

## REVIEW ARTICLE

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# Herbivory on aquatic macrophytes by geese and swans—a review of methods, effects, and management

*Herbivori av gäss och svanar på akvatiska makrofytter – en översikt av metoder, effekter och förvaltning*

Elsie Kjeller<sup>1,2</sup>, Jonas Waldenström<sup>2</sup>, Johan Elmberg<sup>1</sup> and Gunnar Gunnarsson<sup>1</sup>

<sup>1</sup>Department of Environmental Science, Kristianstad University, 291 88 Kristianstad, Sweden | [elsie.kjeller@hkr.se](mailto:elsie.kjeller@hkr.se) | [johan.elmberg@hkr.se](mailto:johan.elmberg@hkr.se) | [gunnar.gunnarsson@hkr.se](mailto:gunnar.gunnarsson@hkr.se) <sup>2</sup>Department of Biology and Environmental Science, Linnaeus University, 391 82 Kalmar, Sweden | [jonas.waldenstrom@lnu.se](mailto:jonas.waldenstrom@lnu.se)



**IN RECENT DECADES**, interest has grown in how increasing populations of herbivorous geese and swans (Anseriformes: Anatidae: Anserinae) affect macrophyte communities in wetlands, especially because many waterbodies are simultaneously subjected to stressors like eutrophication and biodiversity declines. Here, we review the literature on methods applied in grazing experiments that have been conducted in aquatic ecosystems. We also investigate and how different macrophyte characteristics may respond to waterfowl herbivory. Results indicate that both research methodology and responses of macrophytes differ widely among studies. While most experimental studies on grazing pressure employ a ‘paired plot design’ with exclosures and open control plots, the structure, size, and placement of plots vary among studies. Commonly sampled macrophyte variables are biomass (of either above- or below-ground plant parts), density, height, plant cover, and community composition. The literature provides support that geese and swans significantly affect several of these variables, but the outcome depends on additional factors, e.g. waterfowl density, water depth, and timing (within or between seasons/years). Because of the persisting conservation threats to aquatic ecosystems, more knowledge is needed about potential direct and indirect consequences of waterfowl herbivory in these environments.

**Keywords:** exclosure | grazing | vegetation | waterbird | wetland

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## Introduction

Eutrophication, increased turbidity, and browning are but a few of the current environmental changes facing aquatic ecosystems (Porter *et al.* 2013, Kritzberg *et al.* 2020). Past, present, and future deterioration of these ecosystems will likely have negative consequences for economy and human wellbeing (Dudgeon *et al.* 2006, Alikhani *et al.* 2021), and not least for a wide range of organisms that depend on aquatic ecosystems for their survival (Mitsch *et al.* 2015). It is therefore essential to get a better understanding of the causes behind such deterioration, including interactions between organisms within the ecosystems. One interaction of special interest is that between herbivores and aquatic plants (i.e., macrophytes); abundance and composition of these plants contribute to the structure and health of aquatic ecosystems, for example by providing food and shelter, and by enhancing water quality (Scheffer *et al.* 1993, Jeppesen *et al.* 1997, Tabacchi *et al.* 2000, Bayley & Prather 2003, Porter *et al.* 2013, Mitsch *et al.* 2015, Phillips *et al.* 2016, Moomaw *et al.* 2018, Andersen *et al.* 2021). However, many ecological studies have focused on the influence of macrophytes on higher trophic levels (bottom-up effects) rather than the reverse (top-down effects; Kollars *et al.* 2017, Wood *et al.* 2017). In recent years, though, consumption of macrophytes by large vertebrate herbivores has gained more attention, and research indicates that such top-down effects may play a more important role than previously thought (Bakker *et al.* 2016a).

For a long time, effects of herbivory were mainly studied in terrestrial ecosystems, whereas herbivory in aquatic ecosystems was believed to be of less significance (Lodge *et al.* 1998, Bakker *et al.* 2016a). This view primarily concerned freshwater ecosystems and it was based on the assumption that many macrophytes are unpalatable to larger herbivores, being too rigid in structure and having lower nutritional value than their terrestrial counterparts. According to Lodge *et al.* (1998), this view changed due to a growing number of studies in the 1990s demonstrating opposing results. Since then, further research has suggested that herbivory may have an even greater impact in aquatic compared to terrestrial ecosystems, because many aquatic macrophytes lack structural defences and are thus more readily consumed (Cyr & Pace 1993, Lodge & Tyler 2020). Evidence of this can be seen in a review

by Bakker *et al.* (2016b) who found that herbivores in aquatic (both freshwater and marine) ecosystems consume about 30–80% of the annual primary production in general, a considerably higher ratio than the 10–25% observed in terrestrial ecosystems.

Common vertebrate herbivores that feed on macrophytes in aquatic ecosystems in north-western Europe are fish (e.g. roach *Rutilus rutilus* and rudd *Scardinius erythrophthalmus*), common muskrat *Ondatra zibethica*, beaver *Castor* spp., moose *Alces alces*, and various waterbird species (Prejs 1984, Bergman & Bump 2015, Vermaat *et al.* 2016). Geese and swans are the largest herbivorous waterbirds, and since several species have increased in numbers and expanded their geographical range over past decades (Fox & Madsen 2017b, Rees *et al.* 2019), there is growing concern that their foraging influences aquatic ecosystems (Dos Santos *et al.* 2012, Buij *et al.* 2017). In turn, this has sparked a number of studies, most of which have gathered information on waterbird herbivory in natural environments, often by comparing grazed and ungrazed areas in different types of aquatic ecosystems (Van Donk & Otte 1996, Van Onsem & Triest 2018, Madsen *et al.* 2019). In descriptive studies, researchers have also examined connections between increased presence of herbivorous birds and vegetation abundance within an aquatic ecosystem (Pöysä *et al.* 2017). In experimental studies, on the other hand, the impact is often assessed by comparing grazed and ungrazed areas by establishing exclosures, typically fenced plots. Experiments can be designed differently depending on study site, vegetation type, and herbivores of interest. Although some studies are designed exclusively for geese or swans, many also include other herbivorous or omnivorous waterbirds such as Eurasian Coot *Fulica atra* (Perrow *et al.* 1997) and Eurasian Wigeon *Mareca penelope* (Mayhew & Houston 1999).

With time a wide variety of studies on waterbird herbivory has accumulated, not the least experimental studies using exclosures. However, methods applied in these studies have rarely been explored. The aim of this review was therefore: (1) to synthesize the research methodology applied in experimental exclosure studies; and (2) to examine the observed effects by herbivorous waterbirds on aquatic vegetation in experimental as well as descriptive studies. Studies included were found by searching for peer-reviewed papers in Google Scholar and in reference lists of papers thus obtained.

In Google Scholar, we ran separate queries, combining the keywords *herbivor* (short for herbivory, herbivore, and herbivorous) and *macrophyte* with either *goose*, *geese*, *swan*, or *waterbird*. We included studies that had been conducted in various types of aquatic ecosystems (freshwater, marine, as well as brackish) to obtain a wider perspective of applied research methodology and observed grazing effects. Before addressing these aims, the status and foraging ecology of geese and swans in north-western Europe are presented. In the end, we discuss conflicts related to the management of wetlands and waterbirds, followed by a conclusion of our findings.

## Geese and swans in north-western Europe – status and foraging ecology

Geese and swans belong to the subfamily Anserinae (Anseriformes: Anatidae). Geese in north-western Europe belong to two genera: *Anser* (five species) and *Branta* (four species), whereas the swans all belong to the genus *Cygnus* (three species). Amongst the most abundant and increasing goose species in north-western Europe is the Greylag Goose *Anser anser*, the Canada Goose *Branta canadensis*, and the Barnacle Goose *B. leucopsis* (Table 1; Fox *et al.* 2010, Fox & Madsen 2017b). Regarding swans, the Whooper Swan *Cygnus cygnus* has increased considerably in population size and expanded its geographical range in many north-western European countries (Nilsson 2014, Pöysä *et al.* 2018), whereas the Mute Swan *C. olor* has a more unchanged population and distribution (Rees *et al.* 2019). In contrast to the prospering and stable species, populations of Taiga Bean Goose *A. f. fabalis*, Lesser White-fronted Goose *A. erythropus*, and Bewick's Swan *C. columbianus bewickii* are considered threatened due to long-term declines (Nuijten *et al.* 2020, Liljebäck *et al.* 2021).

Several of the species have historically been on the verge of regional extinction due to high hunting pressure and habitat loss (Fox & Madsen 2017b). The Whooper Swan, for instance, was nearly extinct in parts of Fennoscandia in the late 1800s, as were some populations of the Greylag Goose in the early 1900s (Nilsson 2014). Both species began to increase during the 1960–1970s, primarily as a response to changed hunting regulations (Nilsson 2014, Liljebäck *et al.* 2021). Climate

change may also have favoured large herbivorous waterfowl through milder winters and longer growing seasons, not only affecting survival but also migration patterns, as increasing food availability has shifted wintering populations to the north (Guillemain *et al.* 2013, Nilsson 2014). Another factor presumed to have had a central role in promoting population growth of geese and swans is changes in agricultural methods (Laubek 1995, Fox & Madsen 2017b). Present-day agricultural landscapes attract large numbers of geese and swans by providing open areas with easy-to-access, highly nutritious food, available nearly all year round, not least during spring and fall migration (Fox *et al.* 2017a). This in turn has led to conflicts with agriculture due to reduced harvest yields, in some cases resulting in substantial economic losses (Bjerke *et al.* 2021).

Due to their high body mass, geese and swans need to consume considerable amounts of vegetation to meet daily energy needs (Gauthier 2006, Wood *et al.* 2012a, Dessborn *et al.* 2016). While geese and swans are obligate herbivores, they have quite different foraging behaviours. Geese commonly graze both terrestrial and emergent aquatic plants, whereas swans mainly feed on submerged aquatic vegetation (Table 2). Swans feed in open waters up to 1 m deep by either dipping their necks below the water surface, up-ending, or by making vegetative parts emerge to the water surface through bioturbation caused by foot-paddling. These techniques can also be used to facilitate food access for their young. Summer diets of geese and swans mainly consist of green vegetative parts, preferably growing shoots, leaves, and seeds (Cramp *et al.* 1986). In winter, birds in both groups dig for below-ground parts such as tubers and rhizomes, whereas arable crops with time have become a large part of the diet in fall, winter, and spring (Fox *et al.* 2017a).

## Experimental research approaches

Descriptive studies often examine the relation between macrophyte abundance and waterbird density in different locations using observational data (Pöysä *et al.* 2017). In many experiments, macrophytes are protected from waterbird herbivory by fenced enclosures (Veen *et al.* 2013, Svidenský *et al.* 2021). Comparative measurements, for example vegetation biomass and

**TABLE 1.** Estimated sizes of goose and swan populations breeding or wintering in north-western Europe, and their recent long-term (>10 years) population trend classified as increasing (INC) or decreasing (DEC).  
 — Uppskattade populationsstorlekar av gås- och svanarter häckande eller övervintrande i nordvästra Europa, liksom deras sentida långsiktiga (>10 år) trender klassade som ökande (INC) eller minskande (DEC).

Species Art	Population Population	Population estimate Populationsskattning	Year of estimate År för skattning	>10 years trend Trend för > 10 år	Reference Källa
Bean Goose <i>Sädgås</i>					Fox & Madsen 2017b
<i>Anser fabalis rossicus</i>	Russia Ryssland	600,000	2014	INC	
<i>Anser fabalis fabalis</i>	Scandinavia/Russia Skandinavien/Ryssland	52,000	2015	DEC	
Pink-footed Goose <i>Spetsbergsgås</i>	Svalbard Spetsbergen	76,000	2014	INC	Fox & Madsen 2017b
<i>Anser brachyrhynchus</i>					
Greater White-fronted Goose <i>Bläsgås</i>	Russia (several pop.) Ryssland (flera populationer)	1,085,000	2012	INC	Fox & Madsen 2017b
<i>Anser albifrons</i>					
Lesser White-fronted Goose <i>Fjällgås</i>	Fennoscandia/Russia Fennoskandien/Ryssland	80	2010	DEC	Fox & Madsen 2017b
<i>Anser erythropus</i>					
Greylag Goose <i>Grågås</i>	NW Europe NV Europa	960,000	2014	INC	Fox & Madsen 2017b
<i>Anser anser</i>					
Barnacle Goose <i>Vitkindad gås</i>	Russia/Baltic Ryssland/Östersjön	1,200,000	2015	INC	Fox & Madsen 2017b
<i>Branta leucopsis</i>					
Brent Goose <i>Prutgås</i>					Fox & Madsen 2017b
<i>Branta bernicla bernicla</i>	Russia Ryssland	211,000	2011	INC	
<i>Branta bernicla hrota</i>	Svalbard Spetsbergen	7,500	2015	INC	
Canada Goose <i>Kanadagås</i>	Fennoscandia Fennoskandien	90,000	2000s	INC	Fox et al. 2010
<i>Branta canadensis</i>					
Red-breasted Goose <i>Rödalsad gås</i>	N Siberia/Black Sea and Caspian Sea	50,000–	2016	INC	CAFF 2018
<i>Branta ruficollis</i>	N Sibirien/Svarta havet och Kaspiska havet	100,000			
Mute Swan <i>Knölsvan</i>	NW Mainland/Central Europe	250,000	2019	INC	Rees et al. 2019
<i>Cygnus olor</i>	NV och centrala Europa				
Whooper Swan <i>Sångsvan</i>	NW Mainland Europe NV Europa	138,500	2015	INC	Rees et al. 2019
<i>Cygnus cygnus</i>					
Bewick's Swan <i>Mindre sångsvan</i>	NW Europe NV Europa	20,000	2015	DEC	Rees et al. 2019
<i>Cygnus columbianus bewickii</i>					

**TABLE 2.** Breeding season diets of common European geese and swans in aquatic ecosystems (Cramp *et al.* 1986). The table includes plants that grow in water or on adjacent moist land. – Födoväxter för vanliga europeiska gåsararter och svanar i akvatiska ekosystem (Cramp m.fl. 1986). Tabellen innehåller arter som växer i vattnet eller på omgivande fuktig mark.

Plants Växter		Goose/swan species Gås-/svanart				
Common name Namn	Genus Släkte	Greylag Goose Grågås	Canada Goose Kanadagås	Barnacle Goose Vitkindad gås	Mute Swan Knölsvan	Whooper Swan Sångsvan
Floating and submerged <i>Flytande och undervattensväxter</i>						
Algae <i>Alger</i>	<i>Chara</i>				X	X
	<i>Cladophora</i>					X
	<i>Ulva</i>		X			
Seagrass <i>Bandtång</i>	<i>Zostera</i>		X		X	X
Hornworts <i>Särv</i>	<i>Ceratophyllum</i>					X
Waterweeds <i>Vattenpest</i>	<i>Elodea</i>				X	
Duckweeds <i>Andmat</i>	<i>Lemna</i>	X				
Milfoil <i>Slingor</i>	<i>Myriophyllum</i>					X
Naiad <i>Najas</i>	<i>Najas</i>					X
Pondweed <i>Nate</i>	<i>Potamogeton</i>	X	X		X	X
Wigeon grass <i>Nating</i>	<i>Ruppia</i>		X		X	X
Emergent and terrestrial <i>Uppkommande och terrestra</i>						
Horsetail <i>Fräken</i>	<i>Equisetum</i>	X		X	X	
Rushes <i>Tåg</i>	<i>Juncus</i>			X		
Woodrushes <i>Fryle</i>	<i>Luzula</i>			X		
True sedges <i>Starr</i>	<i>Carex</i>		X	X		
Spike-rush <i>Småsåv</i>	<i>Eleocharis</i>		X	X		
Cotton-grass <i>Ull</i>	<i>Eriophorum</i>				X	
Club-rush <i>Säv</i>	<i>Scirpus</i>	X	X	X		X
Bur-reed <i>Igelknopp</i>	<i>Sparganium</i>	X				
Cattail <i>Kaveldun</i>	<i>Typha</i>	X				
Reed <i>Bladvass</i>	<i>Phragmites</i>	X				
Sweet-grass <i>Glyceria</i>	<i>Glyceria</i>	X			X	X
Canary Grass <i>Flen</i>	<i>Phalaris</i>	X				
Bluegrass <i>Gröe</i>	<i>Poa</i>	X				
Willow <i>Vide</i>	<i>Salix</i>			X		X

height, are then subsequently obtained from the protected and unprotected areas to assess grazing pressure. The benefit of experimental studies, and especially exclosures, is thus the possibility to determine not only how macrophytes can be affected by waterbirds, but also to what extent (Lodge *et al.* 1998, Mitchell & Perrow 1998). The downside is that experiments are time consuming, costly, and hard to maintain long-term.

Exclosures used in experimental studies are constructed by poles and nets that prevent certain herbivores from feeding on the vegetation inside the exclosure (Figure 1) and they are often combined with open plots as a control treatment (Figure 2). To discourage birds from entering exclosures from above, rope or barrier tape is sometimes tied diagonally between the poles, above the net (Figure 2). Although the ‘paired plot design’ is referred to as a commonly used methodology (Sarneel *et al.* 2014), the actual design varies greatly when it comes to construction and placement of the paired plots. For example, the size of an exclosure commonly varies from 1 × 1 m (Irfanullah & Moss 2004, Hilt 2006) to 6 × 8 m (Paice *et al.* 2016). Smaller exclosures may be a good choice when studying homogenous stands of macrophytes (Weisner *et al.* 1997, Matuszak *et al.* 2012), while larger ones can contribute with more information on the community composition (Veen *et al.* 2013).



**FIGURE 1.** Exclosure constructed with wooden poles and plastic net (2.5 × 2.5 m). Photo: Gunnar Gunnarsson.  
— Uthägnad av träpölar och plastnät (2,5 × 2,5 m). Foto: Gunnar Gunnarsson.

Open control plots are usually the same size as exclosures, marked by poles at their edges and placed within a distance of 0–25 m from the exclosures (Sarneel *et al.* 2014, Lodge & Tyler 2020). However, there are studies in which no physical markings were used for control plots, often to minimize disturbance. For instance, Stafford *et al.* (2012) randomly outlined control plots within a given distance of the exclosures on the same day vegetation measurements took place.

Often neither the process of selecting placements nor the distance between paired plots is described, which is unfortunate. In studies where details about the selection process are provided, placements are chosen randomly (Lodge & Tyler 2020), by vegetation type and density (Tatu *et al.* 2007), or according to other environmental factors such as water depth, wind direction, wave action, or sediment type (Jupp & Spence 1977, Weisner *et al.* 1997, Marklund *et al.* 2002, Allin & Husband 2003, Hilt 2006). When described, the distance between one pair of plots and another can range from 3 m (Lodge & Tyler 2020) to 50 m (Bakker *et al.* 2018). However, distances may be even greater when plot pairs are placed on different shores in a study area (Gayet *et al.* 2012, Sarneel *et al.* 2014, Jobe *et al.* 2022). The selection process is challenging since there are both pros and cons of choosing placement by randomisation or based on specific criteria. Randomisation may improve independence of samples but can be difficult to apply if the study is targeting specific macrophyte species growing only in specific areas. Randomised plots may also end up in spots not used by the birds, e.g. close to disturbances. To increase independence without randomising placement, it could be wise to use longer distances between the chosen sites of the paired plots. This was done by Nolet (2004) to ensure that tuber biomass samples were not connected in any way when testing if grazing by Bewick's Swans led to compensatory growth of fennel pondweed *Potamogeton pectinatus*. In some exclosure studies, plots were divided into smaller subplots to facilitate estimation of the vegetation and randomisation of sampling (Hidding *et al.* 2010, Stafford *et al.* 2012, Svidenský *et al.* 2021). It is also common to account for ‘edge effects’ within exclosures when sampling, i.e., to exclude the vegetation closest to the fence, as it may be affected by shading or possibly grazing (Figure 3). The width of such a buffer zone is typically 1 m (Tatu *et al.* 2007, Gayet *et al.* 2012),



**FIGURE 2.** Two pairs of enclosure and control plots (2 × 3 m) placed in a systematic design approximately 5 m apart. The centre of each control is marked with a wooden pole. Photo: Thomas Houet.

— Två par av uthägnad och kontrolltytor (2 × 3 m) systematiskt utlagda med ca. 5 m mellanrum. Mittpunkten i varje kontrolltyta är markerad med en trästolpe. Foto: Thomas Houet.

but range from 0.4 m (Marklund *et al.* 2002) to 1.5 m (Hidding *et al.* 2010) in different studies.

Occasionally more than two types of treatments are included, and this, too, may influence the experimental design. For example, Hidding *et al.* (2010) performed a four-year study in a large shallow lake to investigate the impact of herbivorous waterbirds among seasons. They used four treatments: (1) one open (i.e., without fences; control), (2) one closed (i.e., with fences) only during summer to prevent grazing on above-ground plant parts such as leaves and stems, (3) one closed during winter to prevent grazing on below-ground plant parts such as tubers, and (4) one closed during both summer and winter. These four treatments were placed together as a set in a 12 × 12 m area divided into four blocks (6 × 6 m), each block randomly selected to represent one of the treatments. The sets were then replicated eight times in different parts of the lake (Hidding *et al.* 2010). Although a larger variety of treatments in a study can provide more information, the number of plots and treatments may strongly be restricted by resources such as time and manpower. Accordingly, increasing the number of treatments tends to reduce the number of replicates.

Sometimes enclosures are constructed to allow other grazers inside access, apart from the herbivore species of interest, which hence enables estimation of the grazing effect of the latter solely. For example, in enclosure studies where the grazing effect of swans

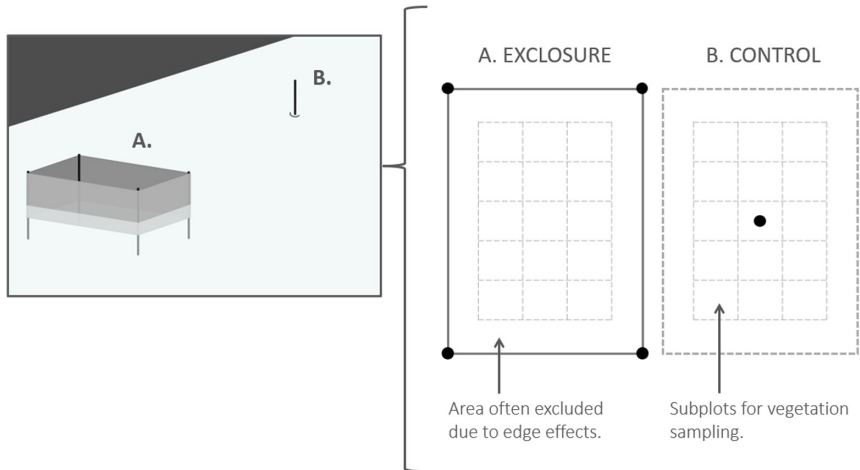
has been studied, a small gap was left open between the water surface and the lower wire to allow entry of other herbivores (e.g. Eurasian Coot; Gayet *et al.* 2011a, Stafford *et al.* 2012). In other cases, enclosures were made accessible for fish either by leaving a gap near the bottom (Tatu *et al.* 2007) or using a net with larger mesh size (Lauridsen *et al.* 1993, Irfanullah & Moss 2004). Some studies have compared the difference between fish and waterbird herbivory by creating additional fish enclosure treatments (Marklund *et al.* 2002, Hilt 2006). There are also other terrestrial or aquatic herbivore species that may influence macrophyte abundance and whose presence should be considered as well, like common muskrat (Danell 1979), moose (Bump *et al.* 2017), and beaver (Law *et al.* 2014).

## VEGETATION SAMPLING

The most common macrophyte variables included in studies of waterbird herbivory are *vegetation biomass, density, height, cover, and community composition*. Each variable is treated under separate headings in the following.

## VEGETATION BIOMASS

Vegetation biomass refers to the weight of macrophytes and is often divided into either above- or below-ground biomass. Above-ground biomass includes all parts of a plant above the sediment surface (e.g. shoots, stems,



**FIGURE 3.** Example of an enclosure (A) and a control (B) plot in an experimental study using the paired plot design. The right side illustrates how subplots as well as the area where sampling is avoided to account for edge effects can be outlined within the larger plots.  
 — Exempel på uthägnad (A) och kontrolllyta (B) i experimentell studie enligt designen parade provtytor. Den högra sidan illustrerar hur delytor och kantområden där provtagning undviks kan användas inom provtytor.

leaves), while below-ground biomass includes parts below it (e.g. rhizomes, tubers). It should be noted that above-ground biomass includes plant parts that grow both above and below the water surface. Furthermore, vegetation biomass can be expressed as either fresh weight, dry weight, or ash free dry weight. Dry weight is the most common measure related to enclosure studies and it is obtained by drying macrophyte samples in an oven after harvest (Rivers & Short 2007, Hidding *et al.* 2010, Sarneel *et al.* 2014). Macrophytes are usually dried at 55–60°C for 48 h (Rivers & Short 2007, Sarneel *et al.* 2014) or 72 h (Hidding *et al.* 2010, Gayet *et al.* 2012). While sampling of above-ground biomass is restricted to the growing season, below-ground biomass can be sampled all-year round. However, the latter is often sampled in fall, winter or spring, as waterfowl feed more on below-ground plant parts during these seasons (Nolet 2004, Hilt 2006).

To avoid biases when harvesting vegetation for biomass estimations, it is important to use a systematic approach, including independent samples. This can be ensured in advance by deciding how many and which subplots to harvest, either by random selection or by a systematic scheme (Marklund *et al.* 2002, Santamaría & Rodríguez-Gironés 2002, Hidding *et al.* 2009). In general, the amount of sampled vegetation varies between studies. By way of illustration, Sarneel *et al.* (2014) took

three 0.2 m<sup>2</sup> samples of above-ground vegetation in their plots, whereas Gayet *et al.* (2012) harvested above-ground vegetation in all nine 1 m<sup>2</sup> subplots (but chose to harvest only half of their total plots). Larger subplots may give more representative samples, i.e., by including larger areas and thereby more of the vegetation. This may be of greater importance when harvesting above-ground biomass compared to below-ground, especially when additional measurements such as macrophyte community composition are assessed. Nonetheless, detailed estimations are very time-consuming, and the area to be harvested is limited by time and manpower.

### VEGETATION DENSITY

To assess vegetation abundance, an alternative to biomass measurements, is to record macrophyte density. This is usually done by counting the number of shoots in a given area (often within enclosure subplots; Van den Wyngaert *et al.* 2003, Svidenský *et al.* 2021). When studying the effect of Greylag Goose herbivory on common reed *Phragmites australis* using the ‘paired plot design’, Bakker *et al.* (2018) used 2 × 6 m plots and delineated five subplots of 0.5 × 0.7 m along a transect in the middle of each plot. In each subplot, they measured reed density by counting each stem emerging above the water surface. Tatu *et al.* (2007) partitioned their plots into nine 1 m<sup>2</sup> squared subplots and chose three



of them, in a diagonal pattern, for vegetation sampling. To estimate shoot density in their subplots, they used a 1 m<sup>2</sup> frame divided into smaller squares to count shoots of submerged macrophyte species (Tatu *et al.* 2007). Shoot density can also be an important measurement in restoration studies in order to evaluate colonization success, i.e., initial shoot density when planting macrophytes compared to shoot density at the end of an experiment (Lauridsen *et al.* 1993). Moreover, density can be a suitable option depending on physical traits, e.g. in *Typha* and *Phragmites* species that have readily distinguishable individual straight shoots that are easy to count. Still, biomass could give a more representative measure of the total amount of vegetative parts available. If waterfowl for instance feed on above-ground plant structures without uprooting the plants, it may not be possible to detect differences in density between treatments. This is exemplified by Jupp and Spence (1997) in their study on the effects of a mixed assemblage of herbivorous waterbirds on fennel pondweed and thread-leaved pondweed *Stuckenia filiformis*.

### VEGETATION HEIGHT

The height of macrophytes is commonly assessed by averaging the three tallest stems of each species in every subplot (Lodge & Tyler 2020). Nonetheless, it is not uncommon to measure stems of all individual plants, especially in studies that examine grazing effects on transplanted macrophytes (Lauridsen *et al.* 1993, Søndergaard *et al.* 1996). The height of a specific plant can be obtained by either measuring the total length from the bottom substrate (Veen *et al.* 2013), or by measuring the part emerging above the water surface (Bakker *et al.* 2018). However, information about this procedure is rarely described. Since the water level may fluctuate between seasons and years, which also affects macrophyte growth (Lawniczak *et al.* 2010), total length measurements could be more representative and comparable as a proxy for height. More rarely, height is measured after macrophytes have been harvested for biomass sampling (Jupp & Spence 1977, Hilt 2006).

### PLANT COVER AND COMMUNITY COMPOSITION

Plant cover is usually visually estimated to gauge total plant cover or to estimate the community composition within a specific area. Typically, plant cover is expressed

in percent, sometimes as interval classes (or ‘cover classes’). Such interval classes are typically divided into five or ten percent units, and some studies include additional classes of narrower intervals for species covering less than 10–15% (Sarneel *et al.* 2014, Jobe *et al.* 2022). Areas with no macrophyte cover, or with dead and decomposing plant material, are in some cases also assessed by percentage cover which is then included as additional data (Jobe *et al.* 2022). Measurements of plant cover can either be obtained in a limited number of subplots chosen for vegetation sampling (Tatu *et al.* 2007) or in all subplots (Gayet *et al.* 2012). Another way to assess community composition is to calculate species’ proportions from density counts or samples of above-ground biomass instead of estimating cover. An example of the latter can be found in Hidding *et al.* (2010). Here, they first harvested the vegetation and sorted the samples by species before drying. Then, proportions were calculated by subtracting the dry weight for each species from the total weight of the sample (Hidding *et al.* 2010). Moreover, to evaluate structures of a macrophyte community, the obtained information of present species is often analysed by using diversity indices such as the Shannon-Weiner Diversity Index (H’; Gayet *et al.* 2011a, Sarneel *et al.* 2014, Lodge & Tyler 2020).

## Effects of waterbird herbivory on aquatic vegetation

In this section we present observed effects on macrophytes in aquatic ecosystems by foraging waterbirds, mainly geese and swans. The findings are not exclusively derived from experiments but include descriptive studies as well. The results focus on the commonly used vegetation variables *vegetation biomass*, *density*, *height*, *cover*, and *community composition* (above).

### VEGETATION BIOMASS

Although herbivorous waterbirds have been found to significantly reduce both above- and below-ground biomass (Van Donk & Otte 1996, Lodge & Tyler 2020), results are not consistent, as no, or even positive effects have been reported as well (Rip *et al.* 2006, Van den Wyngaert *et al.* 2003). Evidence of detrimental grazing effects of geese can be found in an observational study by Rivers & Short (2007). The authors investigated an unusual event where about 100 Canada Geese

wintered on Fishing Island (Maine, USA), in a marine area containing a well-established meadow of eelgrass *Zostera marina*. In only three months the geese reduced the above-ground eelgrass biomass to the extent that the meadow did not recuperate the following growing season (Rivers & Short 2007). The authors stated that the low recovery rate of the eelgrass was due to the fact that Canada Geese not only consumed the leaves, but also reproductive parts of the shoot, thus reducing subsequent vegetative growth. Contrasting results in which grazing by geese has been observed to rather increase above-ground biomass were for instance found by Van den Wyngaert *et al.* (2003). They found significantly higher above-ground biomass of common reed in a marsh where goose grazing occurred compared to a nearby ungrazed marsh. The authors argued that by consuming common reed during summer, geese reduced the amount of standing dead mass over winter, which in turn facilitated growth of new shoots in the start of the following growing season (Van den Wyngaert *et al.* 2003).

Swans have been observed to reduce the biomass of floating as well as submerged macrophytes in several types of aquatic ecosystems. For example, in a river in southwest England, O'Hare *et al.* (2007) found above-ground biomass of stream water-crowfoot *Ranunculus penicillatus* to be significantly lower in areas often used by Mute Swans. Furthermore, the grazing effects of Mute Swans have been of particular interest in USA, where the species is considered invasive (Rees *et al.* 2019). Here, extensive loss of submerged macrophytes has been attributed to the expansion of this species in freshwater as well as coastal ecosystems (e.g. enclosure studies by Allin & Husband 2003 and Stafford *et al.* 2012). The former conducted a four-year experiment in a coastal pond on Rhode Island (USA). By placing paired plots in different water levels they found that Mute Swans could reduce above-ground biomass of submerged macrophytes by up to 95% in shallow areas. The overall treatment effect across all water levels was also significant, but only in two out of three sampling months (July and August, but not June; Allin & Husband 2003). Stafford *et al.* (2012) conducted their experiment in two large freshwater wetlands in Illinois (USA). After one and a half year, the mean below-ground biomass (e.g. tubers, rhizomes) of several submerged macrophyte species was reduced by 51% in the

open control plots. However, there was no significant reduction of above-ground biomass (e.g. leaves, stems; Stafford *et al.* 2012). The authors assumed the decrease of below- but not above-ground biomass to be a result of Mute Swans foraging on below-ground plant parts in winter, or of overcompensation. Concerning the latter, Stafford *et al.* (2012) suggested that submerged macrophytes redirected their energy from below-ground parts to increase photosynthetic above-ground structures, due to defoliation by Mute Swans. This could be a more probable cause than their former assumption, as winter foraging on below-ground parts has been observed to have negligible effects on above-ground biomass of some macrophytes (e.g. fennel pondweed and tape grass *Vallisneria spiralis*) in following growing season (Sponberg & Lodge 2005, Hidding *et al.* 2009).

As demonstrated by Allin and Husband (2003), the amount of vegetation removed by swans is related to water depth, as they prefer to feed on submerged macrophytes in shallow water. This has been illustrated in other studies as well (Tatu *et al.* 2007, Dos Santos *et al.* 2013). Water depth, in turn, may influence how well macrophytes recuperate from herbivory, especially in more turbid waters with lower light penetration (Tatu *et al.* 2007). Moreover, if an aquatic system contains large herbivores of several species, the negative effects on macrophyte biomass can be additive (Van Donk & Otte 1996). For example, Hilt (2006) who conducted an enclosure study in a shallow, eutrophic lake in Germany reported that waterbird herbivory combined with fish herbivory reduced about 90% of the above-ground biomass of fennel pondweed, even at low herbivore densities. In that study, waterbird herbivory was separated from combined herbivory by using two types of enclosures; one with a 25 cm open gap at the bottom (exclusion of waterbirds) and another fully closed (exclusion of waterbirds and fish). In contrast to Hilt (2006), Lauridsen *et al.* (1993) suggested that herbivorous waterbirds alone may have a stronger impact on macrophytes compared to fish. The authors carried out their experiment in a Danish eutrophic lake that had recently been biomanipulated through removal of cyprinid fish. Although the water became clearer and nutrient concentrations lower after restoration, there was still a lack of submerged macrophytes in the lake. To test whether the re-establishment

of submerged macrophytes was suppressed by grazing, Lauridsen *et al.* (1993) planted different species of pondweed in- and outside enclosures. They found that that nearly all attempts to re-establish the pondweed failed in the unprotected areas. Since the mesh size (6 cm) allowed entry to smaller fish, they concluded that grazing activities (feeding and uprooting) by waterbirds were the main reason. As Eurasian Coot and Mallard were the dominant waterbird species during the study period, they were implicated to have the largest impact on submerged macrophytes (Lauridsen *et al.* 1993).

### VEGETATION DENSITY

In enclosure studies, both geese and swans have been shown to significantly reduce macrophyte shoot density. Moreover, the differences in density between enclosures and controls seem to become more apparent over time. When investigating effects of Mute Swans grazing on submerged macrophytes in a shallow estuary, Tatu *et al.* (2007) found that shoot density in control plots was reduced by 41% after one growing season, and by 76% after two growing seasons. Similarly, Bakker *et al.* (2018) discovered that shoot density of common reed was fourfold higher in plots protected from Greylag Geese by the end of a five-year period. However, shoot density may not always correlate to other vegetation measurements, as it has turned out not to differ between paired plots in contrast to measurements of shoot biomass in the same study (Hilt 2006). In addition, vegetation density itself can influence the observed effects, as waterbirds have been seen to cause less damage in dense macrophyte stands compared to sparse stands, possibly as a result of restricted grazing access by thick vegetation (Mitchell & Perrow 1998, Svidenský *et al.* 2021). Reijers *et al.* (2019) tested if Greylag Geese could control the expansion of common reed, and if denser stands inhibited the grazing effects. This was done by constructing large enclosure and control plots in a brackish reed-dominated marsh and then removing the enclosures after two years. The vegetation in the plots were then monitored for one more year after the enclosures had been taken down (Reijers *et al.* 2019). The authors concluded that common reed significantly expanded, especially into previously bare areas during the exclusion of Greylag Geese. They could also confirm that grazing was in fact inhibited after the reed had expanded and become denser since it did not retreat

after the geese were granted access to it again. Instead of grazing on the reed, the Greylag Geese targeted the saltmarsh bulrush *Bolboschoenus maritimus* that had grown in the enclosures (Reijers *et al.* 2019). However, the authors stated that Greylag Geese mainly control the expansion of common reed in its early development stages, and that reed expansion is hard to reverse after about one year of growth. Unlike Bakker *et al.* (2018) who regard the grazing effects on common reed as a conservation threat, Reijers *et al.* (2019) consider goose herbivory to be positive because it increased habitat heterogeneity in their study, thereby favouring the state of the aquatic ecosystem. It is possible that the inhibiting effect of species such as common reed is stronger in productive systems that facilitate growth, and that grazing may be more damaging and have long-term effects in nutrient-poor ecosystems (Reijers *et al.* 2019). However, species that grow in low densities in either type of ecosystem could be particularly vulnerable to herbivory, especially in small waterbodies where both herbivory and plant competition can be greater (Søndergaard *et al.* 1996).

### VEGETATION HEIGHT

Several enclosure studies have demonstrated that waterbirds may reduce macrophyte height (Hilt 2006, Bakker *et al.* 2018), but that the effect may sometimes differ between submerged and emergent vegetation (Lodge & Tyler 2020). As mentioned previously, Hilt (2006) studied the combined grazing effects of waterbirds and fish on the submerged macrophyte fennel pondweed. The author listed six species of waterbirds observed on the lake as potential herbivores: Mute Swan, Eurasian Coot, Mallard, Common Goldeneye *Bucephala clangula*, Tufted Duck *Aythya fuligula*, and Common Pochard *A. ferina*. Along with biomass, Hilt (2006) found length of fennel pondweed to be significantly reduced in the open control plots. Compared to the control plots, the fennel pondweed was significantly longer in enclosures protected against both waterbirds and fish, as well as in those only protected against waterbirds (longest in the former; Hilt 2006). Regarding grazing effects on height of emergent macrophytes, Bakker *et al.* (2018) demonstrated that protecting common reed against Greylag Geese for five years resulted in stems in enclosures being about four times higher than those in control plots (Bakker *et al.*

2018). Interestingly, by analysing grazing effects on various species, [Lodge and Tyler \(2020\)](#) found divergent effects on emergent and submerged macrophytes in one of their two study sites. Here, stem height of emergent macrophytes was reduced by up to 60–70%, while their results indicated no effect or even a significant increase in stem height of submerged macrophytes in open control plots. However, since [Lodge and Tyler \(2020\)](#) analysed the grazing effects on species level, it was possible to detect that not all emergent species were affected by the enclosure treatment. In fact, the effect on the same emergent species sometimes differed between wetlands. For example, great bulrush *Schoenoplectus tabernaemontani* tended to be longer in control plots in one wetland, and longer in enclosures in another. Overall, the grazing effects on emergent macrophytes were greater in the wetland that was permanently flooded compared to the other that was seasonally flooded ([Lodge & Tyler 2020](#)). Thus, the authors presumed that grazing pressure was reduced by the seasonally lower water depth in the latter. The main herbivores in both wetlands were waterbirds (Canada Goose and ducks *Anas* spp.), although [Lodge & Tyler \(2020\)](#) also observed low densities of white-tail deer *Odocoileus virginianus*, North American beaver *Castor canadensis*, and common muskrat. Moreover, filamentous algae may additionally reduce growth of submerged macrophytes as they can cause shading and thereby decrease the light absorption ([Irfanullah & Moss 2004](#)). In conclusion, these cases illustrate that the height of a specific macrophyte species can be affected differently by grazers, and that it is important to account for site-specific differences, as they may influence grazing effects.

## PLANT COVER AND COMMUNITY COMPOSITION

Swans seem to have a particular impact on total plant cover. For example, when studying Mute Swan herbivory in an estuary, [Tatu et al. 2007](#) observed non-breeding flocks to reduce the cover of submerged macrophytes by up to 100%, while breeding pairs reduced by about 90% ([Tatu et al. 2007](#)). The effect on plant cover thus seems to increase with increasing swan density but it may also depend on the number of days swans remain at a specific location ([Gayet et al. 2011a](#), [Guillaume et al. 2014](#)). Similar patterns have been observed for other

waterbird species as well (e.g. Canada Goose), with differences in plant cover between enclosures and open control plots increasing from 5 to 55% over three consecutive years ([Lodge & Tyler 2020](#)). In another enclosure study, including ten Dutch wetlands, the cover of emergent macrophytes expanded in enclosures over two years, while the cover in the open control plots did not ([Sarneel et al. 2014](#)). The authors suggested that waterbirds such as Greylag Goose, Mute Swan, Eurasian Coot, and Mallard restricted the expansion of shoreline vegetation.

In addition to direct impacts on macrophyte physical structure, foraging activities by waterbirds may influence composition and diversity of communities. By creating open patches and reducing the abundance of dominant macrophyte species, herbivores can promote colonization or persistence of less competitive macrophytes, thus increasing diversity ([Hidding et al. 2010](#), [Gayet et al. 2012](#)). However, there are studies in which waterbirds instead reduced plant diversity ([Gayet et al. 2011a](#), [Sarneel et al. 2014](#)). This may especially be the case when waterbirds selectively forage on less dominant species ([Phillips et al. 2016](#)), or on annual species ([Jobe et al. 2022](#)). Interestingly, [Lodge and Tyler \(2020\)](#) obtained contrasting results between their two study sites: one permanently flooded wetland with low nutrient availability and high herbivore densities, and one seasonally flooded wetland with low nutrient availability and low herbivore densities. In the former, macrophyte diversity in open control plots was reduced, while it increased in the latter. The results suggest that the effect of herbivory on community composition as well as vegetation height (above) may be influenced by hydrology and nutrient state of the aquatic ecosystem, along with herbivore density ([Lodge & Tyler 2020](#)).

Some studies have proposed there is a mutualistic relationship between herbivores and their preferred macrophyte food source. [Sandsten & Klaassen \(2008\)](#), for instance, found that the preferred species fennel pondweed better withstood foraging activities of wintering swans compared to a less palatable species, perfoliate pondweed *P. perfoliatus*. They suggested this was due to the life history traits of fennel pondweed, arguing that the small and round tubers of this species more easily escaped complete deterioration by swan trampling. Moreover, the results indicated that herbivory on fennel pondweed led to overcompensation, and that tubers

seemed to extend deeper into the sediment when grazing pressure increased (Sandsten & Klaassen 2008). Santamaría & Rodríguez-Gironés (2002) reached similar conclusions when studying the physical response of fennel pondweed tubers to herbivory by Bewick's Swan.

## Management of wetlands and waterbirds: conservation efforts and conflicts

Efforts to restore aquatic ecosystems and to construct new wetlands have increased over the last decades, but their success may in some cases decrease due to herbivorous waterfowl. Recently, herbivory by Canada Geese was observed to interfere with restoration of a freshwater wetland in the USA by suppressing the establishment and diversity of aquatic vegetation (Jobe *et al.* 2022). Several other studies have obtained similar results, providing further evidence that herbivorous waterbirds may cause severe damage to macrophytes planted to enhance water quality (Lodge *et al.* 1998, Lauridsen *et al.* 2003, Veen *et al.* 2013). Permanent enclosures during the initial stages of macrophyte establishment have been suggested as the most effective protection against waterbird herbivory on submerged and emergent plants (Bakker *et al.* 2018, Temmink *et al.* 2022).

Since macrophytes support the biodiversity and health of aquatic ecosystems, vegetation loss from waterbird herbivory could possibly lead to cascading effects (Hidding *et al.* 2016, van Altena *et al.* 2016). Grazing may for instance lead to a lack of suitable habitats for invertebrates, eventually decreasing the abundance of prey for invertivorous waterbirds and fish alike. Yet, how organisms in other trophic levels are affected by waterbird herbivory is still a quite unexplored topic in aquatic ecosystems (Wood *et al.* 2017). In research about reed management several macroinvertebrate species were found to be affected differently, either increasing or decreasing in abundance when burning or harvesting parts of the reed bed (Valkama *et al.* 2008). Overall abundance of macroinvertebrates seems to decrease with long-term reed management (4–7 years) in contrast to shorter time periods (1–2 years; Valkama *et al.* 2008). Moreover, macroinvertebrate diversity can be negatively affected by intense large-scale harvesting, as more species are found in older reedbeds supporting higher heterogeneity (Andersen *et al.* 2021).

Management can also reduce the abundance of passerine birds living in reed habitats, possibly as a result of increased predation risk (Valkama *et al.* 2008).

Studies do exist in which geese have been demonstrated to cause cascade effects in ecosystems, but most such cases concern herbivory on land adjacent to wetlands and not herbivory in the water *per se*. An example from Canada is Snow Geese *Anser c. caerulescens* degrading the habitat adjacent to coastal marshes (Jefferies & Rockwell 2002). Through overgrazing and grubbing, plant cover of graminoid and shrub species decreased with 46% and 84%, respectively, over 35 years, leaving bare patches of soil to dry out and become hypersaline (Peterson *et al.* 2013). These changes in plant cover and microclimate in turn led to the reduction of invertebrates like spiders and ground beetles, as well as ground nesting bird species other than geese (Milakovic & Jefferies 2003, Peterson *et al.* 2014). However, Flemming *et al.* (2022), who studied the effects of Snow Geese in a different location in Canada, found macroinvertebrate abundance to be higher in areas with moderate levels of goose abundance, compared to areas with either low or high goose abundance. The authors ascribed the abundance of macroinvertebrates in these areas to positive fertilizing effects of geese in aquatic ecosystems (i.e. contributing to more productive ecosystems). Nevertheless, if and how an aquatic ecosystem benefits from faecal decompositions may depend on its nutrient state. In oligotrophic ecosystems, nutrient input may increase macrophyte abundance and diversity with positive bottom-up effects, while it could put more stress on hyper-eutrophic ecosystems that already have high nutrient loads (Green & Elmberg 2014, Dessborn *et al.* 2016, Buij *et al.* 2017).

Corresponding studies about effects of swans on other trophic levels are sparse. In an enclosure study about the influence of Mute Swans on submerged macrophytes and macroinvertebrates, Allin & Husband (2003) found that some invertebrate species decreased in grazed plots, but there was no reduction of total macroinvertebrate abundance. The presence of swans in wetlands have in some cases been linked to higher abundances of other waterbird species, presumably a consequence of sharing similar preferences for productive wetlands, although the reasons have not been unravelled (Gayet *et al.* 2011b, Holopainen & Lehikoinen 2022). It has been suggested, though, that

swans may affect other waterbirds positively through commensal foraging, for example when dabbling ducks and Eurasian Coot get access to plants that surface due to swans trampling and dislodging them from the bottom (Källander 2005, Gyimesi *et al.* 2012).

Worth mentioning is also the role of herbivorous waterbirds as vectors for dispersal of plants and other organisms, as this may alter species composition in aquatic ecosystems (Bauer & Hoyer 2014). According to Green *et al.* (2023), waterbirds may disperse propagules of, e.g. macrophytes, phytoplankton, zooplankton, macroinvertebrates, and fish (eggs), either by endozoochory (internal transport) or epizoochory (external transport). Short distance dispersal may be important to maintain the diversity and richness of local plant species (Bruun *et al.* 2008). As migratory waterbirds can move far in short time, they have been suggested to also disperse propagules over long distances and to even be responsible for the geographical distribution of some plants (Alsos *et al.* 2007, Green *et al.* 2023, Lovas-Kiss *et al.* 2023). The poor digestion and fast passage of ingested macrophytes in geese and swans may increase the survival of seeds and other reproductive parts after gut passage, but it may also restrict the distance of dispersal (Clausen *et al.* 2002, Paolacci *et al.* 2023). Moreover, dispersal success may depend on the timing between the bird's movement and reproductive phase of the plant, and whether the plant can survive in the new habitat it arrives at (Clausen *et al.* 2002). Unfortunately, many waterbird species, including geese and swans, may also disperse alien species that negatively affect aquatic ecosystems, e.g. by outrivalling native flora or fauna (García-Álvarez *et al.* 2015, Navarro-Ramos 2024).

## Conclusions

By examining the literature on waterbird herbivory, we find that both research methodology and observed effects vary greatly among studies. Although many experimental studies have applied the 'paired plot design', the implementation of this approach is far from uniform. Experimental plots vary greatly in size, placement, and overall construction. More importantly, the use of different measurements and sampling techniques differ, which often impedes comparability between studies (Mitchell & Perrow 1998). Further, studying processes in the

natural environment is not an easy task as several confounding factors can influence the outcome. To obtain reliable results about the impact of herbivorous waterbirds on macrophyte abundance, systematic sampling techniques and comparability between paired plots in an experiment are essential. Plots should preferably be placed in areas with representative vegetation, along with considerations about macrophyte diet and foraging technique of the studied waterfowl. This also means taking into account water depth and seasonal water level fluctuations to ensure that plots do not dry out or become inaccessible during the study. Larger plots often include a greater variety of macrophyte species than smaller ones and may therefore be a better choice when studying grazing effects on community composition. By dividing larger plots into subplots, it is possible to save time, i.e., with no need to sample the whole enclosure or control plot. Doing so, it is a good idea to choose beforehand which subplots to sample and apply the same scheme in all plots for consistency and to avoid bias. The methods used for constructing plots and sampling vegetation or other parameters should be described in detail for every study to ensure their reproducibility.

Concerning the observed effects of waterfowl herbivory, there are studies indicating either high reduction or no significant decline of macrophytes. Effects can also be contradicting among various waterbodies within a study and among different macrophyte variables, suggesting that several vegetation variables should be included when sampling macrophytes. There are also additional variables to consider when interpreting results to better understand relationships between herbivory and macrophyte abundance. Such variables are *density of waterfowl* and/or other herbivores, as it can affect grazing pressure (van Altena *et al.* 2016, Wood *et al.* 2017), *seasonal fluctuations* of biotic and abiotic conditions, especially in long-term studies (Mitchell & Perrow 1998, Chaichana *et al.* 2011, Wood *et al.* 2012b), and *local conditions* such as surrounding land use and nutrient concentrations in the water (Kuiper *et al.* 2015, Van Onsem & Triest 2018). Furthermore, it is important to account for life history traits and morphological adaptations of the studied species, as macrophytes may respond differently to herbivore pressure and competitive interactions in the macrophyte community (Nolet 2004, Dar *et al.* 2014).

There is still a large knowledge gap in the literature about how large waterfowl not only affect macrophytes,

but also to what extent they may cause trophic cascades in aquatic ecosystems through direct or indirect interactions. More knowledge is also needed about how alterations in wetlands induced by herbivorous waterfowl are linked to climate change, as this may have synergistic effects further inhibiting the conservation of wetlands and other aquatic organisms (Yallop *et al.* 2004, Phillips *et al.* 2016, Jensen *et al.* 2019).

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## Svensk sammanfattning

De senaste årtiondena har intresset ökat för hur svanar och gäss påverkar växtligheten i våtmarker. För detta finns flera skäl. Ett är att flera arter av dessa fåglar har ökat kraftigt i antal, vissa också i utbredning. Många våtmarker hyser därför avsevärt fler av dessa stora växtätare än förut, i vissa fall fler än någonsin tidigare. Därtill är våtmarker föremål för andra förändringar, såsom eutrofiering, klimatförändringar, brunifiering och negativ utveckling hos delar av deras biologiska mångfald.

I denna artikel ger vi en översikt av den vetenskapliga litteraturen om svanars och gäss bete på vattenvegetation. Dels har vi undersökt vilka undersökningsmetoder som vanligen används i experimentella studier, dels hur olika vegetationsvariabler svarar på bete. Vi finner att både undersökningsmetoder och växternas svar skiljer sig avsevärt mellan olika studier. Många experimentella studier av beteseffekter bygger på en kombination av uthägnade provtytor och öppna kontrolltytor i samma

våtmark, alltså likartade ytor utan respektive med bete. Likväl är det ofta svårt att dra generella slutsatser av dessa studier eftersom provtyornas antal, storlek och placering skiljer sig mycket åt. Än mer problematiskt är att användningen av olika mät- och provtagningsmetoder skiljer sig åt, vilket också försvårar jämförbarheten mellan studier. Vanliga vegetationsvariabler i jämförande studier är biomassa (ovan eller under markytan/botten), täthet, höjd, täckningsgrad och artsammansättning hos växtsamhället. Tidigare forskning stöder uppfattningen att svanar och gäss på ett signifikant sätt kan påverka alla dessa variabler negativt. Graden av påverkan beror dock på olika andra faktorer, såsom vattendjup, tid på året och tätheten av växtätande fåglar. Med tanke på den tidigare och pågående kraftiga antropogena påverkan på våtmarker är det viktigt att ytterligare studera direkta och indirekta effekter av svanars och gäss bete i våtmarksekosystem.



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