



# 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))

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 (Rodriguez 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;

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