

# Herbivory on freshwater and marine macrophytes: A review and perspective<sup>☆</sup>



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## ABSTRACT

Until the 1990s, herbivory on aquatic vascular plants was considered to be of minor importance, and the predominant view was that freshwater and marine macrophytes did not take part in the food web: their primary fate was the detritivorous pathway. In the last 25 years, a substantial body of evidence has developed that shows that herbivory is an important factor in the ecology of vascular macrophytes across freshwater and marine habitats. Herbivores remove on average 40–48% of plant biomass in freshwater and marine ecosystems, which is typically 5–10 times greater than reported for terrestrial ecosystems. This may be explained by the lower C:N stoichiometry found in submerged plants. Herbivores affect plant abundance and species composition by grazing and bioturbation and therewith alter the functioning of aquatic ecosystems, including biogeochemical cycling, carbon stocks and primary production, transport of nutrients and propagules across ecosystem boundaries, habitat for other organisms and the level of shoreline protection by macrophyte beds.

With ongoing global environmental change, herbivore impacts are predicted to increase. There are pressing needs to improve our management of undesirable herbivore impacts on macrophytes (e.g. leading to an ecosystem collapse), and the conflicts between people associated with the impacts of charismatic mega-herbivores. While simultaneously, the long-term future of maintaining both viable herbivore populations and plant beds should be addressed, as both belong in complete ecosystems and have co-evolved in these long before the increasing influence of man. Better integration of the freshwater, marine, and terrestrial herbivory literatures would greatly benefit future research efforts.

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## 1. Introduction: 25 years of research on herbivory on macrophytes

### 1.1. Setting the scene

In the 1990s two seminal papers appeared in Aquatic Botany that urged for a complete change in the paradigm that had been dominating macrophyte ecology. Despite some early work on the impact of waterbirds on freshwater and marine angiosperms (Jupp and Spence, 1977; Jacobs et al., 1981), until then, herbivory on aquatic vascular plants was considered to be of minor importance, and the predominant view was that freshwater and marine macrophytes did not take part in the food web (e.g. Shelford (1918))

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and their primary fate was the detritivorous pathway (Polunin, 1984; Duarte and Cebrian, 1996). But in 1991, Lodge argued that, contrary to conventional wisdom, live freshwater macrophytes are engaged in aquatic food webs. In 1998, Cebrian and Duarte highlighted that, while seagrasses suffered modest herbivory rates on average, such rates were highly variable, and the importance of seagrass-herbivore interactions should not be discounted. Following on from these two papers, Lodge et al. (1998) provided further evidence for the important role of herbivores in freshwater habitats, as compared to other biomes; and Valentine and Heck (1999) demonstrated that grazing on seagrasses is widespread in the world's oceans.

Together, these landmark papers put macrophyte herbivory on the map. Since then, there has been a strong increase in the amount of studies that investigated herbivory on freshwater macrophytes and seagrasses. In this study, we review what we have learned in the 25 years that followed the appearance of Lodge (1991). Furthermore, we identify new topics that have emerged over this time. These new topics include the fast changes that may occur in macrophyte-herbivore relationships with the ongoing global environmental change, as well as the potential conflicts between herbivore conservation and herbivore impacts on aquatic ecosystems. Finally, we discuss how we can improve our understanding of herbivore impacts and what tools may help us in achieving this. Following the approach of the seminal papers listed above, we focus primarily on aquatic angiosperms (submerged, floating and emergent) and address both freshwater and marine ecosystems.

## 1.2. Why thinking about herbivory on macrophytes has changed over the last 25 years

The paradigm shift in our perception of macrophyte herbivory, from being considered negligible to being acknowledged as a key factor shaping benthic ecosystems, is not only caused by an increase in scientific interest fostered by these landmark papers: the effect of herbivory became also more conspicuous over the last 25 years. The reasons for this are methodological, anthropogenic and ecological.

Methodological improvements for estimating herbivory included observation methods, such as bite mark counts (Cebrian and Duarte, 1998), experimental approaches, such as herbivore exclusions (see Poore et al. (2012) and Wood et al. (2016) for syntheses of marine and freshwater habitats, including macroalgae) and direct methods, including video bite counts or isotopic signatures (see Table 4 for details).

Anthropogenic effects included increases in the densities of aquatic and marine herbivores as a result of increased protection, predator removal, food subsidies from agriculture, and the introduction of exotic herbivores (Estes et al., 2011). For example, steep increases in herbivory rates have been reported for sea turtles in the Arabian Sea and Indonesia (Kelkar et al., 2013a,b), (Christianen et al., 2014), for herbivorous fish in the Mediterranean (Pages et al., 2012) and for geese in Northwestern Europe and North America (Jefferies et al., 2003; Van Eerden et al., 2005). However, it should be noted that despite recent local increases in herbivory, which have attracted attention to the role of herbivores in benthic ecosystems, over longer time frames in particularly species of large herbivores have experienced strong global declines (Jackson, 1997; McCauley et al., 2015; Bakker et al., 2016b).

Furthermore, the recent spread of exotic herbivores had major consequences for macrophyte establishment and survival in many areas worldwide. For example, tropical lessepsian rabbitfishes (*Siganus* spp.) cause overgrazing of macroalgae and seagrasses at the Eastern Mediterranean (Verges et al., 2014b), chubs and rabbit fishes (*Kyphosus* spp. and *Siganus* spp., Siganidae) overgraze Australian and Japanese kelp forests (Verges et al., 2014a), North-American red-swamp crayfish (*Procambarus clarkii*) have

depleted submerged plant meadows in shallow lakes across Europe (Rodríguez et al., 2003; Gherardi and Acquistapace, 2007; Van der Wal et al., 2013), and intentional introductions of grass carp (*Ctenopharyngodon idella*) have been considered a threat to native macrophytes (Wittmann et al., 2014).

Ecological effects are related to the oligotrophication of many European freshwater systems, which resulted in their recolonization with submerged macrophytes (Jeppesen et al., 2005). In many systems, however, the impact of aquatic herbivores sufficed to halt or reverse such recolonization (Körner and Dugdale, 2003; Hilt, 2006; Bakker et al., 2013a,b; Hilt et al., 2013; Eigemann et al., 2016).

## 2. Quantitative impacts of herbivores in aquatic systems

### 2.1. Quantitative impact of herbivores on plant biomass across ecosystems

A growing body of primary research has demonstrated herbivore-induced changes in one or more measures of macrophyte abundance, including biomass, two-dimensional cover, volume, and individual density (Kirsch et al., 2002; Marklund et al., 2002; Tomas et al., 2005; Prado et al., 2007; Christianen et al., 2012; Pages et al., 2012; Wood et al., 2012a; Kelkar et al., 2013a,b; Christianen et al., 2014; Bakker et al., 2016b). These studies, synthesized in several reviews (Cyr and Pace, 1993; Valentine and Duffy, 2006; Gruner et al., 2008; Poore et al., 2012), confirmed herbivores as key drivers of benthic ecosystems around the world. The overwhelming majority of studies reported a reduction in macrophyte abundance as a result of herbivory. Indeed, a recent meta-analysis of 326 experiments in which freshwater herbivores were excluded found that herbivory reduced macrophyte biomass by  $47.2 \pm 3.4\%$  (average  $\pm$  CI) (Wood et al., 2016). Of these, 300 experiments reported a reduction in macrophyte biomass, while 26 experiments reported positive effects or no changes. Similarly, a meta-analysis on grazing impacts on marine macrophytes found that herbivores reduce macrophyte abundance (both submerged angiosperms and macroalgae) by 68% on average (Poore et al., 2012).

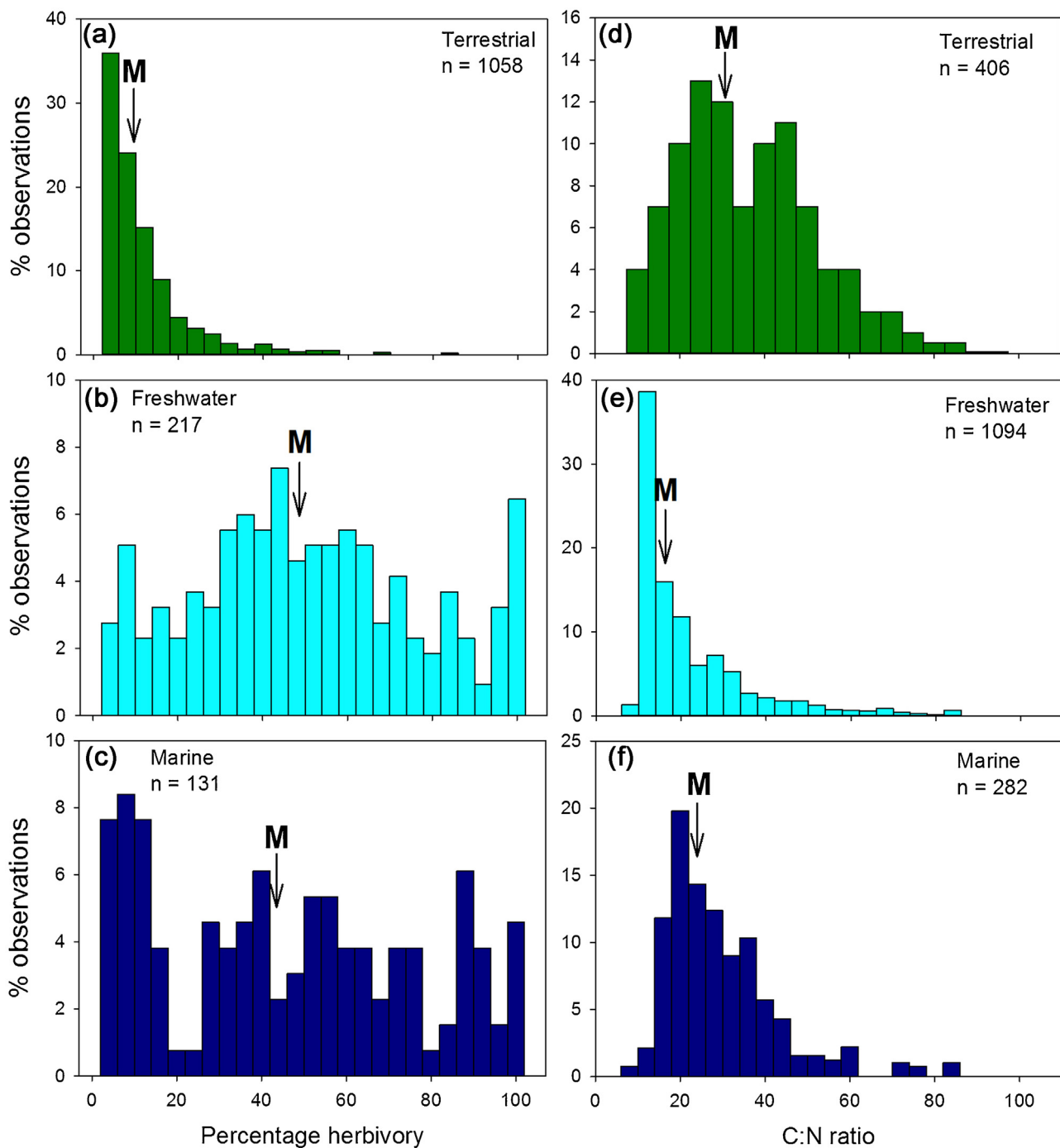
Despite their historical disregard, the removal of vascular plant biomass by herbivores is, on average, much larger in aquatic than in terrestrial ecosystems. The most recent meta-analyses available for terrestrial, freshwater and marine habitats (Turcotte et al., 2014; Wood et al., 2016) show that median biomass removal by herbivores is 4–8% in terrestrial ecosystems, while it is 44–48% in freshwater and 40–44% in marine ecosystems (Fig. 1a–c). Thus, herbivores remove on average 5–10 times more vascular plant biomass in aquatic ecosystems than in terrestrial ones.

Yet, the impact of herbivores on vascular plant biomass removal is much more variable in aquatic than in terrestrial ecosystems, and it ranges as broadly as between 0 and 100% of biomass removal (Fig. 1a–c). Underlying explanations for the large range of herbivore effects in aquatic ecosystems are still unknown. Potential mechanisms involve bottom-up effects, such as variation in plant productivity, nutritional quality, stoichiometry, resistance and tolerance to grazing (Cebrian et al., 2009); and top-down effects, such as variation in herbivore abundance, feeding efficiency, size, taxonomy, mobility, metabolism and predator effects (Borer et al., 2005).

### 2.2. Bottom-up effects: the plant's perspective

#### 2.2.1. Primary productivity and herbivory rates

Studies in aquatic systems traditionally focussed on primary production of phytoplankton in pelagic habitats, and only recently littoral areas received more attention (Vadeboncoeur et al., 2002;

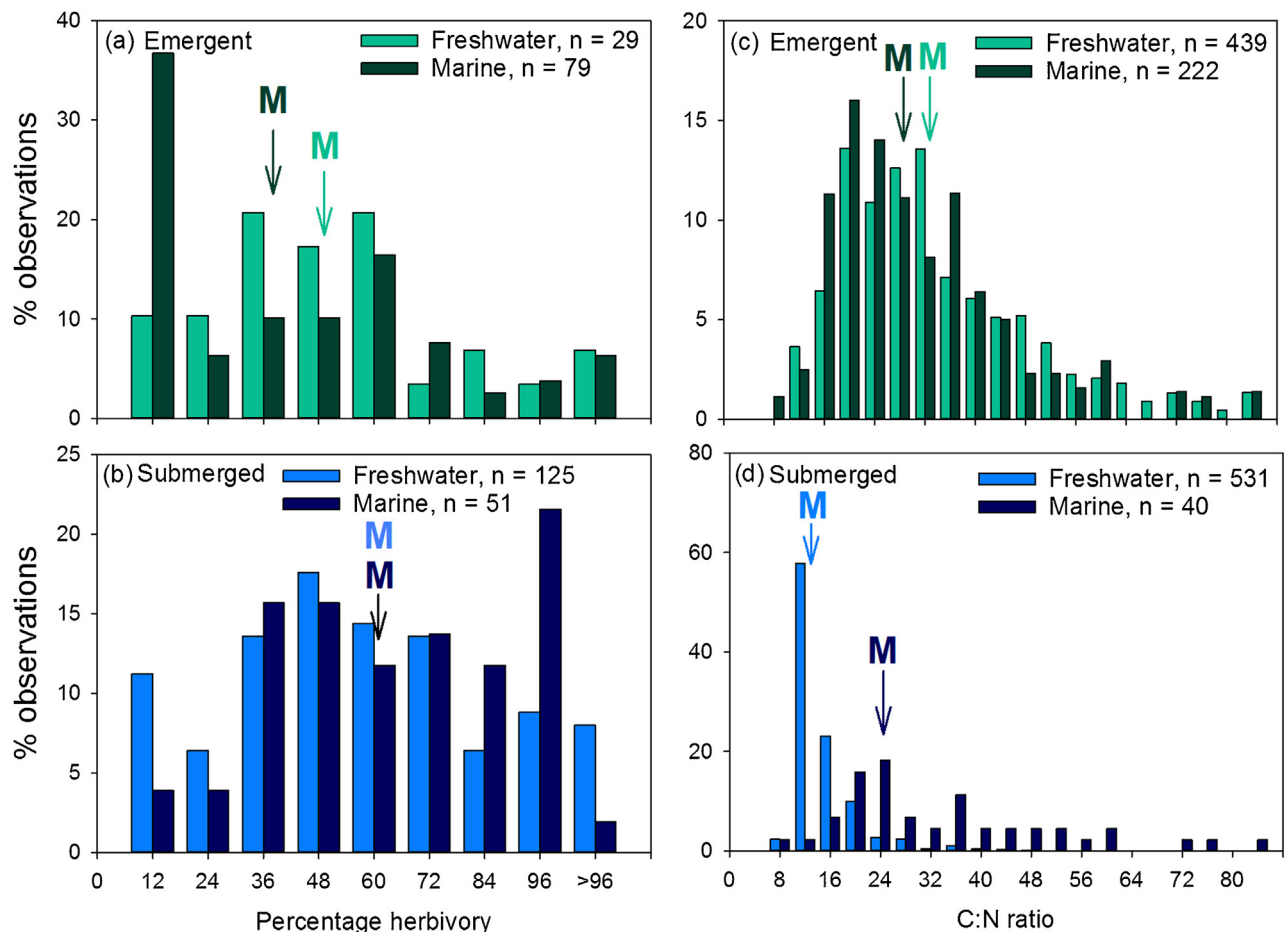


**Fig. 1.** Frequency diagram of percentage of herbivory (% herbivory) on vascular plants (a: mean percent damage; b, c: net primary production removal) and biomass C:N ratio (g/g) across (a,d) terrestrial, (b,e) freshwater and (c,f) marine ecosystems. Freshwater and marine data include both submerged and emergent plants. The median values in each panel are indicated with an arrow accompanied by “M”.

Data sources: terrestrial (a) herbivory: percentage of leaf area damaged (Turcotte et al., 2014), (d) biomass C:N ratio: in foliage (Elser et al., 2000); freshwater (b) herbivory: percentage of emergent and submerged vascular plant biomass removed by herbivores in herbivore enclosure/exclosure or addition/removal experiments (Wood et al., 2016), (e) biomass C:N ratio: in submerged and emergent vascular plants (Cloern et al., 2002; Bakker unpublished data); marine, (c) herbivory: percentage of emergent and submerged vascular plant biomass removed by herbivores in herbivore enclosure/exclosure or addition/removal experiments (Wood et al., 2016), percentage of leaf area damaged in seagrasses (Cebrian and Duarte, 1998) (f) biomass C:N ratio: in seagrass leaves (Atkinson and Smith, 1983; Duarte, 1990; Fourqurean et al., 1993; Cebrian and Duarte, 1998; Fourqurean et al., 2010; Olsen and Valiela, 2010), in salt marsh plants (Cloern et al., 2002). The duration of the herbivory studies varied from instantaneous measurements of percentage leaf damage in terrestrial plants and seagrasses to exclosures studies in freshwater and marine ecosystems ranging from about a week to multiple study years (study durations reported in Wood et al., 2016 who found no effect of study duration on percentage herbivore plant biomass removal).

Brothers et al., 2013). Theoretical predictions based on Lotka-Volterra models suggest that grazing should increase with primary productivity (Gruner et al., 2008), because as plants produce more tissues or do so at faster rates, herbivores can increase their rates

of consumption. This prediction relies in the assumption that herbivory rates are bottom-up regulated by the availability of plant tissues. Empirical evidence is however conflicting. A meta-analysis by Cyr and Pace (1993) concluded that herbivory increases with pri-



**Fig. 2.** Frequency diagram of net primary production removal (% herbivory) and biomass C:N (g/g) for vascular freshwater and marine macrophytes of different growth forms (emergent and submerged). Emergent plants include floating plants and wetland or salt marsh plants. The median values in each panel are indicated with an arrow accompanied by "M". Data sources as in Fig. 1.

mary production in both terrestrial and aquatic systems. However, a more recent meta-analysis found no significant effect of productivity on herbivory (or interaction strength) in aquatic systems (e.g. (Borer et al., 2005)). In fact, it is widely recognized that food quality and defences also have major effects on herbivore performance that might mask any herbivory-productivity relationship. Using a plant growth model, Hidding et al. (2016) suggested that herbivore grazing effects on macrophytes become important above certain thresholds in periphyton shading and thus reduced production of plants.

### 2.2.2. Plant stoichiometry

Differences in herbivory rates across plant taxa have also been attributed to differences in plant quality, as perceived by herbivores (Lodge, 1991; Cronin et al., 2002). Generally, there is a positive relationship between the nitrogen content in the plant's tissue and its consumption by herbivores (Cebrian and Lartigue, 2004). This pattern holds both within and across ecosystems (Elser et al., 2000; Cebrian and Lartigue, 2004; Cebrian et al., 2009). Hence, it has been suggested that higher herbivore consumption rates in aquatic plants might be explained by their higher quality as food – arising from the lack of carbon-rich structural compounds that strengthen cell walls, increase resistance to herbivores, and reduce digestibility in terrestrial plants (Gruner et al., 2008). Unfortunately, most comparisons between aquatic and terrestrial systems undertaken to date restricted their estimates of aquatic herbivory to phytoplankton consumption, thus giving limited or no information on

the consumption of aquatic macrophytes (Elser et al., 2000). Comparing herbivory rates on, and food quality (e.g., nitrogen content) of, aquatic and terrestrial vascular plants would be more informative, because they have a close phylogenetic affinity and most differences could be attributed to the ecosystems they inhabit (Hay, 1991; Gross and Bakker, 2012; Burkepile, 2013).

A compilation of data on C:N ratios of vascular plants in terrestrial, freshwater and marine ecosystems reveals that they differ strongly between these systems (Fig. 1d–f). Median C:N ratio decreased strongly from terrestrial vascular plants (25–30) and marine macrophytes (24–28) to freshwater macrophytes (12–16) (Fig. 1d–f). The high N content (thus low C:N ratio) of freshwater macrophytes may indicate a higher quality to herbivores, potentially explaining the high herbivory rates found in freshwater systems. Taking into account the variation in growth forms that occurs in aquatic ecosystems makes this pattern stronger (Fig. 2a–d). Herbivory rates are lower on emergent macrophytes (median freshwater = 36–48%; median marine = 24–36%) than on submerged macrophytes (median freshwater and marine = 48–60%) in both freshwater and marine ecosystems (Fig. 2a,b). These differences fit closely the C:N ratio of the different plant growth forms, as emergent macrophytes have higher C:N ratios (median freshwater = 28–32; median marine = 24–28) than submerged macrophytes (median freshwater = 8–12; median marine = 20–24), particularly in freshwater ecosystems (Fig. 2c,d).



Our data compilation indicates that differences in plant quality between terrestrial plants and macrophytes show close links to variation in herbivory rates. Submerged plants need less structural components, resulting in higher N content and higher rates of herbivory. In contrast, herbivory rates and N content of emergent macrophytes are similar to those found in terrestrial plants (Figs. 1a,d, 2a–d). Although N content is acknowledged as an important determinant of plant quality to herbivores, other nutrients and secondary compounds may also influence it. For example, freshwater macrophytes and seagrasses have anti-herbivore defenses (Verges et al., 2008; Gross and Bakker, 2012), which may cause low palatability – even in highly nutritious species. Phenolics, terpenoids and nitrogenated compounds can be efficient deterrents of aquatic herbivores, although deterrence of generalist herbivores often comes at the cost of higher preference by specialised consumers (Verges et al., 2007). Interestingly, in freshwater systems, the concentrations of phenolic compounds decrease from emergent to floating to submerged plants (Smolders et al., 2000), suggesting not only higher nutritional quality, but also less defended tissues, resulting in generally higher palatability of submerged plants. However, this issue still deserves more research, since most work has focused on macro-algae (e.g. (Hay, 1996)). Besides the differences between ecosystems discussed above, spatial and temporal variation in herbivory at population and individual-plant level has also been linked to plant quality (C:N, % N) and to the presence of anti-herbivore defences (Hacker and Bertness, 1995; Preen, 1995; Verges et al., 2007; Prado et al., 2010).

### 2.3. Top-down effects: the herbivore's perspective

#### 2.3.1. Herbivore density

Within individual herbivore species, herbivore impact on aquatic plant abundance is positively related to herbivore density (Stott and Robson, 1970; Valentine and Heck, 1991; Wood et al., 2012a; Kelkar et al., 2013b). However, analyses of herbivore impacts across multiple herbivore species have found no relationship between herbivore density and macrophyte abundance, probably due to the confounding effects of interspecific differences in herbivore ecology (Marklund et al., 2002; Wood et al., 2012a). For example, among plant-eating waterfowl, substantial differences exist in mean adult body mass (from the 24 g of ocellated crake, *Micropygia schomburgkii*, to the 12,000 g of trumpeter swan, *Cygnus buccinator*), which is known to influence the species' diet and the absolute quantity of vegetation consumed (Wood et al., 2012a). Consequently, when herbivore densities were estimated as biomass densities (thus accounting for interspecific differences in individual body mass), a significant negative relationship between herbivore biomass density and macrophyte abundance was detected (Wood et al., 2012a, 2016). Only at relatively low herbivore densities were positive changes in plant abundance reported, suggesting that in aquatic systems greater herbivore densities overwhelm plant compensatory growth responses (Wood et al., 2016).

#### 2.3.2. Size, mobility and taxonomy of herbivores

By virtue of their size, large terrestrial herbivores are critical agents of change and maintenance of the ecosystems they inhabit (Owen-Smith, 1988; Bakker et al., 2016a). In aquatic environments, large herbivores have also been identified as key species (McCauley et al., 2015), often considered ecosystem engineers (e.g. (Bakker et al., 2016b)). It is not surprising, thus, that a recent meta-analysis found significantly stronger impacts of macrograzers (fishes, urchins and large molluscs) than mesograzers (amphipods, isopods and small molluscs) on marine macrophytes (algae, seagrasses and salt marshes) (Poore et al., 2012).

Another recent meta-analysis by Wood et al. (2016) found substantial between-taxa differences in effects of herbivores on the abundance of freshwater and marine macrophytes. Echinoderms, molluscs, and fish had relatively large impacts on plants, while insects and birds had relatively low impacts. The reason for these differences may be the mobility and habitat preferences of each of these groups. Fully aquatic species that live underwater permanently, have been shown to produce the greatest impacts on aquatic plants (Bakker et al., 2016b), while facultative aquatic grazers, such as insects and birds, spread their activity more between different ecosystems (thanks to their high mobility), thus spreading also their impact between such ecosystems. Wood et al. (2016) also pointed out the fact that some herbivores (such as echinoderms, crayfish and molluscs) have restricted mobility and produce intense impacts due to their bulk grazing strategies, since they consume multiple tissues types and species, thus affecting a greater proportion of a plant community (Lodge et al., 1998).

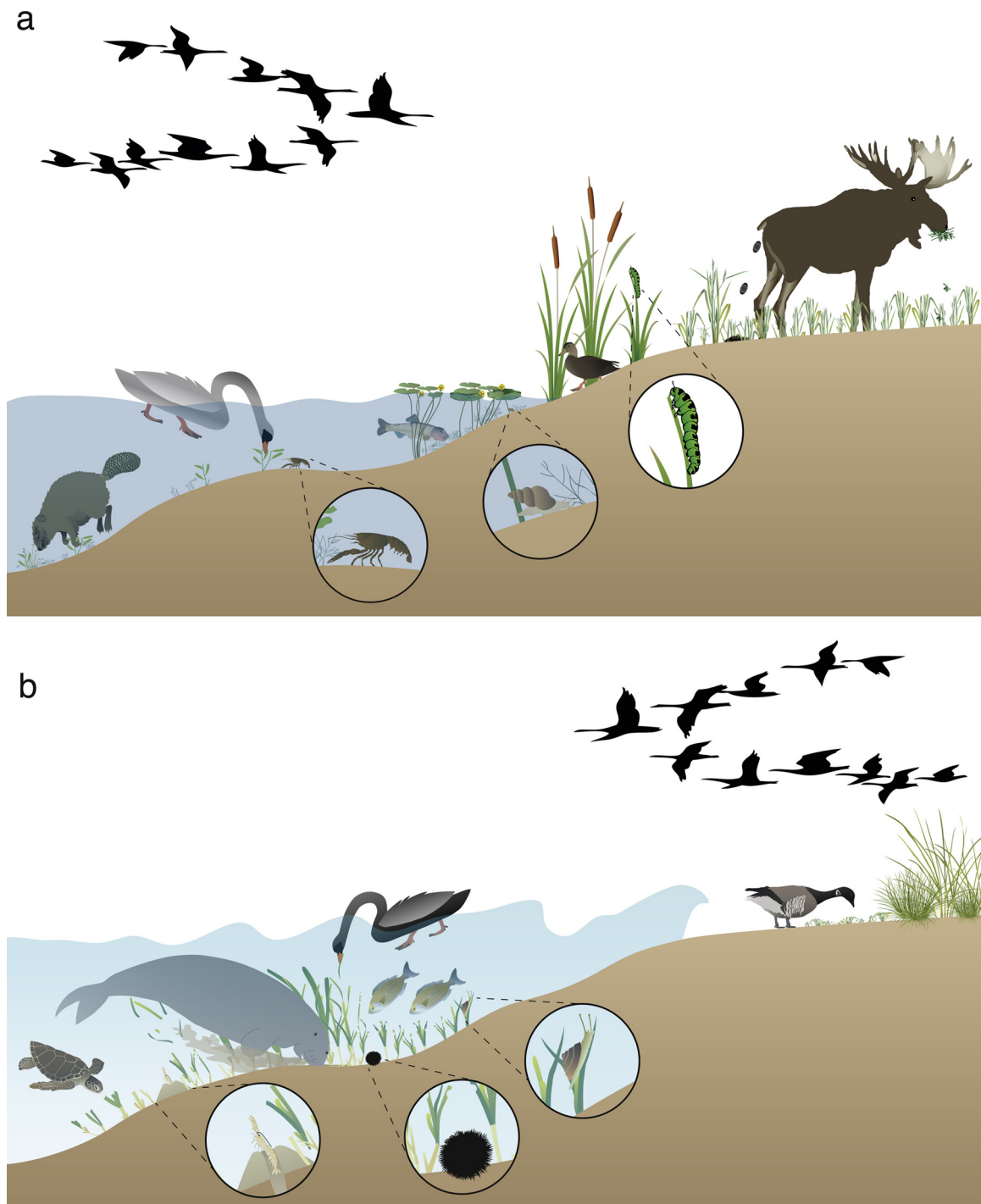
#### 2.3.3. Herbivory and omnivory

Most animals that consume aquatic plants are omnivores, very few are strict herbivores. There is a positive relationship between body size and degree of herbivory in aquatic omnivores: the larger the consumer, the more important plant consumption (granivory and folivory, particularly the latter) is in their diet (Clements et al., 2009; Wood et al., 2012a). Hence, per capita, large herbivores have the largest impact on plant abundance through grazing. The high level of generalistic feeding and omnivory of aquatic plant consumers may be related to the higher impact of herbivory on aquatic plants, because it may relax the effect of direct density dependence on consumers: whenever consumers overgraze plants, they can switch to alternative food sources (algae, detritus or animal prey) within or nearby the water body (Grey and Jackson, 2012). Furthermore, in aquatic systems, large herbivores and omnivores often feed on both aboveground and belowground plant material, which may multiply their impact on plants, due to the depletion of underground plant resources for regrowth.

Herbivore impact may also be enhanced by non-consumptive effects, which are documented to be severe in freshwater and marine macrophytes, e.g. bioturbation (Lodge, 1991). By initiating bare patches, herbivores can create focal points for further erosion of macrophyte meadows by waves in shallow areas (Christianen et al., 2013). Trampling, fecal deposition and increasing nutrient concentrations may also play a role. Whilst previous authors have cautioned against the assumption that herbivore effects on plants represent exclusively grazing losses due to consumption (Mitchell and Wass, 1996b), many studies continue to ignore the roles of non-consumptive effects.

### 2.4. Latitude

Potential variance in herbivore impacts on plant abundance across different latitudes has been a topic of growing interest among ecologists. However, the evidence for a role of latitudinal effects is limited. For example, in macrophyte feeding assays carried out by Morrison and Hay (2012), only one out of three crayfish species showed a preference associated with latitude (a preference for higher latitude plants). Schemske et al. (2009) argued that, across all ecosystems, herbivore impacts are greater at lower latitudes. In contrast, a meta-analysis by Gruner et al. (2008) reported an increase in herbivore effects at higher latitudes in freshwater ecosystems, but not in marine ecosystems. Three more recent meta-analyses with larger sample sizes found no evidence of latitudinal gradients in herbivore impacts on aquatic macrophyte abundances, some including both vascular plants and macro-algae (Moles et al., 2011; Poore et al., 2012; Wood et al., 2016).



**Fig. 3.** Synthesizing scheme indicating the effects of herbivores on macrophyte beds and the functioning of shallow freshwater (a) and marine (b) aquatic ecosystems. Herbivores affect plant abundance and species composition by grazing and bioturbation. Their presence alters biogeochemical cycling and primary production, they transport nutrients and propagules across ecosystem boundaries, modify habitat for other organisms and affect the level of shoreline protection by macrophyte beds. Symbols in the figure are courtesy of the Integration and Application Network, Univ. of Maryland Center for Environmental Science ([ian.umces.edu/symbols/](http://ian.umces.edu/symbols/)).

### 3. Ecosystem consequences of herbivory

With the establishment of herbivory as a an important factor regulating plant abundance, [Lodge \(1991\)](#) ended his review with the conclusion that “the functional importance of grazing remains largely untested”. Indeed, this has been an emerging field of research over the last 25 years, with particular progress over the last 5 years. By their presence, herbivores may induce direct changes in plant dynamics and indirect effects on ecosystem func-

tioning ([Fig. 3](#)). The effects of marine herbivores may include stimulated production of seagrass ([Valentine et al., 1997](#); [Moran and Bjorndal, 2005](#); [Vonk et al., 2008b](#); [Christianen et al., 2012](#)), changes in seagrass meadow structure ([Lal et al., 2010](#)), and the reduction of the flux of organic matter and nutrients to sediments and plants by short circuiting the detrital cycle ([Thayer et al., 1982](#); [Vonk et al., 2008a](#)); or their export to nearby habitats ([Christianen et al., 2012](#)). In salt marshes and aquatic ecosystems, an additional effect of herbivores is the return of nutrients through faeces and

**Table 1**  
Plant and herbivore traits promoting propagule dispersal by aquatic herbivores.

Trait	Effect	References
Herbivores		
Ability to chew or grind food	The presence of a gizzard or grinding teeth reduces propagule survival. Among waterfowl, heavier gizzards reduce seed survival but higher grit content may enhance germination of undigested seeds.	Figuerola et al. (2002)
Furry or sticky appearance of animal body	Animals with a surface on which propagules can attach disperse more propagules	
Diet selection	Targeted feeding on seeds may result in more transport, but also in more seed predation – thus reducing the transport through untargeted feeding which, particularly when mixed with large bulks of food (plant parts, animal food, debris), may result in high propagule survival.	Figuerola et al. (2003)
Travelling distance	Larger travelling distances results in further potential dispersal, particularly for migratory species that cover long distances in single leaps	Viana et al. (2013b)
Habitat use	Animals with specialised use of aquatic habitats are more likely to deposit the propagules in suitable habitat. In particular, targeted arrival to aquatic habitats at stopovers may increase the deposition of propagules ingested at departure sites, especially after the first drinking and feeding bout.	Figuerola and Green (2005)
Plants		
Propagule dimensions	Small, round seeds survive digestive tract better than large, elongated seeds. Small size, in particular, may enhance ingestion mixed with vegetative plant material, increasing propagule ingestion (“foliage is the fruit”, sensu Janzen (1984)) and survival to gut passage.	Mueller and van der Valk (2002), Soons et al. (2008), Figuerola et al. (2010)
Hardness and permeability of seed coat	Thicker, harder and less permeable seed coats increase survival to disperser's gut passage, but may reduce germination in the absence of undigested seeds.	Mueller and van der Valk (2002), Santamaria et al. (2002), Figuerola et al. (2010)
Adaptations for epizoochorous dispersal	Hooks, rough or sticky surface have been proposed to enhance dispersal potential	Van der Pijl (1982)
Resistance to desiccation	Organism's and/or propagule's resistance to desiccation may enhance epizoochorous dispersal of aquatic organisms	Panov and Caceres (2007), Havel et al. (2014)

urine (Bazely and Jefferies, 1985; Hik et al., 1991; Frank et al., 2000), though in seagrass grazed by turtles this effect is reduced by nutrient transport to turtle resting areas (Christianen et al., 2012).

### 3.1. Plant abundance and species composition and diversity

While the largely negative impacts of herbivores on macrophyte abundance have been well documented through short-term enclosure studies, the persistence of such effects it is often less clear. In particular, highly-mobile herbivores such as waterfowl can cause large reductions in plant abundance before switching to ungrazed sites (Wood et al., 2012b). Ecosystem responses to fluctuating grazing pressure have received little attention to date. However, there is some evidence that repeated episodes of grazing over time, such as by breeding colonies of snow geese (*Chen caerulescens*) in wetlands, can cause sustained long-term shifts in species composition and declines in plant abundance (Kerbes et al., 1990). Where non-selective, generalist herbivores feed on mixed assemblages of macrophyte, herbivores can increase species evenness by reducing the abundance of dominant competitors relative to sub-dominant macrophyte species (Hidding et al., 2010b; Wood et al., 2012b). However, when they favor certain subordinate plant species over the dominant, they can reduce evenness (Hidding et al., 2010a).

Herbivory in tropical seagrasses (e.g. by sea urchins and green turtles) can influence species composition (Vonk et al., 2008b; Kelkar et al., 2013b; Hernandez and van Tussenbroek, 2014), but often in contrasting ways. In tropical multispecies meadows, slow growing climax seagrass species (*Thalassia hemprichii*) were promoted by small herbivores (urchins), while in more intensively grazed meadows species difference in herbivore's grazing preferences resulted in the dominance of fast growing pioneer species (Kelkar et al., 2013b). Larger grazers that consume belowground plant parts and create bare sediment patches, such as green turtles and dugongs, also introduce species heterogeneity by setting

back species succession in grazed plots (Aragones et al., 2006; Christianen et al., 2013).

### 3.2. Ecosystem functions and services of aquatic herbivores

#### 3.2.1. Seed and propagule dispersal

Besides their direct effects on their food plants, aquatic herbivores provide a key service for aquatic ecosystems: the passive dispersal of a broad variety of aquatic organisms, including the aforementioned food plants, as well as many other taxa attached or associated to them (Figuerola and Green, 2002a; Brochet et al., 2010a; Van Leeuwen et al., 2012). Dispersal by most inland-water herbivores contributes to the redistribution of individuals within single wetlands and among nearby ones; while waterbirds (most notably, migratory species) are the main vector of long-distance dispersal among wetlands situated at separated watersheds, from regional to continental scales (Viana et al., 2013b; Viana et al., 2016). Among waterbirds, the frequency and scale of long-distance dispersal events is known to vary with the vector's morphology, to depend on the migratory strategy and to scale negative with body mass (Green and Figuerola, 2005; Viana et al., 2013a,b). In the marine environment, biotic dispersal by herbivores (sea turtles, ducks and fish) has been reported for seagrasses (Sumoski and Orth, 2012) and passive transport of other organisms is also known to occur e.g. sessile invertebrates transported by sea turtles and crabs (Winston, 2012). The opposite process may also take place – e.g. anecdotal evidence suggests that green turtle hatchlings use kelp rafts for passive dispersal (Carr and Meylan, 1980).

In terrestrial systems, animal-mediated dispersal is often facilitated by rewards encasing the propagules or attached to the seeds (such as fruits, elaiosomes and some pods). In contrast, aquatic plant seeds typically lack rewards; hence, their dispersal is mediated by the ingestion of plant vegetative parts by herbivores

(ifoliage in the fruit, sensu Janzen (1984)), the occasional survival of seeds ingested by granivores (e.g. teals (Brochet et al., 2010b)) or the accidental ingestion of seeds by carnivores/omnivores notably filter-feeders, such as flamingoes and shovelers (Verhoeven, 1980; Figuerola et al., 2003). This difference results in major differences in selection pressures, which can be traced to differences in predominant seed traits (Table 1). Aquatic plant seeds are typically small, which facilitates their ingestion mixed with the foliage, their survival to gut passage, and a prolonged gut-passage times resulting in longer dispersal distances (Mueller and van der Valk, 2002; Charalambidou and Santamaria, 2005; Soons et al., 2008; Figuerola et al., 2010). Larger seeds often have thick and impermeable coats, necessary to withstand their severe scarification in waterbird guts which tend to retain selectively such larger seeds (Kleyheeg, 2015) and the severe physico-chemical treatment exerted by their guts (Figuerola et al., 2002; Santamaria et al., 2002). Such coat types often result in strong physical dormancies, which may postpone seed germination until ingestion by a potential dispersal vector has taken place e.g. in seeds collected from the sediment bank by granivores and filter feeders (Figuerola et al., 2003). Invertebrate propagules dispersed by waterfowl typically show similar traits: small size, one to several protective coats, and delayed or stochastic hatching (Charalambidou and Santamaria, 2002). In some cases, the encasement of resting eggs in the mother's body may provide both protection against their digestion and a reward to potential dispersers – having thus a function analogous to that of plant fruits, whose functional and adaptive value of such a trait remains to be studied.

External dispersal may take place attached to the animal's fur or plumage, or adhered to mud-stained surfaces in the body or feet (Figuerola and Green, 2002b; Frisch et al., 2007). Available evidence suggests, however, that it is less frequent than internal dispersal (Brochet et al., 2010b). Once again, small propagules are much more likely to become attached or adhered, and remain in such situation long enough for long-distance dispersal to occur. Other traits that have been generally assumed to facilitate external dispersal, such as flat shapes and suitable surface structures (hooks, thorns, hairs), are known to occur in plant and invertebrate propagules (e.g. Vivian-Smith and Stiles (1994)). As above, their functional and adaptive value remains to be studied.

Propagule dispersal, particularly over long distances, influences the population, genetic and community structure of aquatic organisms (Viana et al., 2014). Hence, it is broadly regarded as a key ecosystem service provided by aquatic herbivores. Its effect is, however, more evident when such immigrants encounter empty niches (e.g. colonization of disturbed, new or restored wetlands) than when they face resident genotypes or species, established before their arrival (Louette and De Meester, 2005). In such cases, the immigrant's establishment may be precluded by biotic resistance arising from intra- and inter-specific competition, mortality caused by natural enemies and environmental filtering (e.g. habitat changes caused by other species). Even then, the process of propagule dispersal represents a key element of ecosystem resilience – particularly in inland waters, which are fragmented and isolated by nature. Such resilience may prove vital, in the near future, for ecosystem adaptation to global change – by facilitating rapid range shifts and the readjustment of genetic structure (e.g. locally-adapted genotypes) caused by the accelerating changes in environmental conditions associated to global warming, land use changes and the perturbation of global nutrient cycles (Amezaga et al., 2002; Röckstrom et al., 2009; Robledo-Arnuncio et al., 2014).

Propagule dispersal by aquatic herbivores may also entail negative effects for native species and ecosystems when it mediates the arrival and spread of alien species (Reynolds et al., 2015). Examples include both plant and invertebrate species (Charalambidou et al., 2003; Brochet et al., 2009; Munoz et al., 2013), although the

effect of dispersal on human-mediated dispersal is often predominant or difficult to disentangle (Weisz and Yan, 2010; Van Leeuwen et al., 2013). It is also worth noting that, despite their potential role as seed dispersers, aquatic herbivores may also reduce the frequency of propagule dispersal by reducing propagule production – due to the consumption of plant vegetative parts (e.g. (Wood et al., 2012a; Darnell and Dunton, 2015)) and the invertebrates attached or associated to them.

### 3.2.2. Biogeochemical cycling

Grazing and bioturbation by aquatic herbivores can have direct and indirect effects on biogeochemical cycling. In oligotrophic systems, grazing by smaller herbivores can have positive effects by conserving nutrients within the meadow and closing the cycling of nutrients from leaf material. Leaf material can be shredded (sea urchins, (Vonk et al., 2008b)), burrowed (Alpheid shrimp, (Vonk et al., 2008a)) or excreted after grazing (fish, (Kirsch et al., 2002)), thus stimulating nutrient retention. Larger herbivores such as green turtles and dugongs may travel between different habitats and stimulate export of nutrients between foraging (seagrass) and resting (coral reefs) areas (Christianen et al., 2012).

By foraging and resting in terrestrial and aquatic environments, herbivores provide aquatic-terrestrial linkages, transporting carbon, nutrients and contaminants from land to water (for instance hippopotamus *Hippopotamus amphibius* (Subalusky et al., 2015), waterbirds (Hahn et al., 2008; Chaichana et al., 2010) or large savanna herbivores (Moss, 2015) or vice versa (for instance by moose *Alces* sp. (Bump et al., 2009)). It has recently been suggested that the decline in large herbivore densities and the extinction of Late Pleistocene megafauna caused a strong reduction in the capacity of transport of phosphorus from nutrient hotspots, such as streams or floodplains, towards less fertile inland areas (Doughty et al., 2016). Long distance travel of migratory herbivores also contributes to transport of nutrients across sites of varying fertility (Bauer and Hoyer, 2014).

In seagrass meadows, grazing by mesoherbivores can increase productivity and possibly carbon sequestration. However below-ground grazing (e.g. by dense populations of green turtles) or other factors of disturbance in the seagrass root mat can cause release of ancient carbon, which may contribute to increased global warming (Macreadie et al., 2015). Similarly, early season below-ground foraging by pink-footed geese (*Anser brachyrhynchus*) is sufficient to strongly reduce C sink strength and soil C stocks of arctic tundra (Van der Wal et al., 2007). Recent studies are therefore stressing that it is critical to maintain intact predator populations that control large herbivore densities to prevent grazer aggregation, protect carbon stocks and avoid seagrass meadow collapse (Atwood et al., 2015). In a subtropical seagrass ecosystem, large predators (e.g. tiger sharks) induce plant species shifts by changing the foraging tactics of large grazers, such as turtle and dugongs (Heithaus et al., 2007). Under low predation risk, dugongs and sea turtles foraged by excavating nutrient-rich rhizomes of seagrasses. Under high predation risks, they changed their foraging tactics, which stimulated slow-growing pioneer species and enhanced carbon stocks.

Aquatic herbivores can also enhance methane emission through the damage of emergent plant stems (greylag geese (*Anser anser*) (Dingemans et al., 2011); grasshoppers (Petruzzella et al., 2015)). The stems of emergent macrophytes have well-developed lacunar systems for gas transport; hence, broken stems may act like “chimneys”, providing an open connection between the sediment and the atmosphere that bypasses the water layer. On the other hand, herbivores can reduce methane emission through bioturbation and removal of submerged plant beds (Bodelier et al., 2006).



### 3.2.3. Coastal protection

Seagrasses, mangroves and saltmarshes offer important coastal protection and sediment stabilization services. For seagrasses this function is generally attributed to seagrass canopy properties (Hendriks et al., 2010) and could be altered by herbivory. Although intensively grazed seagrass meadows have been shown to maintain their capacity for effective sediment stabilization, this function degrades when herbivores switch to belowground grazing, which causes decreased bed elevation, erosion and reduced coastal protection (Christianen et al., 2013). Similarly, livestock grazing can lower saltmarshes' accretion rates (Nolte et al., 2015), weakening the resilience and coastal protection function of these systems.

### 3.2.4. Habitat for other organisms

Macrophytes play an important role in structuring aquatic communities because they provide physical structure, increase habitat complexity and heterogeneity, affect oxygen and nutrient concentrations and provide refuge from predation (Carpenter and Lodge, 1986; Jeppesen et al., 1998). Macrophytes also release dissolved organic carbon (DOC) which can be used by microbes in the periphyton or plankton (Findlay et al., 1986). Therefore, by consuming macrophytes, herbivores may deteriorate the habitat for other organisms. Fish productivity was found to be lower in seagrass meadows grazed by green turtles (Arthur et al., 2013) and after meadow collapse caused by overgrazing (reported for turtles in (Christianen et al., 2013). Similarly, herbivorous fishes, dugongs, geese and other waterbirds have been found to drastically reduce invertebrate biomass in seagrass meadows and salt marshes (Marklund et al., 2002; Sherfy and Kirkpatrick, 2003; Skilleter et al., 2007; Pages et al., 2012). Impacts on invertebrates may occur even where the proportional reduction of vegetation is low (Bortolus et al., 1998).

### 3.2.5. Primary production

Submerged and emergent macrophytes can significantly contribute to the primary production of aquatic ecosystems (Blindow et al., 2006; Brothers et al., 2013). This holds especially for small lakes which represent approximately 99% of all lakes (Downing et al., 2006; Verpoorter et al., 2014). Direct studies on the effect of herbivory on aquatic plant growth and production are scarce because quantification of the impact of grazing rates on plant production requires coupled measurements of age-dependent grazing loss and turnover rate of plant tissue (Sand-Jensen et al., 1994). In general, fast turnover of the plant tissue (i.e. high specific growth rate) can compensate for intense herbivory under non-limiting resource conditions (Sand-Jensen and Jacobsen, 2002). Cherry and Gough (2009) found that *Nymphaea odorata* may tolerate moderate levels of herbivory by reallocating biomass and resources aboveground. On the contrary, stands of *Myriophyllum spicatum* retract their resources to belowground parts after defoliation by aquatic caterpillars (Miler and Straile, 2010). Water hyacinths (*Eichhornia crassipes*) were also found to fully compensate for low levels of continuous defoliation, regardless of nutrient availability (Soti and Volin, 2010). In seagrass ecosystems, reported effects of large herbivores were positive for intermediate densities of green turtles (e.g. an increased tolerance to eutrophication), and negative for high densities of green turtles (e.g. switch to belowground grazing causing meadow collapse) (Christianen et al., 2012, 2013). Similarly, moderate levels of simulated fish herbivory stimulated seagrass in primary production (i.e. compensatory growth), while very high levels of herbivory decreased it (Verges et al., 2008).

At whole-ecosystem level, herbivory on submerged macrophytes may have different effects on gross primary production (GPP). If herbivory results in a shift from clear-water to turbid conditions (see below), GPP can be expected to decline, at least under intermediate concentrations of total phosphorus (Brothers et al.,

2013). On the other hand, large grazers that remove old seagrass leaves covered in epiphytes and have been reported to increase primary production (Valentine et al., 1997; Moran and Bjorndal, 2005; Christianen et al., 2012).

### 3.2.6. Regime shifts

Shallow eutrophic lakes and lowland rivers may exist in two alternative stable steady states, a clear-water state dominated by submerged macrophytes and a turbid, phytoplankton-dominated state (Scheffer et al., 1993; Hilt et al., 2011; Hilt, 2015). In deeper lakes, submerged macrophytes may also contribute to the stabilization of clear-water conditions (Hilt et al., 2010; Sachse et al., 2014). Shifts between clear-water and turbid states have been attributed to changes in nutrient loading, in the abundance of zooplanktivorous fish (e.g. by biomanipulation) and/or in macrophyte cover (Scheffer et al., 1993; Søndergaard et al., 2007; Bakker et al., 2010). Herbivory on macrophytes may also play a significant role for shifting macrophyte-dominated systems into the turbid state, or preventing the shift from turbid- into clear-water conditions. Mitchell and Wass (1996a) concluded that the cumulative effect of waterfowl grazing consumption was small but might become critical when other conditions for macrophyte growth become limiting (due e.g. to light limitation caused by high water turbidity). A recent modeling study indeed showed that herbivory on macrophytes often becomes important in combination with additional stress by periphyton shading (Hidding et al., 2016). Herbivory by birds and fish may thus trigger the loss of submerged vegetation under high nutrient loading (Van Donk and Otte, 1996; Paice et al., 2016), possibly in combination with other stress factors. Similarly, after reductions in nutrient loading, herbivorous birds may inhibit the expected recovery of macrophytes (Lauridsen et al., 1993; Søndergaard et al., 1996; Hilt, 2006).

## 4. Perspectives: historical and future changes in herbivore grazing pressure

Herbivore management and global environmental change, including water level fluctuations, eutrophication, temperature rise and invasive species, feedback on herbivore numbers, herbivore distribution and grazing pressure.

### 4.1. Changes in herbivore assemblages over time

There is a growing body of evidence that herbivore assemblages have varied over time considerably in their diversity and abundance, and are likely to continue to vary in the future. Throughout human history, people have exploited many aquatic herbivore species, including waterfowl, Sirenians, beavers, and muskrats, for food, recreation, and animal products such as skins, furs, feathers, and oils (Domning, 1982; Kitchener and Conroy, 1997). Human overexploitation has had catastrophic effects on many herbivore populations, with a wide range of species experiencing reduced population sizes and geographic ranges, and even extinction (Jessen, 1970; Turvey and Risley, 2006). Profound historical changes in herbivore assemblages were particularly evident in shallow seas and coastal habitats, where the diversity and distributions of mammalian mega-herbivores (Sirenians such as manatees and dugongs) were reduced heavily due to hunting by humans (Whitehead, 1978; Jackson, 1997; Turvey and Risley, 2006; McCauley et al., 2015). Freshwater systems have also seen the loss of many large-bodied herbivore species, in particular mammals (Moss, 2015; Bakker et al., 2016b). Additionally, during the twentieth century a range of semi-aquatic herbivore species switched from aquatic to terrestrial feeding, particularly during winter (Laubek, 1995), further reducing herbivore abundance and diversity within aquatic systems. Such

**Table 2**

An overview of reported conservation conflicts that have arisen from the impacts of overgrazing by herbivores on macrophytes.

Herbivore	Issue	Parties in conflict	Location(s)	Duration	Current status	References
Green turtle ( <i>Chelonia mydas</i> )	Overgrazing of seagrasses can undermine conservation efforts in protected areas and reduce fish catches for local people	Turtle and seagrass conservationists, fishermen	Indo-Pacific oceans	1980s – present	Ongoing	Arthur et al. (2013), Christianen et al. (2014)
West Indian manatee ( <i>Trichechus manatus</i> )	Overgrazing has hindered efforts to restore submerged macrophyte beds	Manatee and macrophyte conservationists	Freshwater and brackish ecosystems in south-east USA	1990s – present	Ongoing	Hauxwell et al. (2004)
Beaver ( <i>Castor spp.</i> )	Impacts on aquatic habitats, via effects on vegetation and wider ecosystem (e.g. fish)	Conservationists, animal welfare groups, fishermen, and statutory wildlife management agencies	Freshwater habitats across North America, Russia	Unknown – present	Ongoing	Nolet and Rosell (1998), Collen and Gibson (2001), Halley and Rosell (2002)
Coypu ( <i>Myocastor coypus</i> ) and muskrat ( <i>Ondatra zibethicus</i> )	Overgrazing on emergent macrophytes degrades aquatic habitats	Conservationists, animal welfare groups, and statutory wildlife management agencies	Freshwater lakes and wetlands in Europe	1930s – present	Resolved by 1970s via extirpation of coypu in Britain; ongoing elsewhere in Europe	Gosling and Baker (1989), Barends (2002)
Mute swan ( <i>Cygnus olor</i> )	Overgrazing of macrophytes degrades aquatic habitats	Conservationists, animal welfare groups, and statutory wildlife management agencies	Freshwater habitats in Europe and USA	1950s – present	Ongoing	Perry and Perry (2008), Wood et al. (2014b, 2015)
Geese ( <i>Anser spp.</i> , <i>Branta spp.</i> , and <i>Chen spp.</i> )	Overgrazing of emergent macrophytes degrades wetland habitats	Conservationists, animal welfare groups, and statutory wildlife management agencies	Canadian Arctic and sub-Arctic wetlands, freshwater lakes and wetlands in Europe and North America	1970s – present	Ongoing	Kerbes et al. (1990), Nichols (2014)

habitat shifts have been most widely documented for avian herbivores such as species of swans, geese, ducks and rails (Jefferies et al., 2003; Van Eerden et al., 2005). The substantial effects of humans on aquatic herbivores meant that the twentieth century represented a low point for herbivore abundance and diversity across aquatic systems. Indeed, we find it interesting to note that earlier authors drew their conclusions on the apparent unimportance of plant-herbivore interactions in aquatic ecosystems based on research conducted during a period in which aquatic herbivores were relatively scarce. For Caribbean coastal ecosystems it has even been documented that these were severely degraded long before ecologists began to study them, through the decimation of large vertebrates including green turtles and manatees by about the year 1800 (Jackson, 1997).

Stricter hunting regulations and conservation efforts in the second half of the twentieth century have facilitated recoveries in the range and population sizes of many key aquatic herbivore species (Nolet and Rosell, 1998). An example is the Eurasian beaver (*Castor fiber*), reduced by overhunting at the beginning of the twentieth century to c.1200 individuals in eight isolated populations across Europe (Nolet and Rosell, 1998; Halley and Rosell, 2002). Following greater legal protections from hunting, the Eurasian beaver underwent sustained population recovery and has re-established populations in all areas within its former natural range (with the exception of Portugal, Italy, and the southern Balkans), with a total population of at least 1.04 million individuals (Halley et al., 2012). Many species of herbivorous waterfowl in temperate regions have made similar recoveries (Bellrose, 1976; Ankney, 1996). Of the 21 goose species (*Anser spp.* and *Branta spp.*)

for whose long-term population trends in Europe are known, 16 species are currently increasing (Fox et al., 2010). Recent changes in agricultural practices have resulted in greater terrestrial food availability for overwintering waterfowl, with larger species benefiting more in terms of population growth (Jefferies et al., 2003; Van Eerden et al., 2005). Although many reptilian herbivores remain endangered, certain species such as the green turtle (*Chelonia mydas*) have recently shown signs of population recovery in response to three decades of conservation efforts (Chaloupka et al., 2008).

The recovery of species of aquatic herbivores has been aided by the recent interest in rewinding ecosystems (Donlan et al., 2006). The key roles that extinct or extirpated large herbivores played in the structure and functioning of terrestrial ecosystems has received growing recognition from researchers (Donlan et al., 2006; Sandom et al., 2014; Bakker et al., 2016a; Doughty et al., 2016). Recently, it has been proposed that large herbivores may have played equally-important roles in regulating the structure and functioning of aquatic ecosystems (Moss, 2015; Bakker et al., 2016b). Species of aquatic herbivore which can act as ecosystem engineers, such as the beaver, are typically prime candidates for rewinding projects due to the wider ecosystem benefits that result from such engineering (Collen and Gibson, 2001). The recent finding that beaver's creation of ponds increased the diversity of herbivorous waterfowl within the landscape indicates that natural recolonization and rewinding may result in wider changes to herbivore assemblages than the target species alone, through the

facilitation of different herbivore taxa (Nummi and Holopainen, 2014).

The recovery of predator populations, via natural recovery and conservation efforts, can also affect plant-herbivore interactions (Estes et al., 2011). Evidence from terrestrial and marine systems shows that herbivore impacts on plants can be reduced as predator numbers recover, because predators not only lower herbivore abundance through direct consumption, but also alter herbivore distributions and reduce grazing intensity through indirect effects of predator avoidance behaviour ('landscape of fear' *sensu* Madin et al., (2011); Kuijper et al., (2013)). Similar results could be found for interactions between predators, herbivores, and macrophytes in aquatic systems, but little research has been carried out to date. For example, a recent study found that green turtle (*Chelonia mydas*) habitat use reflected trade-offs between food resources, body condition, and risk of predation by tiger sharks (*Galeocerdo cuvier*) in seagrass beds (Heithaus et al., 2007). A decline in tiger shark numbers may thus result in a strong increase of green turtle grazing on seagrass beds, potentially resulting in a seagrass bed collapse (Heithaus et al., 2014).

#### 4.2. Exotic herbivore species

The spread of non-native species has been a key driver of temporal changes in aquatic herbivore assemblages in recent decades. A wide range of herbivore taxa have established invasive populations known to impact on native macrophytes. Well-documented examples include birds such as the mute swan in North America (Tatu et al., 2007), mammals such as the muskrat in Europe (Danell, 1979; Sarneel et al., 2014), fishes such as the lesser-spined rabbitfishes in the Mediterranean (Verges et al., 2014a), molluscs such as the golden apple snail in Asia (Carlsson et al., 2004), and crustaceans such as red swamp crayfish in Europe (Gherardi and Acquistapace, 2007; Van der Wal et al., 2013). Despite attempts to prevent species transfer and establishment through improved biosecurity, rates of invasion remain at a historic high (Cohen and Carlton, 1998; Jackson and Grey, 2013).

#### 4.3. Climate change and temperature rise

Future environmental change is also predicted to alter herbivore assemblages. In particular, climate-driven factors such as sea-level rise and changes in vegetation phenology and abundance have the potential to alter where, when and how much herbivores feed, and thus have the potential to alter plant-herbivore interactions across aquatic systems (Stillman et al., 2015). For example, northward shifts in wintering range in response to warming have been recorded for several waterfowl species, including semi-aquatic herbivores like greylag geese (Ramo et al., 2015). Furthermore, food requirements change with temperature. With increasing temperatures, the energy requirements of temperate ectotherm animals increase and they consume more food. Furthermore, they may change their diet in response to temperature, which has consequences for the degree of plant consumption. Omnivorous fish increase their relative consumption of plant material with increasing temperatures (Prejs, 1984; Behrens and Lafferty, 2007, 2012), a pattern that is recently also found in copepods feeding on seston (Boersma et al., 2016). For endotherms this pattern may be the opposite, as their energy requirements decrease with increasing temperatures, but this hypothesis awaits empirical testing. Warmer temperatures may also induce higher periphyton shading of macrophytes (Mahdy et al., 2015), making them more prone to herbivory (Hidding et al., 2016).

#### 4.4. Herbivore impacts under human control

Where herbivore impacts on macrophytes affect human activities, such as conservation, recreation, and aquaculture, they may be viewed as undesirable. In most cases it should be noted that problems caused by herbivores are often the direct or indirect consequence of earlier human actions. For instance, ongoing eutrophication of lakes reduces the resilience of submerged plant beds to grazing due to increased shading by periphyton which profits from the nutrient loading (Hidding et al., 2016), and re-establishment of submerged vegetation can be inhibited by grazers as well (Hauxwell et al., 2004). The combined hunting of large predators and the creation of marine protected reserves, as the place where large herbivores are safe, has locally resulted in very strong grazing pressure on seagrass beds by green sea turtles (Christianen et al., 2014).

Such herbivore impacts can lead to conflicts between people interested in herbivore welfare and conservation, and those interested in the activity being affected by the herbivore (Redpath et al., 2015). To date, conflicts have arisen due to overgrazing by reptilian, mammalian, and avian herbivores (Table 2). In contrast, we could find no evidence of conflicts associated with invertebrate herbivory, which may reflect differences in human values rather than ecological impact. Indeed, evidence from a recent meta-analysis showed that vertebrate herbivores do not have consistently greater impacts on macrophytes than invertebrate herbivores (Wood et al., 2016). Vertebrate herbivores such as waterfowl, turtles, and Sirenians are often considered charismatic, and attempts to manage their numbers, behaviour or distributions are likely to attract more opposition from conservation and welfare groups than the management of invertebrate herbivores (Bremner and Park, 2007; Small, 2012). Consequently, it can be difficult to implement management to alleviate the effects of overgrazing (Coluccy et al., 2001).

Despite these conflicts, not all herbivore impacts on macrophytes are viewed as negative by people. Herbivores have proven to be effective biocontrol agents to help reduce and eradicate undesirable macrophytes, such as overabundant or invasive species (Newman, 2004; Cuda et al., 2008). A wide range of herbivore biocontrol agents have been used globally (Table 3). Biocontrol of macrophytes through herbivory has received growing interest from researchers and managers, particularly as some biotypes of invasive macrophytes (e.g. *Hydrilla verticillata*) have developed resistance to commonly-used herbicides (Cuda et al., 2008). More targeted biocontrol can be achieved by invertebrate herbivores, which typically show greater specificity for macrophyte species relative to vertebrate herbivores (Lodge, 1991; Newman, 1991). Since Wilson (1964) argued that "no insects have yet been used for the biological control of aquatic weeds", a wide range of species of coleopteran, lepidopteran, and dipteran biocontrol agents have been used successfully (Newman, 2004; Cuda et al., 2008). Both the conflicts related to overgrazing, and the use of herbivores as biocontrol agents, show the importance of improving our understanding plant-herbivore interactions. For example, understanding the density-dependence of herbivore impacts on macrophyte abundance can inform the densities of biocontrol agents required to reduce overabundant macrophytes (Cuda et al., 2008), or allow lake managers to predict the response of macrophytes to changes in wild herbivore density (Wood et al., 2012a).

### 5. How to improve understanding of herbivore impacts

#### 5.1. Bottom-up versus top-down control across environmental gradients

Lodge (1991) ended his review with the conclusion that "To understand the influence of herbivory (relative to other biotic

**Table 3**

A summary of key herbivore taxa used as biocontrol agents in the management of macrophytes.

Herbivore biocontrol agent	Target macrophyte(s)	Herbivore generalist or specific?	References
West Indian manatee ( <i>Trichechus manatus</i> )	Wide range of macrophyte species, including <i>Cabomba aquatica</i> , <i>Anacharis</i> spp., <i>Leersia</i> spp., <i>Utricularia</i> spp.	Generalist	Allsopp (1960)
Geese ( <i>Anser</i> spp)	Wide range of macrophyte species	Generalist	Ross (1971), Wilson et al. (1977)
Grass carp ( <i>Ctenopharyngodon idella</i> )	Wide range of macrophyte species, including invasive species such as <i>Hydrilla verticillata</i>	Generalist	Clayton (1996), Hanlon et al. (2000)
Cichlid fishes, e.g. blue tilapia ( <i>Oreochromis aureus</i> )	Wide range of macrophyte species	Generalist	Schwartz et al. (1986)
Crayfish, e.g. papershell crayfish ( <i>Orconectes immunis</i> )	Wide range of submerged macrophyte species	Generalist	Letson and Makarewicz (1994)
Weevils, e.g. milfoil weevil ( <i>Euhrychiopsis lecontei</i> ), Hydrilla tuber weevil ( <i>Bagous affinis</i> )	Species-specific biocontrol agents identified for many macrophyte species, e.g. Hydrilla ( <i>Hydrilla verticillata</i> ), Eurasian water milfoil ( <i>Myriophyllum spicatum</i> )	Specialist	Creed and Sheldon (1993), Newman (2004)
Apple snails ( <i>Pomacea</i> spp.)	Wide range of macrophyte species	Generalist	Rushing (1973)
Dipteran larvae, e.g. Asian hydrilla leaf-mining fly ( <i>Hydrellia pakistanae</i> )	Species-specific biocontrol agents identified for many macrophyte species, e.g. <i>Hydrilla verticillata</i>	Specialist	Wheeler and Center (2001), Bownes (2014)
Lepidopteran larvae, e.g. waterlettuce moth ( <i>Spodoptera pectinicornis</i> )	Species-specific biocontrol agents identified for many macrophyte species	Both generalist and specialist species reported	Wheeler et al. (1998), Gross et al. (2001), Newman (2004)
Hemiptera, e.g. <i>Eccritotarsus catarinensis</i>	Species-specific biocontrol agents identified for many macrophyte species, e.g. Water hyacinth ( <i>Eichhornia crassipes</i> )	Specialist	Coetzee et al. (2007), Hernandez et al. (2011)
Orthoptera, e.g. water hyacinth grasshopper ( <i>Cornops aquaticum</i> )	Species-specific biocontrol agents identified for many macrophyte species, e.g. Water hyacinth ( <i>Eichhornia crassipes</i> )	Specialist	Bownes et al. (2010)

and abiotic factors) on macrophyte populations and assemblages, extensive comparisons of grazing damage across environmental gradients and across macrophyte and grazer species must be made." Whereas meta-analyses have provided valuable insight in the impact of different herbivores both on Angiosperms and macroalgae (Poore et al., 2012; Wood et al., 2016), and the relationship between macrophyte palatability and herbivore impact received increasing attention during the last decade, the variation in the intensity and impacts of herbivory along environmental gradients has been scantily explored. Bakker and Nolet (2014) suggested that herbivore impact may increase at nutrient-rich conditions, due to a combination of higher plant palatability and lower tolerance to grazing damage caused by additional stress factors such as reduced light availability due to periphyton shading (Hidding et al., 2016). In an experimental pond system, herbivory by mallards proved to have stronger impact on submerged macrophytes under eutrophic than under oligotrophic conditions. We are not aware, however, of any field tests for this theory. Alternatively, herbivores may facilitate submerged macrophytes with increasing eutrophication, for example when moderate densities of small grazers such as freshwater snails clean submerged plants from epiphytes, which becomes more important under eutrophic conditions (Bakker et al., 2013a,b). Also, when intense grazing stimulates the formation of new shoots, which are not yet colonized by epiphytes, large grazers such as green sea turtles, can compensate the negative effect of eutrophication for seagrass growth to a certain extent (Christianen et al., 2012).

### 5.2. Integrating marine and freshwater studies

Traditionally, freshwater macrophytes and seagrasses have largely been studied separately. To date, the literature on freshwater and marine herbivore impacts have not been integrated, and have largely developed separately despite the obvious areas of overlap. If cross-system comparisons were being made, these were often marine-terrestrial or freshwater-terrestrial comparisons and

can include both vascular plants and algae (Hay, 1991; Elser et al., 2000; Burkepile, 2013). This is unfortunate because, leaving a few obvious differences apart (such as the higher salinity and connectivity of marine systems), the ecology of marine and inland-water vascular macrophytes shows very few differences. Yet, integrative work on freshwater and marine vascular macrophytes still awaits its moment.

### 5.3. Herbivore assemblages: towards functional groups

For a better understanding of herbivore impact, researchers should consider the whole community of herbivores, which compete and facilitate each other. This has already been done for terrestrial systems long ago (McNaughton, 1985), but examples for aquatic systems are rare. One such example is the herbivore community in a shallow freshwater lake that forages on pondweed beds, consisting mainly of *Potamogeton pectinatus*. The sprouting plants are being grazed by resident waterfowl species like mute swans (*Cygnus olor*), mallards (*Anas platyrhynchos*), gadwall (*Anas strepera*) and coots (*Fulica atra*). The intensity and timing of grazing determine how much above-ground plant material is remaining and growing (Hootsmans, 1999). At the end of the summer, below-ground tubers are being formed depending on the amount of above-ground plant material (Van Wijk, 1988). Thus, more and, notably, earlier waterfowl grazing in summer results in less tuber biomass in autumn (Klaassen et al., 2006; Gyimesi et al., 2011). In autumn, tubers are being depleted by migratory swans (Bewick's swans *Cygnus columbianus*) and diving ducks (mainly tufted ducks *Aythya fuligula* and pochards *Aythya ferina*) until a grazing threshold (Nolet et al., 2001). The diving ducks benefit from the trampling activity of the swans, without negatively affecting the swans' intake rate; this therefore classifies as commensalism (Gyimesi et al., 2012). In accordance with a sequential population model (Jonzén et al., 2002), highest tuber biomass and in particular tuber production was generally found at sites foraged down to intermediate thresholds in the previous autumn. In this system a positive feed-



**Table 4**  
Different methodologies used to detect and quantify herbivory on macrophytes.

Methodology	Explanation	References
Exclosures	Installation of cages (fully closed or open at the bottom) to protect macrophytes from different herbivores (fish, muskrats, waterfowl, crayfish, turtles)	Søndergaard et al. (1996), Körner et al. (2002), Hilt (2006), Christianen et al. (2012), Poore et al. (2012), Veen et al. (2013), Van der Wal et al. (2013), Sarneel et al. (2014)
Tethering	Shoot herbivory rates (cm shoot <sup>-1</sup> day <sup>-1</sup> ) are estimated for marked shoots by measuring leaf elongation over time.	Kirsch et al. (2002), Tomas et al. (2005), Prado et al. (2007), Pages et al. (2014)
Underwater videos	Video recording and quantification of fish activities including plucking of leaves	Körner and Dugdale (2003), Bennett and Bellwood (2011), Verges et al. (2014b)
Visual estimation of leaf damage		Franceschini et al. (2010)
Natural gradients	Measure macrophyte performance (e.g. growth rate, biomass, etc) across naturally-occurring gradients in herbivore assemblage properties (e.g. density)	Wood et al. (2012b)
Drones	Identification of muskrat damage in constructed wetlands by digitizing low-altitude aerial photographs	Brandt et al. (2015)
Molecular markers	Assessments of genetic variation in plants across environmental or geographical (latitudinal) gradients using different molecular markers	Mader et al. (1998), Hangelbroek et al. (2002), King et al. (2002), Hidding et al. (2014)
Stable isotope analyses	Measurement of carbon, nitrogen and hydrogen stable isotopes in resources and consumers and application of mixing models	France (1996), Solomon et al. (2011), Dorenbosch and Bakker (2012), Mendonca et al. (2013), Vander Zanden et al. (2013), Scharnweber et al. (2014), De Kluijver et al. (2015), Mao et al. (2014)
Gut analyses and stable isotope analyses	Gut analyses in fish combined with stable isotope analyses of basal food resources and fish	Hanson et al. (2007)
Telemetry	Whole-lake fish telemetry	Dos Santos et al. (2012)
Bird counting and determination of lignin content in faeces		
Laboratory feeding rate determination in fish	Determination of fish feeding rates in aquaria	Körner and Dugdale (2003)
Mechanistic models	Simulations of foraging herbivores or effects on plant growth can predict the location, timing, and magnitude of herbivore effects on macrophytes	Hootsmans (1999), Van Nes et al. (2003), Nolet et al. (2006), Wood et al. (2014a), Nolet et al. (2016), Hidding et al. (2016)

back between tuber grazing and tuber production resulted from a reduction in self-shading or a decrease in neighbour competition (Nolet, 2004).

Together, the interactions within herbivore communities will determine the effect of herbivore diversity, a topic rarely touched upon in aquatic vascular plant beds but see marine macro-algae and seagrass systems, e.g. (Duffy et al., 2003; Burkepile, 2013). Whereas all interactions at the species level are interesting, a way forward can be to generalize beyond species by grouping herbivores in guilds or functional groups and working out which traits best explain their relative effects. Such traits could include body size, diet (herbivory-omnivory), habitat (terrestrial-aquatic linkages), migratory strategy (sedentary versus migratory) and movement ecology (foraging ranges). Recently, grouping of large savanna herbivores proved to be useful to understand their ecosystem impacts (Hempson et al., 2015). Similarly, the ecosystem functions of aquatic large herbivores may be understood from their habitat use, in particular how dependent on the aquatic systems they are in combination with their movement ecology (Bakker et al., 2016b).

#### 5.4. Tools to study herbivore impacts

Practically, the high variance in estimates of macrophyte abundance, even within a single study system, can make herbivore effects difficult to detect in aquatic systems without large sample sizes (Wood et al., 2012b). However, numerous methods have been developed and employed to detect and/or quantify herbivory on macrophytes and seagrasses (Table 4). The most direct approach for detection and quantification of effects is a technique known as tethering (Kirsch et al., 2002; Tomas et al., 2005; Prado et al., 2007; Pages et al., 2014). With this technique it is possible to estimate the biomass (or cm of leaf) eaten daily, i.e. direct herbivory rates (see Table 4). Another direct approach to detect and quantify herbivore effects are in situ exclosure cages with subsequent biomass measurements in- and outside.

Other less direct herbivory detection and quantification methods focusing on macrophytes include visual estimations of leaf damage and measurements of macrophyte performance across naturally-occurring spatial or temporal gradients in herbivore