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# Herbivory on freshwater and marine macrophytes

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## Aquatic Botany

1 **Herbivory on freshwater and marine macrophytes: a review and perspective**

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42    **Abstract**

43

44    Until the 1990s, herbivory on aquatic vascular plants was considered to be of minor importance, and

45    the predominant view was that freshwater and marine macrophytes did not take part in the food

46    web: their primary fate was the detritivorous pathway. In the last 25 years, a substantial body of

47    evidence has developed that shows that herbivory is an important factor in the ecology of vascular

48    macrophytes across freshwater and marine habitats. Herbivores remove on average 40-48% of plant

49    biomass in freshwater and marine ecosystems, which is typically 5-10 times greater than reported for

50    terrestrial ecosystems. This may be explained by the lower C:N stoichiometry found in submerged

51    plants. Herbivores affect plant abundance and species composition by grazing and bioturbation and

52    therewith alter the functioning of aquatic ecosystems, including biogeochemical cycling, carbon

53    stocks and primary production, transport of nutrients and propagules across ecosystem boundaries,

54    habitat for other organisms and the level of shoreline protection by macrophyte beds.

55    With ongoing global environmental change, herbivore impacts are predicted to increase. There are

56    pressing needs to improve our management of undesirable herbivore impacts on macrophytes (e.g.

57    leading to an ecosystem collapse), and the conflicts between people associated with the impacts of

58    charismatic mega-herbivores. While simultaneously, the long-term future of maintaining both viable

59    herbivore populations and plant beds should be addressed, as both belong in complete ecosystems

60    and have co-evolved in these long before the increasing influence of man. Better integration of the

61    freshwater, marine, and terrestrial herbivory literatures would greatly benefit future research

62    efforts.

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64

65    *Keywords: climate change, conservation, ecosystem functions, grazing, seagrass, stoichiometry*

66     **1.    Introduction: 25 years of research on herbivory on macrophytes**

67

68     1.1 *Setting the scene*

69

70         In the 1990s two seminal papers appeared in Aquatic Botany that urged for a complete

71     change in the paradigm that had been dominating macrophyte ecology. Despite some early work on

72     the impact of waterbirds on freshwater and marine angiosperms (Jupp and Spence, 1977; Jacobs et

73     al., 1981), until then, herbivory on aquatic vascular plants was considered to be of minor importance,

74     and the predominant view was that freshwater and marine macrophytes did not take part in the

75     food web (e.g. Shelford (1918) and their primary fate was the detritivorous pathway (Polunin, 1984;

76     Duarte and Cebrian, 1996). But in 1991, Lodge argued that, contrary to conventional wisdom, live

77     freshwater macrophytes are engaged in aquatic food webs. In 1998, Cebrian and Duarte highlighted

78     that, while seagrasses suffered modest herbivory rates on average, such rates were highly variable,

79     and the importance of seagrass-herbivore interactions should not be discounted. Following on from

80     these two papers, Lodge (1998) provided further evidence for the important role of herbivores in

81     freshwater habitats, as compared to other biomes; and Valentine and Heck (1999) demonstrated

82     that grazing on seagrasses is widespread in the world's oceans.

83         Together, these landmark papers put macrophyte herbivory on the map. Since then, there

84     has been a strong increase in the amount of studies that investigated herbivory on freshwater

85     macrophytes and seagrasses. In this study, we review what we have learned in the 25 years that

86     followed the appearance of Lodge (1991). Furthermore, we identify new topics that have emerged

87     over this time. These new topics include the fast changes that may occur in macrophyte-herbivore

88     relationships with the ongoing global environmental change, as well as the potential conflicts

89     between herbivore conservation and herbivore impacts on aquatic ecosystems. Finally, we discuss

90     how we can improve our understanding of herbivore impacts and what tools may help us in

4

91    achieving this. Following the approach of the seminal papers listed above, we focus primarily on

92    aquatic angiosperms (submerged, floating and emergent) and address both freshwater and marine

93    ecosystems.

94

95    1.2 *Why thinking about herbivory on macrophytes has changed over the last 25 years*

96         The paradigm shift in our perception of macrophyte herbivory, from being considered

97    negligible to being acknowledged as a key factor shaping benthic ecosystems, is not only caused by

98    an increase in scientific interest fostered by these landmark papers: the effect of herbivory became

99    also more conspicuous over the last 25 years. The reasons for this are methodological, anthropogenic

100   and ecological.

101        Methodological improvements for estimating herbivory included observation methods, such

102   as bite mark counts (Cebrian and Duarte, 1998), experimental approaches, such as herbivore

103   exclusions (see Poore et al. (2012) and Wood et al. (2016) for syntheses of marine and freshwater

104   habitats, including macro-algae) and direct methods, including video bite counts or isotopic

105   signatures (see Table 4 for details).

106        Anthropogenic effects included increases in the densities of aquatic and marine herbivores as

107   a result of increased protection, predator removal, food subsidies from agriculture, and the

108   introduction of exotic herbivores (Estes et al., 2011). For example, steep increases in herbivory rates

109   have been reported for sea turtles in the Arabian Sea and Indonesia (Kelkar et al., 2013b, a),

110   (Christianen et al., 2014), for herbivorous fish in the Mediterranean (Pages et al., 2012) and for geese

111   in Northwestern Europe and North America  (Jefferies et al., 2003; Van Eerden et al., 2005).

112   However, it should be noted that despite recent local increases in herbivory, which have attracted

113   attention to the role of herbivores in benthic ecosystems, over longer time frames in particularly

114   species of large herbivores have experienced strong global declines (Jackson, 1997; McCauley et al.,

115   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 re-colonization 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., 2013; 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., 2013b, a; 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

141    experiments in which freshwater herbivores were excluded found that herbivory reduced

142    macrophyte biomass by 47.2 ± 3.4 % (average ± CI) (Wood et al., 2016). Of these, 300 experiments

143    reported a reduction in macrophyte biomass, while 26 experiments reported positive effects or no

144    changes. Similarly, a meta-analysis on grazing impacts on marine macrophytes found that herbivores

145    reduce macrophyte abundance (both submerged angiosperms and macro-algae) by 68% on average

146    (Poore et al., 2012).

147    Despite their historical disregard, the removal of vascular plant biomass by herbivores is, on average,

148    much larger in aquatic than in terrestrial ecosystems. The most recent meta-analyses available for

149    terrestrial, freshwater and marine habitats (Turcotte et al., 2014; Wood et al., 2016) show that

150    median biomass removal by herbivores is 4-8 % in terrestrial ecosystems,  while it is  44-48% in

151    freshwater and 40-44% in  marine ecosystems (Fig 1a-c). Thus, herbivores remove on average 5-10

152    times more vascular plant biomass in aquatic ecosystems than in terrestrial ones.

153    Yet, the impact of herbivores on vascular plant biomass removal is much more variable in aquatic

154    than in terrestrial ecosystems, and it ranges as broadly as between 0 and 100% of biomass removal

155    (Fig 1a-c). Underlying explanations for the large range of herbivore effects in aquatic ecosystems are

156    still unknown. Potential mechanisms involve bottom-up effects, such as variation in plant

157    productivity, nutritional quality, stoichiometry, resistance and tolerance to grazing (Cebrian et al.,

158    2009); and top-down effects, such as variation in herbivore abundance, feeding efficiency, size,

159    taxonomy, mobility, metabolism and predator effects (Borer et al., 2005).

160

161    *2.2. Bottom-up effects: the plant's perspective*

162    *2.2.1.   Primary productivity and herbivory rates*

163    Studies in aquatic systems traditionally focussed on primary production of phytoplankton in pelagic

164    habitats, and only recently littoral areas received more attention (Vadeboncoeur et al., 2002;

165 Brothers et al., 2013). Theoretical predictions based on Lotka-Volterra models suggest that grazing

166 should increase with primary productivity (Gruner et al., 2008), because as plants produce more

167 tissues or do so at faster rates, herbivores can increase their rates of consumption. This prediction

168 relies in the assumption that herbivory rates are bottom-up regulated by the availability of plant

169 tissues. Empirical evidence is however conflicting. A meta-analysis by Cyr and Pace (1993) concluded

170 that herbivory increases with primary production in both terrestrial and aquatic systems. However, a

171 more recent meta-analysis found no significant effect of productivity on herbivory (or interaction

172 strength) in aquatic systems (e.g. (Borer et al., 2005)). In fact, it is widely recognized that food quality

173 and defences also have major effects on herbivore performance that might mask any herbivory-

174 productivity relationship. Using a plant growth model, Hidding et al. (2016) suggested that herbivore

175 grazing effects on macrophytes become important above certain thresholds in periphyton shading

176 and thus reduced production of plants.

177

178     *2.2.2. Plant stoichiometry*

179     Differences in herbivory rates across plant taxa have also been attributed to differences in

180 plant quality, as perceived by herbivores (Lodge, 1991; Cronin et al., 2002). Generally, there is a

181 positive relationship between the nitrogen content in the plant's tissue and its consumption by

182 herbivores (Cebrian and Lartigue, 2004). This pattern holds both within and across ecosystems (Elser

183 et al., 2000; Cebrian and Lartigue, 2004; Cebrian et al., 2009). Hence, it has been suggested that

184 higher herbivore consumption rates in aquatic plants might be explained by their higher quality as

185 food – arising from the lack of carbon-rich structural compounds that strengthen cell walls, increase

186 resistance to herbivores, and reduce digestibility in terrestrial plants (Gruner et al., 2008).

187 Unfortunately, most comparisons between aquatic and terrestrial systems undertaken to date

188 restricted their estimates of aquatic herbivory to phytoplankton consumption, thus giving limited or

189 no information on the consumption of aquatic macrophytes (Elser et al., 2000). Comparing herbivory

190  rates on, and food quality (e.g., nitrogen content) of, aquatic and terrestrial vascular plants would be

191  more informative, because they have a close phylogenetic affinity and most differences could be

192  attributed to the ecosystems they inhabit (Hay, 1991; Gross and Bakker, 2012; Burkepile, 2013).

193  A compilation of data on C:N ratios of vascular plants in terrestrial, freshwater and marine

194  ecosystems reveals that they differ strongly between these systems (Fig 1d-f). Median C:N ratio

195  decreased strongly from terrestrial vascular plants (25-30) and marine macrophytes (24-28) to

196  freshwater macrophytes (12-16) (Fig 1d-f). The high N content (thus low C:N ratio) of freshwater

197  macrophytes may indicate a higher quality to herbivores, potentially  explaining the high herbivory

198  rates found in freshwater systems. Taking into account the variation in growth forms that occurs in

199  aquatic ecosystems makes this pattern stronger (Fig 2a-d). Herbivory rates are lower on emergent

200  macrophytes (median freshwater = 36-48%; median marine = 24-36%) than on submerged

201  macrophytes (median freshwater and marine = 48-60%) in both freshwater and marine ecosystems

202  (Fig 2a,b). These differences fit closely the C:N ratio of the different plant growth forms, as emergent

203  macrophytes have higher C:N ratios (median freshwater = 28-32; median marine = 24-28) than

204  submerged macrophytes (median freshwater = 8-12; median marine = 20-24), particularly in

205  freshwater ecosystems (Fig 2c,d).

206  Our data compilation indicates that differences in plant quality between terrestrial plants

207  and macrophytes show close links to variation in herbivory rates. Submerged plants need less

208  structural components, resulting in higher N content and higher rates of herbivory. In contrast,

209  herbivory rates and N content of emergent macrophytes are similar to those found in terrestrial

210  plants (Fig 1a, 1d, 2a-d). Although N content is acknowledged as an important determinant of plant

211  quality to herbivores, other nutrients and secondary compounds may also influence it. For example,

212  freshwater macrophytes and seagrassess have anti-herbivore defenses (Verges et al., 2008; Gross

213  and Bakker, 2012), which may cause low palatability - even in highly nutritious species. Phenolics,

214  terpenoids and nitrogenated compounds can be efficient deterrents of aquatic herbivores, although

215     deterrence of generalist herbivores often comes at the cost of higher preference by specialised

216     consumers (Verges et al., 2007). Interestingly, in freshwater systems, the concentrations of phenolic

217     compounds decrease from emergent to floating to submerged plants (Smolders et al., 2000),

218     suggesting not only higher nutritional quality, but also less defended tissues, resulting in generally

219     higher palatability of submerged plants. However, this issue still deserves more research, since most

220     work has focused on macro-algae (e.g. (Hay, 1996)). Besides the differences between ecosystems

221     discussed above, spatial and temporal variation in herbivory at population and individual-plant level

222     has also been linked to plant quality (C:N, % N) and to the presence of anti-herbivore defences

223     (Hacker and Bertness, 1995; Preen, 1995; Verges et al., 2007; Prado et al., 2010).

224

225     *2.3. Top-down effects: the herbivore's perspective*

226     *2.3.1.    Herbivore density*

227     Within individual herbivore species, herbivore impact on aquatic plant abundance is positively

228     related to herbivore density (Stott and Robson, 1970; Valentine and Heck, 1991; Wood et al., 2012a;

229     Kelkar et al., 2013b). However, analyses of herbivore impacts across multiple herbivore species have

230     found no relationship between herbivore density and macrophyte abundance, probably due to the

231     confounding effects of interspecific differences in herbivore ecology (Marklund et al., 2002; Wood et

232     al., 2012a). For example, among plant-eating waterfowl, substantial differences exist in mean adult

233     body mass (from the 24 g of ocellated crake, *Micropygia schomburgkii*, to the 12,000 g of trumpeter

234     swan, *Cygnus buccinator*), which is known to influence the species' diet and the absolute quantity of

235     vegetation consumed (Wood et al., 2012a). Consequently, when herbivore densities were estimated

236     as biomass densities (thus accounting for interspecific differences in individual body mass), a

237     significant negative relationship between herbivore biomass density and macrophyte abundance was

238     detected (Wood et al., 2012a; Wood et al., 2016). Only at relatively low herbivore densities were

239     positive changes in plant abundance reported, suggesting that in aquatic systems greater herbivore

240     densities overwhelm plant compensatory growth responses (Wood et al., 2016).

241

242     *2.3.2.   Size, mobility and taxonomy of herbivores*

243     By virtue of their size, large terrestrial herbivores are critical agents of change and maintenance of

244     the ecosystems they inhabit (Owen-Smith, 1988; Bakker et al., 2016a). In aquatic environments, large

245     herbivores have also been identified as key species (McCauley et al., 2015), often considered

246     ecosystem engineers (e.g. (Bakker et al., 2016b)). It is not surprising, thus, that a recent meta-analysis

247     found significantly stronger impacts of macrograzers (fishes, urchins and large molluscs) than

248     mesograzers (amphipods, isopods and small molluscs) on marine macrophytes (algae, seagrasses and

249     salt marshes)  (Poore et al., 2012).

250     Another recent meta-analysis by Wood et al (2016) found substantial between-taxa differences in

251     effects of herbivores on the abundance of freshwater and marine macrophytes. Echinoderms,

252     molluscs, and fish had relatively large impacts on plants, while insects and birds had relatively low

253     impacts. The reason for these differences may be the mobility and habitat preferences of each of

254     these groups. Fully aquatic species that live underwater permanently, have been shown to produce

255     the greatest impacts on aquatic plants (Bakker et al., 2016b), while facultative aquatic grazers, such

256     as insects and birds, spread their activity more between different ecosystems (thanks to their high

257     mobility), thus spreading also their impact between such ecosystems. Wood et al. (2016) also

258     pointed out the fact that some herbivores (such as echinoderms, crayfish and molluscs) have

259     restricted mobility and produce intense impacts due to their bulk grazing strategies, since they

260     consume multiple tissues types and species, thus affecting a greater proportion of a plant community

261     (Lodge et al., 1998).

262

263    *2.3.3.  Herbivory and omnivory*

264        Most animals that consume aquatic plants are omnivores, very few are strict herbivores.

265    There is a positive relationship between body size and degree of herbivory in aquatic omnivores: the

266    larger the consumer, the more important plant consumption (granivory and folivory, particularly the

267    latter) is in their diet (Clements et al., 2009; Wood et al., 2012a). Hence, per capita, large herbivores

268    have the largest impact on plant abundance through grazing. The high level of generalistic feeding

269    and omnivory of aquatic plant consumers may be related to the higher impact of herbivory on

270    aquatic plants, because it may relax the effect of direct density dependence on consumers: whenever

271    consumers overgraze plants, they can switch to alternative food sources (algae, detritus or animal

272    prey) within or nearby the water body (Grey and Jackson, 2012). Furthermore, in aquatic systems,

273    large herbivores and omnivores often feed on both aboveground and belowground plant material,

274    which may multiply their impact on plants, due to the depletion of underground plant resources for

275    regrowth.

276        Herbivore impact may also be enhanced by non-consumptive effects, which are documented

277    to be severe in freshwater and marine macrophytes, e.g. bioturbation (Lodge, 1991). By initiating

278    bare patches, herbivores can create focal points for further erosion of macrophyte meadows by

279    waves in shallow areas (Christianen et al., 2013). Trampling, fecal deposition and increasing nutrient

280    concentrations may also play a role. Whilst previous authors have cautioned against the assumption

281    that herbivore effects on plants represent exclusively grazing losses due to consumption (Mitchell

282    and Wass, 1996b), many studies continue to ignore the roles of non-consumptive effects.

283

284    *2.4. Latitude*

285    Potential variance in herbivore impacts on plant abundance across different latitudes has been a

286    topic of growing interest among ecologists. However, the evidence for a role of latitudinal effects is

287  limited. For example, in macrophyte feeding assays carried out by Morrison and Hay (2012), only one

288  out of three crayfish species showed a preference associated with latitude (a preference for higher

289  latitude plants). Schemske et al. (2009) argued that, across all ecosystems, herbivore impacts are

290  greater at lower latitudes. In contrast, a meta-analysis by Gruner et al. (2008) reported an increase in

291  herbivore effects at higher latitudes in freshwater ecosystems, but not in marine ecosystems. Three

292  more recent meta-analyses with larger sample sizes found no evidence of latitudinal gradients in

293  herbivore impacts on aquatic macrophyte abundances, some including both vascular plants and

294  macro-algae (Moles et al., 2011; Poore et al., 2012; Wood et al., 2016).

295

296    **3.  Ecosystem consequences of herbivory**

297  With the establishment of herbivory as a an important factor regulating plant abundance, Lodge

298  (1991) ended his review with the conclusion that "the functional importance of grazing remains

299  largely untested". Indeed, this has been an emerging field of research over the last 25 years, with

300  particular progress over the last 5 years. By their presence, herbivores may induce direct changes in

301  plant dynamics and indirect effects on ecosystem functioning (Fig. 3). The effects of marine

302  herbivores may include stimulated production of seagrass  (Valentine et al., 1997; Moran and

303  Bjorndal, 2005; Vonk et al., 2008b; Christianen et al., 2012), changes in seagrass meadow structure

304  (Lal et al., 2010), and the reduction of the flux of organic matter and nutrients to sediments and

305  plants (by short circuiting the detrital cycle; (Thayer et al., 1982; Vonk et al., 2008a) or their export to

306  nearby habitats (Christianen et al., 2012). In salt marshes and aquatic ecosystems, an additional

307  effect of herbivores is the return of nutrients through faeces and urine (Bazely and Jefferies, 1985;

308  Hik et al., 1991; Frank et al., 2000), though in seagrass grazed by turtles this effect is reduced by

309  nutrient transport to turtle resting areas (Christianen et al., 2012).

310

311    3.1 *Plant abundance and species composition and diversity*

312    While the largely negative impacts of herbivores on macrophyte abundance have been well

313    documented through short-term exclosure studies, the persistence of such effects it is often less

314    clear. In particular, highly-mobile herbivores such as waterfowl can cause large reductions in plant

315    abundance before switching to ungrazed sites (Wood et al., 2012b). Ecosystem responses to

316    fluctuating grazing pressure have received little attention to date. However, there is some evidence

317    that repeated episodes of grazing over time, such as by breeding colonies of snow geese (*Chen*

318    *caerulescens*) in wetlands, can cause sustained long-term shifts in species composition and declines

319    in plant abundance (Kerbes et al., 1990). Where non-selective, generalist herbivores feed on mixed

320    assemblages of macrophyte, herbivores can increase species evenness by reducing the abundance of

321    dominant competitors relative to sub-dominant macrophyte species (Hidding et al., 2010b; Wood et

322    al., 2012b). However, when they favor certain subordinate plant species over the dominant, they can

323    reduce eveness (Hidding et al. 2010a).

324    Herbivory in tropical seagrasses (e.g. by sea urchins and green turtles) can influence species

325    composition (Vonk et al., 2008b; Kelkar et al., 2013b; Hernandez and van Tussenbroek, 2014), but

326    often in contrasting ways. In tropical multispecies meadows, slow growing climax seagrass species

327    (*Thalassia hemprichii*) were promoted by small herbivores (urchins), while in more intensively grazed

328    meadows species difference in herbivore's grazing preferences resulted in the dominance of fast

329    growing pioneer species (Kelkar et al., 2013b). Larger grazers that consume belowground plant parts

330    and create bare sediment patches, such as green turtles and dugongs, also introduce species

331    heterogeneity by setting back species succession in grazed plots (Aragones et al., 2006; Christianen et

332    al., 2013).

333

334    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., in press). 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., 2013b; Viana

et al., 2013a). 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 (´foliage 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

360  gut-passage times resulting in longer dispersal distances (Mueller and van der Valk, 2002;

361  Charalambidou and Santamaria, 2005; Soons et al., 2008; Figuerola et al., 2010). Larger seeds often

362  have thick and impermeable coats, necessary to withstand their severe scarification in waterbird guts

363  (which tend to retain selectively such larger seeds(Kleyheeg, 2015) and the severe physico-chemical

364  treatment exerted by their guts (Figuerola et al., 2002; Santamaria et al., 2002). Such coat types

365  often result in strong physical dormancies, which may postpone seed germination until ingestion by a

366  potential dispersal vector has taken place (e.g. in seeds collected from the sediment bank by

367  granivores and filter feeders (Figuerola et al., 2003). Invertebrate propagules dispersed by waterfowl

368  typically show similar traits: small size, one to several protective coats, and delayed or stochastic

369  hatching (Charalambidou and Santamaria, 2002). In some cases, the encasement of resting eggs in

370  the mother's body may provide both protection against their digestion and a reward to potential

371  dispersers – having thus a function analogous to that of plant fruits, whose functional and adaptive

372  value of such a trait remains to be studied.

373  External dispersal may take place attached to the animal's fur or plumage, or adhered to mud-

374  stained surfaces in the body or feet (Figuerola and Green, 2002b; Frisch et al., 2007). Available

375  evidence suggests, however, that it is less frequent than internal dispersal (Brochet et al., 2010b).

376  Once again, small propagules are much more likely to become attached or adhered, and remain in

377  such situation long enough for long-distance dispersal to occur. Other traits that have been generally

378  assumed to facilitate external dispersal, such as flat shapes and suitable surface structures (hooks,

379  thorns, hairs), are known to occur in plant and invertebrate propagules (e.g. Vivian-Smith and Stiles

380  (1994)). As above, their functional and adaptive value remains to be studied.

381  Propagule dispersal, particularly over long distances, influences the population, genetic and

382  community structure of aquatic organisms (Viana et al., 2014). Hence, it is broadly regarded as a key

383  ecosystem service provided by aquatic herbivores. Its effect is, however, more evident when such

384  immigrants encounter empty niches (e.g. colonization of disturbed, new or restored wetlands) than

385    when they face resident genotypes or species, established before their arrival (Louette and De

386    Meester, 2005). In such cases, the immigrant's establishment may be precluded by biotic resistance

387    arising from intra- and inter-specific competition, mortality caused by natural enemies and

388    environmental filtering (e.g. habitat changes caused by other species). Even then, the process of

389    propagule dispersal represents a key element of ecosystem resilience – particularly in inland waters,

390    which are fragmented and isolated by nature. Such resilience may prove vital, in the near future, for

391    ecosystem adaptation to global change – by facilitating rapid range shifts and the readjustment of

392    genetic structure (e.g. locally-adapted genotypes) caused by the accelerating changes in

393    environmental conditions associated to global warming, land use changes and the perturbation of

394    global nutrient cycles (Amezaga et al., 2002; Röckstrom et al., 2009; Robledo-Arnuncio et al., 2014).

395    Propagule dispersal by aquatic herbivores may also entail negative effects for native species and

396    ecosystems when it mediates the arrival and spread of alien species (Reynolds et al., 2015). Examples

397    include both plant and invertebrate species (Charalambidou et al., 2003; Brochet et al., 2009; Munoz

398    et al., 2013), although the effect of dispersal on human-mediated dispersal is often predominant or

399    difficult to disentangle (Weisz and Yan, 2010; Van Leeuwen et al., 2013). It is also worth noting that,

400    despite their potential role as seed dispersers, aquatic herbivores may also reduce the frequency of

401    propagule dispersal by reducing propagule production – due to the consumption of plant vegetative

402    parts (e.g. (Wood et al., 2012a; Darnell and Dunton, 2015)) and the invertebrates attached or

403    associated to them.

404

405    *3.2.2 Biogeochemical cycling*

406    Grazing and bioturbation by aquatic herbivores can have direct and indirect effects on

407    biogeochemical cycling. In oligotrophic systems, grazing by smaller herbivores can have positive

408    effects by conserving nutrients within the meadow and closing the cycling of nutrients from leaf

409    material. Leaf material can be shredded (sea urchins, (Vonk et al., 2008b)), burrowed (Alpheid

410      shrimp, (Vonk et al., 2008a)) or excreted after grazing (fish, (Kirsch et al., 2002)), thus stimulating

411      nutrient retention. Larger herbivores such as green turtles and dugongs may travel between different

412      habitats and stimulate export of nutrients between foraging (seagrass) and resting (coral reefs) areas

413      (Christianen et al., 2012).

414      By foraging and resting in terrestrial and aquatic environments, herbivores provide aquatic-terrestrial

415      linkages, transporting carbon, nutrients and contaminants from land to water (for instance

416      hippopotamus *Hippopotamus amphibius* (Subalusky et al., 2015), waterbirds (Hahn et al., 2008;

417      Chaichana et al., 2010) or large savanna herbivores(Moss, 2015) or *vice versa* (for instance by moose

418      *Alces sp.* (Bump et al., 2009)). It has recently been suggested that the decline in large herbivore

419      densities and the extinction of Late Pleistocene megafauna caused a strong reduction in the capacity

420      of transport of phosphorus from nutrient hotspots, such as streams or floodplains, towards less

421      fertile inland areas (Doughty et al., 2016). Long distance travel of migratory herbivores also

422      contributes to transport of nutrients across sites of varying fertility (Bauer and Hoye, 2014).

423      In seagrass meadows, grazing by mesoherbivores can increase productivity and possibly carbon

424      sequestration. However below-ground grazing (e.g. by dense populations of green turtles) or other

425      factors of disturbance in the seagrass root mat can cause release of ancient carbon, which may

426      contribute to increased global warming (Macreadie et al., 2015). Similarly, early season below-

427      ground foraging by pink-footed geese (*Anser brachyrhynchus*) is sufficient to strongly reduce C sink

428      strength and soil C stocks of arctic tundra (van der Wal et al., 2007). Recent studies are therefore

429      stressing that it is critical to maintain intact predator populations that control large herbivore

430      densities to prevent grazer aggregation, protect carbon stocks and avoid seagrass meadow collapse

431      (Atwood et al., 2015). In a subtropical seagrass ecosystem, large predators (e.g. tiger sharks) induce

432      plant species shifts by changing the foraging tactics of large grazers, such as turtle and dugongs

433      (Heithaus et al., 2007). Under low predation risk, dugongs and sea turtles foraged by excavating

434      nutrient-rich rhizomes of seagrasses. Under high predation risks, they changed their foraging tactics,

435      which stimulated slow-growing pioneer species and enhanced carbon stocks.

436      Aquatic herbivores can also enhance methane emission through the damage of emergent plant

437      stems (greylag geese (*Anser anser* ) (Dingemans et al., 2011); grasshoppers (Petruzzella et al., 2015)).

438      The stems of emergent macrophytes have well-developed lacunar systems for gas transport; hence,

439      broken stems may act like "chimneys", providing an open connection between the sediment and the

440      atmosphere that bypasses the water layer. On the other hand, herbivores can reduce methane

441      emission through bioturbation and removal of submerged plant beds (Bodelier et al., 2006).

442

443      *3.2.3 Coastal protection*

444      Seagrasses, mangroves and saltmarshes offer important coastal protection and sediment

445      stabilization services. For seagrasses this function is generally attributed to seagrass canopy

446      properties (Hendriks et al., 2010) and could be altered by herbivory. Although intensively grazed

447      seagrass meadows have been shown to maintain their capacity for effective sediment stabilization,

448      this function degrades when herbivores switch to belowground grazing , which causes decreased bed

449      elevation, erosion and reduced coastal protection (Christianen et al., 2013). Similarly, livestock

450      grazing can lower saltmarshes' accretion rates (Nolte et al., 2015), weakening the resilience and

451      coastal protection function of these systems.

452

453      *3.2.4 Habitat for other organisms*

454      Macrophytes play an important role in structuring aquatic communities because they provide

455      physical structure, increase habitat complexity and heterogeneity, affect oxygen and nutrient

456      concentrations and provide refuge from predation (Carpenter and Lodge, 1986; Jeppesen et al.,

457    1998). Macrophytes also release dissolved organic carbon (DOC) which can be used by microbes in

458    the periphyton or plankton (Findlay et al., 1986). Therefore, by consuming macrophytes, herbivores

459    may deteriorate the habitat for other organisms. Fish productivity was found to be lower in seagrass

460    meadows grazed by green turtles (Arthur et al., 2013) and after meadow collapse caused by

461    overgrazing (reported for turtles in (Christianen et al., 2013). Similarly, herbivorous fishes, dugongs,

462    geese and other waterbirds have been found to drastically reduce invertebrate biomass in seagrass

463    meadows and salt marshes (Marklund et al., 2002; Sherfy and Kirkpatrick, 2003; Skilleter et al., 2007;

464    Pages et al., 2012) . Impacts on invertebrates may occur even where the proportional reduction of

465    vegetation is low (Bortolus et al., 1998).

466

467    3.2.5. *Primary production*

468    Submerged and emergent macrophytes can significantly contribute to the primary production of

469    aquatic ecosystems (Blindow et al., 2006; Brothers et al., 2013). This holds especially for small lakes

470    which represent approximately 99% of all lakes (Downing et al., 2006; Verpoorter et al., 2014). Direct

471    studies on the effect of herbivory on aquatic plant growth and production are scarce because

472    quantification of the impact of grazing rates on plant production requires coupled measurements of

473    age-dependent grazing loss and turnover rate of plant tissue (Sand-Jensen et al., 1994). In general,

474    fast turnover of the plant tissue (i.e. high specific growth rate) can compensate for intense herbivory

475    under non-limiting resource conditions (Sand-Jensen and Jacobsen, 2002). Cherry & Gough (2009)

476    found that *Nymphaea odorata* may tolerate moderate levels of herbivory by reallocating biomass

477    and resources aboveground. On the contrary, stands of *Myriophyllum spicatum* retract their

478    resources to belowground parts after defoliation by aquatic caterpillars (Miler and Straile, 2010).

479    Water hyacinths (*Eichhornia crassipes*) were also found to fully compensate for low levels of

480    continuous defoliation, regardless of nutrient availability (Soti and Volin, 2010). In seagrass

481    ecosystems, reported effects of large herbivores were positive for intermediate densities of green

482 turtles (e.g. an increased tolerance to eutrophication), and negative for high densities of green

483 turtles (e.g. switch to belowground grazing causing meadow collapse) (Christianen et al., 2012;

484 Christianen et al., 2013). Similarly, moderate levels of simulated fish herbivory stimulated seagrass in

485 primary production (i.e. compensatory growth), while very high levels of herbivory decreased it

486 (Verges et al., 2008).

487 At whole-ecosystem level, herbivory on submerged macrophytes may have different effects on gross

488 primary production (GPP). If herbivory results in a shift from clear-water to turbid conditions (see

489 below), GPP can be expected to decline, at least under intermediate concentrations of total

490 phosphorus (Brothers et al., 2013). On the other hand, large grazers that remove old seagrass leaves

491 covered in ephiphytes and have been reported to increase primary production (Valentine et al.,

492 1997; Moran and Bjorndal, 2005; Christianen et al., 2012).

493

494 3.2.6. *Regime shifts*

495 Shallow eutrophic lakes and lowland rivers may exist in two alternative stable steady states, a clear-

496 water state dominated by submerged macrophytes and a turbid, phytoplankton-dominated state

497 (Scheffer et al., 1993; Hilt et al., 2011; Hilt, 2015). In deeper lakes, submerged macrophytes may also

498 contribute to the stabilisation of clear-water conditions (Hilt et al., 2010; Sachse et al., 2014). Shifts

499 between clear-water and turbid states have been attributed to changes in nutrient loading, in the

500 abundance of zooplanktivorous fish (e.g. by biomanipulation) and/or in macrophyte cover (Scheffer

501 et al., 1993; Sondergaard et al., 2007; Bakker et al., 2010). Herbivory on macrophytes may also play a

502 significant role for shifting macrophyte-dominated systems into the turbid state, or preventing the

503 shift from turbid- into clear-water conditions. Mitchell & Wass (1996a) concluded that the

504 cumulative effect of waterfowl grazing consumption was small but might become critical when other

505 conditions for macrophyte growth become limiting (due e.g. to light limitation caused by high water

506 turbidity). A recent modeling study indeed showed that herbivory on macrophytes often becomes

507     important in combination with additional stress by periphyton shading (Hidding et al., 2016).

508     Herbivory by birds and fish may thus trigger the loss of submerged vegetation under high nutrient

509     loading (Van Donk and Otte, 1996; Paice et al., in press), possibly in combination with other stress

510     factors. Similarly, after reductions in nutrient loading, herbivorous birds may inhibit the expected

511     recovery of macrophytes (Lauridsen et al., 1993; Søndergaard et al., 1996; Hilt, 2006).

512

513

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

515     Herbivore management and global environmental change, including water level fluctuations,

516     eutrophication, temperature rise and invasive species, feedback on herbivore numbers, herbivore

517     distribution and grazing pressure.

518

519     *4.1 Changes in herbivore assemblages over time*

520     There is a growing body of evidence that herbivore assemblages have varied over time considerably

521     in their diversity and abundance, and are likely to continue to vary in the future. Throughout human

522     history, people have exploited many aquatic herbivore species, including waterfowl, Sirenians,

523     beavers, and muskrats, for food, recreation, and animal products such as skins, furs, feathers, and

524     oils (Domning, 1982; Kitchener and Conroy, 1997). Human overexploitation has had catastrophic

525     effects on many herbivore populations, with a wide range of species experiencing reduced

526     population sizes and geographic ranges, and even extinction (Jessen, 1970; Turvey and Risley, 2006).

527     Profound historical changes in herbivore assemblages were particularly evident in shallow seas and

528     coastal habitats, where the diversity and distributions of mammalian mega-herbivores (Sirenians

529     such as manatees and dugongs) were reduced heavily due to hunting by humans (Whitehead, 1978;

530     Jackson, 1997; Turvey and Risley, 2006; McCauley et al., 2015). Freshwater systems have also seen

531    the loss of many large-bodied herbivore species, in particular mammals (Moss, 2015; Bakker et al.,

532    2016b). Additionally, during the twentieth century a range of semi-aquatic herbivore species

533    switched from aquatic to terrestrial feeding, particularly during winter (Laubek, 1995), further

534    reducing herbivore abundance and diversity within aquatic systems. Such habitat shifts have been

535    most widely documented for avian herbivores such as species of swans, geese, ducks and rails

536    (Jefferies et al., 2003; Van Eerden et al., 2005). The substantial effects of humans on aquatic

537    herbivores meant that the twentieth century represented a low point for herbivore abundance and

538    diversity across aquatic systems. Indeed, we find it interesting to note that earlier authors drew their

539    conclusions on the apparent unimportance of plant-herbivore interactions in aquatic ecosystems

540    based on research conducted during a period in which aquatic herbivores were relatively scarce. For

541    Carribean coastal ecosystems it has even been documented that these were severely degraded long

542    before ecologists began to study them, through the decimation of large vertebrates including green

543    turtles and manatees by about the year 1800 (Jackson 1997).

544    Stricter hunting regulations and conservation efforts in the second half of the twentieth century have

545    facilitated recoveries in the range and population sizes of many key aquatic herbivore species (Nolet

546    and Rosell, 1998). An example is the Eurasian beaver (*Castor fiber*), reduced by overhunting at the

547    beginning of the twentieth century to c.1200 individuals in eight isolated populations across Europe

548    (Nolet and Rosell, 1998; Halley and Rosell, 2002). Following greater legal protections from hunting,

549    the Eurasian beaver underwent sustained population recovery and has re-established populations in

550    all areas within its former natural range (with the exception of Portugal, Italy, and the southern

551    Balkans), with a total population of at least 1.04 million individuals (Halley et al., 2012). Many species

552    of herbivorous waterfowl in temperate regions have made similar recoveries (Bellrose, 1976; Ankney,

553    1996). Of the 21 goose species (*Anser* spp. and *Branta* spp.) for whose long-term population trends in

554    Europe are known, 16 species are currently increasing (Fox et al., 2010). Recent changes in

555    agricultural practices have resulted in greater terrestrial food availability for overwintering

556    waterfowl, with larger species benefiting more in terms of population growth (Jefferies et al., 2003;

557    Van Eerden et al., 2005). Although many reptilian herbivores remain endangered, certain species

558    such as the green turtle (*Chelonia mydas*) have recently shown signs of population recovery in

559    response to three decades of conservation efforts (Chaloupka et al., 2008).

560    The recovery of species of aquatic herbivores has been aided by the recent interest in rewilding

561    ecosystems (Donlan et al., 2006). The key roles that extinct or extirpated large herbivores played in

562    the structure and functioning of terrestrial ecosystems has received growing recognition from

563    researchers (Donlan et al., 2006; Sandom et al., 2014; Bakker et al., 2016a; Doughty et al., 2016).

564    Recently, it has been proposed that large herbivores may have played equally-important roles in

565    regulating the structure and functioning of aquatic ecosystems (Moss, 2015; Bakker et al., 2016b).

566    Species of aquatic herbivore which can act as ecosystem engineers, such as the beaver, are typically

567    prime candidates for rewilding projects due to the wider ecosystem benefits that result from such

568    engineering (Collen and Gibson, 2001). The recent finding that beaver's creation of ponds increased

569    the diversity of herbivorous waterfowl within the landscape indicates that natural recolonization and

570    rewilding may result in wider changes to herbivore assemblages than the target species alone,

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

572    The recovery of predator populations, via natural recovery and conservation efforts, can also affect

573    plant-herbivore interactions (Estes et al., 2011). Evidence from terrestrial and marine systems shows

574    that herbivore impacts on plants can be reduced as predator numbers recover, because predators

575    not only lower herbivore abundance through direct consumption, but also alter herbivore

576    distributions and reduce grazing intensity through indirect effects of predator avoidance behavior

577    ('landscape of fear' *sensu* (Madin et al., 2011; Kuijper et al., 2013). Similar results could be found for

578    interactions between predators, herbivores, and macrophytes in aquatic systems, but little research

579    has been carried out to date. For example, a recent study found that green turtle (*Chelonia mydas*)

580    habitat use reflected trade-offs between food resources, body condition, and risk of predation by

581    tiger sharks (*Galeocerdo cuvier*) in seagrass beds (Heithaus et al., 2007). A decline in tiger shark

582 numbers may thus result in a strong increase of green turtle grazing on seagrass beds, potentially

583 resulting in a seagrass bed collapse (Heithaus et al., 2014).

584

585 *4.2 Exotic herbivore species*

586 The spread of non-native species has been a key driver of temporal changes in aquatic herbivore

587 assemblages in recent decades. A wide range of herbivore taxa have established invasive populations

588 known to impact on native macrophytes. Well-documented examples include birds such as the mute

589 swan in North America (Tatu et al., 2007), mammals such as the muskrat in Europe (Danell, 1979;

590 Sarneel et al., 2014), fishes such as the lessepsian rabbitfishes in the Mediterranean (Verges et al.,

591 2014a), molluscs such as the golden apple snail in Asia (Carlsson et al., 2004), and crustaceans such

592 as red swamp crayfish in Europe (Gherardi and Acquistapace, 2007; Van der Wal et al., 2013). Despite

593 attempts to prevent species transfer and establishment through improved biosecurity, rates of

594 invasion remain at a historic high (Cohen and Carlton, 1998; Jackson and Grey, 2013).

595

596 *4.3 Climate change and temperature rise*

597 Future environmental change is also predicted to alter herbivore assemblages. In particular, climate-

598 driven factors such as sea-level rise and changes in vegetation phenology and abundance have the

599 potential to alter where, when and how much herbivores feed, and thus have the potential to alter

600 plant-herbivore interactions across aquatic systems (Stillman et al., 2015). For example, northward

601 shifts in wintering range in response to warming have been recorded for several waterfowl species,

602 including semi-aquatic herbivores like greylag geese (Ramo et al., 2015). Furthermore, food

603 requirements change with temperature. With increasing temperatures, the energy requirements of

604 temperate ectotherm animals increase and they consume more food. Furthermore, they may change

605 their diet in response to temperature, which has consequences for the degree of plant consumption.

606 Omnivorous fish increase their relative consumption of plant material with increasing temperatures

607 (Prejs, 1984; Behrens and Lafferty, 2007, 2012), a pattern that is recently also found in copepods

608 feeding on seston (Boersma et al., 2016). For endotherms this pattern may be the opposite, as their

609 energy requirements decrease with increasing temperatures, but this hypothesis awaits empirical

610 testing. Warmer temperatures may also induce higher periphyton shading of macrophytes (Mahdy et

611 al., 2015), making them more prone to herbivory (Hidding et al., 2016).

612

613 *4.4 Herbivore impacts under human control*

614 Where herbivore impacts on macrophytes affect human activities, such as conservation, recreation,

615 and aquaculture, they may be viewed as undesirable. In most cases it should be noted that problems

616 caused by herbivores are often the direct or indirect consequence of earlier human actions. For

617 instance, ongoing eutrophication of lakes reduces the resilience of submerged plant beds to grazing

618 due to increased shading by periphyton which profits from the nutrient loading (Hidding et al., 2016),

619 and re-establishment of submerged vegetation can be inhibited by grazers as well (Hauxwell et al.,

620 2004). The combined hunting of large predators and the creation of marine protected reserves, as

621 the place where large herbivores are safe, has locally resulted in very strong grazing pressure on

622 seagrass beds by green sea turtles (Christianen et al. 2014).

623 Such herbivore impacts can lead to conflicts between people interested in herbivore welfare and

624 conservation, and those interested in the activity being affected by the herbivore (Redpath et al.,

625 2015). To date, conflicts have arisen due to overgrazing by reptilian, mammalian, and avian

626 herbivores (Table 2). In contrast, we could find no evidence of conflicts associated with invertebrate

627 herbivory, which may reflect differences in human values rather than ecological impact. Indeed,

628 evidence from a recent meta-analysis showed that vertebrate herbivores do not have consistently

629 greater impacts on macrophytes than invertebrate herbivores (Wood et al., 2016). Vertebrate

630 herbivores such as waterfowl, turtles, and Sirenians are often considered charismatic, and attempts

631    to manage their numbers, behaviour or distributions are likely to attract more opposition from

632    conservation and welfare groups than the management of invertebrate herbivores (Bremner and

633    Park, 2007; Small, 2012). Consequently, it can be difficult to implement management to alleviate the

634    effects of overgrazing (Coluccy et al., 2001).

635    Despite these conflicts, not all herbivore impacts on macrophytes are viewed as negative by people.

636    Herbivores have proven to be effective biocontrol agents to help reduce and eradicate undesirable

637    macrophytes, such as overabundant or invasive species (Newman, 2004; Cuda et al., 2008). A wide

638    range of herbivore biocontrol agents have been used globally (Table 3). Biocontrol of macrophytes

639    through herbivory has received growing interest from researchers and managers, particularly as

640    some biotypes of invasive macrophytes (e.g. *Hydrilla verticillata*) have developed resistance to

641    commonly-used herbicides (Cuda et al., 2008). More targeted biocontrol can be achieved by

642    invertebrate herbivores, which typically show greater specificity for macrophyte species relative to

643    vertebrate herbivores (Lodge, 1991; Newman, 1991). Since Wilson (1964) argued that "no insects

644    have yet been used for the biological control of aquatic weeds", a wide range of species of

645    coleopteran, lepidopteran, and dipteran biocontrol agents have been used successfully (Newman,

646    2004; Cuda et al., 2008). Both the conflicts related to overgrazing, and the use of herbivores as

647    biocontrol agents, show the importance of improving our understanding plant-herbivore

648    interactions. For example, understanding the density-dependence of herbivore impacts on

649    macrophyte abundance can inform the densities of biocontrol agents required to reduce

650    overabundant macrophytes (Cuda et al., 2008), or allow lake managers to predict the response of

651    macrophytes to changes in wild herbivore density (Wood et al., 2012a).

652

653    **5. How to improve understanding of herbivore impacts**

654    *5.1 Bottom-up versus top-down control across environmental gradients*

655    Lodge (1991) ended his review with the conclusion that "To understand the influence of herbivory

656    (relative to other biotic and abiotic factors) on macrophyte populations and assemblages, extensive

657    comparisons of grazing damage across environmental gradients and across macrophyte and grazer

658    species must be made." Whereas meta-analyses have provided valuable insight in the impact of

659    different herbivores both on Angiosperms and macro-algae (Poore et al., 2012; Wood et al., 2016),

660    and the relationship between macrophyte palatability and herbivore impact received increasing

661    attention during the last decade, the variation in the intensity and impacts of herbivory along

662    environmental gradients has been scantly explored. Bakker and Nolet (2014) suggested that

663    herbivore impact may increase at nutrient-rich conditions, due to a combination of higher plant

664    palatability and lower tolerance to grazing damage caused by additional stress factors (such as

665    reduced light availability due to periphyton shading (Hidding et al., 2016). In an experimental pond

666    system, herbivory by mallards proved to have stronger impact on submerged macrophytes under

667    eutrophic than under oligotrophic conditions. We are not aware, however, of any field tests for this

668    theory. Alternatively, herbivores may facilitate submerged macrophytes with increasing

669    eutrophication, for example when moderate densities of small grazers such as freshwater snails clean

670    submerged plants from epiphytes, which becomes more important under eutrophic conditions

671    (Bakker et al., 2013). Also, when intense grazing stimulates the formation of new shoots, which are

672    not yet colonized by epiphytes, large grazers such as green sea turtles, can compensate the negative

673    effect of eutrophication for seagrass growth to a certain extent (Christianen et al., 2012).

674

675    *5.2 Integrating marine and freshwater studies*

676    Traditionally, freshwater macrophytes and seagrasses have largely been studied separately. To date,

677    the literature on freshwater and marine herbivore impacts have not been integrated, and have

678    largely developed separately despite the obvious areas of overlap. If cross-system comparisons were

679    being made, these were often marine-terrestrial or freshwater-terrestrial comparisons and can

680    include both vascular plants and algae (Hay, 1991; Elser et al., 2000; Burkepile, 2013). This is

681    unfortunate because, leaving a few obvious differences apart (such as the higher salinity and

682    connectivity of marine systems), the ecology of marine and inland-water vascular macrophytes

683    shows very few differences. Yet, integrative work on freshwater and marine vascular macrophytes

684    still awaits its moment.

685

686    *5.2 Herbivore assemblages: towards functional groups*

687

688    For a better understanding of herbivore impact, researchers should consider the whole community

689    of herbivores, which compete and facilitate each other. This has already been done for terrestrial

690    systems long ago (McNaughton, 1985), but examples for aquatic systems are rare. One such example

691    is the herbivore community in a shallow freshwater lake that forages on pondweed beds, consisting

692    mainly of *Potamogeton pectinatus*. The sprouting plants are being grazed by resident waterfowl

693    species like mute swans (*Cygnus olor*), mallards (*Anas platyrhynchos*), gadwall (*Anas strepera*) and

694    coots (*Fulica atra*). The intensity and timing of grazing determine how much above-ground plant

695    material is remaining and growing (Hootsmans, 1999). At the end of the summer, below-ground

696    tubers are being formed depending on the amount of above-ground plant material (Van Wijk, 1988).

697    Thus, more and, notably, earlier waterfowl grazing in summer results in less tuber biomass in autumn

698    (Klaassen et al., 2006; Gyimesi et al., 2011). In autumn, tubers are being depleted by migratory swans

699    (Bewick's swans *Cygnus columbianus*) and diving ducks (mainly tufted ducks *Aythya fuligula* and

700    pochards *Aythya ferina*) until a grazing threshold (Nolet et al., 2001). The diving ducks benefit from

701    the trampling activity of the swans, without negatively affecting the swans' intake rate; this therefore

702    classifies as commensalism (Gyimesi et al., 2012). In accordance with a sequential population model

703    (Jonzén et al., 2002), highest tuber biomass and in particular tuber production was generally found at

704    sites foraged down to intermediate thresholds in the previous autumn. In this system a positive

705     feedback between tuber grazing and tuber production resulted from a reduction in self-shading or a

706     decrease in neighbour competition (Nolet, 2004).

707

708     Together, the interactions within herbivore communities will determine the effect of herbivore

709     diversity, a topic rarely touched upon in aquatic vascular plant beds (but see marine macro-algae and

710     seagrass systems, e.g (Duffy et al., 2003; Burkepile, 2013). Whereas all interactions at the species

711     level are interesting, a way forward can be to generalize beyond species by grouping herbivores in

712     guilds or functional groups and working out which traits best explain their relative effects. Such traits

713     could include body size, diet (herbivory-omnivory), habitat (terrestrial-aquatic linkages), migratory

714     strategy (sedentary versus migratory) and movement ecology (foraging ranges). Recently, grouping

715     of large savanna herbivores proved to be useful to understand their ecosystem impacts (Hempson et

716     al., 2015). Similarly, the ecosystem functions of aquatic large herbivores may be understood from

717     their habitat use, in particular how dependent on the aquatic systems they are in combination with

718     their movement ecology (Bakker et al., 2016b).

719

720     5.3 *Tools to study herbivore impacts*

721     Practically, the high variance in estimates of macrophyte abundance, even within a single study

722     system, can make herbivore effects difficult to detect in aquatic systems without large sample sizes

723     (Wood et al., 2012b). However, numerous methods have been developed and employed to detect

724     and/or quantify herbivory on macrophytes and seagrasses (Table 4). The most direct approach for

725     detection and quantification of effects is a technique known as tethering (Kirsch et al., 2002; Tomas

726     et al., 2005; Prado et al., 2007; Pages et al., 2014). With this technique it is possible to estimate the

727     biomass (or cm of leaf) eaten daily, i.e. direct herbivory rates (see Table 4). Another direct approach

728     to detect and quantify herbivore effects are in situ exclosure cages with subsequent biomass

729     measurements in- and outside.

730    Other less direct herbivory detection and quantification methods focusing on macrophytes include

731    visual estimations of leaf damage and measurements of macrophyte performance across naturally-

732    occuring spatial or temporal gradients in herbivore assemblage properties (e.g. density) (Table 4).

733    Aerial photographs taken from drones (Brandt et al., 2015), echo-sounding (Jäger et al., 2004) and

734    remote sensing (Silva et al., 2008) may increasingly being used in the future for larger scale

735    quantifications of macrophyte consumption by herbivores. At the herbivore side, underwater videos,

736    aquarium feeding experiments, molecular markers, stable isotope signatures, gut and faeces

737    analyses, and whole-lake fish telemetry have been applied (Table 4).

738    Finally, mechanistic models allow assessments of herbivory over larger spatial and temporal scales

739    than field-based methods, e.g. long-term predictions of future herbivory. They initially need to be

740    tested against field data to demonstrate accuracy and have been developed for both, the herbivores

741    and the plants (Table 4). Recently, a plant growth models for a specific macrophyte species has been

742    used to detect a synergy between herbivory and shading by periphyton as additional stressor

743    (Hidding et al., 2016). Simulation models of herbivore foraging can be useful tools to predict foraging

744    impacts, and test strategies for grazing management (Wood et al., 2014a; Nolet et al., 2016).

745

746    **6. Conclusions**

747    Over the last 25 years, a substantial body of evidence has developed that shows that herbivory is an

748    important factor in the ecology of macrophytes across freshwater and marine habitats. Compiling the

749    most recent data, we conclude that herbivore impacts in freshwater and marine ecosystems are

750    typically 5-10 times greater than those reported for terrestrial ecosystems. This corresponds with

751    lower C:N stoichiometry of submerged aquatic plants. Furthermore, aquatic habitats are

752    characterized by large variation in grazing pressure. Considerable changes have occurred, and are

753    predicted to occur, in herbivore diversity and abundance, with wide implications for the composition

754    and dynamics of macrophyte communities, as well as for the structure and functioning of aquatic

755   ecosystems. There are pressing needs to improve our management of undesirable herbivore impacts

756   on macrophytes (e.g. leading to an ecosystem collapse), and the conflicts between people associated

757   with the impacts of charismatic mega-herbivores. While simultaneously, the long-term future of

758   maintaining both viable herbivore populations and plant beds should be addressed, as both belong in

759   complete ecosystems and have co-evolved in these long before the increasing influence of man.

760   Most research to date has focused on the short-term impacts of herbivores on macrophyte

761   abundance and community composition. To understand the roles of herbivores more fully we need

762   to consider their longer-term impacts and the role of herbivory in the (co-)evolution of both

763   macrophyte and herbivore species. Furthermore, a better integration of the freshwater, marine, and

764   terrestrial herbivory literatures would greatly benefit future research efforts.

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776    **Literature**

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1460    **Captions to figures**

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1462    Figure 1. Frequency diagram of percentage of herbivory (% herbivory) on vascular plants (a: mean

1463    percent damage; b, c: net primary production removal) and biomass C:N ratio (g/g) across (a,d)

1464    terrestrial, (b,e) freshwater and (c,f) marine ecosystems. Freshwater and marine data include both

1465    submerged and emergent plants. The median values in each panel are indicated with an arrow

1466    accompanied by "M".

1467    Data sources: terrestrial (a) herbivory: percentage of leaf area damaged (Turcotte et al. 2014), (d)

1468    biomass C:N ratio: in foliage (Elser et al. 2000); freshwater (b) herbivory: percentage of emergent and

1469    submerged vascular plant biomass removed by herbivores in herbivore exclosure/enclosure or

1470    addition/removal experiments (Wood et al. 2016), (e) biomass C:N ratio: in submerged and emergent

1471    vascular plants (Cloern et al. 2002; Bakker unpublished data); marine, (c) herbivory: percentage of

1472    emergent and submerged vascular plant biomass removed by herbivores in herbivore

1473    exclosure/enclosure or addition/removal experiments (Wood et al. 2016), percentage of leaf area

1474    damaged in seagrasses (Cebrian and Duarte 1998) (f) biomass C:N ratio: in seagrass leaves (Atkinson

1475    & Smith 1983, Duarte 1990, Fourqurean et al. 1993, Cebrian and Duarte 1998, Fourqurean et al.

1476    2010, Olsen en Valiela 2010), in salt marsh plants (Cloern et al. 2002). The duration of the herbivroy

1477    studies varied from instantaneous measurements of percentage leaf damage in terrestrial plants and

1478    seagrasses to exclosures studies in freshwater and marine ecosystems ranging from about a week to

1479    multiple study years (study durations reported in Wood et al. 2016 who found no effect of study

1480    duration on percentage herbivore plant biomass removal).

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1482    Figure 2. Frequency diagram of net primary production removal (% herbivory) and biomass C:N (g/g)

1483    for vascular freshwater and marine macrophytes of different growth forms (emergent and

1484    submerged). Emergent plants include floating plants and wetland or salt marsh plants. The median

1485    values in each panel are indicated with an arrow accompanied by "M". Data sources as in Fig. 1.

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1487    Figure 3. Synthesizing scheme indicating the effects of herbivores on macrophyte beds and the

1488    functioning of shallow freshwater (a) and marine (b) aquatic ecosystems. Herbivores affect plant

1489    abundance and species composition by grazing and bioturbation. Their presence alters

1490    biogeochemical cycling and primary production, they transport nutrients and propagules across

1491    ecosystem boundaries, modify habitat for other organisms and affect the level of shoreline

1492    protection by macrophyte beds. Symbols in the figure are courtesy of the Integration and Application

1493    Network, Univ. of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

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 specialized use of aquatic habitats are more likely to deposit the propagules in suitable habitat. In particular, targeted arrival to aquatic habitats at stopovers may increased the deposition of | Figuerola and Green (2005) |

propagules  ingested at departure sites, especially after the first drinking and feeding bout.

*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 uningested 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 dessication | Organism's and/or propagule's resistance to dessication may enhance epizoochorous dispersal of aquatic organisms | Panov and Caceres (2007); Havel et al. (2014) |

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1499 Table 2. An overview of reported conservation conflicts that have arisen from the impacts of overgrazing by herbivores on macrophytes.

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| Herbivore | Issue | Parties in conflict | Location(s) | Duration | Current status | References |
|---|---|---|---|---|---|---|
| Green turtle (*Chelonia mydas*) | 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 (*Trichechus manatus*) | 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 (*Castor spp*.) | Impacts on aquatic habitats, via effects on vegetation and wider ecosystem (e.g. fish) | Conservationists, animal welfare groups, fishermen, and statutory wildlife management | Freshwater habitats across North America, Russia | Unknown - present | Ongoing | Nolet and Rosell (1998); Collen and Gibson (2001); Halley and Rosell (2002) |

agencies

| Coypu (*Myocastor coypus*) and muskrat (*Ondatra zibethicus*) | 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 (*Cygnus olor*) | 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 (*Anser* spp., *Branta* spp., and *Chen* spp.) | Overgrazing of emergent macrophytes degrades wetland habitats | Conservationists, animal welfare groups, and statutory wildlife management | Canadian Arctic and sub-Arctic wetlands, freshwater lakes | 1970s - present | Ongoing | Kerbes et al. (1990); Nichols (2014) |

agencies and wetlands in

Europe and

North America

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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 (*Trichechus manatus*) | Wide range of macrophyte species, including *Cabomba aquatica*, *Anacharis* spp., *Leersia* spp., *Utricularia* spp. | Generalist | Allsopp (1960) |
| Geese (*Anser spp*) | Wide range of macrophyte species | Generalist | Ross (1971); Wilson et al. (1977) |
| Grass carp (*Ctenopharyngodon idella*) | Wide range of macrophyte species, including invasive species such as *Hydrilla verticillata* | Generalist | Clayton (1996); Hanlon et al. (2000) |
| Cichlid fishes, e.g. blue tilapia (*Oreochromis aureus*) | Wide range of macrophyte species | Generalist | Schwartz et al. (1986) |
| Crayfish, e.g. papershell crayfish (*Orconectes immunis*) | Wide range of submerged macrophyte species | Generalist | Letson and Makarewicz (1994) |
| Weevils, e.g. milfoil weevil | Species-specific biocontrol agents identified for many macrophyte | Specialist | Creed and Sheldon |

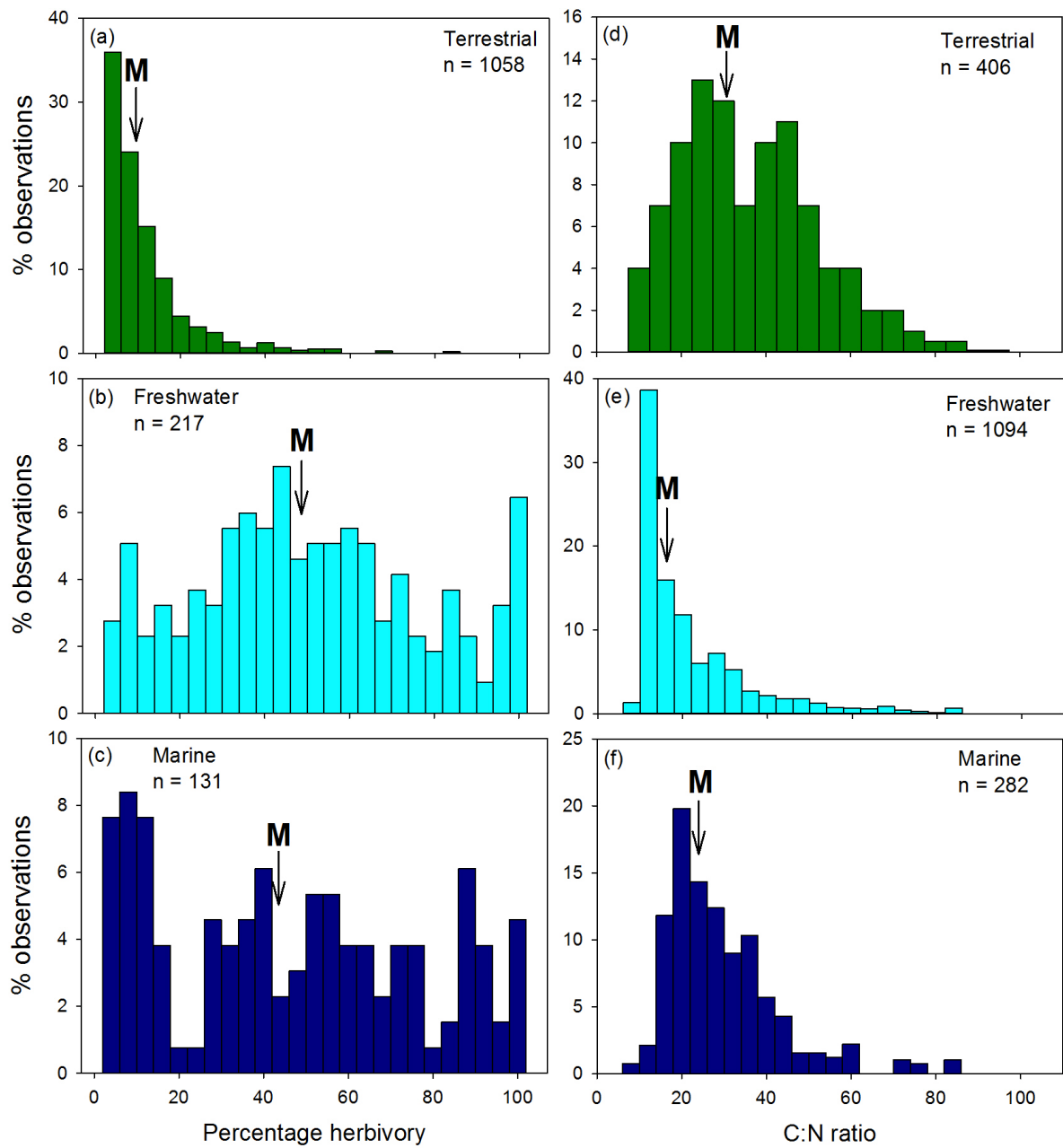| | | | |
|---|---|---|---|
| (*Euhrychiopsis lecontei*), Hydrilla tuber weevil (*Bagous affinis*) | species, e.g. Hydrilla (*Hydrilla verticillata*), Eurasian water milfoil (*Myriophyllum spicatum*) | | (1993); Newman (2004) |
| Apple snails (*Pomacea* spp.) | Wide range of macrophyte species | Generalist | Rushing (1973) |
| Dipteran larvae, e.g. Asian hydrilla leaf-mining fly (*Hydrellia pakistanae*) | Species-specific biocontrol agents identified for many macrophyte species, e.g. *Hydrilla verticillata* | Specialist | Wheeler and Center (2001); Bownes (2014) |
| Lepidopteran larvae, e.g. waterlettuce moth (*Spodoptera pectinicornis*) | 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. *Eccritotarsus catarinensis* | Species-specific biocontrol agents identified for many macrophyte species, e.g. Water hyacinth (*Eichhornia crassipes*) | Specialist | Coetzee et al. (2007); Hernandez et al. (2011) |
| Orthoptera, e.g. water hyacinth grasshopper (*Cornops aquaticum*) | Species-specific biocontrol agents identified for many macrophyte species, e.g. Water hyacinth (*Eichhornia crassipes*) | Specialist | Bownes et al. (2010) |

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1508    Table 4. Different methodologies used to detect and quantify herbivory on macrophytes.

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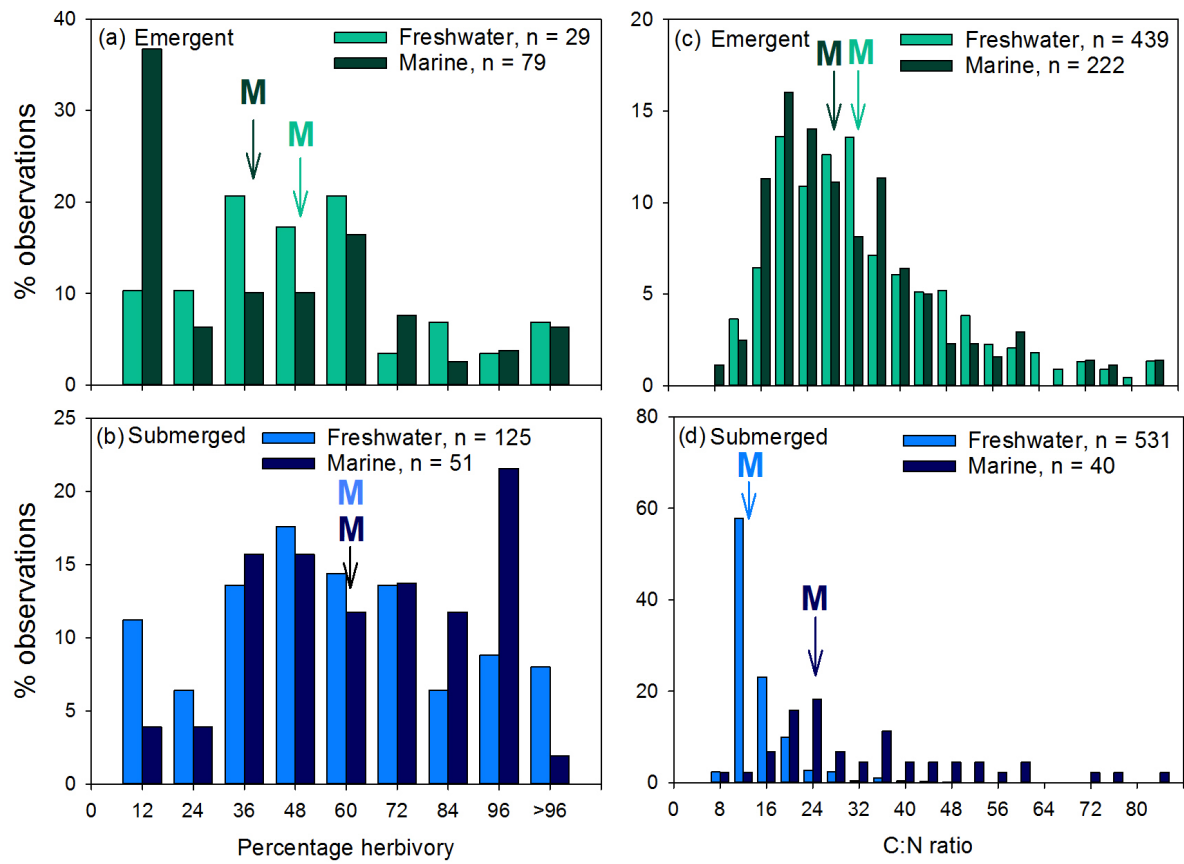| Methodology | Explanation | References |
|---|---|---|
| Exclosures | Installation of cages (fully closed or open at the bottom) to protect macrophytes from different herbivores (fish, muskrats, waterfowl, crayfish, turtles) | Søndergaard et al. (1996); Körner et al. (2002); Hilt (2006); Christianen 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-1 day-1) 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 & Dugdale (2003); Bennett & Bellwood (2011); Verges et al. (2014b) |
| Visual estimation of leaf damage | | Francescini et al. (2010) |

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|---|---|---|
| Natural gradients | Measure macrophyte performance (e.g. growth rate, biomass, etc) across naturally-occuring gradients in herbivore assemblage properties (e.g. density) | Wood et al. (2012b) |
| Drones | Identificaton 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 et al. (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) |
| Gut analyses and stable isotope analyses | Gut analyses in fish combined with stable isotope analyses of basal food resources and fish | Mao et al. (2014) |

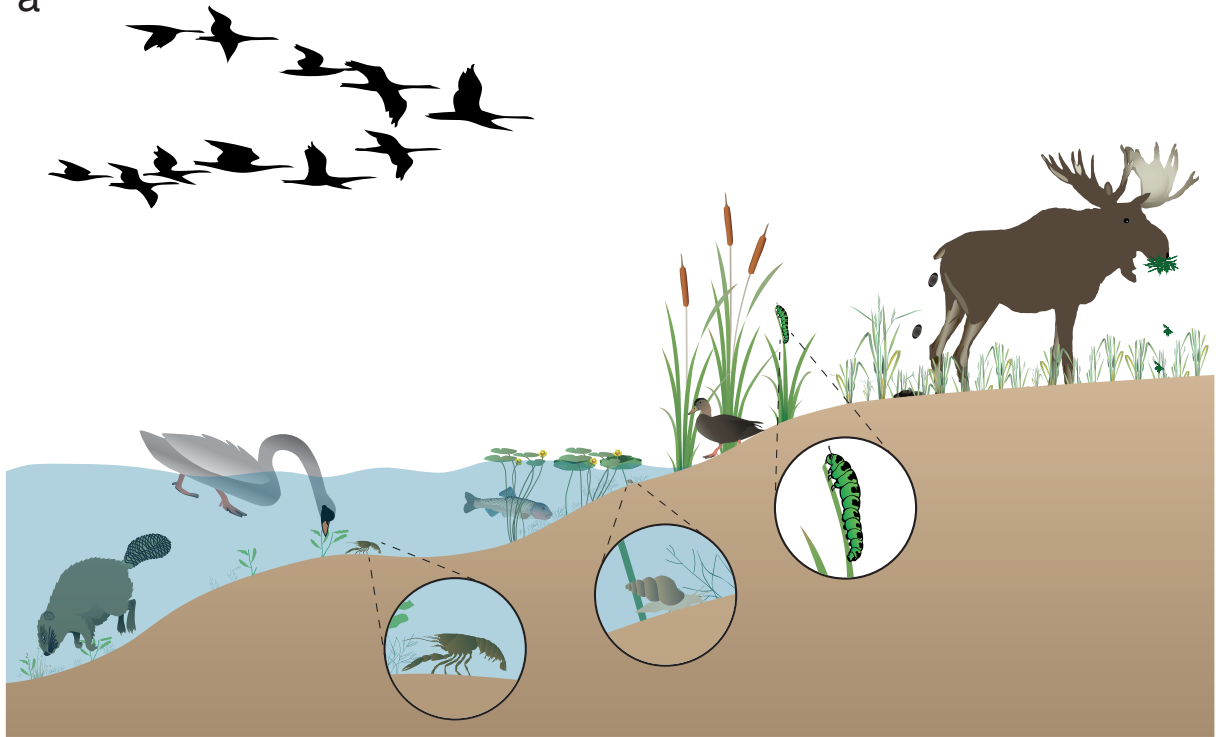| | | |
|---|---|---|
| Telemetry | Whole-lake fish telemetry | Hanson et al. (2007) |
| Bird counting and determination of lignin content in faeces | | Dos Santos et al. (2012) |
| Laboratory feeding rate determination in fish | Determination of fish feeding rates in aquaria | Körner & Dugdale (2003) |
| 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) |

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