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 exclosure 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

Introduction

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

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

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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 km^2

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 °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).

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138   *Water velocity*

139   Daily mean water discharge ($m^3 s^{-1}$) 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    $v = a \cdot (1 - \exp(-b \cdot Q))$,

151   where Q was the mean discharge ($m^3 s^{-1}$), whilst a (1.44) and b (0.12) were the intercept and

152   slope of the relationship between cross-sectional area and discharge.

153

Macrophyte abundance

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

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

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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 (± 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 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).

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Results

Water velocity and swan use of river habitat

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

Carry-over effects of swan grazing

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

Discussion

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

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

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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 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

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removed by the increasing water velocities. High flows during winter flood conditions

increase the physical forces acting on the plant beds and remove large quantities of plant

above-ground tissues in flowing waters (Dawson & Robinson, 1984; Franklin et al., 2008).

Secondly, at grazed river reaches macrophytes were able to regrow from their root network,

which the swans leave largely intact (O'Hare et al., 2007a), until they reach the threshold

abundance determined by flow conditions. Finally, the high winter water velocities forced

swans to leave the river habitat and switch to feeding in adjacent terrestrial pasture fields

(Wood et al., 2013a; Wood et al., 2013b), preventing further grazing at recovering river

reaches. Thus, both grazed and ungrazed sites showed no consistent differences in

macrophyte biomass or cover by the following Spring (**Figure 3**). Overall, water velocity

appears to be a key determinant of macrophyte abundance in shallow rivers over inter-annual

timescales (Riis & Biggs, 2003; Franklin et al., 2008), whilst the effects of swan grazing on

macrophyte abundance do not extend outside the year in which grazing occurred.

The lack of herbivore carry-over effects on aquatic plant abundance in the following growth

seasons suggested that swan grazing did not affect plant overwinter survival. In other systems

herbivory on above-ground tissues can affect plant survival and future growth by causing

reallocation of resources from the roots to compensate for losses due to herbivory (Whittaker,

1982). For example, selective herbivory on *Rumex crispus* leaves led to resource

remobilisation from the roots, decreasing root mass and increasing the wash-out of this plant

under flood conditions (Whittaker, 1982). More detailed research on macrophyte root

biomass dynamics under different levels of herbivory is required to improve our

understanding of the conditions under which resource reallocation can occur, and its potential

impact on plant abundance.

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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-

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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).

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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	R^2 (%)
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

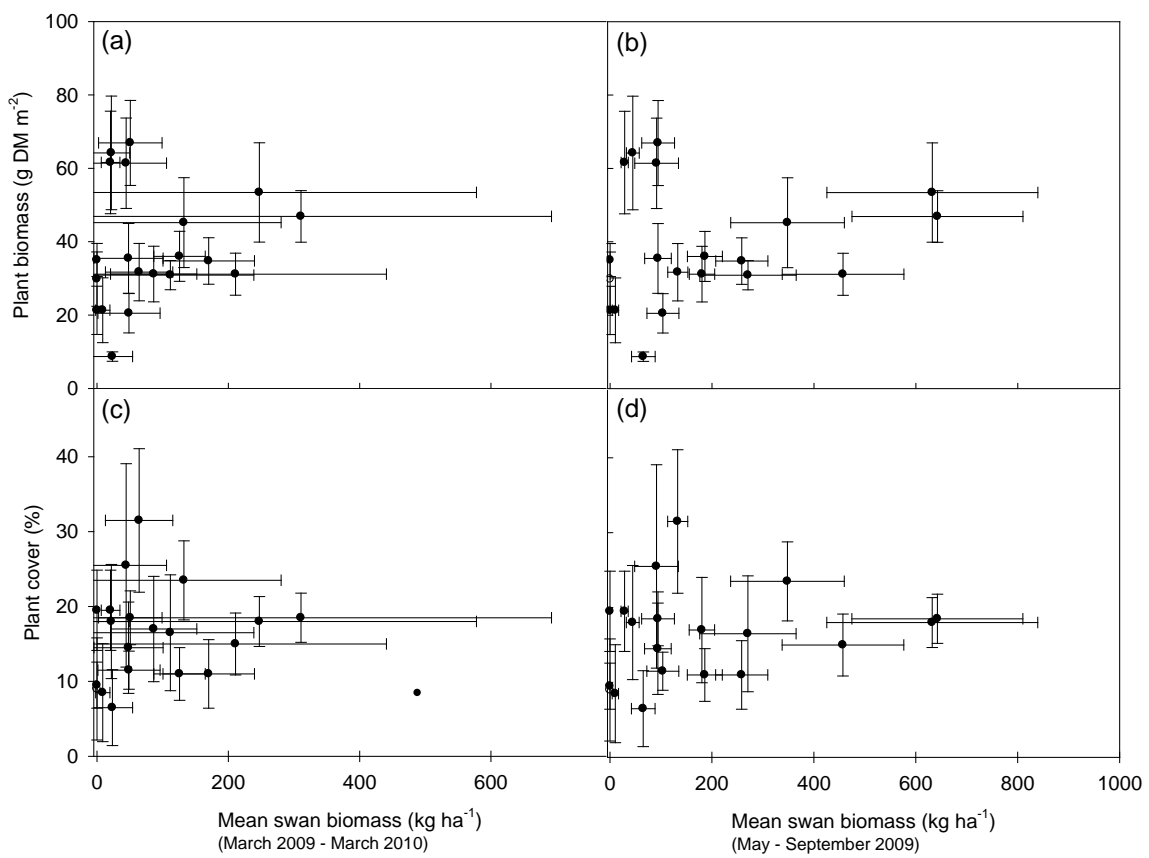568 known to be washed out (see text).
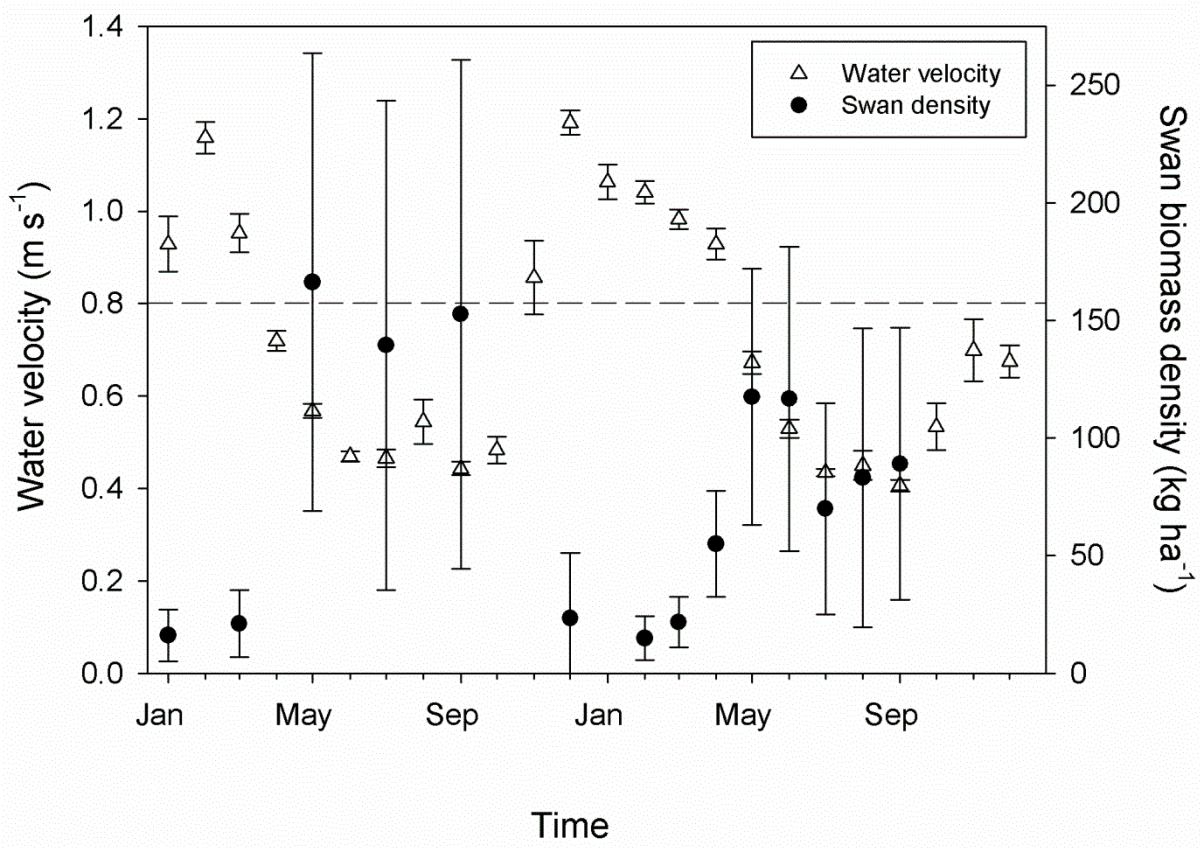
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571 **Figure 2:** The negative relationship between the mean swan biomass density per site and

572 water velocity in the River Frome. Each data point represents one monthly mean (± 95 % CI)

573 value.
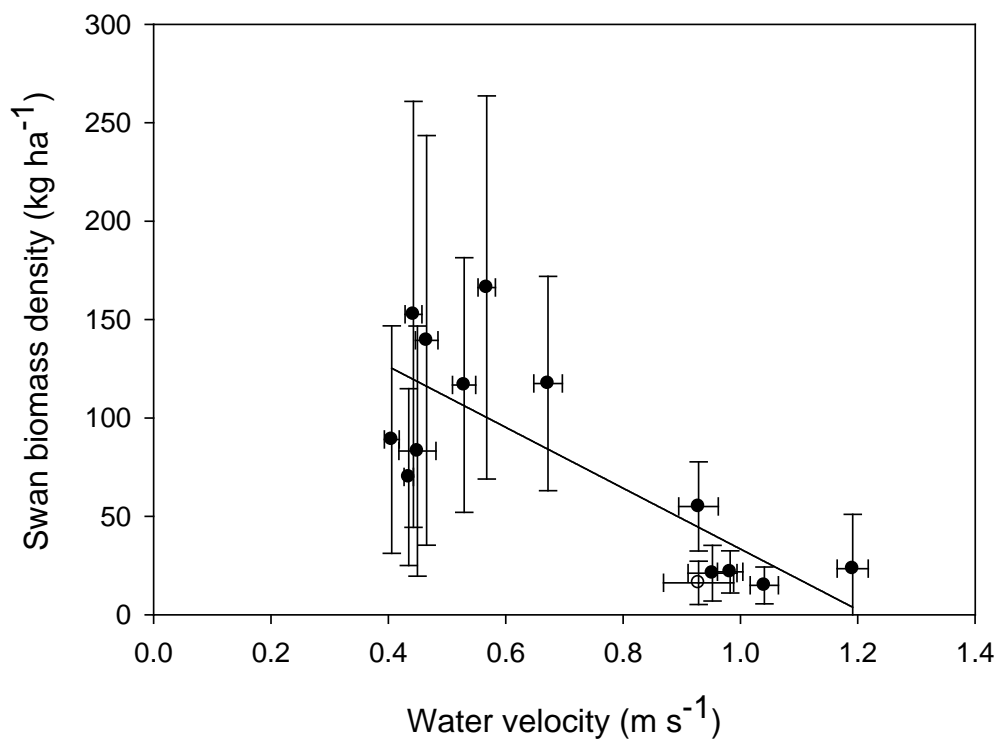
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576 **Figure 3:** The lack of relationship between early season macrophyte abundance and the

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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