

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

Elisabeth S. Bakker, Jordi F. Pagès, Rohan Arthur and Teresa Alcoverro

E. S. Bakker (l.bakker@nioo.knaw.nl), Dept of Aquatic Ecology, Netherlands Inst. of Ecology (NIOO-KNAW), Droevendaalsesteeg 10, NL-6708 PB Wageningen, the Netherlands. – J. F. Pagès, R. Arthur and T. Alcoverro, Centre d'Estudis Avançats de Blanes (CEAB-CSIC), Accés a la cala Sant Francesc, 14. ES-17300 Blanes, Catalonia, Spain. JFP also at: School of Ocean Sciences, Bangor Univ., Menai Bridge, Wales, LL59 5AB, UK. RA and TA also at: Nature Conservation Foundation, 3076/5, 4th Cross, Gokulam Park, IN-570 002 Mysore, Karnataka, India.

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 herbivores are declining, some show remarkable local recoveries with dramatic consequences for the systems they inhabit. A better understanding of these functional roles will help set priorities for the effective management of large aquatic herbivores along with the plant habitats they rely on.

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 (Olf 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 large impacts on the habitats

they inhabit. Large herbivores tend to have more generalised diets, have slower ingestion and defecation rates, and are predominantly herding species that typically occupy larger home ranges than smaller herbivores (Peters 1983, Owen-Smith 1988, Belovsky 1997, Cumming and Cumming 2003). This results in a series of very specific effects on plant communities, habitat structure and critical ecosystems processes. The direct effects on plants include reductions in canopy structure and height (Asner et al. 2009), increases in trampling effects (Cumming and Cumming 2003, Schrama et al. 2013) and increases in seed dispersal rates (Clausen et al. 2002) among others. These, in turn, have a host of indirect effects on ecosystems. These include modifications to plant species competition, to the benefit of grazing-adapted species (McNaughton 1984, Knapp et al. 1999), flow-on effects to structure-dependent species (Pringle et al. 2007, Huntzinger et al. 2008), changes in the productivity of the system which directly and/or indirectly affects carbon and nutrient cycles (Knapp et al. 1999, Olofsson et al. 2004, Bakker et al. 2009), an increase in the heterogeneity of landscapes, increases in nutrient transport between ecosystems or decreases in fire regimes (Asner et al. 2009), among others. Taken together, these effects make large terrestrial herbivores key modifiers and maintainers of ecosystem dynamics and habitat complexity (Jones et al. 1994, Wright et al. 2002, Pringle 2008, Waldrum et al. 2008). Moreover, their decline since the Late Pleistocene due to hunting and other human-related causes has been linked to major shifts in the structure and functioning of the systems they were once abundant in (Johnson 2009, Corlett 2013, Croomsigt and te Beest 2014, Gill 2014). Equally, local increases in their number, either as a result of conservation initiatives or the faster decline of their predators (Estes et al. 2011), has also resulted in serious consequences for the ecosystems they depend on; population overshoots of large herbivores or concentrations within restricted areas (National Parks and reserves for instance) can result in major ecosystem alterations (Cumming et al. 1997).

Aquatic herbivores have, in contrast, received much less attention and little is known of the consequences of the functional roles they perform in freshwater and marine environments. The list of extant species is relatively small, a mere fraction of the large aquatic herbivores that were once present in aquatic ecosystems. Prehistorically, a rich assemblage of large aquatic herbivores coexisted, including sirenians and Hippopotamidae, of which both fully aquatic and semi-aquatic species have been documented (Domning 2001, Boisserie et al. 2011). Furthermore, Oligocene-to-recent proboscideans are thought to be derived from amphibious ancestors, which consumed freshwater vegetation (Liu et al. 2008). Several large-tusked dugongines were also present in ancient seas, some of which may have acted as keystone species, disrupting climax seagrass communities, thereby increasing their productivity and diversity, with presumed positive effects on sirenian diversity (Domning 2001). Unlike most seagrass systems today, which, in the absence of large herbivores, are mostly detritus based, until around 2 ± 3 MA, most primary productivity in seagrass beds was presumably consumed by herbivores (Domning 2001).

Today, even these few contemporary species of large aquatic herbivores are mostly in decline, particularly the fully

aquatic ones. Although the defaunation of aquatic animals began more recently than in terrestrial systems (McCauley et al. 2015), the effect of this reduction on aquatic large herbivores has been dramatic in the last century (Marsh and Lefebvre 1994, McCauley et al. 2015). Effective management has been successful in reversing these trends for some aquatic species such as the moose, Eurasian elk, beavers, green turtles and swans (Nolet and Rosell 1998, Halley and Rosell 2002, Chaloupka et al. 2008, Gayet et al. 2014). However, populations of many large aquatic herbivores like dugongs, manatees or hippopotamuses have been declining to critical levels in the last centuries (Jackson 2001, D'Souza et al. 2013, Pennisi 2014), and they may no longer be sufficiently abundant to effectively perform their functional role in the ecosystems they inhabit (McCauley et al. 2015).

Together with their low numbers, the aquatic environment they inhabit makes it inherently more difficult to track, monitor and gauge any potential influence these species may have on these systems; studies that have examined their ecosystem impacts have been necessarily opportunistic, making use of locally high concentrations (Hauxwell et al. 2004b, Heithaus et al. 2014). On the face of it, there is little to suggest that large aquatic herbivores are qualitatively different from their terrestrial counterparts. Most fully aquatic herbivores such as sirenids have sizes, feeding choices, metabolic requirements, social behaviour and movement patterns comparable to large terrestrial herbivores (Owen-Smith 1988). Additionally, a significant number of large terrestrial herbivores also feed on aquatic systems, including moose, swans or turtles among others. Given these similarities in traits, it is likely that their influence on aquatic habitats may be at least as large as terrestrial systems. From what is known of aquatic macrophyte-dominated communities like kelp beds, seagrass meadows and macro-algal communities, they may be highly modified by herbivory, and large herbivores are likely to play a potentially non-trivial role in contributing to these processes (Burkepile and Hay 2006, Valentine and Duffy 2006). In fact, several aquatic macrophytes show a series of adaptations to herbivory including compensatory growth, protected rhizomes or clonal growth that are typical of highly grazed systems (Valentine and Heck 1999, Nolet 2004, Valentine and Duffy 2006, Vergés et al. 2008).

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 angiosperms may be annual, clonal species of vascular plants (like *Posidonia oceanica*), can have generation times that span millennia (Arnaud-Haond et al. 2012), making them respond in similar ways to herbivory as terrestrial grasslands, also dominated by clonal primary producers (Burkepile 2013).

A final vital contrast between terrestrial and aquatic systems is that the latter are considered to be generally better connected (Tanner 2006), governed by higher flow rates of nutrients and other materials, holoplanktonic organisms and reproductive propagules (Carr et al. 2003). In particular, marine environments present few barriers to movements, enabling large herbivores to travel vast distances (often spanning entire oceans) without impediment. However, while connectivity may be high, the habitats themselves may be highly discontinuous (Goodsell 2009). Marine macrophytes (seagrasses and algae) are clearly limited by light and substrate availability, resulting in marine macrophyte habitats being very patchy in their distribution (Hemminga and Duarte 1999). For herbivores using these systems, the distance between feeding areas could be separated by hundreds or thousands of kilometres, particularly in the open sea. Freshwater macrophyte dominated habitats are also characterised by similar discontinuities. Here though, it is the water bodies themselves that can be highly disconnected. Thus, for both marine and freshwater systems, large herbivores whose forage requirements may not be satisfied at a single location, may necessarily have to undertake much larger-scale movements than their terrestrial counterparts (McCauley et al. 2015). This may make them much less predictable in space and time. The impacts of their herbivory, although locally high, may be distributed over a much wider area than terrestrial species, diluting their overall importance to ecosystem functioning. Clearly, there is no agreement on how foraging and behavioural traits interact with the peculiarities of the aquatic environment to determine the functional importance of large aquatic herbivores on their habitats and ecosystems.

Objectives

We conducted a comprehensive review of extant herbivores in aquatic systems to document the potential impacts of large aquatic herbivores on the structure and function-

ing of aquatic ecosystems. We restrict our review to aquatic angiosperm-dominated systems, because these constitute the primary habitats in which extant large herbivores feed. In particular, our objectives were to determine which large herbivorous species can be classed as consumers of submerged angiosperms. In addition, we documented the direct impacts their foraging and use could have on the habitats and ecosystems they inhabit. Further, we asked if these species have the ability to modify ecosystem structure and function and under what conditions this is likely to take place. Finally, if large aquatic herbivores are capable of ecosystem modification, we ask what implications this has for the way we manage their populations and the ecosystems they depend on.

List of large aquatic herbivores

Large aquatic herbivores: which species consume aquatic angiosperms?

There is no universal definition of large aquatic herbivores. In this review, we included herbivores with a body mass of 10 kg and greater, which represent meso- to megaherbivores according to Owen-Smith (2013). We include animals consuming submerged angiosperms in both marine and freshwater environments. In marine systems this includes dugongs, manatees and turtles. In freshwater systems it is less clear which animals can be considered large aquatic herbivores, and we included aquatic and semi-aquatic animals, as all of them consume aquatic plants. In fact, only freshwater manatees are fully aquatic and depend completely on submerged and floating macrophytes as a food source. The group of semi-aquatic animals consists of animals that are frequently found in aquatic systems. We acknowledge that this category is somewhat arbitrary. We identified three distinct vertebrate classes that could be considered large aquatic or semi-aquatic herbivores: mammals, birds and reptiles (Table 1). We did not find examples of herbivore fish greater than 10 kg that graze on submerged vascular macrophytes; therefore fish were left out of this review. The body mass of the selected aquatic herbivores ranges from about 10 kg (swans) to 3200 kg (hippopotamus). Interestingly, the list includes the largest species from a variety of guilds/families of animals. Whereas a swan of 10 kg will likely have less per capita impact on submerged plants than a manatee of 300 kg, within the guild of water birds, swans have disproportionate impacts, which is directly related to their body size (Wood et al. 2012a).

Diets

The diets of all the large aquatic herbivores included in this review are presented in Table 1. None feed exclusively on submerged angiosperms. In fact, although most of the species in Table 1 are primarily plant consumers, they generally also feed on algae, invertebrates (e.g. cnidarians) and other animal material (O'Hare et al. 2007, Cardona et al. 2009, Reisser et al. 2013). The marine dugong appears to be the most specialist feeder, with a diet of mostly seagrass (Heinsohn et al. 1977). It feeds indiscriminately on above-ground and belowground parts, just as beavers and swans. While migrating, swans apparently depend largely on tubers as their principal food source (Nolet and Drent 1998, Nolet et al. 2002, LaMontagne et al. 2003). Recently, green turtles

Table 1. List of large aquatic and semi-aquatic herbivores (> 10 kg) that consume submerged angiosperms, with indication of their body mass, home range, diet and conservation status, according to IUCN. EN = endangered, VU = vulnerable, LC = least concern. Several other large herbivore species occasionally consume submerged angiosperms, including other cervids, mainly based on availability and comprising only a minor fraction of their diets, as far as data are available. Sources: data on habitat, diet and range for mammals from MacDonald (2001), for waterbirds from Kear (2005), for turtles the Encyclopaedia of Life ($< \text{www.eol.org} >$); data supplemented with references indicated in the table. Data on conservation status, population size and population trend from IUCN: $< \text{www.iucnredlist.org} >$, accessed 26 Jan 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	<i>Chelonia mydas</i> (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	<i>Caretta caretta</i> (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	<i>Trichechus inunguis</i> (Natterer)	Freshwater; floodplain lakes, rivers and channels; fully aquatic	Amazon river drainage basin	Unknown; resident	Herbivorous; emergent, floating or submerged mostly freshwater vegetation	120–270	VU; population size and trend unknown
West-Indian manatee (subspecies: Florida and Caribbean)	<i>Trichechus manatus</i> (L.)	Marine to freshwater; shallow coastal waters, estuaries and rivers; fully aquatic	Atlantic coast from Florida and Caribbean to central Brazil	202–5156 (Castelblanco-Márquez et al. 2013); migratory	Herbivorous; seagrass, algae, cnidarians, freshwater macrophytes, mangroves	200–600	VU; $< 10\,000$ animals; declining
West African manatee	<i>Trichechus senegalensis</i> (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	<i>Dugong dugon</i> (Müller)	Marine; coastal shallows; fully aquatic	South-West Pacific Ocean and Indian Ocean	4.1–43.4 (longh 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	<i>Cygnus olor</i> (Gmelin)	Lakes, rivers, freshwater and brackish marshes; semi-aquatic	Eurasia	Mostly resident, can be migratory (< 200 km) EOL	Herbivorous (mostly); 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	<i>Cygnus buccinator</i> (Richardson)	Freshwater and brackish wetlands; semi-aquatic	North America	Migratory (> 200 km) EOL	Herbivorous (mostly); aquatic vegetation, cereals and root crops	9.5–13.5	LC; population size unknown; increasing
Whooper swan	<i>Cygnus cygnus</i> (L.)	Wetlands; semi-aquatic	Eurasia	Migratory (> 200 km, even 945 km) (Gardarsson 1991)	Omnivorous; mostly aquatic vegetation, cereal crops, mussels	7.4–14.0	LC; $> 180\,000$ animals; trend unknown

(Continued)

Table 1. (Continued)

English name	Latin name	Habitat	Geographic range	Home range (km ²) and migration	Diet selection	Body mass (kg)	Conservation status; population size; trend (IUCN)
Capybara	<i>Hydrochoerus hydrochaeris</i> (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	<i>Hippopotamus amphibius</i> (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 longh 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	<i>Hexaprotodon liberiensis</i> (Morton)	Lowland forests and swamps; semi-aquatic	West Africa	0.4–1.5 (Roth et al. 2004); resident	Herbivorous; fallen fruits, ferns, dicots and grasses	180–275	EN; < 2000–3000 animals; declining
North American beaver	<i>Castor canadensis</i> (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, 2013b)	13–32	LC; population size unknown; stable
Eurasian beaver	<i>Castor fiber</i> (L.)	Riparian wetlands; semi-aquatic	North-west and central Eurasia	Unknown; 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	<i>Tapirus terrestris</i> (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	<i>Bubalus arnee</i> (Kerr)	Freshwater; near and in large rivers in grass jungles and marshes, riparian forests; largely terrestrial	India and (southeast) Asia	3.6 EOL; resident	Herbivorous; predominantly a grazer on grasses; also eats herbs; aquatic plants, leaves, agricultural crops	800–1200	EN; < 4000 or < 200 or no purebreds existent; decreasing
Moose	<i>Alces americanus</i> (Clinton)	Freshwater; boreal and mixed deciduous forests; largely terrestrial	North America	27.6–42.9 (Murray et al. 2012); resident	Herbivorous; both terrestrial and aquatic vegetation	360–800	LC; population size unknown; stable
Eurasian elk	<i>Alces alces</i> (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	<i>Blastocerus dichotomus</i> (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 unknown; decline
Swamp deer (Barasingha)	<i>Cervus duvaucelii</i> (G. Cuvier)	Freshwater; swamps, grassy plains; largely terrestrial	North and central India, south Nepal	14.1–20.0 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

have also been observed to dig up and eat belowground tissues of seagrasses, which has been interpreted as a sign of local turtle overpopulation and food limitation (Christianen et al. 2014). The belowground parts of vascular plants are rich in carbohydrates and starch, which provides energy-rich food to aquatic herbivores (Nolet and Klaassen 2005).

Several species feed both on marine and freshwater angiosperms, including the west-Indian and west African manatee as well as the swan species (Table 1). All manatees are fully aquatic and feed mostly on submerged and floating macrophytes, occasionally feeding on emergent species. Most herbivores that consume submerged macrophytes in freshwater systems also consume terrestrial plants, with aquatic angiosperms often being a very small component of their diet. Even semi-aquatic herbivorous species such as the hippopotamus, the capybara and the beaver, which are adapted to spend much of their time half submerged, having their eyes and nostrils on the upper part of their head, feed mostly on land and only occasionally consume submerged macrophytes (Creed 2004). It should however, be noted that the diets of these species have not been very intensively investigated; it is therefore possible that aquatic macrophytes may be a larger portion of their diet than is presumed.

The other mammals that sporadically consume freshwater vascular plants are perhaps more rightly terrestrial animals that frequent swamps and marshy areas, including moose, Eurasian elk and several other deer species (Table 1). A recent review shows that their incidence of feeding on submerged angiosperms may be seriously underestimated as all better studied cervid species occasionally consume submerged vascular plants and macro-algae (Ceacero et al. 2014). This suggests that less studied species may also opportunistically consume aquatic angiosperms when these are available. In fact, some terrestrial herbivores (e.g. moose) may specifically seek out aquatic angiosperms to obtain valuable nutrients, such as sodium, the concentrations of which are higher in aquatic vascular plants than terrestrial plants (Belovsky and Jordan 1978). In addition, other minerals or proteins could drive herbivores to use aquatic angiosperms as a supplementary source to a primarily terrestrial diet, particularly in periods of high physiological demand (Ceacero et al. 2014).

Impact on aquatic vascular plant abundance and species composition

Herbivory rates compared to primary production

Current rates of herbivory in terrestrial habitats are relatively low. In a recent review, Turcotte et al. (2014) showed that, when averaged across all major lineages of vascular plants, herbivores consume 5.3% of the leaf tissue produced annually. Previous estimates of the mean annual rate of leaf herbivory across terrestrial plants ranged between 10 and 20% (Cyr and Pace 1993, Frank et al. 1998, Cebrian and Lartigue 2004, Maron and Crone 2006). By any estimate, these values are clearly lower than rates reported in aquatic systems, where herbivores have been shown to consume between 30–80% of primary production on average (Lodge 1991, Cyr and Pace 1993, Burkpile 2013, Gruner and Mooney 2013). At the highest extremes, large aquatic herbivores can consume well above 100% of annual primary production

(Table 2); it is not uncommon for turtles and swans to consume ca 100% of primary production in a given season (Rivers and Short 2007, Hidding et al. 2009, Kelkar et al. 2013a, Christianen et al. 2014). A lot of the variation in herbivory rates observed among studies is likely due to variation in herbivore densities (Wood et al. 2012a).

Effects on canopy height and above and below ground biomass

Large aquatic herbivores significantly affect plant abundance and vegetation structure (Table 2). Reduction of the above-ground standing crop varies considerably, but can be very high at some locations (see above) resulting in an almost complete removal of submerged vegetation beds. By removing aboveground plant material, aquatic herbivores alter the vegetation structure (Christianen et al. 2014) or increase the patchiness on a small spatial scale (Dos Santos et al. 2012, Christianen et al. 2013). Thus, by grazing on the upper plant parts, aquatic herbivores reduce shoot length and the mean height of the vegetation (Tatu et al. 2007). More importantly, some large aquatic herbivores appear to specifically target belowground storage. In fact, this may be a key difference between terrestrial and aquatic herbivores: while terrestrial species seldom consume belowground parts, large aquatic herbivores can, on average, reduce belowground biomass by 60% (comparing grazed versus ungrazed areas; Table 2) (Preen 1995). While mute swans do consume roots and rhizomes, this is often a minor portion of their diet that mostly consists of aboveground plant material (Bailey et al. 2008). Other species, in contrast, specifically target belowground plant parts while feeding. Dugongs, manatees, hippopotamuses, cervids, beavers and whooper and trumpeter swans, have all been identified as consumers of below ground biomass (Preen 1995, Nacken and Reise 2000, LaMontagne et al. 2003, Källander 2005, Dos Santos et al. 2012, Law et al. 2014). Indeed, dense populations of green turtles overgrazing above ground biomass have been reported (in Indonesian seagrass meadows) to exploit the below ground compartment by digging up the rhizomes (Christianen et al. 2014, Heithaus et al. 2014). Similarly, black swans (*Cygnus atratus*), Bewick swans and whooper swans (the former two at the limit of what we class as large herbivores (> 10 kg) in this review), forage on leaves, rhizomes and roots on macrophyte meadows, producing a pitted waterscape (Hidding et al. 2010a, Dos Santos et al. 2012). Dugongs (and also manatees) are specialist belowground feeders, and the feeding trails they produce have a 50–87% lower shoot density, and 51–75% reduction in belowground biomass (Table 2).

Changes in species composition

All of the examined large aquatic herbivores (for which sufficient data was available) have impacts on plant species composition, usually transforming meadows dominated by slow growing, large plants into meadows dominated by fast-growing smaller species that cope better with herbivore-induced disturbances in the above- and below-ground compartments (Preen 1995, Burkholder et al. 2013, Kelkar et al. 2013b). They can alter species composition and diversity of macrophyte beds by preferentially grazing on certain species or by unselective bulk grazing, which will mostly affect the dominant or most sensitive species, thus

Table 2. Impact of large aquatic herbivores on submerged angiosperm abundance and species composition. – = no data available. Data refer to natural vegetation, apart from the first study, where *Trichechus manatus* consumed introduced *Vallisneria* plants. * = mixed emergent and submerged species.

Herbivore	Location	Herbivory rate	Plant height	Effects on				References
				Shoot density and cover	Above-ground biomass	Below-ground biomass	Species composition	
<i>Trichechus manatus</i>	Central and North America	80% of introduced <i>Vallisneria americana</i> consumed	–	–	–	–	–	(Hauxwell et al. 2004b)
<i>Dugong dugon</i>	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)
<i>Chelonia mydas</i>	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 Bjørndal 2005, Christianen et al. 2012, 2014, Arthur et al. 2013, Burkholder et al. 2013, Kelkar et al. 2013a, 2013b, Heithaus et al. 2014)
<i>Cygnus olor</i>	North America, Europe	30–60% of primary production consumed	40% reduction	0–79% reduction in cover 76% reduction in shoot density	0–95% reduction	0–34% reduction	Changes in species composition 0–~20% reduction in diversity	(Conover and Kania 1994, Allin and Husband 2003, O'Hare et al. 2007, Tatu et al. 2007, Hidding et al. 2009, 2010a, 2010b, Gayet et al. 2011, 2012, Wood et al. 2012b, Stafford et al. 2012)
<i>Cygnus buccinator</i>	North America	–	–	–	No effect of spring tuber grazing on aboveground biomass in summer	24% reduction	Changes in species composition	(LaMontagne et al. 2003)
<i>Castor canadensis</i> and <i>C. fiber</i>	North America, UK	–	–	–	45–60% reduction*	–	Changes in species composition* 70% increase in species richness*	(Ray et al. 2001, Parker et al. 2007, Law et al. 2014)
<i>Alces americanus</i>	North America	–	–	–	45% reduction	–	Lower species richness (72%) and diversity (95%) in grazed plots	(Quarnemark and Sheldon 2004)

changing the relative abundance among species assemblages. This can promote species diversity when herbivores graze on the dominant plant species, thereby releasing subordinates from competition or creating generation niches for subordinates (Olf and Ritchie 1998). Equally though, they reduce diversity by selectively removing the subordinate species. These alternative impacts can be illustrated by the grazing of mute swans, which like to feed on *Potamogeton pectinatus*. They preferentially consumed *P. pectinatus* amongst vegetation dominated by charophytes, thus enhancing charophyte dominance (Hidding et al. 2010a), whereas in vegetation dominated by *P. pectinatus*, they strongly reduced its biomass, which favoured the subordinate species *Potamogeton pusillus* that would otherwise be outcompeted (Hidding et al. 2010b). Interestingly, herbivores can also reduce the biomass of a species, while simultaneously increasing its relative share in species composition. In a brackish lagoon, grazing impacts by waterfowl on *Zostera noltii* was dual, mainly favouring its relative abundance by reducing competing macroalgae, but conversely reducing its biomass through direct impact (Gayet et al. 2012). Similar examples can be found in marine systems. Green turtles in the Lakshadweep archipelago precipitate species shifts in meadows from the long-lived, slow-growing seagrass *Thalassia heimprichii*, on which they preferentially feed, to the faster growing small seagrass *Cymodocea rotundata*; with sustained grazing, turtles can cause meadows to shift to monospecific *C. rotundata* stands (Kelkar et al. 2013b). This is similar to some reports of dugongs that appear to be responsible for maintaining seagrass meadows with short-lived *Halophila* spp. and *Halodule* spp. species (Preen 1995). In contrast, in freshwater systems, belowground foraging on *P. pectinatus* tubers in autumn or spring by whooper swans and Bewick swans, generally enhances species diversity, as it reduces the dominance of *P. pectinatus* in the following growing season and creates regeneration niches through sediment disturbance, to which particularly annual species, such as *Najas marina* and *Zannichellia palustris*, respond favourably (Hidding et al. 2010a, 2010b). Even when no net effect on aboveground plant standing crop is measured, early season tuber foraging by trumpeter or whooper swans may result in a shift of species composition, with increased abundance of subordinate species in the aboveground vegetation (LaMontagne et al. 2003, Hidding et al. 2010b). Moose grazing can also reduce aquatic plant species richness, but the underlying mechanism remains unknown (Qvarnemark and Sheldon 2004).

Direct and indirect effects of large aquatic herbivores on ecosystem functioning

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

productivity, modifying geomorphology, altering nutrient cycling and transport of organisms.

Habitat modification for other organisms

Not unlike terrestrial grasslands, in the presence of large herbivores, many aquatic vascular plant systems are transformed to low canopy habitats, with low above ground biomass and high turnover of plant tissues, often referred to as grazing lawns (McNaughton 1984, Frank et al. 1998, Table 3). Green turtles, dugongs and swans can produce strong habitat modifications by reducing shoot densities, above and belowground biomass, changing species composition and reducing canopies of the submerged plant ecosystems they feed on (Lock 1972, Nolet 2004, Skilleter et al. 2007, Sandsten and Klaassen 2008, Arthur et al. 2013, Table 3). Hippopotamuses create grazing lawns on land, thereby enhancing larger scale spatial heterogeneity of vegetation (Lock 1972), which attracts a rich herbivore assemblage (Eltringham 1974, Verweij et al. 2006, Waldram et al. 2008, Kanga et al. 2013). However, facilitative effects will depend strongly on large herbivore density. Hippopotamuses may facilitate other herbivores by creating grazing lawns, but at very high densities, they reduce the standing crop of vegetation to a level that makes it difficult for other herbivores to find enough food, causing them to compete with each other (Eltringham 1974). The circumstances under which facilitative effects can be found may further depend on the type of ecosystem and the availability of resources for plant (re)growth.

Altogether, the removal of plant material, changes in species composition or changes to the structural complexity provided by the vegetation due to grazing by large aquatic herbivores has indirect implications for other organisms that use this spatially heterogeneous habitat for foraging, breeding, and as a refuge from predation (Coen et al. 1981, Marklund et al. 2002, Skilleter et al. 2007). Skilleter et al. (2007) found that up to 85% fewer animals were present in dugong feeding trails, and that the overall composition of benthic infaunal assemblages in the grazed areas was different from that in ungrazed areas. Similarly, Arthur et al. (2013) found that total biomass density of seagrass-associated fish recruits was about 12 times lower in seagrass meadows grazed by green turtles. At its extreme, high populations of large herbivores such as green turtles, dugongs or manatees concentrate in space, resulting in habitats that can be completely overgrazed (Preen 1995, Hauxwell et al. 2004a, Skilleter et al. 2007, Christianen et al. 2012, Table 3).

Production modification

In aquatic systems, herbivores are more often reported to suppress primary productivity rather than facilitate growth, prompting a 49–68% decrease in producer abundance on average (Gruner et al. 2008, Hillebrand et al. 2009, Poore et al. 2012, Table 3). However, large grazers have also been reported to increase primary production by up to 40% compared to ungrazed areas by removing heavily-epiphytized seagrass blades, which presumably reduces light limitation and facilitates the production of new, fast growing shoots (Moran and Bjørndal 2005, Valentine et al. 2014, Table 3). Similarly, autumn foraging by Bewick's swans (which are just below 10 kg) enhanced the production of tubers of *Potamogeton*

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)
Production modification	Increasing primary production	Increasing primary production of submerged plants	Green turtle, dugong, whooper swan (Preen 1995, Nolet 2004, Moran and Bjorndal 2005, Aragones et al. 2006, Kuiper-Linley et al. 2007, Valentine et al. 2014)
	Decreasing primary production	Suppressing primary production	Green turtle, dugong, black swan (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 (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 (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, Subalusi et al. 2015)
	Nutrient alleviation	Reduction of nutrient stress in the system under high nutrient loads	Green turtle (Christianen et al. 2012)
Transport modification	Transport of other organisms	Dispersal of aquatic plants and animals through endo- and exozoochory	Swans, moose (Clausen et al. 2002, Van Leeuwen et al. 2012, Jaroszewicz et al. 2013, Green and Elmberg 2014)
	Geomorphological engineering	Dam creation	Beaver (Naiman et al. 1986, Wright et al. 2002, Rosell et al. 2005)
Geomorphological modification		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)

pectinatus, at intermediate grazing pressure, through an over-compensation response of the remaining tubers (Nolet 2004).

Geomorphological modification

Perhaps one of the strongest effects large aquatic herbivores can exert on systems is the modification of sediment characteristics (e.g. granulometry) while foraging, that mobilizes fine particles and increases water turbidity (Skilleter et al. 2007, Christianen et al. 2014, Green and Elmerberg 2014, Table 3). Sediment mobilization by herbivores may influence primary producers by increasing rates of plant burial or by reducing transparency (Christianen et al. 2014). It may also influence other organisms living in these habitats either through direct mortality as a result of burial or reduced visibility (Skilleter et al. 2007), incidental consumption (as seen in terrestrial systems, Gomez and Gonzalez-Megias 2002), or indirectly because of the close association between soft sediment fauna and sedimentary parameters (Skilleter et al. 2007, Table 3). Large herbivores may also cause a reduction in sediment stability, not just through the loss of submerged plants, but due to the loss of features such as animal tubes (Luckenbach 1986). This is not the only effect. Trampling by large herbivores damages plants directly, resulting in bare soil, but also compacts the soil, and on land, prevents rapid infiltration of rain water, resulting in wetter habitats (Lock 1972, Schrama et al. 2013). Furthermore, in freshwater habitats, large herbivores have two principal effects on the geomorphology of their habitat: they alter the areas where they reside and, due to their foraging movements between water to land, impact the entire riparian zone (Naiman and Rogers 1997). Hippopotamuses create pathways through wetland vegetation during their nightly foraging bouts on land as they consistently use the same trails (McCarthy et al. 1998, Mosepele et al. 2009). These maintained trails can potentially become water or rivers channels, pools alongside rivers, or even lakes (Lock 1972, Naiman and Rogers 1997, McCarthy et al. 1998, Mosepele et al. 2009), that serve as a habitat for fish, invasive red-swamp crayfish and larger animals such as crocodiles (Naiman and Rogers 1997, Mosepele et al. 2009, Grey and Jackson 2012, Table 3).

Analogous patterns of strong engineering effects of large aquatic herbivores can be found in northern latitudes. Beavers strongly modify channel geomorphology and hydraulic conditions through their dam building activities (Naiman et al. 1986, Wright et al. 2002, Rosell et al. 2005, Hood and Larson 2015). The creation of ponds and stream diversions has profound long-term consequences for the entire drainage network (Naiman et al. 1986), by reducing water flow and increasing sedimentation rates (Naiman and Rogers 1997, McCarthy et al. 1998, Rosell et al. 2005). As a result, beavers can act as a whole-community facilitator for a wide variety of aquatic animals, making the habitat structurally more diverse and productive (Jones et al. 1994, Wright et al. 2002, Rosell et al. 2005, Nummi and Holopainen 2014). Moose and elk also create a dense network of foraging trails in the riparian zone when moving between water and land (Naiman and Rogers 1997).

Nutrient cycle modification

Large herbivores can modify nutrient cycling in two main ways: alteration of nutrient cycling and transport of nutri-

ents in or out of the system. Direct consumption by large herbivores can accelerate the detrital cycle by accelerating decomposition, but also modifies the nutrient cycle in plants themselves. Sustained grazing has been shown to modify the nutrient content of plants, particularly through enhanced nitrogen content, in both aquatic (Hunter 1980, Aragones et al. 2006, Moran and Bjorndal 2006) and terrestrial habitats (McNaughton 1979, Knapp et al. 1999, Bakker et al. 2009). In this way, by gardening plants, large aquatic herbivores may increase foraging quality for themselves and other herbivores in the system (Aragones et al. 2006, Moran and Bjorndal 2006). Herbivores may indirectly fertilize benthic primary producers. The shortened grazed canopy facilitates the flux of nutrients from the water column to producers, thereby decreasing nutrient limitation (Carpenter and Williams 2007). However, the most common mechanism by which large aquatic herbivores increase plant nutrient levels is by stimulating the plant's compensatory growth (Moran and Bjorndal 2006, Vergés et al. 2008, Christianen et al. 2012).

Nutrient flows in aquatic systems can be radically different from terrestrial habitats, where fertilization through urine and dung are recycled largely within the same broad area (McNaughton et al. 1997, Subaluski et al. 2015). In contrast, in freshwater and marine systems, water motion and currents on the one hand, and the larger home ranges of herbivores on the other hand, make it unlikely that herbivores could fertilize the same benthic primary producers they have consumed directly via their excretions (Burkpile 2013). Many marine animals have on average significantly larger adult home ranges (McCauley et al. 2015) and disperse greater distances as juveniles than their terrestrial counterparts (Kinlan and Gaines 2003). In addition, larger animals usually display larger home ranges (McCauley et al. 2015). This makes large aquatic fauna potentially important mobile links, capable of being long-distance vectors of nutrients between habitats and ecosystems (Lundberg and Moberg 2003, Heck et al. 2008, Green and Elmerberg 2014). Most large aquatic herbivores may have the potential to transfer nutrients within and between the habitats within their home range, and those that use both terrestrial and aquatic habitats, may even be cross-ecosystem links. This has been shown for the moose (Belovsky and Jordan 1978, Bump et al. 2009), green turtles (Vander Zanden et al. 2012), beavers (Rosell et al. 2005), hippopotamuses (Subaluski et al. 2015) and swans (Hahn et al. 2008, Wood et al. 2013). By eating in one system and defecating and excreting in another, these species may serve as powerful links and be considered ecosystem engineers. Thanks to this capacity of exporting nutrients out of the system, large aquatic herbivores may also function as alleviators of anthropogenic nutrient inputs to seagrass or macrophyte meadows. This has been confirmed for seagrass meadows grazed by green turtles (Christianen et al. 2012). Grazing increases seagrass production, thereby increasing the food availability for green turtles and the amount of seagrass biomass and nutrients exported by the turtles out of the system. According to Christianen et al. (2012), this export by large aquatic herbivores is probably the most important controlling factor for seagrass under grazing and high nutrient loads. When nutrients increase, grazing can potentially improve conditions for seagrass.

Transport of organisms

Apart from transporting nutrients, large herbivorous fauna can transport propagules of aquatic plants and animals when moving between wetlands or aquatic plant beds. This dispersal ability has been mainly examined in waterbirds (Green and Elmberg 2014), but may be extended to other large aquatic herbivores. Seeds of aquatic plants and resting stages of numerous invertebrate species are transported both by endo- and exozoochorous means (Clausen et al. 2002, van Leeuwen et al. 2012). Internal transport is the most common form of dispersal (Brochet et al. 2010). The maximum distance of endozoochorous dispersal depends strongly on the body size of the vector: larger waterbirds fly faster and have longer gut retention times, which allows for a longer travel distance before the last propagule is excreted (Clausen et al. 2002, van Leeuwen et al. 2012). Furthermore, the viability of seeds after gut passage is higher in larger birds (Van Leeuwen et al. 2012), even though seeds excreted after shorter retention times are generally more viable (Charalambidou et al. 2003). Whereas large waterbirds consume relatively fewer seeds and more green plant material than smaller birds (Wood et al. 2012a), they inadvertently consume large amounts of macro-invertebrates and seeds while feeding on green plant material (O'Hare et al. 2007). Altogether, this makes larger species, such as swans, suitable vectors for long distance travel of propagules. While most propagules will be lost as they may be digested or excreted in unsuitable habitats, rare, successful long distance dispersal events can be of high significance for instance in promoting species range expansions or in maintaining gene flow between distant populations (Figuerola et al. 2005, Brochet et al. 2009, Sanchez et al. 2012). Whereas for other groups of large aquatic herbivores little information on dispersal is available, similar processes may occur in marine environments, where large herbivores transport seeds of seagrasses (Sumoski and Orth 2012, McMahon et al. 2014) whereas in freshwater habitats mammalian herbivores can also carry seeds (Jaroszewicz et al. 2013). Their potential as dispersal vectors of submerged plants will depend strongly on the digestion physiology and movement ecology of the species.

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)

Their diets consist mostly of submerged vascular plants and they live most of the time fully submerged.

(b) Semi-aquatic species adapted to life on the water, but frequent both water and land, and can be both resident and migratory (swans)

They consume a lot of submerged vascular plants and can sustain themselves for prolonged periods on submerged vascular plants but can also survive on terrestrial vegetation.

(c) Semi-aquatic species that live in the water and forage mainly on land according to a central-place foraging pattern; they are residents (hippopotamuses, beavers, capybara)

They are adapted to spend extended periods almost submerged, leaving only their ears, eyes and nose above the water surface. They retreat to the water when scared. While they do consume submerged angiosperms, this appears to generally be a minor part of their diet, although most species are data deficient when it comes to foraging on submerged vascular plants.

(d) Terrestrial species that frequent aquatic habitats; resident species with relatively large home ranges (cervids, water buffalo, lowland tapir)

They are adapted to frequent wetlands: interdigital membranes, extended hooves or relatively long limbs, their nose may function as a snorkel as in case of the tapir. They consume submerged vascular plants; this is a minor but seemingly important part of their diet, although also most of these species are data deficient when it comes to quantification of foraging on submerged angiosperms.

The ecosystem functions of large aquatic herbivores differ between these four groups (Fig. 2). The strongest impacts on submerged plant production, both positive and negative, are found for the fully submerged herbivore species that live most closely associated with submerged angiosperms (Fig. 1a). Both the fully submerged grazers and the swans (Fig. 1b) can reduce plant standing crop considerably, which is also due to their habit of foraging on belowground plant parts. The removal or reduction of plant beds has flow-on effects on other fauna, mostly reducing their abundance. The central-place foragers (Fig. 1c) that forage mostly on land, typically create gradients of grazing pressure, most intense in or close to the water and less intense further away on land (Lock 1972, Fryxell 1999, Kanga et al. 2013). As a result they create strong spatial heterogeneity in vegetation structure (Fig. 1c), which has positive effects on other flora and fauna. It should be noted that no data are available for capybara. Unsurprisingly, both beavers and hippopotamuses

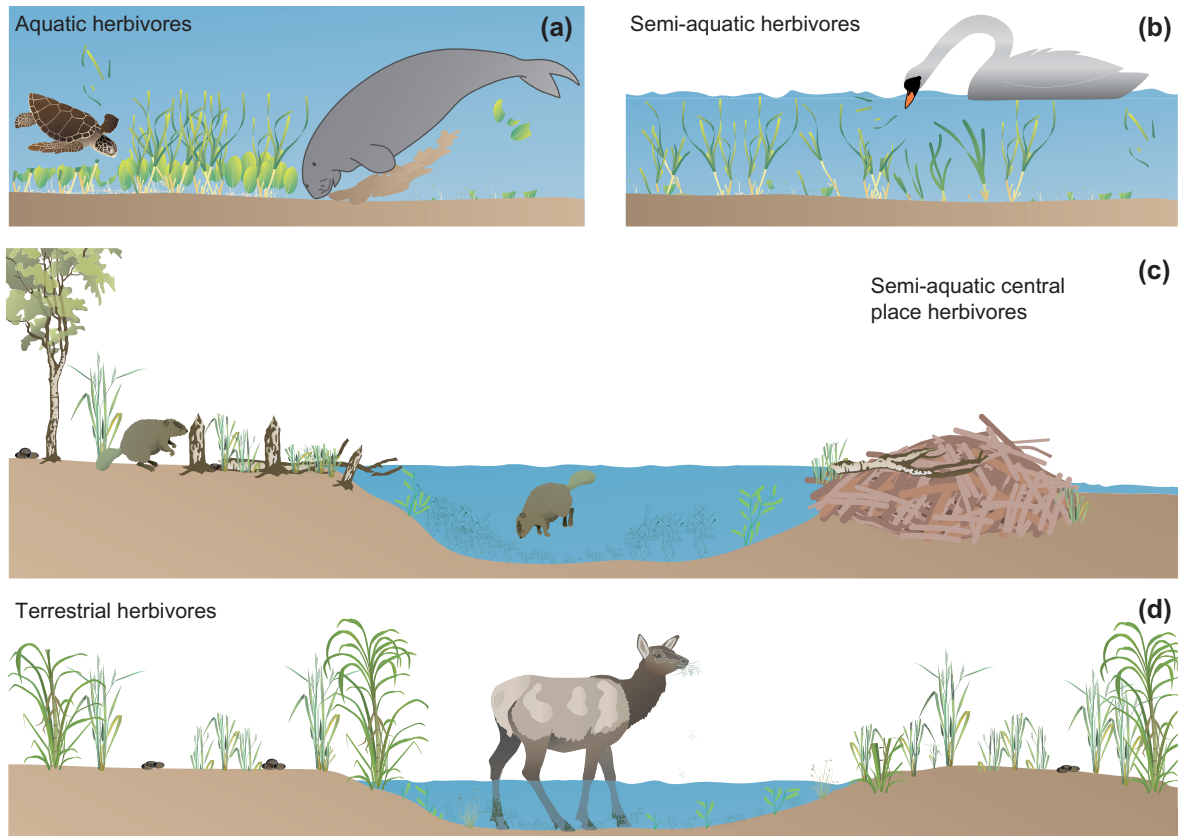


Figure 1. Large aquatic herbivore categories: (a) fully aquatic herbivores (dugongs, turtles and manatees) that live and forage under water. They may be resident or migrant. They strongly impact plant beds, especially if resident. They may transport nutrients and plant material within their large home range. (b) semi-aquatic species (swans) adapted to life on water, but that frequent both water and terrestrial habitats. They usually display migration behaviour. (c) semi-aquatic central place foragers (hippopotamus, beaver, capybara). They are residents and have strong impacts on plants within their core areas. (d) terrestrial species that frequent aquatic habitats (cervids, water buffalos, lowland tapir) in search of food supplements/complements (e.g. sodium).

(category c) also have the strongest geomorphological and hydrological engineering effects.

The transport of nutrients and dispersal of submerged angiosperm propagules is closely linked to the travelling distance of the animals as well as their targeted movement between habitats or habitat patches (Bauer and Hoyer 2014, Green and Elmer 2014). Semi-aquatic species have strong roles linking aquatic and terrestrial habitats and import nutrients mainly into the water (category b and c) or on land (category d). Long distance migrants (category a and b) can be of particular importance in propagule dispersal between unconnected habitat patches; large terrestrial herbivores moving between aquatic habitats in their large home ranges (category d) likely also perform this function, but data on their role as dispersal agents of submerged vascular plants are lacking.

Trophic downgrading and ecosystem collapse

Whereas large aquatic herbivores have a number of important ecosystem effects, their actual impact depends strongly on their density (Wood et al. 2012a, Kelkar et al. 2013b). Where the largest herbivores (> 1000 kg), such as elephants and rhinoceroses, are considered to be predation free due to their size (Owen-Smith 1988), at least as adults, most aquatic large herbivores are too small (< 500 kg, Table 1)

to be completely predation free under natural conditions. Large roving predators may have direct impact on the survival of large aquatic herbivores, but even more so through their indirect effect of inducing a landscape of fear where foraging movements of herbivores are restricted to less risky habitats (Burkholder et al. 2013). Of the large aquatic herbivores only the hippopotamus is a true megaherbivore (> 1000 kg), which may be considered predation free under natural conditions. However, other species of large aquatic herbivores like dugongs or green turtles are seldom preyed in today's waters due to the lack of predators. Indeed, megafauna is generally declining, and this decline is not random. The largest species typically experience the strongest decline (Dirzo et al. 2014, Ripple et al. 2015), but also, predators decline faster than herbivores (Estes et al. 2011, McCauley et al. 2015). This has led to the phenomenon of trophic downgrading, where the relative abundance of herbivores increases, due to the faster decline of predators and a subsequent release from predation (Estes et al. 2011). A similar effect is observed when herbivores are protected from hunting or other forms of human disturbance and there are no natural predators to compensate for the release of hunting pressure. In these cases, herbivores can become locally very numerous, and exert very strong grazing pressure on the submerged vegetation, such as in marine reserves, where locally

Ecosystem impacts and functions

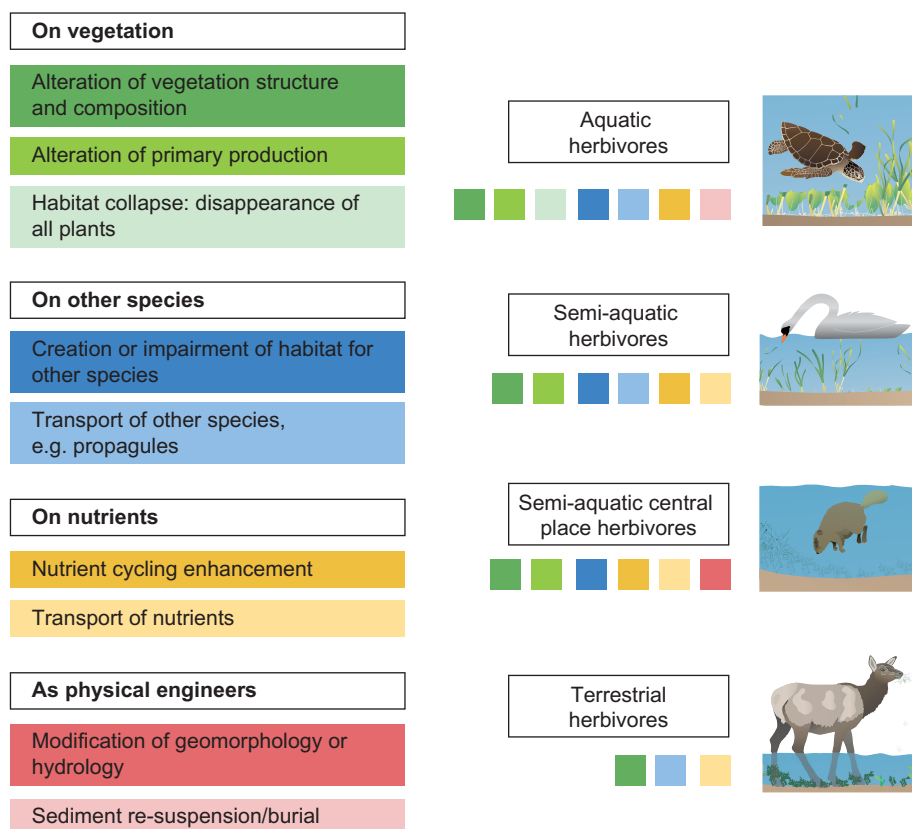


Figure 2. Ecosystem processes modified by large aquatic herbivores. The figure provides a key to the range of impacts and functions that are mediated by the four aquatic herbivore functional groups (Fig. 1). The colour codes associated with each functional group refer to the processes listed in the key on the left. See Table 3 for species-specific details of functional roles and impacts.

large populations of green turtles can seriously threaten ecosystem stability by removing seagrass beds, which could lead to ecosystem collapse (Christianen et al. 2014, Heithaus et al. 2014). This is because, unlike most terrestrial mega-herbivores, many aquatic species (both marine and freshwater) consume not merely the above-ground biomass but sometimes target the below-ground storage of the primary producers that structure aquatic plant communities. It is well established that these belowground reserves are critical to ensure the buffer capacity of these ecosystems, and by targeting these reserves, large aquatic herbivores may contribute to considerable ecosystem instability in the systems they inhabit. Similarly, very high densities of hippopotamus result in hypertrophic pools and rivers (Subalusi et al. 2015), particularly at periods of low water levels, which can result in algal blooms, anoxia and fish kills (Pennisi 2014). In some instances, ecosystems modified by large aquatic herbivores go through a pattern of rotational collapse and recovery, spurred by large-scale movements of herbivore populations (Arthur et al. 2013, Heithaus et al. 2014). In other cases, systems may even collapse beyond recovery thresholds. A confinement of large aquatic herbivores to reserves, without the possibility to follow their natural migration patterns, and a lack of natural predation in combination are the root cause of recorded detrimental effects of large herbivore grazing and the collapse of entire plant beds. Other species have recovered successfully from population declines, such as the mute

swan, which has expanded its range through introductions in new habitats, particularly the USA. Here, the mute swan is an exotic species and rapidly increasing in population size, with concomitant effects on submerged plant beds (Conover and Kania 1994, Tatu et al. 2007, Gayet et al. 2014).

Conserving large aquatic herbivores and the ecosystems they rely on

Taken together, this evaluation raises important questions for the management of large marine and freshwater herbivores. Many of these species are globally threatened and conserving their populations is a critical concern. For large herbivores, their size itself becomes a clear threat as has already been observed in terrestrial large herbivores (Dirzo et al. 2014). Large animals are more difficult to conserve because they have higher food requirements, larger home ranges, longer life spans and lower reproductive success among other size-specific traits that limit their reproduction and impede conservation efforts (Owen-Smith 1988). Large aquatic herbivores have to deal with additional issues. They have, on average, larger home ranges (Peters 1983, McCauley et al. 2015) that makes conservation a significant challenge as species move freely between different conservation jurisdictions (Bauer and Hoyer 2014). Unlike their terrestrial counterparts, large aquatic herbivores cannot be protected with fences within restricted areas where protection can be maximized; most marine protected areas are not large enough to protect