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Do mute swan (*Cygnus olor*) grazing, swan residence and fishpond nutrient availability interactively control macrophyte communities?

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ABSTRACT

The mute swan (*Cygnus olor* Gmelin) is one of the largest herbivorous waterbirds in the world. Its population increased dramatically over the last decades in Western Europe, leading to concerns about its potential impact on aquatic ecosystems. Indeed, swan consequences on fishponds remain poorly investigated, although fishpond animal communities and economic value both largely depend on aquatic macrophytes. We carried out an experiment in the Dombes region (Eastern France) with 96 exclosures on 24 fishponds. Our aim was to assess the impact of swan grazing on aquatic macrophyte presence, abundance and community structure (diversity and evenness) during the growing season (April to July). We also considered the potential effect of swan stay (i.e. number of swan days ha^{-1}) and nutrient availability on macrophyte depletion. Swan grazing negatively affected the presence and abundance (% cover) of macrophyte beds, particularly at high swan density. No significant effect on dry biomass was found. Furthermore, swan grazing negatively affected community structure, suggesting that mute swan promoted the dominance of a few species in macrophyte communities. Whatever the macrophyte variable considered, nutrient availability in fishponds did not affect macrophyte depletion rate. It is speculated that both the repeated use of the same fishponds by birds and their expansion within the landscape may lead to more acute and broader consequences for macrophyte beds over the longer term.

1. Introduction

Although herbivory has long been considered to have a minor impact on aquatic macrophytes, Lodge (1991) demonstrated that grazers can affect these plants, and such relationships have since received a growing interest. It is now a recognized fact that waterfowl grazing can have a wide range of possible effects on aquatic plant communities. Within macrophyte communities, waterfowl can modify dominance relationships by consuming preferred species (Santamaria, 2002; Rodriguez-Villafane et al., 2007; Sandsten and Klaassen, 2008) and limit macrophyte production (Idestam-Almquist, 1998; Rodriguez-Perez and Green, 2006; Schmieder et al., 2006).

Numerous studies carried out on wetlands reported a decrease in plant biomass associated with grazing by large herbivorous birds (Esselink et al., 1997; Gauthier et al., 2006; Tatu et al., 2006; O'Hare et al., 2007), which likely has carry-over effects onto associated animal communities. The mute swan (*Cygnus olor* Gmelin), as one of the largest waterbird species (ca. 10 kg, Cramp et al., 1986), may disturb macrophyte beds over large areas in aquatic ecosystems. Indeed, a mute swan is considered to consume 3–4 kg of aquatic vegetation daily (Cramp et al., 1986) plus losses generated by non-consumptive destruction, e.g. disturbance generated during foraging activities (see Lodge, 1991). Given the recent expansion of Mute swan populations in fishpond regions (Musil and Fuchs, 1994; Fouque et al., 2007), their depletion of macrophytes in these ecosystems is of major concern. It is thus crucial to quantify their impact on fishponds, where both ecological and socioeconomical stakes depend on macrophytes. Some fishpond macrophyte communities are indeed listed in the European Habitat directive, and Common carp (*Cyprinus carpio* L.) bred by landowners uses macrophyte beds as a spawning support (Crivelli, 1983; Rozas and Odum, 1988).

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It is likely that the potential impact of grazers on plants may vary during the growing season, owing to grazing intensity as well as nutrient availability for plants (see Maschinski and Whitham, 1989). Indeed, the relatively short stay of numerous swans in moulting flocks and the repeated use of the same waterbody by a territorial nesting pair over the breeding season should cause different grazing pressures and have different consequences on macrophytes (Tatu et al., 2006). Plant productivity also depends on the interaction between grazers and nutrient availability (Maschinski and Whitham, 1989; Power, 1992; Hawkes and Sullivan, 2001), just like plant species richness (Gough and Grace, 1998; Proulx and Mazumder, 1998). However, such interactions may have potentially opposite directions according to nutrient availability and are difficult to predict *a priori*. Furthermore, most earlier studies on grazing processes in aquatic ecosystems have considered the potential effects of grazing, herbivore residence and nutrient availability in a waterbody separately, although it is likely that these factors have combined effects. In order to investigate if and to what extent mute swan grazing affects macrophyte communities we considered here how these factors simultaneously interact with grazing in affecting the dynamics of macrophyte communities:

We tested (1) if grazing affects macrophyte presence, expecting more frequent bare sediment where swans could graze. We were also interested in (2) the effect of grazing on macrophyte abundance, expecting lower plant cover and/or biomass in areas available to swans. Finally, we predicted (3) that swan grazing would affect macrophyte community structural though the direction of the effect is uncertain. We were further interested in assessing what modulates macrophyte depletion rate by swans: we thus tested if the above potential effects were more acute when swan stay was more extended or if they differed depending on fishpond nutrient availability.

2. Methods

2.1. Study area

The study took place in the Dombes region (Eastern France 45°57′N, 05°02′E), which contains 1450 freshwater fishponds of 7.3 ha (±0.2 SE) on average. Most fishponds have a depth lower than 1 m and transparency varies from a very clear water to a highly turbid state. Mostly also have a reedbed, though its extent is highly variable too. The main macrophytes in the area are Eurasian water-milfoil (*Myriophyllum spicatum* L.), various-leaved pondweed (*Potamogeton gramineus* L.), curled pondweed (*Potamogeton crispus* L.), holly-leaved naiad (*Najas marina* L.), brittle naiad (*Najas minor* All.) and pond water-crowfoot (*Ranunculus peltatus* Schrank) (Curtet, unpublished data), but macrophyte communities differ greatly between fishponds. Mute swans nested in the area for the first time during the 1970s. The population has gradually increased to ca. 1000 individuals nowadays (Benmergui et al., 2005).

2.2. Study sites, period and experimental design

Since aquatic macrophyte beds vary strongly between fishponds in terms of macrophyte abundance and community composition, numerous fishponds were sampled. The experiment to assess the impact of mute swan on aquatic macrophytes was carried out in 24 fishponds (mean area: 15.8 ha ± 2 SE) in 2008 and 2009, from early April until the end of July. Fishponds known to be regularly used by nesting and moulting swans were selected.

The experimental set comprised an open plot (accessible to all species including swans) and an exclosure that was inaccessible to mute swans but accessible to the other herbivores such as coot *Fulica atra* L., and coypu *Myocastor coypus* Molina, which were indeed observed inside the exclosures. The exclosure was made of 1.2 m high wire netting (mesh size 0.15 m) delimiting an area of 5 × 5 m^2. Two threads between the opposite corners of the exclosure prevented swans from entering the area from above. Due to potential consumption by swans from the outside, the outer 1 m of the exclosure was not considered in the analyses, so that effective exclosure area was 9 m^2. The associated open plot was positioned at 10 m from the exclosure, and positioned in areas of similar depth to the exclosure. The open plot represented an area of 9 m^2. We identified quadrats of 1 m^2 in both open plots and exclosures. Four such experimental sets (one exclosure and its associated open plot) were used per fishpond, hence a total of 96 experimental sets.

2.3. Fishpond nutrient availability

One of the aims of the study was to unravel the relative effect of nutrient availability compared to the potential effect of swans. Since it was impractical to regularly measure nutrients in the water column, we measured nutrient concentration in interstitial water following Enell and Löfgren (1988). Nutrients in the interstitial water were considered to measure nutrient availability to plants. It has been measured before the growing season. Once the growing season started, plants can store a non-negligible amount of nutrients which can no more be measured (Kufel and Kufel, 2002). Sediment samples were taken with an Ekman grab at three random points per fishpond in March. Interstitial water was obtained by aqueous extraction after mixing of the three samples. Physico-chemical parameters measured were total phosphorus, Kjeldahl nitrogen, pH, Ca^{2+} and orthophosphates. In order to get a compound index for nutrient availability we ranked the fishponds on the first axis of a Principal Component Analysis (PCA).

2.4. Swan days and non-destructive vegetation measurements

Swans were counted weekly from April until the end of July. The total number of swan days (number of birds multiplied by their length of stay) from the beginning of the experiment was then calculated monthly to obtain an estimate of swan grazing intensity on macrophytes. In order to control for the influence of fishpond size in assessing the effect of swan stay, the total number of swan days was calculated per area unit, i.e. swan days ha^{-1}. Swan days ha^{-1} thus represents the grazing intensity exerted on macrophytes for a given site.

Plant cover was estimated in each 1 m^2 quadrat within exclosures (n = 9 quadrats each) and associated open plots (n = 9 quadrats each), the last week of May, June and July by wading. In each quadrat, total plant cover and species composition (10% percentage classes) were visually estimated.

2.5. Vegetation biomass

At the end of the monitoring period, we took destructive measurements of vegetation biomass through plant harvest (i.e. before the exclosures were taken out from fishponds in July). This provided an exhaustive measurement of the absolute response of the macrophyte community to swan depletion (i.e. all plant species in the water column were recorded) at the end of the experiment. Vegetation was sampled on 85 of the 96 experimental sets (11 experimental sets were removed due to minor problems in July). Vegetation biomass however varied greatly between fishponds, and was so high in some cases (i.e. >3 kg fresh mass m^{-2}) that it was impractical to sample all quadrats of the 85 sets: four quadrats systematically selected per set were therefore sampled (2 in the exclosure plus 2 in the associated open plot). Biomass samples were