlated processes, and the average number of swans observed during each period, were entered as putative explanatory variables. Significance was assessed by dropping each of the latter terms from the full model. The average swans seen per site visit of apparent significance were found to be strongly influenced by the constant used in logarithmic transformation. Hence average swans seen per site visit were converted into a factor with four levels (average swan numbers/visit of 0, 0.01-2.99, 3.00-8.99, > 9.00). These levels were intended to approximate to no swans, pair, pair plus young, and herd, respectively.

In the above 'biomass change' model, distance from river source was clearly confounded with starting biomass (because the river has more volume and holds more weed in its lower reaches), and there was evidence of density-dependent reduction of growth rate. We therefore finally adopted a 'standing crop' model in which the section biomass at the end of each time period (B or C) was related to the section biomass at the beginning, and to the average number of swans seen (as a 4-level factor). The regression model used had the basic form:

$$(1)\ \log_{10}(biomass_{\text{sample } t+1} + 0.1) = \alpha + \beta swans + \gamma\log_{10}(biomass_{\text{sample } t} + 0.1)$$

Equation (1) can be re-arranged as:

$$(2)\ \log_{10}(biomass_{\text{sample } t+1} + 0.1) - \log_{10}(biomass_{\text{sample } t} + 0.1) = \alpha + \beta swans + (\gamma-1)\log_{10}(biomass_{\text{sample } t} + 0.1)$$

In this form, the left-hand side of the equation represents growth in section biomass, and the right-hand term represents density-dependent inhibition of growth. Thus in the regression equation (1), a value of γ significantly different from 1 implies density-dependence. The model and data were adjusted to allow for variation in the number of days lapsed between consecutive samples, and predictions were standardised to give biomass change over a realistic lapse.

Results

Swan presence

In spring 2004 swans in the valley comprised 21 pairs and approximately 65 non-breeders, a total of 107 birds. A total of 17 nest sites were found during May 2004, broadly similar to the findings of Trump *et al.* (1994). Three nests successfully hatched a total of 14 cygnets. All other nests failed. Three of these were found to have eggs outside the nest, perhaps indicating disturbance by a predator.

There were two flocks of approximately 15 and 35 non-breeding swans. From January-April 2004, the larger herd appeared to feed exclusively on silage grass and oilseed rape in fields adjacent to the river channel. Aggressive territorial behaviour by mated swans particularly during the moulting season restricted the movement of non-breeding swans to a few stretches of river. During the moult, river keepers also herded non-breeders to restrict their impact to certain ‘sacrificial’ stretches.

Presence/absence of Ranunculus and percentage cover

Ranunculus was present in at least trace quantities somewhere in every 100 m river section, at all three sampling dates. On each date the average percentage cover by area among sites was about 20%, and this figure varied little between samples (Table 1). Among sites, no consistent pattern of change in percentage cover was apparent between dates, and we observed no correlation between percentage cover on a given date and swan abundance in the previous period. We found no relationship between maximum frond length on a given date and swan numbers during the preceding period.

Ranunculus standing crop biomass and changes in biomass

Biomass estimates for *Ranunculus* were highly variable between sites and sample occasions, ranging from 0 to 357 kg dry weight per 100 m river section. Mean biomass (± S.E.) at samples 1, 2 and 3 was estimated to be 44(10), 67(16) and 64(19) kg dry weight per 100 m river section (equivalent to 61(13), 87(15) and 80(17) g dry weight per m^2) respectively. The highest biomass recorded at any site on the Wylye in this study was at sample 3.

Out of 27 sites 18 (67%) showed positive growth during period B, but only 7/20 (35%) during period C. Maximum seasonal growth (between samples 1 and 2, or 1 and 3) was 263.48 kg dry weight per 100 m river section, equivalent to 2.40 kg dry weight per 100 m river section per day^{-1} or 29.45 kg fresh weight per 100 m river section day^{-1}. At many sites *Ranunculus* failed to achieve positive growth at all during period B or C or both (Table 1).

The percentage of river volume formed by *Ranunculus* never exceeded 1% (mean 0.13%, 0.2% and 0.2% at samples 1, 2 and 3 respectively; range 0.0-0.8%).

Ranunculus biomass vs. swan presence

For period B, the regression model of biomass at sample 2, against biomass at sample 1 and swan numbers (as a four-level factor), explained 62% of the variation ($F_{4,25}$= 12.58, P < 0.001). Swan numbers accounted for 15% of the variation ($F_{3,25}$= 4.63, P = 0.01). Coefficients for all levels of the swan term were negative and, in absolute value, progressively larger and more significant for increasing numbers of swans (Table 2). Model predictions within the data range are illustrated in figure 4a for different levels of swan numbers.

Fig.4a

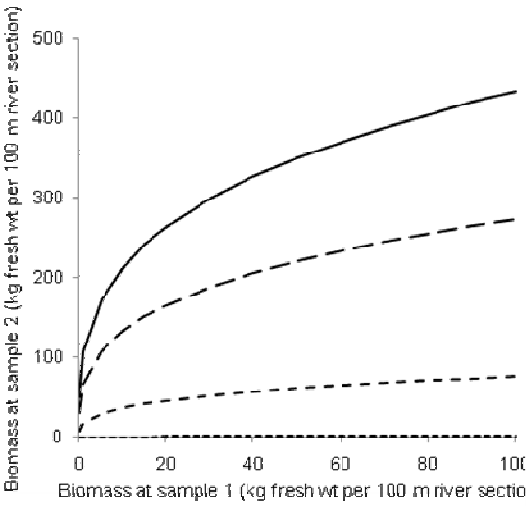
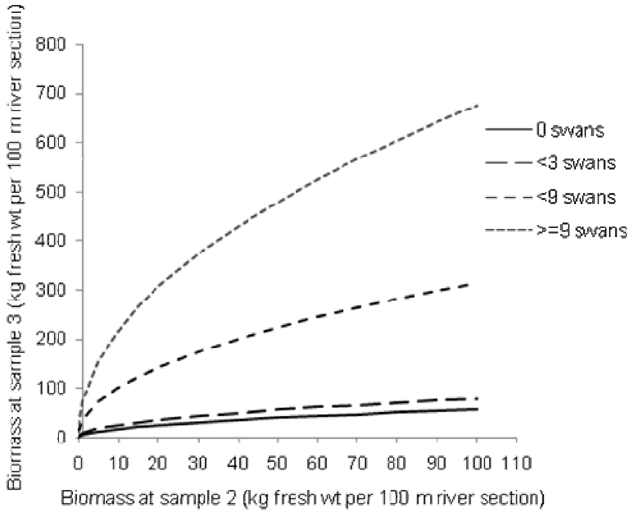


Fig. 4b



For Period C, the equivalent regression was not significant. The dataset available to compare samples 2 and 3 was smaller (n = 20 sites), but there was no evidence that the negative pattern for swans noted in Period B persisted in Period C.

Discussion

Ranunculus biomass and growth

Biomass estimates for *Ranunculus* were considerably lower than previous estimates for *Ranunculus penicillatus var. calcareous* (202g dry weight per m^2; Dawson 1976) and *Ranunculus penicillatus pseudofluitans* on ungrazed sites (240g dry weight per m^2; O'Hare *et al.,* 2007) on Southern chalk streams. The highest biomass recorded in this study (466 g dry weight per m^2) was somewhat higher than that obtained by Dawson (1976) (380g dry weight per m^2) on the River Piddle.

Growth of *Ranunculus penicillatus* var. *calcareous* was estimated by Dawson (1976) to be about 25 g m^{-2} given a water depth of 2.5 m, in the Frome/Piddle catchment. This is presumably dry weight, but the paper does not state what time-scale the estimate refers to, making comparison impossible. In the present study, the maximum estimated growth for the entire season (i.e. samples 1 to 2, or 1 to 3) was 0.33 kg dry weight m^{-2}, equivalent to 4.08 kg fresh weight m^{-2}. This equates to a daily growth of 3.0 g dry weight m^{-2} day^{-1} or 37.1 g fresh weight m^{-2} day^{-1}, and to a daily growth factor of 1.009.

Impact of swan grazing

Flow rates are recognised to be one of the most important factors affecting *Ranunculus* growth (Environment Agency, 2001; Cranston & Darby, 2002), both directly by wash-out and indirectly by controlling epiphytic algae growth (Wade *et al.,* 2002). When flow rates are low, sediment (with its associated nutrients) and temperature can build up, creating a suite of factors which favour algal epiphytes. In 1990 stretches of the River Wylye normally abundant with *Ranunculus* were dominated by algae following two successive years of low aquifer recharge (A. Simmons, pers. comm.). With changes in land-use and agricultural practices combined with greater variability in flow rates due to higher fluctuating rainfalls and over-abstraction, algae-dominated stretches on chalk streams may become a more frequent occurrence (Cotton *et al.,* 2006).

Nevertheless, a previous study (German & Sear, 2003) of *Ranunculus* abundance (2-dimensional coverage of the river bed estimated by eye) along the Wylye found no significant relationship with any geomorphologic measure. Worse, abundance was unrelated to pre-established definitions of what constituted optimal, sub-optimal and poor conditions for the species. In this study, by contrast, we measured *Ranunculus* abundance in three dimensions as biomass, and found a significant relationship between growth in mid-summer and swan grazing pressure during the first 6 months of the year, after accounting for starting biomass and thus density-dependent retardation of growth.

On the nearby River Frome in Dorset, O'Hare *et al*. (2007) estimated early summer (May-June) *Ranunculus* biomass and plant damage in relation to a simple categorisation of sites as recently 'grazed' or 'ungrazed'. Evidence of grazing on surviving plants was clearly demonstrated, and standing biomass was 50% lower in 'grazed' sites. As discussed above (Methods), the consequences of grazing for the standing crop of *Ranunculus* at any point in time will exceed the actual biomass eaten, partly because swans pull up more than they eat, but particularly because of the lost capacity for growth. O'Hare *et al*. (2007) go on to construct a foraging model for swans at a single site, from which they infer that swan grazing must have restricted plant growth, otherwise it would have supported more swans than were observed at the site. Although we question the logic of this step, our own study - using field evidence to estimate the impact of grazing by swans across a number of randomly selected sites - affirms that swan grazing does have an appreciable impact on the growth of *Ranunculus*.

So how much potential increase in biomass was lost per swan? At the average site, growth was positive during period B for all starting biomass levels and swan grazing pressures, except for ≥ 9 swans (Fig. 4a). However, the impact of even a pair of swans on biomass at sample 2 was substantial. It is likely that biomass at the first sample in early summer itself carries a legacy of earlier grazing pressure (O'Hare *et al*., 2007). Because mid-summer biomass builds on early-summer biomass, and because the effects of swan grazing prior to and after our first sample (i.e. periods A and B) were inseparable, the full impact of swan grazing on mid-summer biomass may well be greater than indicated by our regression.

The impact of swans on biomass change in late summer and autumn (period C) remains unclear (Fig. 4b). A scatter-plot suggests that if anything, the relationship is positive, implying that in this period swans congregate in stretches with plentiful weed. At this time of year, most *Ranunculus* in the river has flowered and is senescent, so that 'growth' is negative; but flowering and senescence are uneven between sites, being delayed by mid-season grazing or (deliberately) by weed-cutting. This variability may have masked the effects of swan grazing during period C. However, it is also clear from anecdote and our own direct observation that large aggregations of swans at this season (we observed up to 30 swans in a 100 m stretch) can completely denude stretches of river of *Ranunculus* in a few weeks. In extreme cases this can include pulling up the roots (P. Hayes, pers. comm.). The process of denudation is aided by low water flow at this season, and by the fact that water depth drops as weed is consumed. As noted earlier (Introduction), an adult swan can consume about 5.0 kg fresh weight per day. Thus the largest biomass observed in this study (4,387 kg fresh wt per 100 m at sample 3) could be entirely consumed in 29 days by a herd of 30 swans, assuming no further growth and no wastage. The mean biomass predicted from the regression model for sample 2, given maximum observed starting biomass and zero grazing by swans, was only 10% of this extreme (i.e. 427 kg fresh wt per 100 m) and would last 30 swans no longer than 3 days.

Clearly any process that physically removed *Ranunculus* biomass in a manner similar to grazing by swans would have an equivalent effect on growth. Dawson (1976) showed that intensive weed cutting caused a steady reduction of *Ranunculus* biomass over 4 years. Nevertheless he noted that where the plant grew vigorously it would still require management. Growth in the best stretches of the Wylye in our study was no less vigorous than in Dawson's. Weed-cutting can be used to create a diverse stream flow, limit maximum biomass, delay flowering and senescence, or simply to create clear lanes between weed stands in which fly fishing is possible. Any weed cutting done early in the season has to anticipate likely growth rates. Potential dangers are that subsequent grazing pressure by swans cannot be foreseen, and that too much or too little weed-cutting in itself may lead to a heavy impact by swans. However, it should be noted that in the present-day context of the Wylye, where the concern is too little *Ranunculus* rather than too much, river-keepers are well aware of the vulnerability of the system and weed-cutting is far more moderate than in Dawson's study. In our study, weed-cutting was not quantified, hence it would have contributed to the 39% of unexplained variation in biomass at sample 2, rather than to the apparent impact of swans.

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Table 1 Summary of *Ranunculus* percentage cover and biomass at each sample period, averaged across each site. Figures in parentheses denote the range (DW = dry weight).

	Sample 1	**Sample 2**	**Sample 3**
Sampling Period	24 May – 22 June	19 July – 31 August	13 September – 5 October
Proportion of grid sections positive for *Ranunculus* (excl. trace occurrence)	20% (0-68)	23% (0-87)	21% (0-75)
Proportion of grid sections positive for *Ranunculus* (incl. trace occurrence)	37% (3-83)	39% (1.4-90)	35% (1.4-84)
Mean sample biomass (kg DW)	0.002 (0-0.01)	0.003 (0-0.01)	0.003 (0-0.01)
Estimated section biomass (kg DW per 100 m river section)	44 (0-224)	67 (0-271)	64 (2-357)
Fresh weight (kg per 100 m)	544 (0-2752)	818 (0-3328)	781 (25-4388)
Volume (m^3 per 100 m)	622 (0-3147)	936 (0-3807)	893 (28-5018)

Table 2 Coefficients for the regression of $\log_{10}$(biomass at sample 2) across n = 28 sites where biomass was estimated at both sample 1 and sample 2. Coefficients for levels of the factor *swans* are expressed relative to level 1, corresponding to zero swans. In total, the regression explained 62% of the variation in growth rate.

Variable	**Factor Level**	**Regression Coefficient**	**± S.E.**	**t(25)**	**P value**
Constant	-	0.911	0.277	3.29	0.003
Log biomass at sample 1	-	0.309	0.054	5.74	< 0.001
Average swans per visit < 3	2	-0.200	0.299	-0.67	0.509
Average swans per visit < 9	3	-0.745	0.400	-1.86	0.074
Average swans per visit >= 9	4	-2.170	0.652	-3.33	0.003

Figure Legends

Fig. 1 Location of study site, (inset) and map of River Wylye showing mink raft (black circles) and Wessex Water sampling sites (grey circles).

Fig. 2 The tool used for sampling *Ranunculus* biomass (a) construction details; (b) method of use.

Fig. 3 (a) Regression of dry weight (g) against fresh weight of *Ranunculus* (g) (n = 5); (b) regression of dry weight (g) against volume of *Ranunculus* (cm^3) (n = 8); symbols represent different sites.

Fig. 4 Biomass growth model, indicating the impact of different intensities of swans on the growth of *Ranunculus,* standardised over a 60-day period (a) period B – between late May and late July); (b) period C – between late July and September).