

1 **Water velocity limits the temporal extent of herbivore effects on aquatic plants in a**
2 **lowland river**

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14 *olor*; Plant senescence; Trophic interactions; Water velocity; Waterfowl grazing and
15 herbivory

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18 *Running title:* Flow limits herbivore effects

19

20 **Abstract**

21 The role of herbivores in regulating aquatic plant dynamics has received growing recognition
22 from researchers and managers. However, the evidence for herbivore impacts on aquatic
23 plants is largely based on short-term enclosure studies conducted within a single plant
24 growing season. Thus, it is unclear how long herbivore impacts on aquatic plant abundance
25 can persist for. We addressed this knowledge gap by testing whether mute swan (*Cygnus*
26 *olor*) grazing on lowland river macrophytes could be detected in the following growing
27 season. Furthermore, we investigated the role of seasonal changes in water current speed in
28 limiting the temporal extent of grazing. We found no relationship between swan biomass
29 density in one year and aquatic plant cover or biomass in the following spring. No such carry-
30 over effects were detected despite observing high swan biomass densities in the previous year
31 from which we inferred grazing impacts on macrophytes. Seasonal increases in water
32 velocity were associated with reduced grazing pressure as swans abandoned river habitat.
33 Furthermore, our study highlights the role of seasonal changes in water velocity in
34 determining the length of the mute swan grazing season in shallow lowland rivers, and thus in
35 limiting the temporal extent of herbivore impacts on aquatic plant abundance.

36

37 **Introduction**

38 Herbivory on macrophytes is a key biotic process in aquatic ecosystems that can regulate
39 macrophyte abundance, and control energy and nutrient fluxes between macrophytes and
40 higher trophic levels (Cyr & Pace, 1993; Bakker et al., 2016). Thus, the interactions between
41 macrophytes and their herbivores play key roles in determining the structure, functioning and
42 service provision associated with aquatic ecosystems (Lodge, 1991; Newman, 1991; Klaassen
43 & Nolet, 2007). Across aquatic ecosystems, herbivory has been documented on submerged,
44 floating, and emergent macrophyte species by a wide range of animal taxa, including birds,
45 mammals, reptiles, fishes, crustaceans, molluscs, echinoderms, and insects (Lodge, 1991;
46 Newman, 1991; Heck & Valentine, 2006).

47 Herbivores can reduce plant abundance, with the magnitude of reduction related positively to
48 herbivore biomass density (Wood et al., 2012a; Bakker et al., 2016; Wood et al., in revision).
49 Therefore, regular periods of reduced herbivore densities may allow grazed macrophyte beds
50 to regrow and thus prevent long-term declines in plant abundance (Chaichana et al., 2011).
51 To date, the evidence for herbivore impacts on aquatic plants is largely based on short-term
52 enclosure studies conducted within a single plant growing season (e.g. Søndergaard et al.,
53 2006; Miller & Crowl, 2006; Gayet et al., 2011a; van der Wal et al., 2013). The
54 quantification of short-term changes in plant abundance has yielded important, but partial,
55 understanding of herbivore impacts; in particular, short-term experiments may not account
56 for impairment of future growth, and indirect impacts of herbivores such as altered nutrient
57 and light availability, which are thought to emerge over longer time periods (Wass &
58 Mitchell, 1998). Thus, we currently lack the evidence base to assess the temporal extent of
59 herbivore impacts on aquatic plants. In particular, it is unclear whether herbivore reductions

60 in plant abundance in one plant growing season can carry-over into subsequent growing
61 seasons.

62 In shallow, lowland rivers in temperate regions in the northern hemisphere macrophyte
63 abundance shows a seasonal pattern related to the plant growing season, with abundance
64 reaching a minima during late winter, before increasing to a seasonal maxima in summer
65 (Dawson, 1976; Haury & Aïdara, 1999; Wood et al., 2012b). After summer, macrophytes
66 typically senesce and high flows during winter can remove all but a residual overwintering
67 above-ground biomass (Dawson, 1976; Franklin et al., 2008). High water velocities during
68 winter ($> 1 \text{ m s}^{-1}$) cause physical and mechanical stresses on macrophyte tissues due to
69 increased drag forces, which promotes stem breakage and uprooting (Franklin et al., 2008).

70 The short-term, within-season impacts of mute swans (*Cygnus olor*) on lowland river
71 macrophytes have been well documented in previous research, with reported reductions of up
72 to 100 % of above-ground macrophyte abundance (range = 0 – 100 %) during summer due to
73 the direct and indirect effects of grazing (O'Hare et al., 2007a; Porteus et al., 2011; Wood et
74 al., 2012b; Wood et al., 2012c). O'Hare et al. (2007a) compared macrophyte biomass in
75 reaches with low and high swan densities, and reported that abundance was 49 % lower
76 where high swan densities were recorded due to the presence of large numbers of non-
77 breeding individuals gathered in flocks. Similar reductions in lowland river macrophyte
78 biomass during summer due to high density mute swan grazing were reported by Porteus et
79 al. (2008). Thus, the within season reductions in lowland river macrophyte abundance caused
80 by high swan densities have been demonstrated, and in this current study we focused on
81 understanding whether these impacts of swan grazing could carry-over, through the dynamic
82 overwinter changes to macrophyte beds caused by high water velocity, into subsequent
83 growing years.

84 In this study, we tested two predictions regarding the temporal limit of swan grazing in
85 shallow lowland rivers. Firstly, we predicted that swan use of river habitat would be
86 negatively related to water velocity. Riverine birds such as swans are known to show strong
87 numerical responses to changes in river flow, for example by avoiding in-stream river habitat
88 at high water velocities (Royan et al., 2013; Wood et al., 2013). The seasonal reduction in
89 herbivore densities in river habitat during winter led to our second prediction, that there
90 would be no relationship between aquatic plant abundance (measured as biomass and cover)
91 in spring and swan biomass densities in the previous year. Aside from reduced herbivore
92 grazing pressure during winter, seasonal increases in water velocity during winter can remove
93 large quantities of senescent macrophyte tissues from ungrazed riverine ecosystems
94 (Chambers et al., 1991; Madsen et al., 2001; Franklin et al., 2008). Thus, we expected both
95 swan-grazed and ungrazed river reaches to have achieved equivalent plant abundance by the
96 following spring.

97

98

99 **Methods**

100 *Study system*

101 The River Frome (Dorset, UK) is a mesotrophic chalk river within a largely agriculture
102 landscape, with a total river length of 143.3 km and a catchment area of 414 km²
103 (Environment Agency, 2004; Bowes et al., 2009). The River Frome features an abundant
104 macrophyte community typical of such chalk rivers (Berrie, 1992). The macrophyte
105 community is dominated by stream water crowfoot (*Ranunculus penicillatus* ssp.
106 *pseudofluitans*), which comprises ca.90 % of macrophyte cover within river reaches

107 (Dawson, 1976; Wood et al., 2012b). Stream water crowfoot is a herbaceous perennial which
108 follows a well-established pattern of overwintering with reduced biomass in a procumbent
109 form, biomass increases in late spring to a summer peak when the plant flowers, thereafter
110 the plant begins to senesce and excess biomass is washed out between October and
111 November, typically leaving the roots intact and *in situ* (Dawson, 1976; Wood et al., 2012b).
112 The exact velocity at which the plants are washed out in autumn is dependent on a
113 combination of factors, including the shear stresses exerted by the water, the duration of those
114 stresses, the plants frontal area, its ability to reconfigure and the strength of the stems
115 (Usherwood et al., 1997; O'Hare et al., 2007b; Miler et al., 2014). Stream water crowfoot and
116 other submerged lotic macrophyte species (in particular other species within the genus
117 *Ranunculus*; Miler et al., 2012) typically have a weak point at the base of the stems and field
118 observations and flume studies indicate that at river mean cross sectional water velocities of \geq
119 0.8 m s^{-1} plants respond by reconfiguring and stem breakages can occur, causing a gradual
120 wash out of senescent tissues (O'Hare et al., 2008; Gurnell et al., 2010; Albayrak et al.,
121 2014). Smaller quantities of perfoliate pondweed (*Potamogeton perfoliatus*), Canadian
122 pondweed (*Elodea canadensis*), horned pondweed (*Zannichellia palustris*), blunt-fruited
123 starwort (*Callitriche obtusangula*), European bur-reed (*Sparganium emersum*), watercress
124 (*Nasturtium officinale*), and Eurasian watermilfoil (*Myriophyllum spicatum*), are also present
125 within the catchment and show seasonal patterns of growth and senescence similar to stream
126 water crowfoot (Gurnell et al., 2006; O'Hare et al., 2007a; Wood et al., 2012b). Due to the
127 mild climate of southern England, together with the influx of groundwater, water
128 temperatures remain above $5 \text{ }^{\circ}\text{C}$ throughout the year and so ice formation does not occur
129 (Berrie, 1992; Wood et al., 2012b).

130 The River Frome catchment has a mean mute swan population size of ca.300 individuals,
131 comprising both breeding and non-breeding adults, as well as juveniles (Wood et al., 2013b).
132 Grazing by mute swans on the in-stream macrophyte community has been documented
133 previously (Wood et al., 2015). Whilst territorial breeding pairs are present on the river
134 throughout the year, non-breeding birds use river habitat between May and September, which
135 forms the period of peak grazing pressure on macrophytes (Wood et al., 2013a; Wood et al.,
136 2013b).

137

138 *Water velocity*

139 Daily mean water discharge ($\text{m}^3 \text{s}^{-1}$) measurements between 1st March 2009 and 31st March
140 2010 were provided by the Environment Agency for the East Stoke gauging station (station
141 number 44001; 50°41'N, 02°11'W), from which daily mean water velocity (m s^{-1}) values
142 were calculated. Because water discharge, velocity, and channel cross sectional area (width
143 multiplied by depth) are interrelated according to the relationship, discharge = velocity · cross
144 sectional area, we carried out a back calculation of velocity that was based on the standard
145 technique used to derive depth–discharge relationships for gauging station rating curves,
146 although in this instance velocity, not depth was derived (Bovee & Milhouse, 1978; Gordon,
147 1992). River cross sections were available for East Stoke, recorded using the methodology
148 and values described in Wood et al. (2012d). Mean cross sectional velocity (v , in m s^{-1}) was
149 calculated according to the formula:

$$150 \quad v = a \cdot (1 - \exp(-b \cdot Q)),$$

151 where Q was the mean discharge ($\text{m}^3 \text{s}^{-1}$), whilst a (1.44) and b (0.12) were the intercept and
152 slope of the relationship between cross-sectional area and discharge.

153

154 *Macrophyte abundance*

155 For this study we selected 20 x 500 m lengths of river along a 44 km length of main river
156 channel between Maiden Newton (50°46'N, 02°34'W) and West Holme (50°41'N, 02°10'W).
157 We chose these 20 river reaches to be representative of the River Frome catchment in terms
158 of land use, river morphology, riparian vegetation structure, hydrology, and sediment
159 characteristics; all of our river reaches were on the main channel, and featured $\geq 75\%$ gravel
160 substrate and adjacent terrestrial pasture fields, which reflected the dominant characteristics
161 of our study system (Dawson, 1976; Berrie, 1992; Gurnell et al., 2006; Wood et al., 2012b).

162 In March 2010 aquatic plant cover and biomass were sampled using the methodology
163 described in Wood et al. (2012b). The mean percentage plant cover of all species (to within
164 the nearest 5 %) within the river channel at each river reach was estimated from a visual
165 inspection by a single observer from the river bank for 10 m reaches spaced equally over the
166 site (two reaches per 100 m length of riverbank; total 10 reaches per site). To reduce
167 sampling variance the same observer (KAW) made all estimates of macrophyte cover. A
168 previous study found that visual observations yield estimates of plant cover that are strongly
169 related ($R^2_{\text{adj}} = 59\%$) to values gained by in-stream measurements, although there is a
170 tendency for visual observations to over-estimate macrophyte cover by 27 % (Wood et al.,
171 2012d). However, given that this overestimate is consistent across river reaches, it should not
172 have influenced our ability to detect between-site differences. At each site, 10 plant samples
173 were taken using a 0.00785 m² cylindrical hand corer. Previous work concluded that a sample
174 size of 10 represented an efficient trade-off between sampling effort and accuracy of
175 measurement (Wood et al., 2012b). To select a 10 m reach for in-stream sampling, each 500
176 m site was divided into 50 equally sized sections, and a random number generator was used

177 to select the biomass sampling reach. Within each reach, corer sampling locations were
178 selected by generating random co-ordinates that were located in-stream (± 0.25 m) using fixed
179 tape measures along the bank and across the river. For each core the centre of the plant stand,
180 of whichever species were present, closest to the co-ordinates was sampled. In the laboratory,
181 non-plant material was removed and discarded, after which the sample was dried to a
182 constant mass at 60 °C using a Heraeus Kelvitron T oven (Thermo Fisher Scientific,
183 Loughborough, UK); constant mass was typically achieved after 72 hours. We measured
184 macrophyte dry mass (hereafter DM) to the nearest ± 0.01 g using a Sartorius PT120 balance
185 (Sartorius GMBH, Germany).

186 It was necessary to test the effects of swan grazing on both macrophyte biomass and cover
187 because these two different measures of plant abundance, whilst typically correlated, may not
188 show the same response to consumers (Wood et al., 2012b). For example, both Gayet et al.
189 (2011) and Wood et al. (2012b) detected strong negative effects of mute swans on
190 macrophyte cover, but not on biomass, during the seasonal period of peak macrophyte
191 abundance. Conversely, in a two-month mesocosm experiment Barrat-Segretain & Lemoine
192 (2007) found that the great pond snail (*Lymnaea stagnalis*) reduced the biomass, but not
193 cover, of Nuttall's waterweed (*Elodea nuttallii*).

194

195 *Mute swan abundance*

196 For each of our 20 river reaches we recorded the total number of swans of each age class
197 (adults, juveniles and cygnets) present during bankside surveys conducted in March 2009,
198 May 2009, July 2009, September 2009, December 2009, February 2009, and March 2010.
199 Age classes were determined based on plumage and bill characteristics following Birkhead &

200 Perrins (1986); cygnets (≤ 6 months old) have greyish-brown plumage; juveniles (7–18
201 months old) possess pinkish-grey bill colouration and some greyish-brown feathers; adults ($>$
202 18 months old) possess all-white plumage and orange bill colouration (Birkhead &
203 Perrins 1986). We used a tripod-mounted Swarovski STS 80HD (20 x 60) telescope
204 (Swarovski AG, Austria) to identify swans during surveys. Mute swans have a very high
205 detection probability (e.g. 0.94; Gayet et al., 2011b) due to their large body size, conspicuous
206 plumage, and tolerance of encroachment by humans; thus we could be confident that our
207 survey method quantified accurately the number of swans using each river site. Each survey
208 of our study river reaches was conducted over four days during daylight hours only. We
209 cannot exclude the possibility that swan movements during a survey may have resulted in
210 individuals being either undetected or double-counted. However, we argue that this was
211 unlikely as approximately one third of the swan population within the River Frome catchment
212 were fitted with a coloured leg ring, allowing individual identification as part of a long-term
213 monitoring project in southern England (Watola et al., 2003). Over our study period, we
214 observed a mean (\pm SE) of 28 ± 5 colour ringed swans per survey, with no ringed individual
215 ever observed twice during the same survey. After each survey, the swan biomass density (kg
216 ha^{-1}) at each site was calculated according to the formula:

$$217 \text{ Swan biomass density} = ((\text{Count}_A \cdot \text{Mass}_A) + (\text{Count}_J \cdot \text{Mass}_J) + (\text{Count}_C \cdot \text{Mass}_C)) / A,$$

218 where Count_A , Count_J , and Count_C represented the total numbers of adults, juveniles, and
219 cygnets, respectively, observed at the site during the month. Mass_A , Mass_J , and Mass_C were
220 mean mass (kg) of adults (10.8 kg), juveniles (8.8 kg), and cygnets (May = 0.3 kg, June =
221 2.8 kg, July = 5.5 kg, August = 7.3 kg, September = 8.8 kg), respectively (Bacon & Coleman,
222 1986). Although juveniles and cygnets have the same mass by the end of summer, the
223 differences in early summer made it necessary to separate juveniles and cygnets. Finally, A

224 was the total area (ha) of the river reach. For each river reach we calculated the mean swan
225 biomass density (kg ha^{-1}) in (i) the previous year (March 2009 to March 2010, inclusive), and
226 (ii) the previous peak grazing season (May 2009 to September 2009, inclusive).

227

228 *Statistical analyses*

229 We used a linear regression analysis to test the relationship between mean swan biomass
230 density per river reach (kg ha^{-1}) and mean water velocity (m s^{-1}) across all months in our
231 study. Similarly, linear regression analyses were used to test the relationships between (i)
232 plant biomass (g DW m^{-2}) and (ii) plant cover (%) in March 2010 and mean swan biomass
233 density (kg ha^{-1}) in (a) the previous year (March 2009 to March 2010, inclusive), and (b) the
234 previous peak grazing season (May 2009 to September 2009, inclusive). Whilst there was
235 some overlap between these time periods (5 out of 13 months overlap), these analyses
236 allowed both the core grazing period and extended grazing periods to be tested as contiguous
237 time periods, and thus represented the most comprehensive test of our predictions with our
238 data set. Testing the carry-over effects of the periods of low swan densities would have
239 involved testing across non-consecutive months, which would not have been valid as the
240 effects of grazing are not independent in time (Mitchell & Wass, 1996). We carried out all
241 analyses using R version 3.1.2 (R Development Core Team, 2015), with a statistically
242 significant result attributed where $p < 0.05$. Cook's Distances of <1 confirmed the absence of
243 outliers among residuals, whilst normality and homogeneity of variance of residuals were
244 confirmed visually for all models (Zuur et al., 2010).

245

246

247 **Results**

248 *Water velocity and swan use of river habitat*

249 Water velocity within the River Frome varied seasonally, with peak values observed during
250 winter (November-February), whilst summer and autumn (July-September) exhibited the
251 lowest values; mean monthly velocity values ranged from 0.4 m s⁻¹ in September 2010 to 1.2
252 m s⁻¹ in December 2009 (**Figure 1**). Across our study period we found a significant negative
253 relationship between the mean swan biomass density per site and water velocity ($F_{1,12} =$
254 19.73, $p < 0.001$, $R^2 = 62.2\%$; **Figure 2**). The relationship between the mean swan biomass
255 density per river reach (D , in kg ha⁻¹) and water velocity (v , in m s⁻¹) was described by the
256 equation: $D = 188.02 (\pm 26.52) + (-154.64 (\pm 34.81) \cdot v)$.

257

258 *Carry-over effects of swan grazing*

259 Our measure of plant abundance and swan biomass densities varied across our 20 river
260 reaches within the catchment (**Table 1**). We found no statistically significant relationship
261 between macrophyte biomass in March 2010 and the mean swan biomass density in the
262 previous year (**Table 2; Figure 3a**). Similarly, no relationship with macrophyte biomass was
263 found when only swan biomass densities during the previous peak grazing season (May to
264 September, inclusive) were considered (**Table 2; Figure 3c**). Furthermore, no significant
265 relationships were found between macrophyte cover in March 2010 and mean swan biomass
266 density in either the previous full year (**Table 2; Figure 3b**) or previous peak grazing season
267 (**Table 2; Figure 3d**).

268

269 **Discussion**

270 In this study we presented evidence that the densities of a key herbivore species in lowland
271 rivers, the mute swan, were related negatively to water velocity. Furthermore, we found that
272 swan biomass densities, of the magnitude shown previously to reduce up to 100 % of above-
273 ground plant abundance, were not related to macrophyte cover or biomass at the start of the
274 subsequent growing season in the following year. We argue that high overwinter water
275 velocities, which reached up to 1.2 m s^{-1} in December, removed large quantities of ungrazed
276 macrophyte tissue, and thus forced swans off the river due to the high energetic cost of
277 feeding in fast flows, allowing potentially grazed macrophyte beds to recover from any
278 grazing damage that may have occurred. Our findings suggest that seasonal changes in
279 hydrology may regulate herbivore impacts on aquatic plant communities in shallow lowland
280 riverine ecosystems.

281 We found evidence that high water flows were associated with low use of in-stream river
282 habitat by mute swans, in accordance with our first prediction. Several previous studies have
283 highlighted the sensitivity of mute swans to water velocities in river ecosystems, with high
284 velocities avoided (e.g. Vaughan et al., 2007; Royan et al., 2013). Wood et al. (2013a)
285 demonstrated that in-stream feeding on river macrophytes is less profitable for swans than
286 terrestrial feeding on pasture grasses until April-May (when velocity falls below 0.7 m s^{-1}),
287 due to the high energy expenditure required in fast flows. Our relationship between swan
288 densities and water velocity indicated that, above the 0.7 m s^{-1} value of Wood et al. (2013a),
289 swan densities were low; our field observations confirmed that this was due to non-breeding
290 flocks switching to terrestrial habitat. River temperatures are known to be correlated
291 negatively with velocity, as winter months have both the coldest temperatures and highest
292 velocities (Webb et al., 2003; Garner et al., 2014). However, Wood et al. (2013a) have shown

293 previously that water velocity has a much greater relative contribution to the profitability of
294 river habitat compared with temperatures, and thus we argue that seasonal changes in water
295 velocity, not temperature, explained our findings.

296 The effects of the seasonal changes in hydrology on swan use of river habitat also have
297 implications for swan grazing impacts on terrestrial vegetation which the swans feed on
298 during periods of high water velocity (Trump et al., 1994; Wood et al., 2013b). Swan
299 herbivory in pasture fields adjacent to a shallow lowland river in southern England caused a
300 mean pasture grass yield loss of 11.4 % (Harrison, 1984). Changes in the date on which water
301 velocity forces swans to switch from riverine to terrestrial habitat will affect the duration of
302 the grazing season in these terrestrial habitats as well as aquatic habitats. Increased duration
303 of swan grazing in agricultural fields may increase grazing impacts on crops and exacerbate
304 existing conflicts between farmers and conservationists (Wood et al., 2015).

305 The results of our study indicated no carry-over effect of herbivore biomass densities in one
306 year on plant abundance in the following year, in accordance with our second prediction.

307 Although we did not test the effects of swans on macrophyte abundance within a season and
308 grazing impacts were thus inferred, such short-term impacts have been well documented by
309 previous studies (O'Hare et al., 2007a; Porteus et al., 2011; Wood et al., 2012b; Wood et al.,
310 2012c). Indeed, based on the relationship between swan biomass densities and macrophyte
311 abundance reported for our study system by Wood et al. (2012b), the swan biomass densities
312 of $>190 \text{ kg ha}^{-1}$ observed in our current study would have eliminated macrophyte above-
313 ground biomass within the growing season (i.e. a reduction of 100 %). We argue that our
314 observed lack of herbivore carry-over effects were linked to high overwinter water velocities
315 via two mechanisms. Firstly, at river reaches which had not been grazed by swans, and thus
316 still had relatively high macrophyte abundance, large quantities of macrophyte tissues were

317 removed by the increasing water velocities. High flows during winter flood conditions
318 increase the physical forces acting on the plant beds and remove large quantities of plant
319 above-ground tissues in flowing waters (Dawson & Robinson, 1984; Franklin et al., 2008).
320 Secondly, at grazed river reaches macrophytes were able to regrow from their root network,
321 which the swans leave largely intact (O'Hare et al., 2007a), until they reach the threshold
322 abundance determined by flow conditions. Finally, the high winter water velocities forced
323 swans to leave the river habitat and switch to feeding in adjacent terrestrial pasture fields
324 (Wood et al., 2013a; Wood et al., 2013b), preventing further grazing at recovering river
325 reaches. Thus, both grazed and ungrazed sites showed no consistent differences in
326 macrophyte biomass or cover by the following Spring (**Figure 3**). Overall, water velocity
327 appears to be a key determinant of macrophyte abundance in shallow rivers over inter-annual
328 timescales (Riis & Biggs, 2003; Franklin et al., 2008), whilst the effects of swan grazing on
329 macrophyte abundance do not extend outside the year in which grazing occurred.

330 The lack of herbivore carry-over effects on aquatic plant abundance in the following growth
331 seasons suggested that swan grazing did not affect plant overwinter survival. In other systems
332 herbivory on above-ground tissues can affect plant survival and future growth by causing
333 reallocation of resources from the roots to compensate for losses due to herbivory (Whittaker,
334 1982). For example, selective herbivory on *Rumex crispus* leaves led to resource
335 remobilisation from the roots, decreasing root mass and increasing the wash-out of this plant
336 under flood conditions (Whittaker, 1982). More detailed research on macrophyte root
337 biomass dynamics under different levels of herbivory is required to improve our
338 understanding of the conditions under which resource reallocation can occur, and its potential
339 impact on plant abundance.

340 Globally, marked changes in river flows have occurred due to climate change, over-
341 abstraction of water, and physical modification of rivers related to energy and water demand
342 (Arnell, 2003). Water velocities during winter are expected to increase for lowland rivers
343 such as the River Frome, although the magnitude of increase is highly variable and will likely
344 reflect local conditions (Hannaford & Buys, 2012; Wilby, 2006). Future changes in flow
345 conditions may also alter the suitability of river reaches for waterbirds, altering the spatial
346 distributions of species (Royan et al., 2015). Thus, future changes in flow conditions will
347 likely have implications for the timing and duration of the herbivore grazing season in rivers.

348 Across aquatic ecosystems, there may be other physical processes that could limit herbivore
349 impact on aquatic plants. For example, temporal fluctuations in water levels are common in
350 lentic ecosystems, and increased depth may limit the ability of non-diving waterbirds such as
351 swans and geese to feed on submerged plants (Clausen, 2000; Stillman et al., 2015).

352 Similarly, the formation of ice during cold weather will prevent semi-aquatic herbivores such
353 as waterfowl from reaching submerged macrophyte beds. Indeed, migratory herbivorous
354 waterfowl are known to time their migrations so that they arrive at aquatic stopover river
355 reaches during ice-free periods, to allow foraging on submerged macrophytes (e.g. Nolet *et*
356 *al.*, 2001).

357 Here, we have provided the first evidence that seasonal hydrological changes may limit the
358 temporal extent of herbivore impacts in aquatic ecosystems. Such knowledge of the temporal
359 scale over which herbivores can impact plant abundance is important for three key reasons.

360 Firstly, recent authors have highlighted the need to incorporate herbivory on macrophytes
361 into our theories of the structure and functioning of aquatic ecosystems (Bakker et al., 2016).

362 Secondly, research on terrestrial ecosystems has shown that quantifying temporal links
363 between aquatic plants and their herbivores is necessary to understand plant-herbivore co-

364 evolution (Jermy, 1984; Milchunas & Lauenroth, 1993). Finally, elucidating the conditions
365 under which herbivore grazing of aquatic plants occurs will help ecosystem managers
366 understand when and where grazing impacts are likely to occur, which will aid in the
367 management of grazing impacts and associated conflicts (Wood et al. 2015).

368

369

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378

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552 **TABLES**

553 **Table 1:** A summary of the values associated with plant abundance and swan densities at our
 554 20 study river reaches. Following convention, swan biomass densities are expressed as live
 555 mass, whilst macrophyte biomass is expressed as dry mass (DM).

Variable	Unit	Time period	Mean	SD	Min.	Max.
Macrophyte biomass	g DM m ⁻²	March 2010	38.4	16.2	8.7	66.9
Macrophyte cover	%	March 2010	16.1	6.3	6.5	31.5
Swan density (all year)	kg ha ⁻¹	March 2009 – March 2010	96.0	99.1	0.0	342.8
Swan density (peak grazing season)	kg ha ⁻¹	May – September 2009	182.0	198.5	0.0	642.4

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558 **Table 2:** The results of linear regression analyses of two measures of plant abundance
 559 (biomass and cover) in March 2010 modelled as swan biomass density in one of two periods
 560 in the previous year: ‘all year’ (March 2009 – March 2010, inclusive) or ‘peak grazing
 561 season’ (May – September 2009).

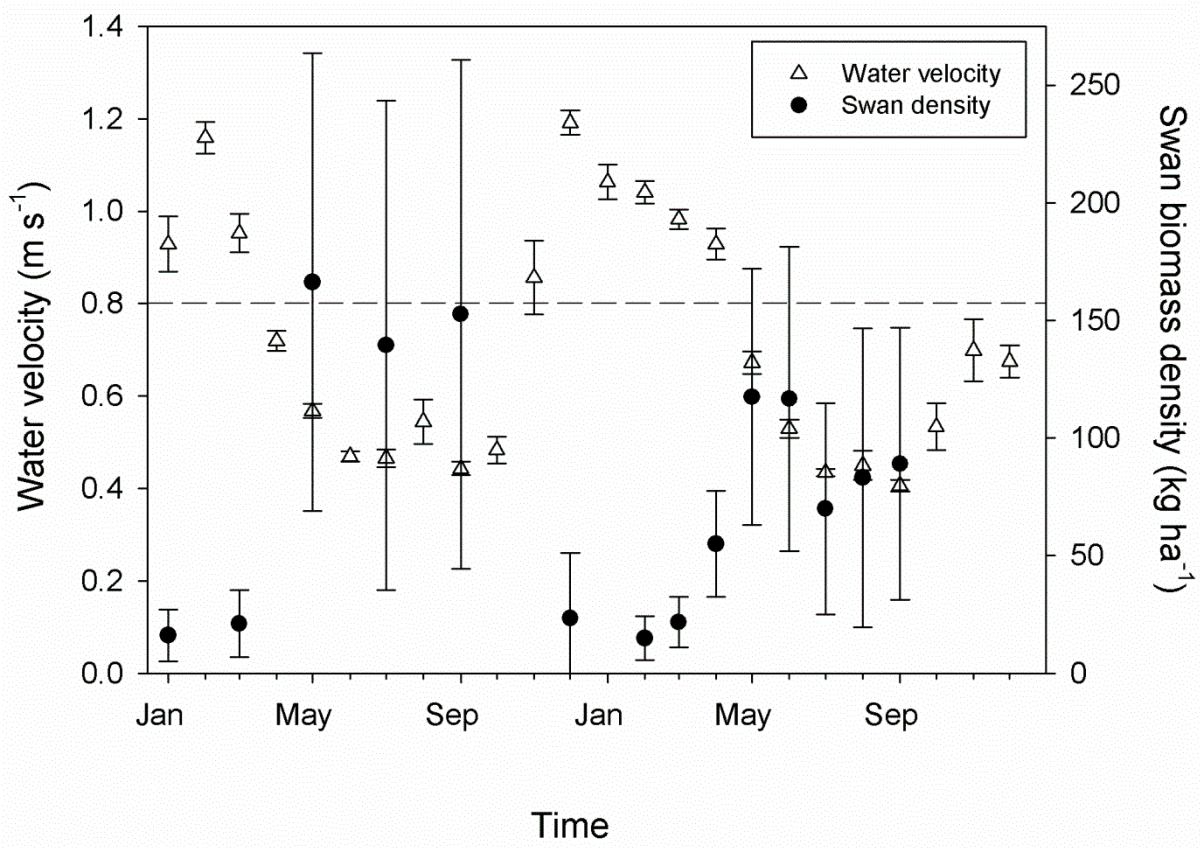
Plant abundance	Timing of swan grazing	F	n	p	R² (%)
Biomass	March 2009 – March 2010	0.53	20	0.477	2.9
Biomass	May – September 2009	0.59	20	0.454	3.2
Cover	March 2009 – March 2010	0.40	20	0.534	2.2
Cover	May – September 2009	0.75	20	0.399	4.0

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564 **FIGURES**

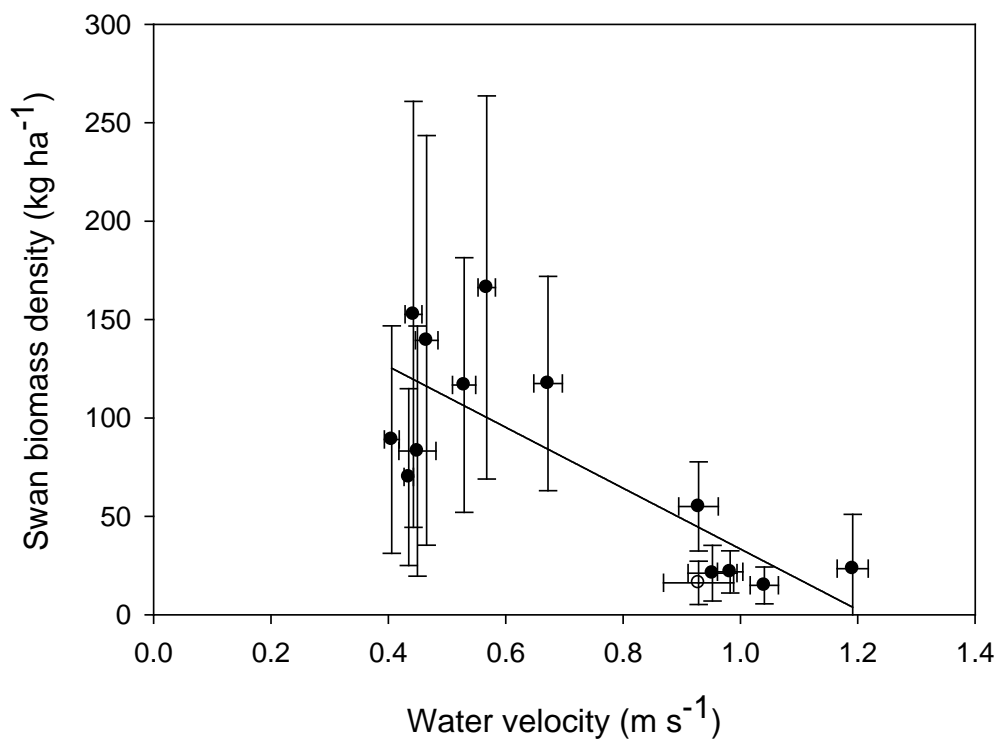
565 **Figure 1:** The seasonal variation in mean monthly water velocity in the River Frome and the
566 mean swan biomass density across our 20 river river reaches. The dashed line indicates the
567 threshold water velocity value of 0.8 m s^{-1} , above which senescent macrophyte tissues are
568 known to be washed out (see text).



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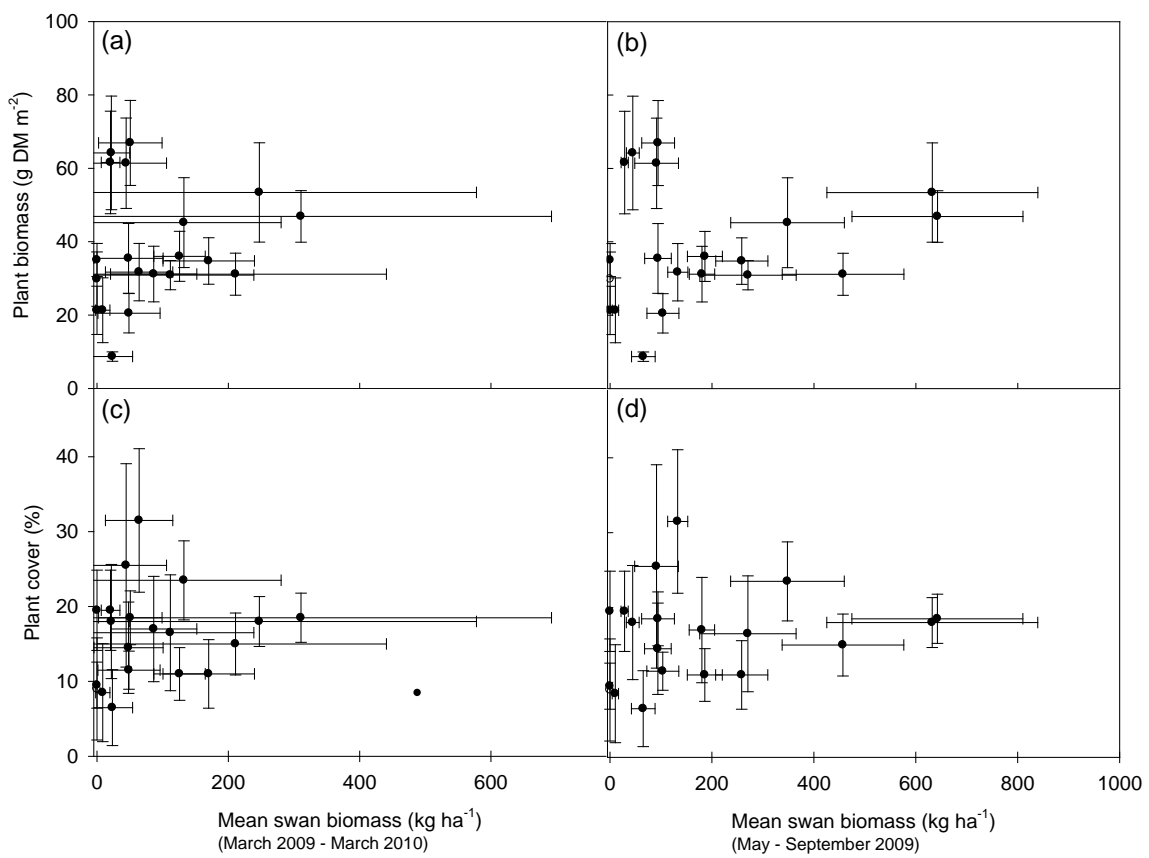
571 **Figure 2:** The negative relationship between the mean swan biomass density per site and
572 water velocity in the River Frome. Each data point represents one monthly mean (\pm 95 % CI)
573 value.



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576 **Figure 3:** The lack of relationship between early season macrophyte abundance and the
577 grazing pressure experienced in the previous growing season. All plant abundance
578 measurements were taken in March 2010. Mean swan biomass density between March 2009
579 and March 2010 was not related to mean aquatic plant biomass (a) or cover (c) in March
580 2010. The 95 % CI associated with plant abundance and swan biomass densities at each site
581 are indicated.



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