**Assessing the role of large herbivores in the structuring and functioning of freshwater and marine angiosperm ecosystems**

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**Assessing the role of large herbivores in the structuring and**

**functioning of freshwater and marine angiosperm ecosystems**

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## Abstract

While large herbivores can have strong impacts on terrestrial ecosystems, much less is known of their role in aquatic systems. We reviewed the literature to determine: (1) which large herbivores (>10 kg) have a (semi-)aquatic lifestyle and are important consumers of submerged vascular plants, (2) their impact on submerged plant abundance and species composition and (3) their ecosystem functions.

We grouped herbivores according to diet, habitat selection and movement ecology: (1) Fully aquatic species, either resident or migratory (manatees, dugongs, turtles), (2) Semi-aquatic species that live both in water and on land, either resident or migratory (swans), (3) Resident semi-aquatic species that live in water and forage mainly on land (hippopotamuses, beavers, capybara), (4) Resident terrestrial species with relatively large home ranges that frequent aquatic habitats (cervids, water buffalo, lowland tapir).

Fully aquatic species and swans have the strongest impact on submerged plant abundance and species composition. They may maintain grazing lawns. Because they sometimes target belowground parts, their activity can result in local collapse of plant beds. Semi-aquatic species and turtles serve as important aquatic-terrestrial linkages, by transporting nutrients across ecosystem boundaries. Hippopotamuses and beavers are important geomorphological engineers, capable of altering the land and hydrology at landscape scales. Migratory species and terrestrial species with large home ranges are potentially important dispersal vectors of plant propagules and nutrients. Clearly, large aquatic herbivores have strong impacts on associated species and can be critical ecosystem engineers of aquatic systems, with the ability to modify direct and indirect functional pathways in ecosystems. While global populations of large aquatic

42 herbivores are declining, some show remarkable local recoveries with dramatic

43 consequences for the systems they inhabit. A better understanding of these functional

44 roles will help set priorities for the effective management of large aquatic herbivores

45 along with the plant habitats they rely on.

46

## Introduction

By virtue of their size, large herbivores are critical agents of change and maintenance of the ecosystems they inhabit (Owen-Smith 1988). However, while their functional roles in terrestrial ecosystems are well established, it is unclear if, and how, aquatic ecosystems are modified by the activity of large herbivores. Marine and freshwater systems differ in important ways from terrestrial systems and may respond very differently to herbivory impact. In addition, large aquatic herbivores are not a species-rich group, and their numbers are on the decline (Marsh and Lefebvre 1994, McCauley et al. 2015). However, these species share many common traits with their terrestrial counterparts, and from what is known of the impacts of terrestrial species on their ecosystems, it raises the question of whether large aquatic herbivores may be at least as capable of modifying aquatic ecosystems in potentially significant ways.

### The role of large herbivores across ecosystems

The effect of large terrestrial herbivores on the structure and functioning of the ecosystems they inhabit is linked to the particular requirements of being large. Their size, feeding choices, metabolic requirements, social behaviour, movement patterns and other life history traits work together to make many large herbivores important ecosystem engineers (Jones et al. 1994), with the ability to change grazing plant communities (Olff and Ritchie 1998, Knapp et al. 1999, Bakker et al. 2006) habitat structure (Asner et al. 2009), nutrient flows (McNaughton et al. 1997, Augustine and Frank 2001) and trophic dynamics through direct and indirect pathways (Pringle et al. 2007). Apart from the direct consequences of their high consumption rates, several traits associated with allometric scaling of herbivore body size result in disproportionately

71 large impacts on the habitats they inhabit. Large herbivores tend to have more

72 generalised diets, have slower ingestion and defecation rates, and are predominantly

73 herding species that typically occupy larger home ranges than smaller herbivores (Peters

74 1983, Owen-Smith 1988, Belovsky 1997, Cumming and Cumming 2003). This results

75 in a series of very specific effects on plant communities, habitat structure and critical

76 ecosystems processes. The direct effects on plants include reductions in canopy

77 structure and height (Asner et al. 2009), increases in trampling effects (Cumming and

78 Cumming 2003, Schrama et al. 2013) and increases in seed dispersal rates (Clausen et

79 al. 2002) among others. These, in turn, have a host of indirect effects on ecosystems.

80 These include modifications to plant species competition, to the benefit of grazing-

81 adapted species (McNaughton 1984, Knapp et al. 1999), flow-on effects to structure-

82 dependent species (Pringle et al. 2007, Huntzinger et al. 2008), changes in the

83 productivity of the system which directly and/or indirectly affects carbon and nutrient

84 cycles (Knapp et al. 1999, Olofsson et al. 2004, Bakker et al. 2009), an increase in the

85 heterogeneity of landscapes, increases in nutrient transport between ecosystems or

86 decreases in fire regimes (Asner et al. 2009), among others. Taken together, these

87 effects make large terrestrial herbivores key modifiers and maintainers of ecosystem

88 dynamics and habitat complexity (Jones et al. 1994, Wright et al. 2002, Pringle 2008,

89 Waldram et al. 2008). Moreover, their decline since the Late Pleistocene due to hunting

90 and other human-related causes has been linked to major shifts in the structure and

91 functioning of the systems they were once abundant in (Johnson 2009, Corlett 2013,

92 Cromsigt and te Beest 2014, Gill 2014). Equally, local increases in their number, either

93 as a result of conservation initiatives or the faster decline of their predators (Estes et al.

94 2011), has also resulted in serious consequences for the ecosystems they depend on;

95 population overshoots of large herbivores or concentrations within restricted areas

96  (National Parks and reserves for instance) can result in major ecosystem alterations (e.g.

97  Cumming et al. 1997).

98      Aquatic herbivores have, in contrast, received much less attention and little is

99  known of the consequences of the functional roles they perform in freshwater and

100  marine environments. The list of extant species is relatively small, a mere fraction of the

101  large aquatic herbivores that were once present in aquatic ecosystems. Prehistorically, a

102  rich assemblage of large aquatic herbivores coexisted, including sirenians and

103  Hippopotamidae, of which both fully aquatic and semi-aquatic species have been

104  documented (Domning 2001, Boisserie et al. 2011). Furthermore, Oligocene-to-recent

105  proboscideans are thought to be derived from amphibious ancestors, which consumed

106  freshwater vegetation (Liu et al. 2008). Several large-tusked dugongines were also

107  present in ancient seas, some of which may have acted as keystone species, disrupting

108  climax seagrass communities, thereby increasing their productivity and diversity, with

109  presumed positive effects on sirenian diversity (Domning 2001). Unlike most seagrass

110  systems today, which, in the absence of large herbivores, are mostly detritus based, until

111  around $2\pm3$ Ma, most primary productivity in seagrass beds was presumably consumed

112  by herbivores (Domning 2001).

113      Today, even these few contemporary species of large aquatic herbivores are

114  mostly in decline, particularly the fully aquatic ones. Although the defaunation of

115  aquatic animals began more recently than in terrestrial systems (McCauley et al. 2015),

116  the effect of this reduction on aquatic large herbivores has been dramatic in the last

117  century (Marsh and Lefebvre 1994, McCauley et al. 2015). Effective management has

118  been successful in reversing these trends for some aquatic species such as the moose,

119  Eurasian elk, beavers, green turtles and swans (Nolet and Rosell 1998, Halley and

120  Rosell 2002, Chaloupka et al. 2008, Gayet et al. 2014). However, populations of many

121    large aquatic herbivores like dugongs, manatees or hippopotamuses have been declining

122    to critical levels in the last centuries (Jackson 2001, D'Souza et al. 2013, Pennisi 2014),

123    and they may no longer be sufficiently abundant to effectively perform their functional

124    role in the ecosystems they inhabit (McCauley et al. 2015).

125        Together with their low numbers, the aquatic environment they inhabit makes it

126    inherently more difficult to track, monitor and gauge any potential influence these

127    species may have on these systems; studies that have examined their ecosystem impacts

128    have been necessarily opportunistic, making use of locally high concentrations

129    (Hauxwell et al. 2004b, Heithaus et al. 2014). On the face of it, there is little to suggest

130    that large aquatic herbivores are qualitatively different from their terrestrial

131    counterparts. Most fully aquatic herbivores such as sirenids have sizes, feeding choices,

132    metabolic requirements, social behaviours and movement patterns comparable to large

133    terrestrial herbivores (Owen-Smith 1988). Additionally, a significant number of large

134    terrestrial herbivores also feed on aquatic systems, including moose, swans or turtles

135    among others. Given these similarities in traits, it is likely that their influence on aquatic

136    habitats may be at least as large as terrestrial systems. From what is known of aquatic

137    macrophyte-dominated communities like kelp beds, seagrass meadows and macroalgal

138    communities, they may be highly modified by herbivory, and large herbivores are likely

139    to play a potentially non-trivial role in contributing to these processes (Burkepile and

140    Hay 2006, Valentine and Duffy 2006). In fact, several aquatic macrophytes show a

141    series of adaptations to herbivory including compensatory growth, protected rhizomes

142    or clonal growth that are typical of highly grazed systems (Valentine and Heck 1999,

143    Nolet 2004, Valentine and Duffy 2006, Vergés et al. 2008).

144

**Ecosystem characteristics that can influence aquatic plant-large herbivore interactions**

Despite the evident similarities between terrestrial and aquatic systems, it must be remembered that aquatic systems may respond very differently to large herbivores compared to terrestrial ecosystems, as a function of inherent differences in plant reproductive strategies and generation times, plant size and structure or differences in ecosystem scale and connectivity; each of these can have major implications for the way aquatic herbivores use and influence these systems.

For a start, the bulk of aquatic primary production is mostly unavailable for large herbivores to consume, dominated as it is by phytoplankton, which large herbivores are generally incapable of harvesting. This restricts them to feed close to shores where they can access benthic primary production, principally dominated by macroalgae and aquatic angiosperms. In terrestrial systems, the structural tissue produced by woody species is, for the most part, unsuitable as a primary food source to large herbivores, even though large browsers and mixed feeders do consume twigs and bark (Bakker et al. 2015). In contrast, aquatic macrophytes in general have fewer structural defences than their terrestrial counterparts, yielding them more edible, although macroalgae can strongly compensate with chemical defences (Hay and Fenical 1988).

The reproductive strategies and population dynamics of aquatic plants may also strongly mediate the ability of these systems to cope with large herbivore foraging. Generation times may differ greatly between aquatic primary producers, in particular the smaller algae having rapid turnover rates, making them differentially susceptible to sustained herbivory, an important consideration particularly when evaluating the prevalence and strength of trophic cascades in aquatic systems. While submerged

169    angiosperms may be annual, clonal species of vascular plants (like *Posidonia oceanica*),

170    can have generation times that span millennia (Arnaud-Haond et al. 2012), making them

171    respond in similar ways to herbivory as terrestrial grasslands, also dominated by clonal

172    primary producers (Burkepile 2013).

173        A final vital contrast between terrestrial and aquatic systems is that the latter are

174    considered to be generally better connected (e.g. Tanner 2006), governed by higher flow

175    rates of nutrients and other materials, holoplanktonic organisms and reproductive

176    propagules (Carr et al. 2003). In particular, marine environments present few barriers to

177    movements, enabling large herbivores to travel vast distances (often spanning entire

178    oceans) without impediment. However, while connectivity may be high, the habitats

179    themselves may be highly discontinuous (Goodsell 2009). Marine macrophytes

180    (seagrasses and algae) are clearly limited by light and substrate availability, resulting in

181    marine macrophyte habitats being very patchy in their distribution (Hemminga and

182    Duarte 1999). For herbivores using these systems, the distance between feeding areas

183    could be separated by hundreds or thousands of kilometres, particularly in the open sea.

184    Freshwater macrophyte dominated habitats are also characterised by similar

185    discontinuities. Here though, it is the water bodies themselves that can be highly

186    disconnected. Thus, for both marine and freshwater systems, large herbivores whose

187    forage requirements may not be satisfied at a single location, may necessarily have to

188    undertake much larger-scale movements than their terrestrial counterparts (McCauley et

189    al. 2015). This may make them much less predictable in space and time. The impacts of

190    their herbivory, although locally high, may be distributed over a much wider area than

191    terrestrial species, diluting their overall importance to ecosystem functioning.  Clearly,

192    there is no agreement on how foraging and behavioural traits interact with the

193    peculiarities of the aquatic environment to determine the functional importance of large

194    aquatic herbivores on their habitats and ecosystems.

195

196    **Objectives**

197    We conducted a comprehensive review of extant herbivores in aquatic systems

198    to document the potential impacts of large aquatic herbivores on the structure and

199    functioning of aquatic ecosystems. We restrict our review to aquatic angiosperm-

200    dominated systems, since these constitute the primary habitats in which extant large

201    herbivores feed. In particular, our objectives were to determine which large herbivorous

202    species can be classed as consumers of submerged angiosperms. In addition, we

203    documented the direct impacts their foraging and use could have on the habitats and

204    ecosystems they inhabit. Further, we asked if these species have the ability to modify

205    ecosystem structure and function and under what conditions this is likely to take place.

206    Finally, if large aquatic herbivores are capable of ecosystem modification, we ask what

207    implications this has for the way we manage their populations and the ecosystems they

208    depend on.

209

210    **List of large aquatic herbivores**

211    *Large aquatic herbivores: which species consume aquatic angiosperms?*

212    There is no universal definition of large aquatic herbivores. In this review, we

213    included herbivores with a body mass of 10 kg and greater, which represent meso- to

214    megaherbivores according to Owen-Smith (2013). We include animals consuming

215    submerged angiosperms in both marine and freshwater environments. In marine systems

216    this includes dugongs, manatees and turtles. In freshwater systems it is less clear which

217    animals can be considered large aquatic herbivores, and we included aquatic and semi-

218    aquatic animals, as all of them consume aquatic plants. In fact, only freshwater

219    manatees are fully aquatic and depend completely on submerged and floating

220    macrophytes as a food source. The group of semi-aquatic animals consists of animals

221    that are frequently found in aquatic systems. We acknowledge that this category is

222    somewhat arbitrary. We identified three distinct vertebrate classes that could be

223    considered large aquatic or semi-aquatic herbivores: mammals, birds and reptiles (Table

224    1). We did not find examples of herbivore fish greater than 10 kg that graze on

225    submerged vascular macrophytes; therefore fish were left out of this review. The body

226    mass of the selected aquatic herbivores ranges from about 10 kg (swans) to 3200 kg

227    (hippopotamus). Interestingly, the list includes the largest species from a variety of

228    guilds/families of animals. Whereas a swan of 10 kg will likely have less per capita

229    impact on submerged plants than a manatee of 300 kg, within the guild of water birds,

230    swans have disproportionate impacts, which is directly related to their body size (Wood

231    et al. 2012a).

232

233    *Diets*

234        The diets of all the large aquatic herbivores included in this review are presented

235    in Table 1. None feed exclusively on submerged angiosperms. In fact, although most of

236    the species in Table 1 are primarily plant consumers, they generally also feed on algae,

237    invertebrates (e.g. cnidarians) and other animal material (O'Hare et al. 2007, Cardona et

238    al. 2009, Reisser et al. 2013). The marine dugong appears to be the most specialist

239    feeder, with a diet of mostly seagrass (Heinsohn et al. 1977). It feeds indiscriminately

240    on aboveground and belowground parts, just as beavers and swans. While migrating,

241    swans apparently depend largely on tubers as their principal food source (Nolet and

242    Drent 1998, Nolet et al. 2002, LaMontagne et al. 2003). Recently, green turtles have

243    also been observed to dig up and eat belowground tissues of seagrasses, which has been

244    interpreted as a sign of local turtle overpopulation and food limitation (Christianen et al.

245    2014). The belowground parts of vascular plants are rich in carbohydrates and starch,

246    which provides energy-rich food to aquatic herbivores (Nolet and Klaassen 2005).

247          Several species feed both on marine and freshwater angiosperms, including the

248    West-Indian and West African manatee as well as the swan species (Table 1). All

249    manatees are fully aquatic and feed mostly on submerged and floating macrophytes,

250    occasionally feeding on emergent species. Most herbivores that consume submerged

251    macrophytes in freshwater systems also consume terrestrial plants, with aquatic

252    angiosperms often being a very small component of their diet. Even semi-aquatic

253    herbivorous species such as the hippopotamus, the capybara and the beaver, which are

254    adapted to spend much of their time half submerged, having their eyes and nostrils on

255    the upper part of their head, feed mostly on land and only occasionally consume

256    submerged macrophytes (Creed 2004). It should however, be noted that the diets of

257    these species have not been very intensively investigated; it is therefore possible that

258    aquatic macrophytes may be a larger portion of their diet than is presumed.

259          The other mammals that sporadically consume freshwater vascular plants are

260    perhaps more rightly terrestrial animals that frequent swamps and marshy areas,

261    including moose, Eurasian elk and several other deer species (Table 1). A recent review

262    shows that their incidence of feeding on submerged angiosperms may be seriously

263    underestimated as all better studied cervid species occasionally consume submerged

264    vascular plants and macro-algae (Ceacero et al. 2014). This suggests that less studied

265 species may also opportunistically consume aquatic angiosperms when these are

266 available. In fact, some terrestrial herbivores (e.g. moose) may specifically seek out

267 aquatic angiosperms to obtain valuable nutrients, such as sodium, the concentrations of

268 which are higher in aquatic vascular plants than terrestrial plants (Belovsky and Jordan

269 1978). In addition, other minerals or proteins could drive herbivores to use aquatic

270 angiosperms as a supplementary source to a primarily terrestrial diet, particularly in

271 periods of high physiological demand (Ceacero et al. 2014).

272

## Impact on aquatic vascular plant abundance and species composition

274 *Herbivory rates compared to primary production*

275 Current rates of herbivory in terrestrial habitats are relatively low. In a recent

276 review, Turcotte et al. (2014) showed that, when averaged across all major lineages of

277 vascular plants, herbivores consume 5.3% of the leaf tissue produced annually. Previous

278 estimates of the mean annual rate of leaf herbivory across terrestrial plants ranged

279 between 10 and 20% (Cyr and Pace 1993, Frank et al. 1998, Cebrian and Lartigue 2004,

280 Maron and Crone 2006). By any estimate, these values are clearly lower than rates

281 reported in aquatic systems, where herbivores have been shown to consume between

282 30-80% of primary production on average (Lodge 1991, Cyr and Pace 1993, Burkepile

283 2013, Gruner and Mooney 2013). At the highest extremes, large aquatic herbivores can

284 consume well above 100% of annual primary production (Table 2); it is not uncommon

285 for turtles and swans to consume ca. 100% of primary production in a given season

286 (Rivers and Short 2007, Hidding et al. 2009, Kelkar et al. 2013a, Christianen et al.

287 2014). A lot of the variation in herbivory rates observed among studies is likely due to

288 variation in herbivore densities (e.g. Wood et al. 2012a).

13

289

290    *Effects on canopy height and above and below ground biomass*

291        Large aquatic herbivores significantly affect plant abundance and vegetation

292    structure (Table 2). Reduction of the aboveground standing crop varies considerably,

293    but can be very high at some locations (see above) resulting in an almost complete

294    removal of submerged vegetation beds. By removing aboveground plant material,

295    aquatic herbivores alter the vegetation structure (e.g. Christianen et al. 2014) or increase

296    the patchiness on a small spatial scale (Dos Santos et al. 2012, Christianen et al. 2013).

297    Thus, by grazing on the upper plant parts, aquatic herbivores reduce shoot length and

298    the mean height of the vegetation (Tatu et al. 2007).  More importantly, some large

299    aquatic herbivores appear to specifically target belowground storage. In fact, this may

300    be a key difference between terrestrial and aquatic herbivores: while terrestrial species

301    seldom consume belowground parts, large aquatic herbivores can, on average, reduce

302    belowground biomass by 60% (comparing grazed versus ungrazed areas; see Table 2)

303    (Preen 1995). While mute swans do consume roots and rhizomes, this is often a minor

304    portion of their diet that mostly consists of aboveground plant material (Bailey et al.

305    2008). Other species, in contrast, specifically target belowground plant parts while

306    feeding. Dugongs, manatees, hippopotamuses, cervids, beavers and whooper and

307    trumpeter swans, have all been identified as consumers of plant below ground biomass

308    (Preen 1995, Nacken and Reise 2000, LaMontagne et al. 2003, Källander 2005, Dos

309    Santos et al. 2012, Law et al. 2014). Indeed, dense populations of green turtles

310    overgrazing above ground biomass have been reported (in Indonesian seagrass

311    meadows) to exploit the below ground compartment by digging up the rhizomes

312    (Christianen et al. 2014, Heithaus et al. 2014). Similarly, black swans (*Cygnus atratus*),

313    Bewick swans and whooper swans (the former two at the limit of what we class as large

314    herbivores (>10 kg) in this review), forage on leaves, rhizomes and roots on macrophyte

315    meadows, producing a pitted waterscape (Hidding et al. 2010a, Dos Santos et al. 2012).

316    Dugongs (and also manatees) are specialist belowground feeders, and the feeding trails

317    they produce have a 50-87% lower shoot density, and 51-75% reduction in

318    belowground biomass (see Table 2).

319

320    *Changes in species composition*

321        All of the large aquatic herbivores examined (for which sufficient data was

322    available) have impacts on plant species composition, usually transforming meadows

323    dominated by slow growing, large plants into meadows dominated by fast-growing

324    smaller species that cope better with herbivore-induced disturbances in the above- and

325    below-ground compartments (Preen 1995, Burkholder et al. 2013, Kelkar et al. 2013b).

326    They can alter species composition and diversity of macrophyte beds by preferentially

327    grazing on certain species or by unselective bulk grazing, which will mostly affect the

328    dominant or most sensitive species, thus changing the relative abundance among species

329    assemblages. This can promote species diversity when herbivores graze on the

330    dominant plant species, thereby releasing subordinates from competition or creating

331    generation niches for subordinates (Olff and Ritchie 1998). Equally though, they reduce

332    diversity by selectively removing the subordinate species. These alternative impacts can

333    be illustrated by the grazing of mute swans, which like to feed on *Potamogeton*

334    *pectinatus*. They preferentially consumed *P. pectinatus* amongst vegetation dominated

335    by charophytes, thus enhancing charophyte dominance (Hidding et al. 2010a), whereas

336    in vegetation dominated by *P. pectinatus*, they strongly reduced its biomass, which

337    favoured the subordinate species *Potamogeton pusillus* that would otherwise be

338  outcompeted (Hidding et al. 2010b). Interestingly, herbivores can also reduce the

339  biomass of a species, while simultaneously increasing its relative share in species

340  composition. In a brackish lagoon, grazing impacts by waterfowl on *Zostera noltii* was

341  dual, mainly favouring its relative abundance by reducing competing macroalgae, but

342  conversely reducing its biomass through direct impact (Gayet et al. 2012). Similar

343  examples can be found in marine systems. Green turtles in the Lakshadweep

344  archipelago precipitate species shifts in meadows from the long-lived, slow-growing

345  seagrass *Thalassia heimprichii*, on which they preferentially feed, to the faster growing

346  small seagrass *Cymodocea rotundata*; with sustained grazing, turtles can cause

347  meadows to shift to monospecific *C. rotundata* stands (Kelkar et al. 2013b). This is

348  similar to some reports of dugongs that appear to be responsible for maintaining

349  seagrass meadows with short-lived *Halophila spp.* and *Halodule spp.* species (Preen

350  1995). In contrast, in freshwater systems, belowground foraging on *P. pectinatus* tubers

351  in autumn or spring by whooper swans and Bewick swans, generally enhances species

352  diversity, as it reduces the dominance of *P. pectinatus* in the following growing season

353  and creates regeneration niches through sediment disturbance, to which particularly

354  annual species, such as *Najas marina* and *Zannichellia palustris*, respond favourably

355  (Hidding et al. 2010a, b). Even when no net effect on aboveground plant standing crop

356  is measured, early season tuber foraging by trumpeter or whooper swans may result in a

357  shift of species composition, with increased abundance of subordinate species in the

358  aboveground vegetation (LaMontagne et al. 2003, Hidding et al. 2010b). Moose grazing

359  can also reduce aquatic plant species richness, but the underlying mechanism remains

360  unknown (Qvarnemark and Sheldon 2004).

361

**Direct and indirect effects of large aquatic herbivores on ecosystem functioning**

362
363

364     Given the review above, it is unsurprising that large herbivores may have the
365     ability to influence aquatic ecosystem functioning. By consuming submerged vegetation
366     they have strong direct and indirect effects on their habitat, often cascading to other
367     organisms. Due to their size, large aquatic herbivores can transform entire landscapes,
368     and promote spatial heterogeneity in plant beds, wetlands and river valleys, with very
369     strong consequences for other organisms (Table 3). We discuss five main ecosystem
370     functions that large aquatic herbivores may contribute to: structuring habitat, modifying
371     productivity, modifying geomorphology, altering nutrient cycling and transport of
372     organisms.

373

374     *Habitat modification for other organisms*

375     Not unlike terrestrial grasslands, in the presence of large herbivores, many
376     aquatic vascular plant systems are transformed to low canopy habitats, with low above
377     ground biomass and high turnover of plant tissues, often referred to as grazing lawns
378     (McNaughton 1984, Frank et al. 1998, Table 3). Green turtles, dugongs and swans can
379     produce strong habitat modifications by reducing shoot densities, above and
380     belowground biomass, changing species composition and reducing canopies of the
381     submerged plant ecosystems they feed on (Lock 1972, Nolet 2004, Skilleter et al. 2007,
382     Sandsten and Klaassen 2008, Arthur et al. 2013, Table 3). Hippopotamuses create
383     grazing lawns on land, thereby enhancing larger scale spatial heterogeneity of
384     vegetation (Lock 1972), which attracts a rich herbivore assemblage (Eltringham 1974,
385     Verweij et al. 2006, Waldram et al. 2008, Kanga et al. 2013). However, facilitative

386 effects will depend strongly on large herbivore density. Hippopotamuses may facilitate

387 other herbivores by creating grazing lawns, but at very high densities, they reduce the

388 standing crop of vegetation to a level that makes it difficult for other herbivores to find

389 enough food, causing them to compete with each other (Eltringham 1974). The

390 circumstances under which facilitative effects can be found may further depend on the

391 type of ecosystem and the availability of resources for plant (re)growth.

392       Altogether, the removal of plant material, changes in species composition or

393 changes to the structural complexity provided by the vegetation due to grazing by large

394 aquatic herbivores has indirect implications for other organisms that use this spatially

395 heterogeneous habitat for foraging, breeding, and as a refuge from predation (Coen et

396 al. 1981, Marklund et al. 2002, Skilleter et al. 2007). Skilleter et al. (2007) found that up

397 to 85% fewer animals were present in dugong feeding trails, and that the overall

398 composition of benthic infaunal assemblages in the grazed areas was different from that

399 in ungrazed areas. Similarly, Arthur et al. (2013) found that total biomass density of

400 seagrass-associated fish recruits was about 12 times lower in seagrass meadows grazed

401 by green turtles. At its extreme, high populations of large herbivores such as green

402 turtles, dugongs or manatees concentrate in space, resulting in habitats that can be

403 completely overgrazed (Preen 1995, Hauxwell et al. 2004a, Skilleter et al. 2007,

404 Christianen et al. 2012, Table 3).

405

406 *Production modification*

407       In aquatic systems, herbivores are more often reported to suppress primary

408 productivity rather than facilitate growth, prompting a 49-68% decrease in producer

409 abundance on average (Gruner et al. 2008, Hillebrand et al. 2009, Poore et al. 2012,

410    Table 3). However, large grazers have also been reported to increase primary

411    production by up to 40% compared to ungrazed areas by removing heavily-epiphytized

412    seagrass blades, which presumably reduces light limitation and facilitates the production

413    of new, fast growing shoots (Moran and Bjorndal 2005, Valentine et al. 2014, Table 3).

414    Similarly, autumn foraging by Bewick's swans (which are just below 10 kg) enhanced

415    the production of tubers of *Potamogeton pectinatus*, at intermediate grazing pressure,

416    through an overcompensation response of the remaining tubers (Nolet 2004).

417

418    *Geomorphological modification*

419         Perhaps one of the strongest effects large aquatic herbivores can exert on

420    systems is the modification of sediment characteristics (e.g. granulometry) while

421    foraging, that mobilizes fine particles and increases water turbidity (Skilleter et al. 2007,

422    Christianen et al. 2014, Green and Elmberg 2014, Table 3). Sediment mobilization by

423    herbivores may influence primary producers by increasing rates of plant burial or by

424    reducing transparency (Christianen et al. 2014). It may also influence other organisms

425    living in these habitats either through direct mortality as a result of burial or reduced

426    visibility (Skilleter et al. 2007), incidental consumption (as seen in terrestrial systems,

427    Gomez and Gonzalez-Megias 2002), or indirectly because of the close association

428    between soft sediment fauna and sedimentary parameters (Skilleter et al. 2007 Table 3).

429    Large herbivores may also cause a reduction in sediment stability, not just through the

430    loss of submerged plants, but due to the loss of features such as animal tubes

431    (Luckenbach 1986). This is not the only effect. Trampling by large herbivores damages

432    plants directly, resulting in bare soil, but also compacts the soil, and on land, prevents

433    rapid infiltration of rain water, resulting in wetter habitats (Lock 1972, Schrama et al.

434   2013). Furthermore, in freshwater habitats, large herbivores have two principal effects

435   on the geomorphology of their habitat: they alter the areas where they reside and, due to

436   their foraging movements between water to land, impact the entire riparian zone

437   (Naiman and Rogers 1997). Hippopotamuses create pathways through wetland

438   vegetation during their nightly foraging bouts on land as they consistently use the same

439   trails (McCarthy et al. 1998, Mosepele et al. 2009). These maintained trails can

440   potentially become water or rivers channels, pools alongside rivers, or even lakes (Lock

441   1972, Naiman and Rogers 1997, McCarthy et al. 1998, Mosepele et al. 2009), that serve

442   as a habitat for fish, invasive red-swamp crayfish and larger animals such as crocodiles

443   (Naiman and Rogers 1997, Mosepele et al. 2009, Grey and Jackson 2012, Table 3).

444        Analogous patterns of strong engineering effects of large aquatic herbivores can

445   be found in northern latitudes. Beavers strongly modify channel geomorphology and

446   hydraulic conditions through their dam building activities (Naiman et al. 1986, Wright

447   et al. 2002, Rosell et al. 2005, Hood and Larson 2015). The creation of ponds and

448   stream diversions has profound long-term consequences for the entire drainage network

449   (Naiman et al. 1986), by reducing water flow and increasing sedimentation rates

450   (Naiman and Rogers 1997, McCarthy et al. 1998, Rosell et al. 2005). As a result,

451   beavers can act as a whole-community facilitator for a wide variety of aquatic animals,

452   making the habitat structurally more diverse and productive (Jones et al. 1994, Wright

453   et al. 2002, Rosell et al. 2005, Nummi and Holopainen 2014). Moose and elk also create

454   a dense network of foraging trails in the riparian zone when moving between water and

455   land (Naiman and Rogers 1997).

456

457   *Nutrient cycle modification*

458        Large herbivores can modify nutrient cycling in two main ways: alteration of

459    nutrient cycling and transport of nutrients in or out of the system. Direct consumption

460    by large herbivores can accelerate the detrital cycle by accelerating decomposition, but

461    also modifies the nutrient cycle in plants themselves. Sustained grazing has been shown

462    to modify the nutrient content of plants, particularly through enhanced nitrogen content,

463    in both aquatic (Hunter 1980, Moran and Bjorndal 2006, Aragones et al. 2006) and

464    terrestrial habitats (McNaughton 1979, Knapp et al. 1999, Bakker et al. 2009). In this

465    way, by gardening plants, large aquatic herbivores may increase forage quality for

466    themselves and other herbivores in the system (Moran and Bjorndal 2006, Aragones et

467    al. 2006). Herbivores may indirectly fertilize benthic primary producers; the shortened

468    grazed canopy facilitates the flux of nutrients from the water column to producers,

469    thereby decreasing nutrient limitation (Carpenter and Williams 2007). However, the

470    most common mechanism by which large aquatic herbivores increase plant nutrient

471    levels is by stimulating the plant's compensatory growth (Moran and Bjorndal 2006,

472    Vergés et al. 2008, Christianen et al. 2012).

473        Nutrient flows in aquatic systems can be radically different from terrestrial

474    habitats, where fertilization through urine and dung are recycled largely within the same

475    broad area (McNaughton et al. 1997, Subaluski et al. 2015). In contrast, in freshwater

476    and marine systems, water motion and currents on the one hand, and the larger home

477    ranges of herbivores on the other, make it unlikely that herbivores could fertilize the

478    same benthic primary producers they have consumed directly via their excretions

479    (Burkepile 2013). Many marine animals have on average significantly larger adult home

480    ranges (McCauley et al. 2015) and disperse greater distances as juveniles than their

481    terrestrial counterparts (Kinlan and Gaines 2003). In addition, larger animals usually

482    display larger home ranges (McCauley et al. 2015). This makes large aquatic fauna

483    potentially important mobile links, capable of being long-distance vectors of nutrients

484    between habitats and ecosystems (Lundberg and Moberg 2003, Heck et al. 2008, Green

485    and Elmberg 2014). Most large aquatic herbivores may have the potential to transfer

486    nutrients within and between the habitats within their home range, and those that use

487    both terrestrial and aquatic habitats, may even be cross-ecosystem links. This has been

488    shown for the moose (Belovsky and Jordan 1978, Bump et al. 2009), green turtles

489    (Vander Zanden et al. 2012), beavers (Rosell et al. 2005), hippopotamuses (Subaluski et

490    al. 2015) and swans (Hahn et al. 2008, Wood et al. 2013); by eating in one system and

491    defecating and excreting in another, these species may serve as powerful links and be

492    considered ecosystem engineers. Thanks to this capacity of exporting nutrients out of

493    the system, large aquatic herbivores may also function as alleviators of anthropogenic

494    nutrient inputs to seagrass or macrophyte meadows. This has been confirmed for

495    seagrass meadows grazed by green turtles (Christianen et al. 2012).  Grazing increases

496    seagrass production, thereby increasing the food availability for green turtles and the

497    amount of seagrass biomass and nutrients exported by the turtles out of the system.

498    According to Christianen et al. (2012), this export by large aquatic herbivores is

499    probably the most important controlling factor for seagrass under grazing and high

500    nutrient loads. When nutrients increase, grazing can potentially improve conditions for

501    seagrass.

502

503    *Transport of organisms*

504    Apart from transporting nutrients, large herbivorous fauna can transport

505    propagules of aquatic plants and animals when moving between wetlands or aquatic

506    plant beds. This dispersal ability has been mainly examined in waterbirds (Green and

507 Elmberg 2014), but may be extended to other large aquatic herbivores. Seeds of aquatic

508 plants and resting stages of numerous invertebrate species are transported both by endo-

509 and exozoochorous means (Clausen et al. 2002, van Leeuwen et al. 2012). Internal

510 transport is the most common form of dispersal (Brochet et al. 2010). The maximum

511 distance of endozoochorous dispersal depends strongly on the body size of the vector:

512 larger waterbirds fly faster and have longer gut retention times, which allows for a

513 longer travel distance before the last propagule is excreted (Clausen et al. 2002, van

514 Leeuwen et al. 2012). Furthermore, the viability of seeds after gut passage is higher in

515 larger birds (van Leeuwen et al. 2012), even though seeds excreted after shorter

516 retention times are generally more viable (Charalambidou et al. 2003). Whereas large

517 waterbirds consume relatively fewer seeds and more green plant material than smaller

518 birds (Wood et al. 2012a), they inadvertently consume large amounts of macro-

519 invertebrates and seeds while feeding on green plant material (O'Hare et al. 2007).

520 Altogether, this makes larger species, such as swans, suitable vectors for long distance

521 travel of propagules. While most propagules will be lost as they may be digested or

522 excreted in unsuitable habitats, rare, successful long distance dispersal events can be of

523 high significance for instance in promoting species range expansions or in maintaining

524 gene flow between distant populations (Figuerola et al. 2005, Brochet et al. 2009,

525 Sanchez et al. 2012). Whereas for other groups of large aquatic herbivores little

526 information on dispersal is available, similar processes may occur in marine

527 environments, where large herbivores transport seeds of seagrasses (Sumoski and Orth

528 2012, McMahon et al. 2014) whereas in freshwater habitats mammalian herbivores can

529 also carry seeds (Jaroszewicz et al. 2013). Their potential as dispersal vectors of

530 submerged plants will depend strongly on the digestion physiology and movement

531 ecology of the species.

532

## **Outlook and conclusions**

*Large aquatic herbivores as ecosystem engineers: from species to functional groups*

Our review highlights that much research on large aquatic herbivores has focused on species forage or habitat requirements, without much consideration of the influence of this foraging on the aquatic habitats themselves. Even for the beaver, a classic textbook example of an ecosystem engineer capable of modifying entire landscapes (Jones et al. 1994, Marshall et al. 2013, Hood and Larson 2015), there is limited knowledge of its impact on submerged freshwater vegetation (Parker et al. 2007). However, from an early discounting of any potential impact herbivory may have as a dominant ecosystem pathway (Lodge 1991, Lodge et al. 1998), more recent evaluations have shown that large aquatic herbivores could, under some circumstances, become key agents of aquatic ecosystem functioning (Christianen et al. 2014, Green and Elmberg 2014, Pennisi 2014, Heithaus et al. 2014).

While large aquatic herbivores all consume submerged angiosperms and have an aquatic lifestyle, there are enough differences between species to make it impossible to generalise on the impact of a generic large aquatic herbivore. Instead, it is helpful to classify large aquatic herbivores on the basis of shared traits according to their diet, habitat selection and movement ecology. Based on these criteria we divided the large aquatic herbivores listed in Table 1 into four categories (Fig. 1):

(a) *Fully aquatic species that may be both resident or migratory (manatees, dugongs, turtles)*

554        Their diets consist mostly of submerged vascular plants and they live most of the

555        time fully submerged.

556        (b) *Semi-aquatic species adapted to life on the water, but frequent both water*

557        *and land, and can be both resident and migratory (swans)*

558        They consume a lot of submerged vascular plants and can sustain themselves for

559        prolonged periods on submerged vascular plants but can also survive on

560        terrestrial vegetation.

561        (c) *Semi-aquatic species that live in the water and forage mainly on land*

562        *according to a central-place foraging pattern; they are residents*

563        *(hippopotamuses, beavers, capybara)*

564        They are adapted to spend extended periods almost submerged, leaving only

565        their ears, eyes and nose above the water surface. They retreat to the water when

566        scared. While they do consume submerged angiosperms, this appears to

567        generally be a minor part of their diet, although most species are data deficient

568        when it comes to foraging on submerged vascular plants.

569        (d) *Terrestrial species that frequent aquatic habitats; resident species with*

570        *relatively large home ranges (cervids, water buffalo, lowland tapir)*

571        They are adapted to frequent wetlands: interdigital membranes, extended hooves

572        or relatively long limbs, their nose may function as a snorkel as in case of the

573        tapir. They consume submerged vascular plants; this is a minor but seemingly

574        important part of their diet, although also most of these species are data deficient

575        when it comes to quantification of foraging on submerged angiosperms.

576     The ecosystem functions of large aquatic herbivores differ between these four

577     groups (Fig. 2). The strongest impacts on submerged plant production, both positive and

578     negative, are found for the fully submerged herbivore species that live most closely

579     associated with submerged angiosperms (Fig. 1a). Both the fully submerged grazers and

580     the swans (Fig. 1b) can reduce plant standing crop considerably, which is also due to

581     their habit of foraging on belowground plant parts. The removal or reduction of plant

582     beds has flow-on effects on other fauna, mostly reducing their abundance. The central-

583     place foragers (Fig. 1c) that forage mostly on land, typically create gradients of grazing

584     pressure, most intense in or close to the water and less intense further away on land

585     (Lock 1972, Fryxell 1999, Kanga et al. 2013). As a result they create strong spatial

586     heterogeneity in vegetation structure (see Fig. 1c), which has positive effects on other

587     flora and fauna. It should be noted that no data are available for capybara's.

588     Unsurprisingly, both beavers and hippopotamuses (category c) also have the strongest

589     geomorphological and hydrological engineering effects.

590     The transport of nutrients and dispersal of submerged angiosperm propagules is

591     closely linked to the travelling distance of the animals as well as their targeted

592     movement between habitats or habitat patches (Bauer and Hoye 2014, Green and

593     Elmberg 2014). Semi-aquatic species have strong roles linking aquatic and terrestrial

594     habitats and import nutrients mainly into the water (category b and c) or on land

595     (category d). Long distance migrants (category a and b) can be of particular importance

596     in propagule dispersal between unconnected habitat patches; large terrestrial herbivores

597     moving between aquatic habitats in their large home ranges (category d) likely also

598     perform this function, but data on their role as dispersal agents of submerged vascular

599     plants are lacking.

600

*Trophic downgrading and ecosystem collapse*

602     Whereas large aquatic herbivores have a number of important ecosystem effects,

603   their actual impact depends strongly on their density (Wood et al. 2012a, Kelkar et al.

604   2013b). Where the largest herbivores (> 1000 kg), such as elephants and rhinoceroses,

605   are considered to be predation free due to their size (Owen-Smith 1988), at least as

606   adults, most aquatic large herbivores are too small (< 500 kg, see Table 1) to be

607   completely predation free under natural conditions. Large roving predators may have

608   direct impact on the survival of large aquatic herbivores, but even more so through their

609   indirect effect of inducing a landscape of fear where foraging movements of herbivores

610   are restricted to less risky habitats (Burkholder et al. 2013). Of the large aquatic

611   herbivores only the hippopotamus is a true megaherbivore (>1000 kg), which may be

612   considered predation free under natural conditions. However, other species of large

613   aquatic herbivores like dugongs or green turtles are seldom predated in today´s waters

614   due to the lack of predators. Indeed, megafauna is generally declining, and this decline

615   is not random. The largest species typically experience the strongest decline (Dirzo et

616   al. 2014, Ripple et al. 2015), but also, predators decline faster than herbivores (Estes et

617   al. 2011, McCauley et al. 2015). This has led to the phenomenon of trophic

618   downgrading, where the relative abundance of herbivores increases, due to the faster

619   decline of predators and a subsequent release from predation (Estes et al. 2011). A

620   similar effect is observed when herbivores are protected from hunting or other forms of

621   human disturbance and there are no natural predators to compensate for the release of

622   hunting pressure. In these cases, herbivores can become locally very numerous, and

623   exert very strong grazing pressure on the submerged vegetation, such as in marine

624   reserves, where locally large populations of green turtles can seriously threaten

625   ecosystem stability by removing seagrass beds, which could lead to ecosystem collapse

626 (Christianen et al. 2014, Heithaus et al. 2014). This is because, unlike most terrestrial

627 megaherbivores, many aquatic species (both marine and fresh water) consume not

628 merely the above-ground biomass but sometimes target the below-ground storage of the

629 primary producers that structure aquatic plant communities. It is well established that

630 these belowground reserves are critical to ensure the buffer capacity of these ecosystem,

631 and by targeting these reserves large aquatic herbivores may contribute to considerable

632 ecosystem instability in the systems they inhabit. Similarly, very high densities of

633 hippopotamus result in hypertrophic pools and rivers (Subaluski et al. 2015),

634 particularly at periods of low water levels, which can result in algal blooms, anoxia and

635 fish kills (Pennisi 2014). In some instances, ecosystems modified by large aquatic

636 herbivores go through a pattern of rotational collapse and recovery, spurred by large-

637 scale movements of herbivore populations (Arthur et al. 2013, Heithaus et al. 2014). In

638 other cases, systems may even collapse beyond recovery thresholds. A confinement of

639 large aquatic herbivores to reserves, without the possibility to follow their natural

640 migration patterns, and a lack of natural predation in combination are the root cause of

641 recorded detrimental effects of large herbivore grazing and the collapse of entire plant

642 beds. Other species have recovered successfully from population declines, such as the

643 mute swan, which has expanded its range through introductions in new habitats,

644 particularly the USA. Here, the mute swan is an exotic species and rapidly increasing in

645 population size, with concomitant effects on submerged plant beds (Conover and Kania

646 1994, Tatu et al. 2007, Gayet et al. 2014).

647

648 *Conserving large aquatic herbivores and the ecosystems they rely on*

649        Taken together, this evaluation raises important questions for the management of

650    large marine and freshwater herbivores. Many of these species are globally threatened

651    and conserving their populations is a critical concern. As a first, for large herbivores,

652    their size itself becomes a clear threat as has already been observed in terrestrial large

653    herbivores (Dirzo et al. 2014). Large animals are more difficult to conserve because

654    they have higher food requirements, larger home ranges, longer life spans and lower

655    reproductive success among other size-specific traits that limit their reproduction and

656    impede conservation efforts (Owen-Smith 1988). Large aquatic herbivores have to deal

657    with additional issues. They have, on average, larger home ranges (Peters 1983,

658    McCauley et al. 2015) that makes conservation a significant challenge as species move

659    freely between different conservation jurisdictions (Bauer and Hoye 2014). Unlike their

660    terrestrial counterparts, large aquatic herbivores cannot be protected with fences within

661    restricted areas where protection can be maximized; most marine protected areas are not

662    large enough to protect these species (McCauley et al. 2015). This results in locally

663    difficult-to-resolve artefacts, such as the dilemma how freshwater plant beds can be

664    restored in the presence of manatees, which immediately consume newly planted shoots

665    – whereas they also rely on healthy meadows for survival (Hauxwell et al. 2004b).

666

667    *Conclusions*

668        It is clear that large herbivores that feed on aquatic systems can be critical

669    ecosystem engineers, with the ability to modify both direct and indirect functional

670    pathways in the ecosystems they inhabit. It is evident that extant aquatic herbivores may

671    play roles very similar or even greater than their terrestrial counterparts and, in

672    conditions of decline or over-abundance, may precipitate large, ecosystem-wide effects,

673　　including entire collapse (Strong 1992, Shurin et al. 2006). Management of large

674　　aquatic herbivores requires a careful understanding of the roles they play in aquatic

675　　vascular plant communities. Currently we know very little about the ecosystem impacts

676　　of some of the most charismatic animals in the world, such as manatees, dugongs, sea

677　　turtles, hippopotamuses and swan species, and next to nothing about some less

678　　charismatic animals, such as capybara, water buffalo, lowland tapir and swamp and

679　　marsh deer. Tourism alone could be an ecosystem service that economically justifies the

680　　preservation of charismatic large aquatic animals (Sala et al. 2013, Roman et al. 2014).

681　　However, beyond conserving these species as flagships, we need further studies to

682　　examine how best to manage the populations of large aquatic herbivores at appropriate

683　　scales, keeping in mind the capacity of extant aquatic plant communities to sustain these

684　　populations. Furthermore, a much better understanding of their roles in aquatic

685　　ecosystems is warranted. This will help understand the ecology of aquatic vascular

686　　plants and their habitats that have evolved in the presence of a diversity of large aquatic

687　　and semi-aquatic herbivores, and will lead to a better appreciation of the importance to

688　　strive for the conservation of complete ecosystems.

689

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**Table 1.** List of large aquatic and semi-aquatic herbivores (>10 kg) that consume submerged angiosperms, with indication of their body mass, home range,

1147 diet and conservation status, according to IUCN. EN- endangered, VU-vulnerable, LC- least concern. Several other large herbivore species occasionally

1148 consume submerged angiosperms, including other cervids, mainly based on availability and comprising only a minor fraction of their diets, as far as data are

1149 available. ***Sources:*** Data on habitat, diet and range for mammals from MacDonald (2001), for waterbirds from Kear (2005), for turtles the Encyclopaedia of

1150 Life (EOL www.eol.org); data supplemented with references indicated in the Table. Data on conservation status, population size and population trend from

1151 IUCN: The IUCN Red List of Threatened Species. Version 2014.3. www.iucnredlist.org. Downloaded on 26 January 2015.

| English name | Latin name | Habitat | Geographic range | Home range (km$^2$) and migration | Diet selection | Body mass (kg) | Conservation status; population size; -trend (IUCN) |
|---|---|---|---|---|---|---|---|
| Green sea turtle | *Chelonia mydas* (L.) | Marine; fully aquatic | Circumglobal, tropical-subtropical | 4-39 (Seminoff et al. 2002); migratory | Herbivorous: mostly seagrass, algae, but also cnidarians, mangroves (Cardona et al. 2009, Reisser et al. 2013) | 68–190 | EN; unknown number; declining |
| Loggerhead sea turtle | *Caretta caretta* (L.) | Marine; fully aquatic | Circumglobal, tropical-subtropical | 300-1900 (Marcovaldi et al. 2010); migratory | Omnivorous: Seagrass, algae, cnidarians and other invertebrates | 80-200 | EN; population size and trend unknown |
| Amazonian manatee | *Trichechus inunguis* (Natterer) | Freshwater; floodplain lakes, rivers and | Amazon river drainage basin | Unknown; resident | Herbivorous: Emergent, floating or submerged mostly freshwater | 120-270 | VU; population size and trend unknown |

| | | channels; fully aquatic | | | vegetation | | |
|---|---|---|---|---|---|---|---|
| West-Indian manatee (subspecies: Florida and Caribbean) | *Trichechus manatus* (L.) | Marine to freshwater; shallow coastal waters, estuaries and rivers; fully aquatic | Atlantic coast from Florida and Caribbean to central Brazil | 202-5156 (Castelblanco-Martínez et al. 2013); migratory | Herbivorous: Seagrass, algae, cnidarians, freshwater macrophytes, mangroves | 200-600 | VU; <10.000 animals, declining |
| West African manatee | *Trichechus senegalensis* (Link) | Marine to freshwater; similar to West-Indian manatee; fully aquatic | West-Africa (Senegal to Angola) | Unknown; resident | Herbivorous (mostly); seagrass and other marine and freshwater plants | 450 | VU: population size and trend unknown |
| Dugong | *Dugong dugon* (Müller) | Marine; coastal shallows; fully aquatic | South-West Pacific Ocean and Indian Ocean | 4.1-43.4 (Iongh et al. 1998, Sheppard et al. 2010); resident | Herbivorous: mostly seagrass (above and belowground biomass) | 290-360 | VU; population size and trend unknown |
| Mute swan | *Cygnus olor* (Gmelin) | Lakes, rivers, freshwater and brackish marshes; semi-aquatic | Eurasia | Mostly resident, can be migratory (<200 km) EOL | Submerged and emergent aquatic vegetation, grasses and cereals, below-ground parts of aquatic plants infrequently (Bailey et al. 2008) | 7-16 | LC; 600.000-610.000 animals; increasing |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Trumpeter swan | *Cygnus buccinator* (Richardson) | Freshwater and brackish wetlands; semi-aquatic | North America | Migratory (>200 km) EOL | Aquatic vegetation, cereals and root crops | 9.5-13.5 | LC; population size unknown; increasing |
| Whooper swan | *Cygnus cygnus* (L.) | Wetlands; semi-aquatic | Eurasia | Migratory (>200 km, even 945 km) (Gardarsson 1991) | Omnivorous; mostly aquatic vegetation, cereal crops, mussels | 7.4-14 | LC; >180.000 animals; trend unknown |
| Capybara | *Hydrochoerus hydrochaeris* (L.) | Freshwater; flooded savanna or grassland next to water holes, also along poles and rivers in tropical forest; semi-aquatic | South-America | 0.1-0.3; resident | Herbivorous, mostly (aquatic) grasses (Do Valle Borges and Gonçalves Colares 2007, Corriale et al. 2011, Desbiez et al. 2011), coprophagy (Borges et al. 1996) | 50 | LC, regulated hunting and harvesting; population size and trend unknown |
| Hippopotamus | *Hippopotamus amphibius* (L.) | Freshwater; short grasslands (at night), rivers, wallows and lakes (by day); semi-aquatic | Sub-Saharan Africa | Hippos seldom travel more than 2–3 km from water to feed (Lock 1972, O'Connor and Campbell 1986); resident | Herbivorous (mostly); terrestrial grasses (de Iongh et al. 2011) and dicots (Codron et al. 2007, Cerling et al. 2008, Michez et al. 2013), supplementary aquatic vegetation (Grey and Harper 2002) | 1600-3200 | VU; 125.000-150.000 animals; declining |
| Pygmy hippopotamus | *Hexaprotodon liberiensis* | Lowland forests and swamps; | West Africa | 0.4-1.5 (Roth et al. 2004); resident | Herbivorous; fallen fruits, ferns, dicots and grasses | 180-275 | EN; <2000-3000 animals; |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | (Morton) | semi-aquatic | | | | | declining |
| North American beaver | *Castor canadensis* (Kuhl) | Riparian wetlands; semi-aquatic | North America | 0.04-0.25 (Bloomquist et al. 2012); resident | Herbivorous; wood, grasses, roots (Parker et al. 2007, Severud et al. 2013a, b) | 13-32 | LC; population size unknown; stable |
| Eurasian beaver | *Castor fiber* (L.) | Riparian wetlands; semi-aquatic | North West and Central Eurasia | -; resident | Herbivorous; woody plants, herbs, grasses, roots (Krojerová-Prokešová et al. 2010, Law et al. 2014) | 13-35 | LC; > 639.000 animals; increasing |
| Lowland tapir | *Tapirus terrestris* (L.) | Freshwater; lowland rain forest and lower montane forest; largely terrestrial | South America | Big; resident | Herbivorous; leaves, fruits, seeds, stems, aquatic plants (Allin et al. 2011, Chalukian et al. 2013, Prado et al. 2013) | 150-250 | VU; population size unknown, decreasing |
| Wild water buffalo | *Bubalus arnee* (Kerr) | Freshwater; near and in large rivers in grass jungles and marshes, riparian forests; largely terrestrial | India and (South East) Asia | 3.6 EOL; resident | Herbivorous; predominately a grazer on grasses; also eats herbs; aquatic plants, leaves, agricultural crops | 800-1200 | EN; <4000 or <200 or no purebreds existent; decreasing |
| Moose | *Alces americanus* | Freshwater; boreal and mixed | North-America | 27.6-42.9 (Murray et al. 2012); resident | Herbivorous; both terrestrial and aquatic | 360-800 | LC; population size unknown; |

| | | (Clinton) | deciduous forests; largely terretrial | | | vegetation | | stable |
|---|---|---|---|---|---|---|---|---|
| Eurasian elk | *Alces alces* (L.) | Freshwater; boreal and mixed deciduous forests; largely terrestrial | Northern Europe and Russia | 15.6-52.2 (Olsson et al. 2010); resident | Herbivorous; both terrestrial and aquatic vegetation (Ohlson and Staaland 2011) | 270-770 | LC; ~1.5 million animals; increasing |
| Marsh deer | *Blastocerus dichotomus* (Illiger) | Freshwater; marshes, floodplains, savannas; largely terrestrial | Central Brazil to North Argentina | Unknown; resident | Herbivorous; aquatic plants (Tomas and Salis 2000, Allin et al. 2011) | 89-125 | VU; population size; decline |
| Swamp deer (Barasingha) | *Cervus duvaucelii* (G. Cuvier) | Freshwater; swamps, grassy plains; largely terrestrial | North and Central India, South Nepal | 14.1-20<br><br>Can walk 2-3 km straight line daily (Nandy et al. 2012); resident | Herbivorous; mostly grasses, some woody species (Wegge et al. 2006) and aquatic plants | 172-181 | VU; 3500-5100 animals; declining |

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1154 **Table 2.** Impact of large aquatic herbivores on submerged angiosperm abundance and species composition. "-" No data available. Data refer to natural
1155 vegetation, apart from the first study, where *Trichechus manatus* consumed introduced *Vallisneria* plants.

| Herbivore | Location | Herbivory rate | Effects on | | | | | References |
|---|---|---|---|---|---|---|---|---|
| | | | **Plant height** | **Shoot density and cover** | **Above-ground biomass** | **Below-ground biomass** | **Species composition** | |
| *Trichechus manatus* | Central and North America | 80% of introduced *Vallisneria americana* consumed | - | - | | - | - | (Hauxwell et al. 2004b) |
| *Dugong dugon* | Indian, Pacific oceans | 15% of primary production consumed (range 4-40 %) | - | 50-87% lower shoot density | 60-86 % removal | 51-75 % decrease | Changes in species composition | (Heinsohn et al. 1977, Preen 1995, Masini et al. 2001, Skilleter et al. 2007) |
| *Chelonia mydas* | Indian, Pacific, Atlantic oceans | 40-200% of primary production consumed | 40-70% reduction | 45-67% decrease in shoot density | 40% removal | 65 % reduction | Changes in species composition | (Moran and Bjorndal 2005, Christianen et al. 2012, 2014, Arthur et al. 2013, Burkholder et al. 2013, Kelkar et al. 2013a, b, Heithaus et al. 2014) |
| *Cygnus olor* | North | 30-60% of | 40% | 0-79% | 0-95% reduction | 0-34% | Changes in | (Conover and Kania 1994, |

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| | Region | | | | | | | References |
|---|---|---|---|---|---|---|---|---|
| | America, Europe | primary production consumed | reduction | reduction in cover<br><br>76% reduction in shoot density | | reduction | species composition<br><br>0- ~20% reduction in diversity | Allin and Husband 2003, O'Hare et al. 2007, Tatu et al. 2007, Hidding et al. 2009, 2010a, b, Gayet et al. 2011, 2012, Wood et al. 2012b, Stafford et al. 2012) |
| *Cygnus buccinator* | North America | - | - | - | No effect of spring tuber grazing on aboveground biomass in summer | 24% reduction | Changes in species composition | (LaMontagne et al. 2003) |
| *Castor canadensis* and *C. fiber* | North America, UK | - | - | - | 45-60% reduction* | - | Changes in species composition*<br><br>70% increase in species richness* | (Ray et al. 2001, Parker et al. 2007, Law et al. 2014) |
| *Alces americanus* | North America | - | - | - | 45% reduction | - | Lower species richness (72%) and diversity (95%) in grazed plots | (Qvarnemark and Sheldon 2004) |

1156    * mixed emergent and submerged species.

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1158 **Table 3.** Ecosystem functions of large aquatic herbivores.

| Ecosystem Function | Specific Function | Description | Species (plus references) |
|---|---|---|---|
| *Habitat modification* | Altering the structure of plant beds | Decreased structure (biomass, density, or canopy height of plants), grazing lawn formation | Hippopotamus, dugong, green turtle, mute swan, moose (Lock 1972, Eltringham 1974, Preen 1995, Qvarnemark and Sheldon 2004, Källander 2005, Verweij et al. 2006, O'Hare et al. 2007, Skilleter et al. 2007, Tatu et al. 2007, Hidding et al. 2009, Arthur et al. 2013) |
| | Increasing access to food source | Digging up belowground plant parts or removing tough green plant structures which benefits smaller herbivores (feeding facilitation) | Hippopotamus, whooper swans (Källander 2005, Gyimesi et al. 2012, Kanga et al. 2013) |
| | Increasing heterogeneity in the landscape | Increasing structural diversity of the habitat that benefits other species (habitat facilitation) | Beaver, hippopotamus, swan (Eltringham 1974, Wright et al. 2002, Källander 2005, Verweij et al. 2006, Waldram et al. 2008, Gyimesi et al. 2012, Kanga et al. 2013, Nummi and Holopainen 2014) |
| | Impairing habitat for other species | Decreasing habitat structural complexity that harms other species (habitat destruction) | Dugong, green turtles, swans (Marklund et al. 2002, Skilleter et al. 2007, Arthur et al. 2013) |
| | Habitat collapse | Trophic cascades and potential ecosystem collapse | Dugong, green turtles (Skilleter et al. 2007, Christianen et al. 2014) |

| | Increasing primary production | Increasing primary production of submerged plants | Green turtle, dugong, whooper swan<br><br>(Preen 1995, Nolet 2004, Moran and Bjorndal 2005, Aragones et al. 2006, Kuiper-Linley et al. 2007, Valentine et al. 2014) |
|---|---|---|---|
| *Production modification* | Decreasing primary production | Suppressing primary production | Green turtle, dugong, black swan<br><br>(Gruner et al. 2008, Hillebrand et al. 2009, Poore et al. 2012, Dos Santos et al. 2012, Kelkar et al. 2013a) |
| | Nutrient cycling enhancement | Increasing nutrient recycling by consumption, increasing compensatory growth in plants, increasing or decreasing nutrient content in plants | Green turtle, dugong<br><br>(Moran and Bjorndal 2006, Aragones et al. 2006) |
| *Nutrient cycle modification* | Nutrient export to other habitats | Transport of nutrients by commuting animals between patches or habitats or from aquatic to terrestrial habitats or vice versa | Green turtle, waterfowl, swan, hippopotamus, moose, beaver<br><br>(Wolanski and Gereta 1999, Rosell et al. 2005, Hahn et al. 2008, Bump et al. 2009, Mosepele et al. 2009, Chaichana et al. 2010, Vander Zanden et al. 2012, Wood et al. 2013, Pennisi 2014, Subaluski et al. 2015) |
| | Nutrient alleviation | Reduction of nutrient stress in the system under high nutrient loads | Green turtle<br><br>(Christianen et al. 2012) |
| *Transport* | Transport of other | Dispersal of aquatic plants and animals | Swans, moose |

| *modification* | organisms | through endo- and exozoochory | (Clausen et al. 2002, van Leeuwen et al. 2012, Jaroszewicz et al. 2013, Green and Elmberg 2014) |
|---|---|---|---|
| *Geomorphological* *modification* | Geomorphological engineering | Dam creation | Beaver (Naiman et al. 1986, Wright et al. 2002, Rosell et al. 2005) |
| | | Increasing burial, holes, wallows and trails, increasing erosion and trampling impacts, maintaining ponds during draw periods | Hippopotamus, green turtle, moose, elk, beaver, dugongs, water buffalo (Luckenbach 1986, Naiman and Rogers 1997, McCarthy et al. 1998, MacDonald 2001, Deocampo 2002, Skilleter et al. 2007, Mosepele et al. 2009, Grey and Jackson 2012, Heithaus et al. 2014, Hood and Larson 2015) |
| | Hydrological engineering | Altering water levels and flow of water through the landscape by construction work | Beaver, hippopotamus (McCarthy et al. 1998, Mosepele et al. 2009, Marshall et al. 2013, Hood and Larson 2015) |
| | Mixing of water layers | Improving oxygen availability through moving water | Hippopotamus (Wolanski and Gereta 1999, Pennisi 2014) |
| | | Re-suspending sediment and increasing of water turbidity | Dugong, green turtle, waterfowl (Skilleter et al. 2007, Christianen et al. 2014, Green and Elmberg 2014) |

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**Figure captions**

1162

**Fig. 1.** Large aquatic herbivore categories: (a) Fully aquatic herbivores (dugongs, turtles

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and manatees) that live and forage under water. They may be resident or migrant. They

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strongly impact plant beds, especially if resident. They may transport nutrients and plant

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material within their large home range. (b) Semi-aquatic species (swans) adapted to life

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on water, but that frequent both water and terrestrial habitats. They usually display

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migration behaviour. (c) Semi-aquatic central place foragers (hippopotamus, beaver,

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capybara). They are residents and have strong impacts on plants within their core areas.

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(d) Terrestrial species that frequent aquatic habitats (cervids, water buffalos, lowland

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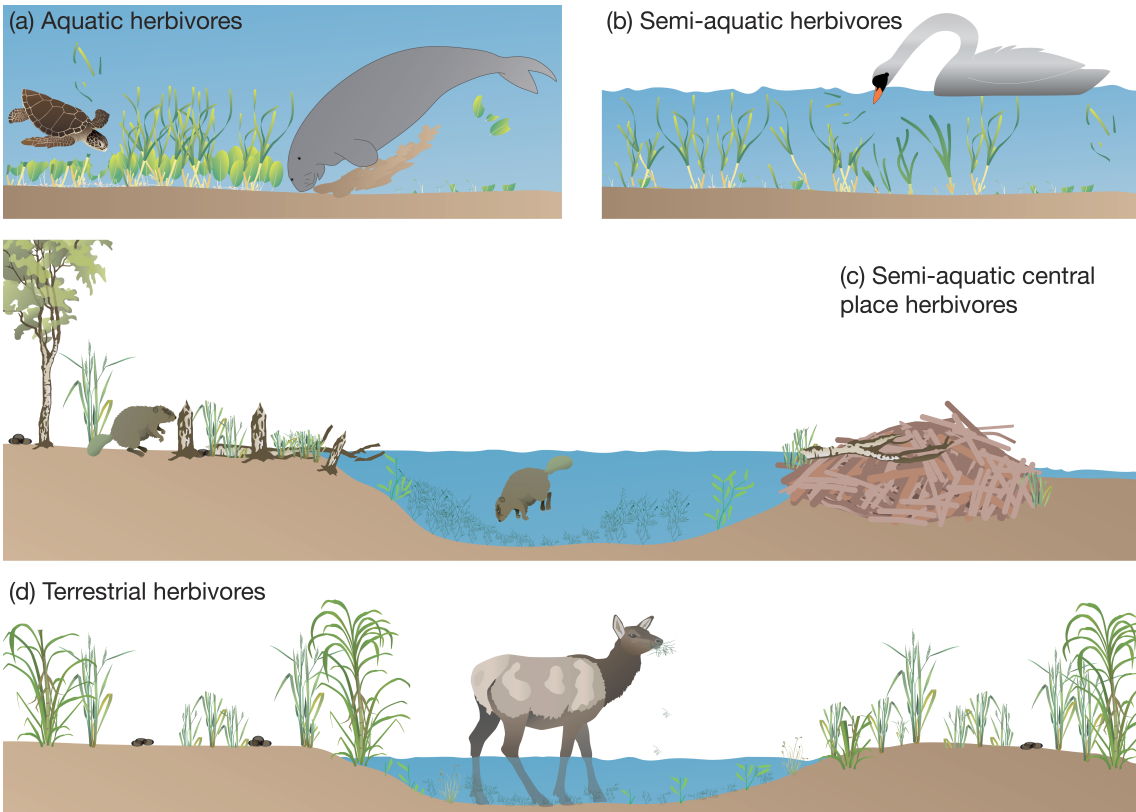tapir) in search of food supplements/complements (e.g. sodium).

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**Fig. 2.** Ecosystem processes modified by large aquatic herbivores. The figure provides a

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key to the range of impacts and functions that are mediated by the four aquatic

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herbivore functional groups (see Fig. 1). The colour codes associated with each

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functional group refer to the processes listed in the key on the left. See Table 3 for

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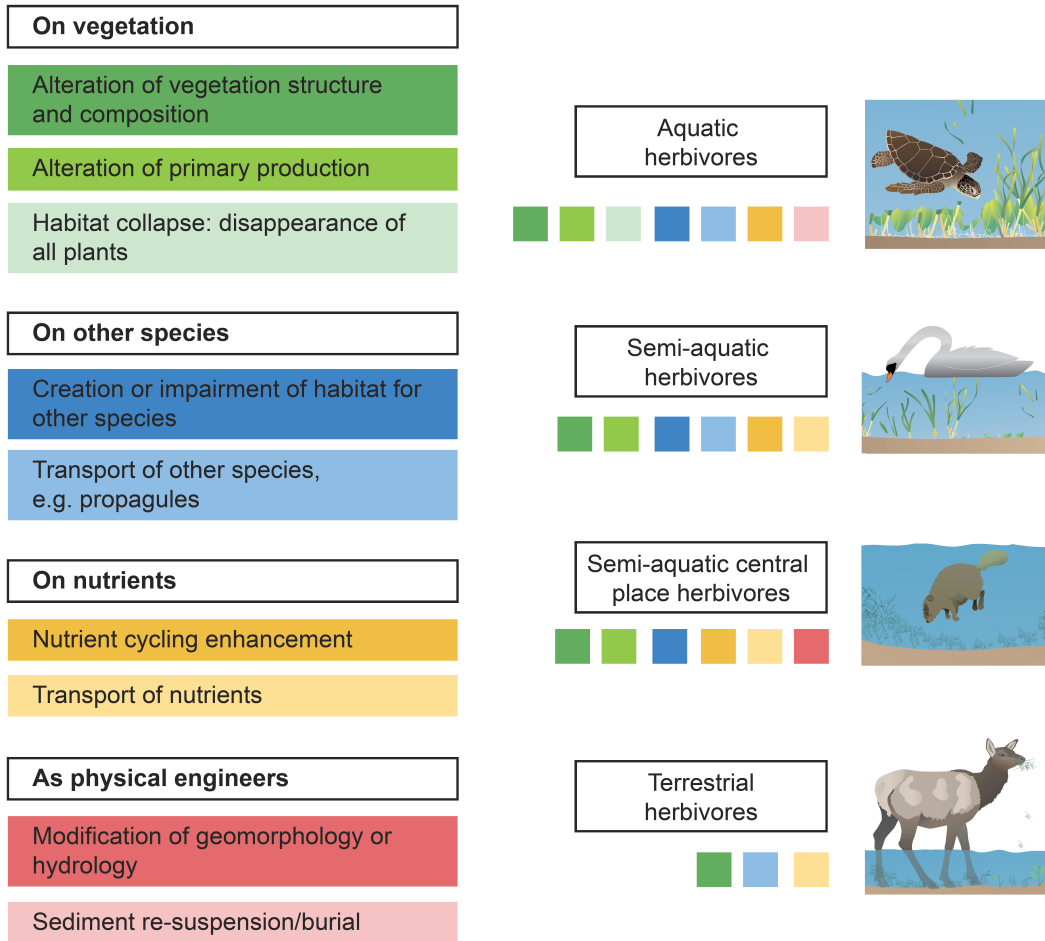species-specific details of functional roles and impacts.

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1179 Figure 1



(a) Aquatic herbivores

(b) Semi-aquatic herbivores

(c) Semi-aquatic central place herbivores

(d) Terrestrial herbivores

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## Ecosystem impacts and functions

| On vegetation |
| --- |
| Alteration of vegetation structure and composition |
| Alteration of primary production |
| Habitat collapse: disappearance of all plants |

| On other species |
| --- |
| Creation or impairment of habitat for other species |
| Transport of other species, e.g. propagules |

| On nutrients |
| --- |
| Nutrient cycling enhancement |
| Transport of nutrients |

| As physical engineers |
| --- |
| Modification of geomorphology or hydrology |
| Sediment re-suspension/burial |

Aquatic herbivores

Semi-aquatic herbivores

Semi-aquatic central place herbivores

Terrestrial herbivores

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