Review

Heike K. Lotze*, Inka Milewski, Julia Fast, Lauren Kay and Boris Worm

Ecosystem-based management of seaweed harvesting

https://doi.org/10.1515/bot-2019-0027
Received 29 April, 2019; accepted 30 July, 2019; online first 23 August, 2019

Abstract: Harvesting wild seaweeds has a long history and is still relevant today, even though aquaculture now supplies >96% of global seaweed production. Current wild harvests mostly target canopy-forming kelp, rockweed and red macroalgae that provide important ecosystem roles, including primary production, carbon storage, nutrient cycling, habitat provision, biodiversity and fisheries support. Harvest methods range from selective hand-cutting to bottom trawling. Resulting ecosystem impacts depend on extraction method and scale, ranging from changes in primary production to habitat disruption, fragmentation, food-web alterations and bycatch of non-target species. Current management often aims for sustainable harvesting in a single-species context, although some agencies acknowledge the wider ecosystem structure, functions and services seaweeds provide. We outline potential ecosystem-based management approaches that would help sustain productive and diverse seaweed-based ecosystems. These include maintaining high canopy biomass, recovery potential, habitat structure and connectivity, limiting bycatch and discards, while incorporating seasonal closures and harvest-exclusion zones into spatial management plans. Other sustainability considerations concern monitoring, enforcement and certification standards, a shift to aquaculture, and addressing cumulative human impacts, invasive species and climate change. Our review provides a concise overview on how to define and operationalize ecosystem-based management of seaweed harvesting that can inform ongoing management and conservation efforts.

Keywords: canopy structure; community composition; ecosystem effects; functions and services; habitat impacts.

***Corresponding author: Heike K. Lotze,** Department of Biology, Dalhousie University, 1355 Oxford Street, PO BOX 15000, Halifax, NS, B3H 4R2, Canada, e-mail: hlotze@dal.ca. https://orcid.org/0000-0001-6258-1304
Inka Milewski, Julia Fast, Lauren Kay and Boris Worm: Department of Biology, Dalhousie University, 1355 Oxford Street, PO BOX 15000, Halifax, NS, B3H 4R2, Canada

Introduction

Over the past decades, there has been increasing recognition worldwide of the importance of moving towards an ecosystem-based management (EBM) approach for marine fisheries (Pikitch et al. 2004, Arkema et al. 2006, UNEP 2011, Long et al. 2015). The overall goal of EBM is to sustain healthy, productive and diverse marine ecosystems, which can support fisheries and human well-being over the long term. Generally, EBM should avoid ecosystem degradation and irreversible changes to species communities and ecosystem processes. Key objectives include the maintenance of ecosystem characteristics, such as biodiversity and trophic interactions, the protection of habitats and threatened species, and the reduction of bycatch, destructive and unselective fishing. This is particularly important in the face of current and future climate change (Worm and Lotze 2016). Despite general agreement on overall direction, there is a variety of definitions of EBM used in policy documents and management plans around the world and implementation has been slow so far (Pitcher et al. 2009, Long et al. 2015).

Developing an EBM approach requires basic knowledge of underlying ecosystem processes to understand the likely consequences of exploitation or other human activities. The ecosystem effects of fishing have been widely studied for marine fish and invertebrates, and include the effects of habitat destruction, bycatch, overexploitation and food-web alterations on biodiversity and ecosystem stability (e.g. Jennings and Kaiser 1998, Dayton et al. 2002, Eddy et al. 2017). Studies on the ecosystem consequences of seaweed harvesting are less prominent (Lorentsen et al. 2010, Stagnol et al. 2013, Krumhansl et al. 2017, Pérez-Matus et al. 2017) but highlight the importance of kelp forests, rockweed beds and other seaweed stands in providing critical ecosystem structure, functions and services. As foundation species and ecosystem engineers, many seaweed species create complex three-dimensional canopies that provide essential habitat and food for a wide range of associated fauna and flora, play critical roles in coastal carbon and nutrient cycling, primary production, detritus formation and wave-buffering of shorelines (Schmidt et al. 2011, Krumhansl and Scheibling 2012, Arkema et al. 2013, Hyndes et al. 2014, Kay et al. 2016, Bustamante et al. 2017). Direct harvesting often alters the structure and functions of these vegetated habitats and the services they provide, depending on the methods used, species harvested, and the scale, duration and frequency of the harvest (Waage-Nielsen et al. 2003, Seeley and Schlesinger 2012, Stagnol et al. 2016, Steen et al. 2016).

In the following, we first provide a brief overview on past and current trends in seaweed harvesting, including trends in global production, species harvested, countries involved, harvest methods, regulatory and management approaches. We then review the ecosystem effects of seaweed harvesting, from which we derive principles for ecosystem-based management of this species group. We conclude with considerations for the sustainability of seaweed harvesting today and into the future, particularly with respect to climate change.

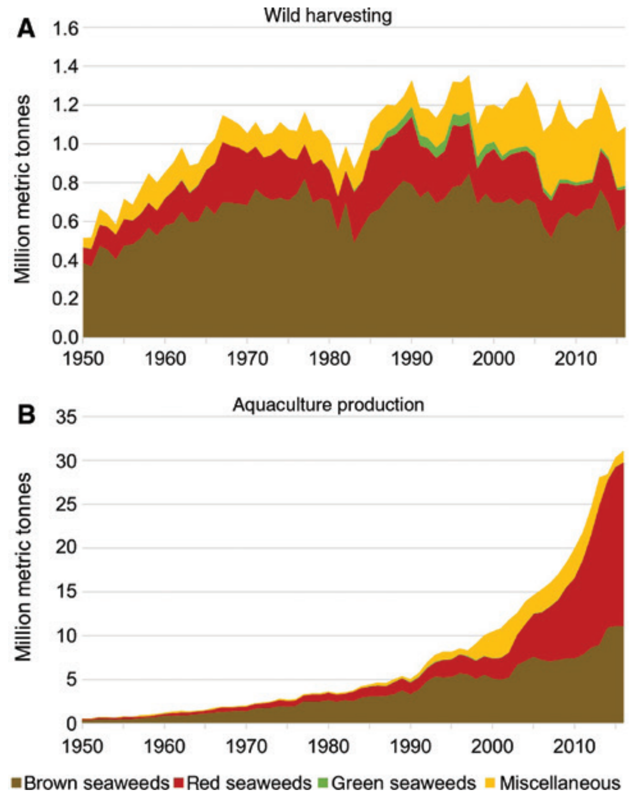

Figure 1: Shown is the relatively stable trend of wild harvest levels compared to the rapid rise in aquaculture production over past decades.
Overview of global trends in (A) wild seaweed harvesting (capture production) and (B) aquaculture production from 1950 to 2016 (FAO 2018b). Note the difference in y-axis scales.

Trends in seaweed harvesting

Throughout history, coastal people have used marine macroalgae (seaweeds) and seagrasses for a variety of purposes, including food, feed, fertilizer, medicine, fibers and insulation (Delaney et al. 2016, Anis et al. 2017). Harvesters either gathered washed-up material along shorelines or cut/raked those accessible in shallow waters (Mac Monagail et al. 2017). Over the 20th century, the direct use of seagrasses has mostly ceased, but seaweed production has continued to rise, mostly due to the widespread adoption of aquaculture (Figure 1). Also, the use of seaweeds is now dominated by industrial applications, such as the production of carrageenan, alginates, agar, and specialty fertilizer, feed, iodine, and substances for the cosmetic, nutrition and pharmaceutical industry (Buschmann et al. 2017). Another potential future use of both wild and cultivated seaweeds is bioenergy production (Fernand et al. 2016). Although harvesting of wild seaweeds continues in many coastal societies (Mac Monagail et al. 2017), wild seaweed stands are increasingly recognized for their value in providing essential ecosystem structure, functions and services (Schmidt et al. 2011, Seeley and Schlesinger 2012, Arkema et al. 2013, Smale et al. 2013).

In the early 1950s, wild harvesting and aquaculture of seaweeds contributed similar amounts to global production (~0.5 million mt each), yet their trajectories have drastically diverged since then (Figure 1). Wild (capture) harvesting surpassed >1 million mt in the late 1960s and has fluctuated around this level until today, while aquaculture production exponentially increased to >31 million mt in 2016 (FAO 2018a,b), contributing 96.5% of total seaweed production today. Both wild and aquaculture production have been dominated by brown seaweeds, although aquaculture of red seaweeds has increased most rapidly over time (Figure 1, Table 1).

The wild harvest of brown seaweeds is currently dominated by Chile and Norway, red seaweeds by Chile and Indonesia, and green seaweeds by India (Figure 2). More than 40 countries have reported wild harvest of ~30 species or groups to the Food and Agriculture Organization (FAO 2018b), but this includes large bulk categories of unspecified seaweeds (Table 1) and likely underestimates the total number of species (Zemke-White and Ohno 1999). For example, harvesting of tropical seaweeds includes hundreds of red, green and brown macroalgal species and provides a significant food source and income for small coastal

Table 1: Overview of wild harvest (mean annual capture production) of seaweeds and unidentified aquatic plants by major species and groups in the earliest and most recent period reported by FAO (2018b).

Common name	Scientific name	Order	1950–1966[a]		2000–2016[a]	
			mt yr^{-1}	%	mt yr^{-1}	%
Brown seaweeds total			**529,117**	**100.00**	**653,155**	**100.00**
North Atlantic rockweed	*Ascophyllum nodosum* (Linnaeus) Le Jolis	Fucales	1978	0.37	60,712	9.30
Bull kelp	*Durvillaea antarctica* (Chamisso) Hariot	Fucales	0	0.00	4726	0.72
Tangle	*Laminaria digitata* (Hudson) J.V. Lamouroux	Laminariales	0	0.00	35723	5.47
North European kelp	*Laminaria hyperborea* (Gunnerus) Foslie	Laminariales	0	0.00	8674	1.33
Japanese kelp	*Laminaria japonica* Areschoug	Laminariales	178,661	33.77	77,806	11.91
Chilean kelp	*Lessonia nigrescens* Bory	Laminariales	0	0.00	172,907	26.47
Kelp - Chile	*Lessonia trabeculata* Villouta & Santelices	Laminariales	0	0.00	45,211	6.92
Giant kelps nei	*Macrocystis* spp. (Linnaeus) C. Agardh	Laminariales	113,638	21.48	34,410	5.27
Wakame	*Undaria pinnatifida* (Harvey) Suringar	Laminariales	0	0.00	4145	0.63
Brown seaweeds general[b]			234,848	44.38	208,834	31.97
Red seaweeds total			**142,265**	**100.00**	**200,870**	**100.00**
Carragheen (Irish) moss	*Chondrus crispus* Stackhouse	Gigartinales	1422	1.00	4	0.00
Gigartina seaweeds nei	*Gigartinaceae* Kützing	Gigartinales	0	0.00	3993	1.99
Skottsberg's gigartina	*Gigartina skottsbergii* Setchell & N.L. Gardner	Gigartinales	0	0.00	27,948	13.91
Leister	*Sarcothalia crispata* (Bory) Leister	Gigartinales	0	0.00	23,549	11.72
	Chondracanthus chamissoi (C. Agardh) Kützing	Gigartinales	0	0.00	3727	1.86
	Mazzaella laminarioides (Bory) Fredericq	Gigartinales	0	0.00	3518	1.75
Gelidium seaweeds	*Gelidium* spp. J.V. Lamouroux	Gelidiales	115	0.08	1647	0.82
Gracilaria seaweeds	*Gracilaria* spp. Greville	Gracilariales	9127	6.42	51,863	25.82
Red seaweeds general[b]			131,601	92.50	84,612	42.13
Green seaweeds total			**1459**	**100.00**	**21,222**	**100.00**
Fragile codium	*Codium fragile* (Suringar) Hariot	Bryopsidales	0	0.00	875	4.12
Green laver	*Monostroma nitidum* Wittrock	Ulotrichales	0	0.00	346	1.63
Green seaweeds general[b]			1459	100.00	20,001	93.25
Miscellaneous total			**108,750**	**100.00**	**295,229**	**100.00**
Aquatic plants nei[c]			108,750	100.00	291,395	98.70
Seaweeds nei[b]			0	0.00	3833	1.29

[a]Shown is the mean annual harvest in metric tonnes (mt) and the percent (%) for each species within its group; only species with >1000 mt yr^{-1} or 1% within their group are shown.
[b]Includes other species.
[c]nei, Not identified.

communities, particularly in the Indo-Pacific region (Trono 1999, Zemke-White and Ohno 1999, Chennubhotla et al. 2015). This points to reporting issues that impair a proper global assessment of species-specific harvests and their potential ecosystem consequences (Nayar and Bott 2014). Importantly, almost all identified brown seaweeds represent canopy-forming rockweeds (Fucales) or kelps (Laminariales), and most red seaweeds belong to the Gigartinales, Gracilariales and Gelidiales (Table 1) which also form three-dimensional habitats. Most green seaweeds and miscellaneous aquatic plants were not identified by species, and only few, such as *Codium fragile* (Suringar) Hariot, form three-dimensional canopies.

Current harvesting methods and regulations

The current wild seaweed harvesting methods, regulations and management regimes vary widely across species and countries (for detail on country- and species-specific regulations see Supplementary Text S1). For example, kelp harvesters use hand-held cutting tools in Chile and Japan, whereas bottom trawls or dredges are employed in Norway and France (Frangoudes 2011, Fujita 2011). Beach-cast harvesting of kelp is still an important harvesting method in several countries, such as South Africa, Australia, and New Zealand (Zemke-White et al. 2005, Anderson et al.

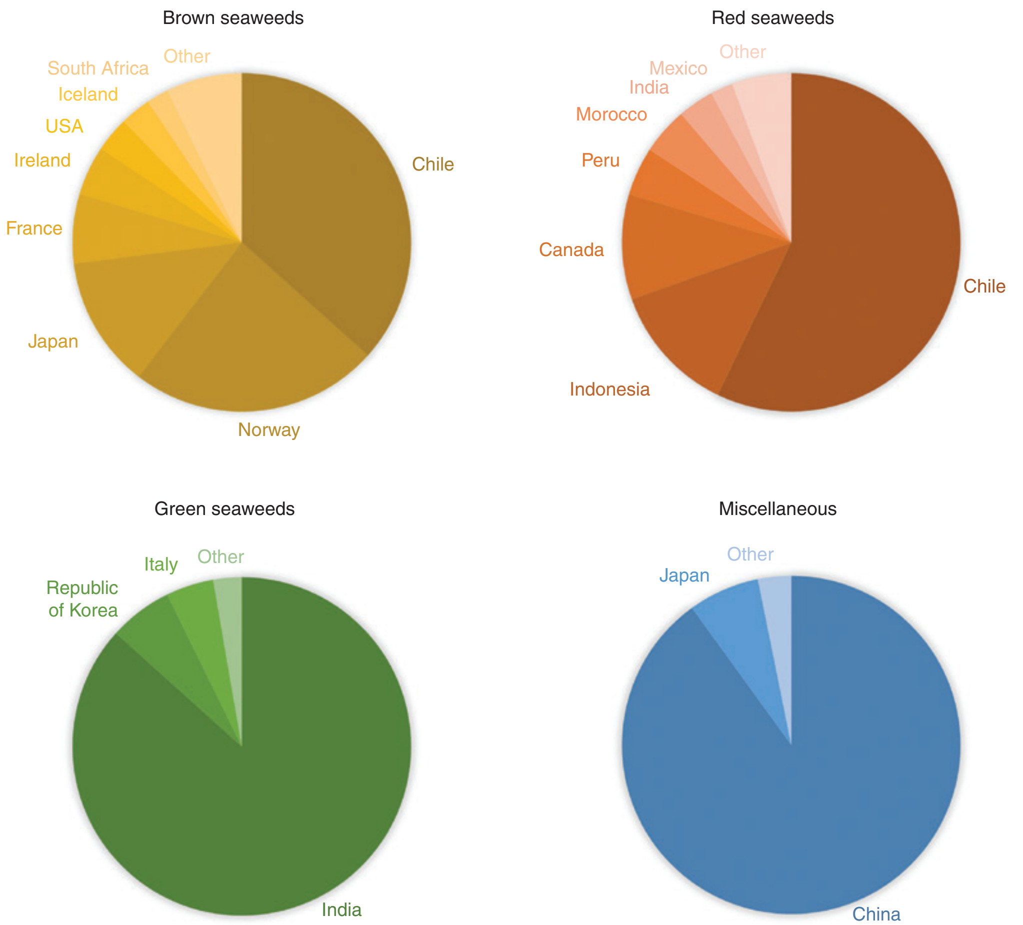

Figure 2: Overview of main countries harvesting seaweeds from the wild.
Shown are all countries contributing >2% of annual harvests within each group from 2000 to 2016 (FAO 2018b).

2007, PIRSA 2014). Rockweed is harvested by hand-raking or cutting in Ireland, France and Canada and by mechanical harvesters in Iceland, Scotland, Norway, France, and the US (Meland and Rebours 2012, Seeley and Schlesinger 2012, Angus 2017, Mac Monagail et al. 2017). Red seaweeds are generally cut by hand in Chile and Indonesia (Buschmann et al. 2008, Chennubhotla et al. 2013) and raked from boats in Canada (DFO 2013). Green seaweeds are cut by hand in India (Subba Rao and Mantri 2006). Overall, harvests range from small-scale traditional to industrial-scale operations.

Generally, information on management and regulations in different countries is difficult to find, and existing management plans often lack detail. Several countries employ some form of single-species management (see details in Supplementary Text S1), which includes licenses or permits to regulate access and effort, limits on harvest amounts (quotas), gear restrictions, and regulations on specific cutting methods (frond size, cutting height, spacing between fronds). Some countries also have temporal restrictions, such as seasonal closures or fallow periods, and spatial restrictions such as area management, no-take zones or closed areas. However, most countries only employ few of these management strategies and regulations vary widely among jurisdictions; for example, the minimum cutting height for rockweed is 12.7 cm in Atlantic Canada but 40.6 cm in neighboring Maine (Seeley and Schlesinger 2012). Generally, the management focus is on the regeneration of the seaweed resource itself, with no or limited consideration of other species that are associated with the target species and may therefore be affected by bycatch or habitat loss and alterations. Few countries prohibit seaweed harvesting in areas important to other species, such as in seabird protection areas in Norway (Vea and Ask 2011).

The management of wild seaweed harvesting is generally in the hands of state or provincial governments, but some countries have co-management schemes where harvesting rights are granted to artisanal fishers or fisheries co-operatives (e.g. Chile and Japan, Fujita 2011, Vásquez et al. 2012, Vega et al. 2014, Supplementary Text S1). Also, some countries perform regular monitoring and assessment, which can be industry-led or independent, but again mostly focusing on the impacts of harvesting on the regeneration of the resource itself (e.g. Norway and Japan, Fujita 2011, Meland and Rebours 2012). However, basic estimates of species-specific standing stock, growth rates, reproduction, regeneration, and associated species are often lacking (Werner and Kraan 2004, Springer et al. 2010, Araújo et al. 2016, Filbee-Dexter et al. 2019). This is similar to many traditional and emerging fisheries where basic population and ecosystem knowledge is often lacking (Anderson et al. 2011), although the assessment and management of individual high-value species has improved over past decades (Worm et al. 2009).

Ecosystem structure, functions and services

Canopy-forming seaweeds, including kelps, rockweeds and many red seaweeds are widely acknowledged as foundation species that form important three-dimensional structure in marine coastal environments which contribute important functions and services (Table 2). First, seaweed stands contribute to energy capture and transfer, including primary, secondary and detritus production as well as carbon storage and nutrient cycling (Fredriksen 2003, Krumhansl and Scheibling 2012, Hyndes et al. 2014). Through their direct provision of food and structural habitat, seaweed forests also support higher levels of biodiversity, fuel food webs and provide biological links between marine ecosystems (Vetter and Dayton 1999, Gaylord et al. 2007, Hyndes et al. 2014, Bustamante et al. 2017, Teagle et al. 2017, Holden et al. 2018). Seaweed beds not only provide habitat for year-round residents but also for species that use the habitat as foraging grounds such as birds and otters, as breeding and nursery areas particularly for fishes, and as refugia from predators (Seitz et al. 2014, Bertocci et al. 2015, Teagle et al. 2017). Lastly, seaweed beds buffer coastlines from waves and storm surges and can act as natural filters for coastal runoff (Gaylord et al. 2007, Arkema et al. 2013). The scale of the different ecosystem roles depends on a range of ecosystem characteristics, such as the type of the foundation species, its frond size and morphology, its area-specific biomass (standing stock), three-dimensional canopy structure, and habitat distribution and connectivity across the seascape (Gaylord et al. 2007, Schmidt et al. 2011, Smale et al. 2013, Kay et al. 2016, Olds et al. 2016, Stagnol et al. 2016). All these characteristics can be affected by harvesting and can result in a wide range of ecosystem effects (Table 2).

Ecosystem effects of seaweed harvesting

Despite the ecological importance of seaweed canopies and their long history of harvesting, relatively few studies have directly examined the effects of harvesting beyond the resource species itself on ecosystem structure, functions and services (details on species-specific case studies are provided in Supplementary Text S2 including Table S2.1).

Harvesting directly affects the biomass and structure of seaweed beds, both individual frond morphology and three-dimensional canopy composition as well as their regrowth and regeneration after harvesting (Christie et al. 1998, Anderson et al. 2006, Seeley and Schlesinger 2012, Stagnol et al. 2013, Kay 2015, Steen et al. 2016). The reduced standing stock, which may include epiphytic algal biomass, can lower primary and secondary production, carbon storage and nutrient retention, and the shoreline buffer and filter function of seaweed stands (Table 2; Graham 2004, Springer et al. 2010, Schmidt et al. 2011, Smale et al. 2013, Stagnol et al. 2013, Pessarrodona et al. 2018). The regeneration of fronds and canopies can compensate for some of these losses but can take between months and decades depending on target species, whether it is perennial or annual, as well as harvest intensity (Christie et al. 1998, Jenkins et al. 2004, Kay 2015, Steen et al. 2016). Also, continuous harvesting can permanently lower the overall standing biomass, as harvested fronds have lower average size and age compared to unharvested beds (Sharp and Pringle 1990, Kay 2015). Harvesting will also lower detritus production from seaweeds, thereby affecting communities in adjacent detritus accumulation areas, such as beaches and deeper waters (Krumhansl and Scheibling 2012, Holden et al. 2018).

Any harvesting method will affect the extent and three-dimensional structure of a seaweed canopy, but the magnitude and range of consequences will depend on the gear type, the harvest intensity and scale, and the cutting methods applied (see details in Supplementary Text S2 with Table S2.1). While mechanical clear-cutting or trawling will remove most of the canopy with years to decades needed for recovery, even lower level hand-harvesting changes canopy structure through a truncation of larger, older and more voluminous fronds. Cutting height plays a crucial role in frond regrowth, such as for perennial

Table 2: Ecosystem functions and services of canopy-forming seaweeds, the associated ecosystem characteristic that can be measured, generalized effects of harvesting, and potential ecosystem-based management (EBM) strategies.[a]

Ecosystem roles	Ecosystem characteristic		Effects of harvesting	EBM strategies
Energy capture and transfer	Canopy biomass/standing stock	=>	Reduced	Harvest limits (quota)
– Primary production	Plant mass/growth	=>	Altered (decrease/increase)	Cutting methods (height/spacing/plant size)
– Secondary production	Canopy/plant regeneration	=>	Altered (decrease/increase)	Gear restrictions (mechanical/clear-cut)
– Detrital production	Detritus accumulation	=>	Reduced	Seasonal closures (peak growth/reproduction)
– Carbon storage				Spatial management (area limits/rotation/ exclusion)
Nutrient cycling/retention	Canopy biomass/standing stock	=>	Reduced	Harvest limits
	Tissue nutrient content	=>	None	Spatial management
	Detritus decomposition/release	=>	Reduced	
Habitat provision (quantity/quality)	Seaweed species	=>	Shift in dominance/diversity	Harvest limits
– Settlement (epiphytes, holdfast)	Plant morphology:	=>	Altered	Cutting methods
– Spawning/breeding	– Plant height	=>	Reduced	Gear restrictions
– Nursery	– Plant mass/size	=>	Reduced	By-catch limits (holdfasts/epiphytes)
– Feeding/foraging	– Plant circumference	=>	Reduced	Seasonal closures (breeding/nursery periods)
– Connectivity	– Holdfast size/age	=>	Reduced	No-take protected areas (refuge/reference)
	Canopy structure:	=>	Altered	Spatial management
	– Density	=>	Altered (decrease/increase)	Community co-management (governance)
	– Branching	=>	Altered (decrease/increase)	
	Habitat patchiness/fragmentation	=>	Increased	
	Habitat diversity/linkages	=>	Reduced	
Community organization	Species abundance/diversity	=>	Altered (decrease/increase)	Harvest limits, Cutting methods
– Biodiversity	Functional abundance/diversity	=>	Altered (decrease/increase)	Gear restrictions
– Community structure	Habitat diversity/linkages	=>	Altered (decrease/increase)	By-catch limits (vulnerable species)
– Species interactions	Habitat patchiness/fragmentation	=>	Altered (decrease/increase)	Seasonal closures
– Food webs	Genetic diversity/fragmentation	=>	Altered (decrease/increase)	No-take protected areas
– Connectivity	Vulnerable species	=>	Reduced	Spatial management, Community co-management
Fisheries support	Species abundance	=>	Reduced	Harvest limit, Cutting methods
	Species richness	=>	Reduced	Gear restrictions, By-catch limits
				Seasonal closures, No-take protected areas
				Spatial management, Community co-management
Shoreline protection	Canopy biomass/structure	=>	Reduced	Spatial management
Buffer/filter zone				Community co-management

[a]See Supplementary Text S2 for further details and references.

rockweed, and repeated cutting can change the branching, size, and density of seaweed fronds (Ugarte et al. 2006, Borras-Chavez et al. 2012, Kay 2015). Such changes in the amount and structure of the seaweed canopy will affect the quantity and quality of habitat provision and community organization (Table 2). Also, more complex epiphyte communities on older or unharvested fronds further increase habitat heterogeneity, create refuges for a variety of small animals, provide food for grazers, and contribute to overall primary, secondary and detrital production of seaweed beds (Anderson et al. 2006, Christie et al. 2009). Where beach-cast harvesting occurs, a reduction of detrital export from beach systems can cause declines in the richness, abundance, and biomass of coastal macrofauna and shorebirds (Krumhansl and Scheibling 2012).

Often, the amount of seaweed habitat (patch size/biomass) is more important in determining associated animal abundances, whereas habitat structure (architecture) and complexity are more important in determining species diversity and composition (Christie et al. 2009). For example in Spain, red seaweed canopy availability significantly influenced the abundance of species and functional groups, while a simplification of habitat structure (e.g. reduced density or complexity) decreased species and functional group diversity and density, and a complete canopy loss impoverished the entire community (Bustamante et al. 2017). A partially protected kelp forest in Chile had higher kelp density, higher fish biomass, and higher richness of sessile species in the understory compared to a harvested kelp area (Pérez-Matus et al. 2017). In Eastern Canadian rockweed beds, canopy structure composed of frond length and circumference was more important in explaining associated community composition than canopy biomass (Kay et al. 2016).

The disruption and fragmentation of habitats caused by clear-cutting or trawling can also affect community composition, organization and connectivity (Christie et al. 2009, Olds et al. 2016), but has received little study in seaweed systems. In a trawled kelp-harvesting area in Norway, short-term dispersal and movement of kelp-associated fauna depended on habitat structure post-trawling, with remaining holdfasts or small fronds serving as refugia (Waage-Nielson et al. 2003). Also, while many species were able to disperse rapidly across trawl tracks, they strongly varied in the speed of re-colonizing a cleared area. Thus, the most crucial factor for the re-establishment of an ecologically mature kelp forest community was sufficient time between harvests (Waage-Nielsen et al. 2003).

Generally, the largest ecosystem effects of seaweed harvesting have been observed for target species that created a dominant and monospecific canopy prior to the disturbance (Stagnol et al. 2016). Overharvesting can lead to a shift in foundation species composition with ripple effects on associated ecosystem roles. In Atlantic Canada, a shift from Irish moss to coralline algae has been observed multiple times over past decades due to overharvesting and did not easily or rapidly reverse (DFO 2013). Also, overharvested rockweed (*Ascophyllum nodosum* (Linnaeus) Le Jolis) beds have seen an encroachment of other fucoids, such as *Fucus vesiculosus* L., with lower harvest value and habitat quality (Text S2 with Table S2.1, Kay 2015), and kelp beds can be replaced by turf algae after perturbation by harvesting or other human activities (Benedetti-Cecchi et al. 2015, Filbee-Dexter and Wernberg 2018). In India, overharvesting has reportedly led to a significant decline in seaweed diversity, particularly in the Gulf of Mannar from 200 species in the 1970s to 80 in the 1980s (Chennubhotla et al. 2015).

Bycatch is another common issue in seaweed harvesting, depending on gear selectivity. While seaweed trawling or dredging is most prone to involve significant bycatch, even hand-raking and cutting will remove a certain amount of epiphytes and slow-moving animals attached to the target fronds as well as the occasional holdfast with its own species community (Seeley and Schlesinger 2012). Monospecific stands of Irish moss in Atlantic Canada harbor up to 36 animal and 19 major algal species that are vulnerable to removal as bycatch (Sharp and Pringle 1990). Rockweed beds can harbor >100 species of invertebrate taxa and numerous algal species (Seeley and Schlesinger 2012, Kay et al. 2016), yet only the bycatch of the periwinkle, *Littorina littorea* L. has received some attention due to its commercial interest (Sharp et al. 2006). A study on South African kelps recommended that harvesting should be restricted to only the distal portion of fronds which would result in only a 50% reduction of epiphytes (Anderson et al. 2006).

Seaweed habitats are also important in supporting fisheries by providing breeding, spawning, nursery and foraging grounds, and can be important in the connectivity among different coastal habitats. Rockweed beds in the Northwest Atlantic, for example, harbor a wide variety of commercially important fish as juveniles or adults, including Atlantic cod (*Gadus morhua* L.), pollock (*Pollachius virens* L.) and Atlantic herring (*Clupea harengus* L.), and invertebrates such as American lobster (*Homarus americanus* H. Milne Edwards), several crabs, bivalves and gastropods (Schmidt et al. 2011, Seeley and Schlesinger 2012, Kay et al. 2016). In tropical regions, 17–49% of reef fish species have juveniles using macroalgal habitats whereas adults are mostly found in coral reefs, highlighting the importance of connectivity among multiple habitats

(Fulton et al. 2019). In Norwegian kelp beds, the number of juvenile gadoids (<15 cm) was 92% lower in recently harvested compared to unharvested areas and 85% lower in areas harvested one year earlier (Lorentsen et al. 2010). Isopods and amphipods, an important food source for juvenile gadoids, were slow to recover post-harvesting of kelp (Christie et al. 1998, 2009) and may directly affect gadoid abundance, with further indirect effects on higher trophic levels. Cormorants, for example, performed significantly more feeding dives in unharvested than harvested areas suggesting that kelp harvesting not only affects juvenile fish abundance but also decreases foraging efficiency of coastal seabirds (Lorentsen et al. 2010).

In summary, harvesting canopy-forming seaweeds affects the morphology, canopy structure, standing stock and species composition of the foundation species which in turn affects their ecological roles in marine ecosystems (Table 2). The magnitude and range of ecosystem impacts depend on the species being harvested, the harvest methods employed, the intensity of biomass removal and its spatial and temporal extent (Supplementary Text S2 and Table S2.1). The broader ecosystem effects further depend on the recovery of seaweed fronds and regeneration of seaweed canopies after harvesting, and the ability of associated flora and fauna to recolonize and reorganize associated communities (Waage-Nielsen et al. 2003, Steen et al. 2016). Depending on harvest intensity this can take months to decades and can be influenced by oceanographic conditions (Christie et al. 1998, 2009, Steen et al. 2016), species interactions such as grazing and top-down control (Oritz 2010, Oróstica et al. 2014) and concurrent anthropogenic stressors including climate change (Rangeley and Davies 2000, Worm and Lotze 2006, Bulleri et al. 2017, Falace et al. 2018). Ideally, these factors would be considered in an ecosystem-based management plan for wild seaweed harvesting to minimize the ecosystem impacts.

Ecosystem-based approaches to seaweed harvesting

Over the past decade, several efforts have aimed to define and outline ecosystem-based management (EBM) approaches to exploitation (Pikitch et al. 2004, Arkema et al. 2006, UNEP 2011, Long et al. 2015). With the overall goal to ensure healthy, productive and diverse marine ecosystems, EBM aims to (i) maintain ecosystem characteristics to protect non-target species, vulnerable species, habitats and trophic interactions, (ii) protect essential habitats to sustain species diversity and abundance, (iii) protect endangered, threatened and vulnerable species, (iv) reduce bycatch and discards, and eliminate destructive and unselective methods of exploitation, and (v) manage target species in the context of the overall state of the ecosystem, habitat, protected species and non-target species (Pikitch et al. 2004, UNEP 2011).

Based on our above review we outline below how these goals could be applied to the context of wild harvesting of canopy-forming seaweeds (see also Table 2):

(i) To maintain the ecosystem characteristics of seaweed canopies, the overarching goal should be to maintain high canopy biomass (standing stock) and connectivity and allow for rapid frond regrowth and canopy regeneration after harvesting. This could be implemented with harvest limits (quotas) to constrain biomass removal. Regulation of cutting height, spacing and limits on holdfast removal will allow for more rapid regrowth, avoid canopy fragmentation, and seasonal closures during peak seaweed growth and reproduction will ensure that vital rates remain more natural. Also, overharvesting should be avoided to prevent any replacement of foundation species. These measures would ensure the continued primary, secondary and detritus production to fuel associated food webs and fisheries, and continued levels of carbon storage, nutrient cycling, shoreline protection and buffer zones. This could be further supported with spatial management, including area rotations to ensure enough recovery time and exclusion zones to support recolonization. Exclusion zones would also provide insurance against unforeseen effects of harvesting and help track ecosystem changes in the absence of harvesting, for example changes due to climate change, essentially providing ecosystem-level control sites (Pikitch et al. 2004, UNEP 2011).

(ii) To protect essential habitats to sustain species diversity and abundance, the overarching goal should be to minimize disruptions to the three-dimensional canopy structure, habitat architecture and connectivity. This could be achieved through strict harvest quotas limiting the amount of biomass removal and gear regulations prohibiting mechanical clear-cutting and limiting habitat fragmentation. Cutting methods should aim to minimize alterations of the canopy structure, such as elevated cutting heights and spacing between fronds and strict limits on holdfast removal. Seasonal closures should be implemented during peak breeding, spawning and nursery periods of associated species (e.g. common eider *Somateria mollissima* L., herring spawning, pollock nursery, Rangeley and Davies 2000, Seeley and Schlesinger 2012) and no-take protected areas could serve as year-round refuges (e.g. seabird colonies, Vea and Ask 2011). Spatial management could support these efforts by ensuring population (including genetic) and community connectivity among patches of the same or different habitats across the seascape (Durrant et al. 2018, Fulton et al. 2019), and minimize overlap with other resource uses; ideally this would be implemented in a community co-management framework (e.g. Tognelli et al. 2009).

(iii) To protect endangered, threatened and vulnerable species that depend on seaweed habitats, the overarching goal should be to meet their needs for settlement, food, growth, reproduction, and shelter, depending on the species in question. This means that management needs to address both the direct and indirect effects of seaweed harvesting, including impacts on essential habitat availability, structure and connectivity, food production, and detritus production that supports species farther away dependent on beach cast (e.g. shorebirds) or accumulation areas in open or deeper waters (e.g. sea turtles, sea urchins; Krumhansl and Scheibling 2012). As above, harvest limits to reduce biomass removal, gear restrictions to avoid habitat destruction or fragmentation, and cutting methods to maintain canopy structure should be priorities. Seasonal closures should aim to protect essential reproductive or feeding periods of vulnerable species, and no-take reserves can provide year-round refuges. Further spatial management should ensure connectivity among habitat patches and along migration routes (Durrant et al. 2018, Fulton et al. 2019).

(iv) To reduce bycatch and discards, the overarching goal of seaweed harvesting should be to use the least habitat-destructive and frond-damaging gear and employ the most selective methods for cutting and removing frond material. Trawling and dredging generally entrain a wide range of non-target species and have the most damaging effects on seafloor habitats, including the seaweed canopy (Christie et al. 1998, Jennings and Kaiser 1998, Dayton et al. 2002). Hand-cutting is much less destructive to the habitat itself but can still remove large amounts of epiphytic and slow-moving animals as bycatch (Anderson et al. 2006, Seeley and Schlesinger 2012). Also, the damage or removal of holdfasts should be avoided to support frond regrowth and maintain holdfast communities (Waage-Nielson et al. 2003, Sharp et al. 2006).

(v) Finally, to manage the target species in the context of the overall state of the ecosystem, habitat, protected species and non-target species, management plans need to consider a range of abiotic, biotic and anthropogenic factors in coastal ecosystems, including changing environmental conditions due to climate change. Integrated coastal-zone or ocean management, including zoning of multiple ocean uses, land-sea connections, and cumulative human impacts, should focus on supporting the conditions under which seaweed canopies thrive. This also needs to consider current and future range shifts in foundation species with climate change (Wernberg et al. 2016, Wilson et al. 2019) and the management of invasive species (Maggi et al. 2015, Epstein and Smale 2017). Spatial management should allow for no-take protected areas to provide refuge areas and reference sites for ecosystem assessments (Arkema et al. 2006) as well as ensure connectivity among multiple habitats, such as coral reefs and macroalgal beds (Fulton et al. 2019). Community management needs to balance traditional user rights with industrial interests (Armitage et al. 2009) and co-harvesting in areas with multiple harvesting interests (Tognelli et al. 2009). This requires the engagement of multiple stakeholders as well as the general public.

Other considerations for sustainability

Implementing an EBM approach to seaweed harvesting would lay a proper foundation for the sustainable use of canopy-forming seaweeds while allowing them to continue to provide essential ecosystem functions and services for the benefit of coastal communities around the world (Table 2). Similarly, implementing EBM into other commercial fisheries can be beneficial for fishers, marine ecosystems and society alike (Worm et al. 2009, Eddy et al. 2017). As with other management strategies, an EBM approach would require proper governance and regulations, implementation on the ground, as well as monitoring and enforcement to meet goals and targets (Pitcher et al. 2009, Worm et al. 2009). However, other factors also play a role in the overall sustainability of utilizing wild seaweed canopies.

Firstly, wild seaweeds are facing increasing pressures from growing human demands and global markets for sustainable nutrition, health or superfoods, medicine, cosmetics and a wide range of industrial products including bioenergy production (Fernand et al. 2016, Anis et al. 2017, Mac Monagail et al. 2017). The question is whether we should aim to meet growing global demands by harvesting wild canopy-forming seaweeds that provide a range of essential ecosystem functions and services, or rather by cultivating seaweeds, which seems feasible given the strong rise in aquaculture (Figure 1). The development and transitioning to seaweed aquaculture could be supported by management agencies while maintaining small-scale traditional, subsistence and recreational seaweed harvesting. Also, placing a monetary value on the ecosystem services provided by wild seaweeds could allow for a proper comparison of the economic and environmental benefits and drawbacks of wild seaweed harvesting versus cultivation (Blamey and Bolton 2018).

Another consideration involves cumulative human impacts from activities both on land and in the sea. The growth and survival of seaweeds can be affected by nutrient loading and chemical pollution from land-based sources or aquaculture activities, sediment runoff, physical disturbance from fishing, boating or constructions, shading from overwater structures, and invasive species to name a few (Rangeley and Davies 2000, Worm and Lotze 2006, Murray et al. 2015, Murphy et al. 2019). Because wild seaweeds are harvested directly from the ocean, they are often considered and marketed as “organic” without evaluation of their tissue content or environmental conditions they were grown in; however, seaweeds are known to accumulate chemical substances and toxins (Chen et al. 2018, Falace et al. 2018). Proper evaluation, monitoring, certification and labelling, such as through the Marine Stewardship Council (MSC; ASC-MSC 2018), would help shed a light on growing conditions and harvesting practices of wild seaweeds around the world and ensure the quality and safety of food and feed made from seaweeds.

Also, because many species are impacted by a suite of human activities, the protection of important marine habitats is a growing priority for marine management and conservation worldwide (European Commission 2008, Cullen-Unsworth and Unsworth 2016, Murphy et al. 2019). Essential fish habitats, for example, which many seaweeds and seagrasses provide, are often conservation priorities which is counter to the continued harvesting of canopy-forming seaweeds. In Atlantic Canada, seagrass (*Zostera marina* L.) has been identified as an Ecologically Significant Species (ESS; DFO 2009) because of the important roles it plays in coastal ecosystems, and management efforts aim to reduce or prevent harmful human disturbances (Murphy et al. 2019). In contrast, rockweed and kelp play similar roles in marine environments, yet have not received similar recognition and commercial harvesting continues (DFO 2013). Across the European Union, a wide range of species and habitats, including seaweed beds, can be protected as Special Areas of Conservation under the Natura 2000 network of protected areas (European Commission 2008).

Climate change creates another urgent issue in temperate to polar marine environments where many canopy-forming seaweeds are found (Harley et al. 2012). Warming waters are already affecting the distribution of kelps and rockweeds around the world, with range contractions at their warm-water distribution boundaries, population declines or disappearances in some regions, as well as changes in the composition of foundation species or replacements with turf algae or invasive seaweeds (Ugarte et al. 2010, Wernberg et al. 2016, Jonsson et al. 2018, Wilson et al. 2019), all of which is affecting the quantity and quality of available seaweeds habitats and their connectivity across the seascape (Durrant et al. 2018). Ocean acidification is also an issue for some species, and increased storminess and more severe physical disturbances affect seaweed canopies particularly in shallower waters (Harley et al. 2012). In some instances, range expansions into higher latitudes or invasions by non-native seaweeds may create new opportunities for ecosystem configurations as well as harvesting (Epstein and Smale 2017, Wilson et al. 2019).

Finally, there is no pre-exploitation baseline data for many seaweed stands, and the ecosystems they create, which makes it difficult to evaluate the full scale of population and ecosystem changes (Lotze and Worm 2009, Seeley and Schlesinger 2012, Kay 2015). In the absence of such knowledge, robust and precautionary management measures should be adopted, and the incorporation of harvest exclusion zones or no-take protected areas should be mandatory in every management plan to provide a reference for ecosystem evaluations (Pikitch et al. 2004, Long et al. 2015). Also, species-specific harvest statistics should be collected and reported for all seaweeds to allow for the assessment of harvest trends nationally and globally. Currently, only some statistics are reported for individual seaweed species (Table 1), while many are reported in bulk categories. We also found considerable mismatches between what was reported at FAO compared to country-specific statistics, for example an underreporting of Atlantic Canada rockweed catches at FAO (DFO 2013, FAO 2018b). In addition to biomass removals, reporting, at least to national agencies, should also include the effort employed to allow for proper catch-per-unit-effort assessments as in other fisheries, as well as monitoring and reporting of bycatch (flora, fauna), holdfast removals, and specific harvest locations to allow for evaluations of some ecosystem consequences.

Conclusions

Canopy-forming seaweeds have played – and continue to play – important roles in the history of human coastal resource use and in the functioning of marine ecosystems. In an era of increasing human demands for seaweed products and applications, but also increasing pressures on coastal ecosystems, there is a growing need to balance the value of the functions and services seaweeds provide as living ecosystems against their value as harvested resources. Also, the value of seaweeds for traditional small-scale and subsistence harvesting needs to be preserved in the presence of industrial operations. The growth of seaweed aquaculture could alleviate some pressure on wild seaweed habitats, but the location and scale of such operations should be carefully evaluated to prevent negative environmental impacts (Campbell et al. 2019). Many jurisdictions already employ some regulations to the harvesting of wild seaweeds but usually only in a single-species context and not comprehensive enough to also maintain the ecosystem structure, functions and services they provide. We argue that a comprehensive ecosystem-based management approach would be instrumental for the maintenance of the ecological and economic values of seaweed canopies and help build resilience in the face of growing cumulative and climate-change impacts affecting coastal ecosystems.

Acknowledgments: Financial support was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC, Funder Id: http://dx.doi.org/10.13039/501100000038, Grant Numbers: RGPIN-2014-04491 and RGPIN-2017-05118) with grants to HKL and BW.

References

Anderson, R.J., M.D. Rothman, A. Share and H. Drummond. 2006. Harvesting of the kelp *Ecklonia maxima* in South Africa affects its three obligate, red algal epiphytes. *J. Appl. Phycol. 18*: 343–349.

Anderson, R.J., A. Rand, M.D. Rothman and J.J. Bolton. 2007. Mapping and quantifying the South African kelp resource. *Afr. J. Mar. Sci. 29*: 369–378.

Anderson, S.C., J. Mills-Flemming, R. Watson and H.K. Lotze. 2011. Rapid global expansion of invertebrate fisheries: trends, drivers and ecosystem effects. *PLoS One 6*: e14735.

Angus, S. 2017. Modern seaweed harvesting in Scotland: the legal and ecological context. *Scot. Geogr. J. 133*: 101–114.

Anis, M., S. Ahmed and M. Hasan. 2017. Algae as nutrition, medicine and cosmetic: the forgotten history, present status and future trend. *World J. Pharm. Sci. 6*: 1934–1959.

Araújo, R.M., J. Assis, R. Aguillar, L. Airoldi, I. Barbara, I. Bartsch, T. Bekkby, H. Christie, D. Davoult, S. Derrien-Courtel, C. Fernandez, S. Fredriksen, F. Gevaert, H. Gundersen, A. Le Gal, L. Leveque, N. Mieszkowska, K.M. Norderhaug, P. Oliveira, A. Puente, J.M. Rico, E. Rinde, H. Schubert, E.M. Strain, M. Valero, F. Viard and I. Sousa-Pinto. 2016. Status, trends and drivers of kelp forests in Europe: an expert assessment. *Biodiv. Cons. 25*: 1319–1348.

Arkema, K.K., S.C. Abramson and B.M. Dewsbury. 2006. Marine ecosystem-based management: from characterization to implementation. *Front. Ecol. Environ. 4*: 525–532.

Arkema, K.K., G. Guannel, G. Verutes, S.A. Wood, A. Guerry, M. Ruckelshaus, P. Kareiva, M. Lacayo and J.M. Silver. 2013. Coastal habitats shield people and property from sea-level rise and storms. *Nat. Clim. Change 3*: 913–918.

Armitage, D.R., R. Plummer, F. Berkes, R.I. Arthur, A.T. Charles, I.J. Davidson-Hunt, A.P. Diduck, N.C. Doubleday, D.S. Johnson, M. Marschke, P. McConney, E.W. Pinkerton and E.K. Wollenberg. 2009. Adaptive co-management for social–ecological complexity. *Front. Ecol. Environ. 7*: 95–102.

ASC-MSC. 2018. Seaweed (Algae) Standard Version 1.01. Aquaculture Stewardship Council (ASC) and Marine Stewardship Council (MSC). Available online at https://www.asc-aqua.org/wp-content/uploads/2017/11/ASC-MSC-Seaweed-Algae-Standard-v1.01.pdf.

Benedetti-Cecchi, L., L. Tamburello, E. Maggi and F. Bulleri. 2015. Experimental perturbations modify the performance of early warming indicators of regime shift. *Curr. Biol. 25*: 1867–1872.

Bertocci, I., R. Araújo, P. Oliveira and I. Sousa-Pinto. 2015. Potential effects of kelp species on local fisheries. *J. Appl. Ecol. 52*: 1216–1226.

Blamey, L. and J.J. Bolton. 2018. The economic value of South African kelp forests and temperate reefs: past, present and future. *J. Mar. Syst. 188*: 172–181.

Borras-Chavez, R., M. Edwards and J.A. Vásquez. 2012. Testing sustainable management in Northern Chile: harvesting *Macrocystis pyrifera* (Phaeophyceae, Laminariales). A case study. *J. Appl. Phycol. 24*: 1655–1665.

Bulleri, F., L. Benedetti-Cecchi, G. Ceccherelli and L. Tamburello. 2017. A few is enough: a low cover of a non-native seaweed reduces the resilience of Mediterranean macroalgal stands to disturbances of varying extent. *Biol. Inv. 19*: 2291–2305.

Buschmann, A.H., M.C. Hernández-González and D. Varela. 2008. Seaweed future cultivation in Chile: perspectives and challenges. *Int. J. Environ. Pollut. 33*: 432–456.

Buschmann, A.H., C. Camus, J. Infante, A. Neori, Á. Israel, M.C. Hernández-González, S.V. Pereda, J.L. Gomez-Pinchetti, A. Goldberg, N. Tadmor-Shalev and A.T. Critchley. 2017. Seaweed production: overview of the global state of exploitation, farming and emerging research activity. *Eur. J. Phycol. 52*: 391–406.

Bustamante, M., J. Tajadura, I. Díez and J.I. Saiz-Salinas. 2017. The potential role of habitat-forming seaweeds in modeling benthic ecosystem properties. *J. Sea Res. 130*: 123–133.

Campbell, I., A. McLeod, C. Sahlmann, L. Neves, J. Funderud, M. Øverland, A.D. Hughes and M. Stanley. 2019. The environmental risks associated with the development of seaweed farming in Europe – prioritizing key knowledge gaps. *Front. Mar. Sci. 6*: 107.

Chen, Q., X.-D. Pan, B.-F. Huang and J.-L. Han. 2018. Distribution of metals and metalloids in dried seaweeds and health risk to population in southeastern China. *Sci. Rep. 8*: 3578.

Chennubhotla, V.S., M.U. Rao and K.S. Rao. 2013. Exploitation of marine algae in Indo-Pacific region. *Seaweed Res. Util. 35*: 1–77.

Chennubhotla, V.S.K., K.S. Rao and N. Kaliaperumal. 2015. Effect of some adverse factors on the diversity and distribution of marine macro algae along the Indian Coasts. *Seaweed Res. Util. 36*: 5–11.

Christie, H., S. Fredriksen and E. Rinde. 1998. Regrowth of kelp and colonization of epiphyte and fauna community after kelp trawling at the coast of Norway. *Hydrobiologia 375*: 49–58.

Christie, H., K.M. Norderhaug and S. Fredriksen. 2009. Macrophytes as habitat for fauna. *Mar. Ecol. Prog. Ser. 396*: 221–233.

Cullen-Unsworth, L.C. and R.K.F. Unsworth. 2016. Strategies to enhance the resilience of the world's seagrass meadows. *J. Appl. Ecol. 53*: 967–972.

Dayton, P.K., S.F. Thrush and F.C. Coleman. 2002. Ecological effects of fishing in marine ecosystems of the United States. Pew Ocean Commission, Arlington. pp. 45.

Delaney, A., K. Frangoudes and S.-A. Li. 2016. Society and seaweed: understanding the past and present. *In:* (Fleurence, J. and I. Levine, eds) *Seaweed in*. Elsevier Academic Press, London. pp. 7–40.

DFO. 2009. Does eelgrass (*Zostera marina*) meet the criteria as an ecologically significant species? Department of Fisheries and Oceans, CSAS Sci. Advis. Rep. 2009/018.

DFO. 2013. Assessment of information on Irish moss, rockweed, and kelp harvests in Nova Scotia. Department of Fisheries and Oceans, CSAS Sci. Advis. Rep. 2013/004.

Durrant, H.M.S., N.S. Barrett, G.J. Edgar, M.A. Coleman and C.P. Burridge. 2018. Seascape habitat patchiness and hydrodynamics explain genetic structuring of kelp populations. *Mar. Ecol. Prog. Ser*. *587*: 81–92.

Eddy, T.D., H.K. Lotze, E.A. Fulton, M. Coll, C.H. Ainsworth, J.N. Araújo, C. Bulman, A. Bundy, V. Christensen, J.C. Field, N. Gribble, M. Hasan, S. Mackinson and H. Townsend. 2017. Ecosystem effects of invertebrate fisheries. *Fish Fish. 18*: 40–53.

Epstein, G. and D.A. Smale. 2017. *Undaria pinnatifida*: a case study to highlight challenges in marine invasion ecology and management. *Ecol. Evol. 7*: 8624–8642.

European Commission. 2008. Natura 2000: Protecting Europe's biodiversity. European Commission, Directorate General for the Environment, Brussels, Belgium. pp. 292.

Falace, A., L. Tamburello, G. Guarnieri, S. Kalbe, L. Papa and S. Fraschetti. 2018. Effects of a glyphosate-based herbicide on *Fucus virsoides* (Fucales, Ochrophyta) photosynthetic efficiency. *Environ. Pollut. 243*: 912–918.

FAO. 2018a. The state of world fisheries and aquaculture 2018. Food and Agriculture Organization of the United Nations. Rome, Italy. pp. 227.

FAO. 2018b. Fishery statistical collections. Food and Agriculture Organization of the United Nations. Rome, Italy. http://www.fao.org/fishery/statistics/.

Fernand, F., A. Israel, J. Skjermo, T. Wichard, K.R. Timmermans and A. Golberg. 2016. Offshore macroalgae biomass for bioenergy production: environmental aspects, technological achievements and challenges. *Renew. Sust. Energ. Rev. 75*: 35–45.

Filbee-Dexter, K. and T. Wernberg. 2018. Rise of turfs: a new battle front for globally declining kelp forests. *Bioscience 68*: 4–76.

Filbee-Dexter, K., T. Wernberg, S. Fredriksen, K.M. Norderhaug and M.F. Pedersen. 2019. Arctic kelp forests: diversity, resilience and future. *Glob. Planet. Change 172*: 1–14.

Frangoudes, K. 2011. Seaweeds fisheries management in France, Japan, Chile and Norway. *Cah. Biol. Mar. 52*: 517–525.

Fredriksen, S. 2003. Food web studies in a Norwegian kelp forest based on stable isotope analysis. *Mar. Ecol. Prog. Ser. 260*: 71–81.

Fujita, D. 2011 Management of kelp ecosystem in Japan. *Cah. Biol. Mar. 52*: 499–505.

Fulton, C.J., R.A. Abesamis, C. Berkström, M. Depczynski, N.A.J. Graham, T.H. Holmes, M. Kulbicki, M.M. Noble, B.T. Radford, S. Tano, P. Tinkler, T. Wernberg and S.K. Wilson. 2019. Form and function of tropical macroalgal reefs in the Anthropocene. *Funct. Ecol. 33*: 989–999.

Gaylord, B., J.H. Rosman, D.C. Reed, J.R. Koseff, J. Fram, S. MacIntyre, K. Arkema, C. McDonald, M.A. Brzezinski, J.L. Largier, S.G. Monismith, R.T. Raimondi and B. Mardian. 2007. Spatial patterns of flow and their modification within and around a giant kelp forest. *Limnol. Oceanogr. 52*: 1838–1852.

Graham, M.H. 2004. Effects of local deforestation on the diversity and structure of Southern California giant kelp forest food webs. *Ecosystems 7*: 341–357.

Harley, C.D.G., K.M. Anderson, K.W. Demes, J.P. Jorve, R.L. Kordas, T.A. Coyle and M.H. Graham. 2012. Effects of climate change on global seaweed communities. *J. Phycol. 48*: 1064–1078.

Holden, J.J., S.K. MacNeill, F. Juanes and S.E. Dudas. 2018. Beach-cast deposition and commercial harvesting of a non-indigenous alga, *Mazzaella japonica*: Implications for macrofauna communities in Baynes Sound, British Columbia. *Est. Coast. Shelf Sci. 210*: 162–171.

Hyndes, G.A., I. Nagelkerken, R.J. McLeod, R.M. Connolly, P.S. Lavery and M.A. Vanderklift. 2014. Mechanisms and ecological role of carbon transfer within coastal seascapes. *Biol. Rev. 89*: 232–254.

Jenkins, S.R., T.A. Norton and S.J. Hawkins. 2004. Long term effects of *Ascophyllum nodosum* canopy removal on mid shore community structure. *J. Mar. Biol. Assoc. UK 84*: 327–329.

Jennings, S. and M.J. Kaiser. 1998. The effects of fishing on marine ecosystems. *In:* (Blaxter, J.H.S., A.J. Southward and P.A. Tyler, eds) *Advances in marine biology*. Academic Press, London. pp. 201–352.

Jonsson, R.R., J. Kotta, H.C. Andersson, K. Herkül, E. Virtanen, A.N. Sandman and K. Johannesson. 2018. High climate velocity and population fragmentation may constrain climate-driven range shift of the key habitat former *Fucus vesiculosus*. *Div. Distr*. *24*: 892–905.

Kay, L. 2015. Canopy and community structure of rockweed beds in Nova Scotia and New Brunswick: regional variation and effects of commercial harvest and proximity to aquaculture. Master's thesis, Dalhousie University, Halifax, Canada. pp. 234.

Kay, L., T.D. Eddy, A.L. Schmidt and H.K. Lotze. 2016. Regional differences and linkage between canopy structure and community composition of rockweed habitats in Atlantic Canada. *Mar. Biol. 163*: 251.

Krumhansl, K.A. and R.E. Scheibling. 2012. Production and fate of kelp detritus. *Mar. Ecol. Prog. Ser. 467*: 281–302.

Krumhansl, K.A., J.N. Bergman and A.K. Salomon. 2017. Assessing the ecosystem-level consequences of a small-scale artisanal kelp fishery within the context of climate change. *Ecol. Appl. 27*: 799–813.

Long, R.D., A. Charles and R.L. Stephenson. 2015. Key principles of marine ecosystem-based management. *Mar. Policy 57*: 53–60.

Lorentsen, S.-H., K. Sjøtun and D. Grémillet. 2010. Multi-trophic consequences of kelp harvest. *Biol. Cons. 143*: 2054–2062.

Lotze, H.K. and B. Worm. 2009. Historical baselines for large marine animals. *Trends Ecol. Evol. 24*: 254–262.

Mac Monagail, M., L. Cornish, L. Morrison, R. Araújo and A.T. Critchley. 2017. Sustainable harvesting of wild seaweed resources. *Eur. J. Phycol. 52*: 371–390.

Maggi, E., L. Benedetti-Cecchi, A. Castelli, E. Chatzinikolaou, T.P. Crowe, G. Ghedini, J. Kotta, D.A. Lyons, C. Ravaglioli, G. Rilov, L. Rindi and F. Bulleri. 2015. Ecological impacts of invading seaweeds: a meta-analysis of their effects at different trophic levels. *Div. Distr*. *21*: 1–12.

Meland, M. and C. Rebours. 2012. Short description of the Norwegian seaweed industry. *Bioforsk Fokus 7*: 278–279.

Murphy, G.E.P., M. Wong and H.K. Lotze. 2019. A human impact metric for coastal ecosystems with application to seagrass beds in Atlantic Canada. *Facets 4*: 210–237.

Murray, C.C., S. Agbayani, H.M. Alidini and N.C. Ban. 2015. Advancing marine cumulative effects mapping: an update in Canada's Pacific waters. *Mar. Policy 58*: 71–77.

Nayar, S. and K. Bott. 2014. Current status of global cultivate seaweed production and markets. *World Aquacult. 45*: 32–37.

Olds, A.D., R.M. Connolly, K.A. Pitt, S.J. Pittman, P.S. Maxwell, C.M. Huijbers, B.R. Moore, S. Albert, D. Rissik, R.C. Babcock and T.A. Schlacher. 2016. Quantifying the conservation value of seascape connectivity: a global synthesis. *Glob. Ecol. Biogeogr*. *25*: 3–15.

Oróstica, M.H., M.A. Aguilera, G.A. Donoso, J.A. Vásquez and B.R. Broitman. 2014. Effect of grazing on distribution and recovery of harvested stands of *Lessonia berteroana* kelp in northern Chile. *Mar. Ecol. Prog. Ser. 511*: 71–78.

Ortiz, M. 2010. Dynamic and spatial models of kelp forest of *Macrocystis pyrifera* and *Lessonia trabeculata* (SE Pacific) for assessment harvest scenarios: short-term responses. *Aquat. Cons. 20*: 494–506.

Pérez-Matus, A., S.A. Carrasco, S. Gelcich, M. Fernandez and E.A. Wieters. 2017. Exploring the effects of fishing pressure and upwelling intensity over subtidal kelp forest communities in central Chile. *Ecosphere 8*: e01808.

Pessarrodona, A., P.J. Moore, M.D.J. Sayer and D.A. Smale. 2018. Carbon assimilation and transfer through kelp forests in the NE Atlantic is diminished under a warmer ocean climate. *Glob. Chang. Biol. 24*: 4386–4398.

Pikitch, E.K., C. Santora, E.A. Babcock, A. Bakun, R. Bonfil, D.O. Conover, P. Dayton, P. Doukakis, D. Fluharty, B. Heneman, E.D. Houde, J. Link, P.A. Livingston, M. Mangel, M.K. McAllister, J. Pope and K.J. Sainsbury. 2004. Ecosystem-based fishery management. *Science 305*: 346–347.

PIRSA. 2014. Ecological assessment of the South Australian beachcast seagrass and marine algae fishery. Primary Industries and Resources South Australia, Adelaide. pp. 60.

Pitcher, T.J., D. Kalikoski, K. Short, D. Varkey and G. Pramod. 2009. An evaluation of progress in implementing ecosystem-based management of fisheries in 33 countries. *Mar. Policy 33*: 223–232.

Rangeley, R.W. and J. Davies. 2000. Gulf of Maine rockweed: management in the face of scientific uncertainty. Huntsman Marine Science Centre Occasional Report No. 00/1.

Schmidt, A.L., M. Coll, T. Romanuk and H.K. Lotze. 2011. Ecosystem structure and services in eelgrass (*Zostera marina*) and rockweed (*Ascophyllum nodosum*) habitats. *Mar. Ecol. Prog. Ser. 437*: 51–68.

Seeley, R.H. and W.H. Schlesinger. 2012. Sustainable seaweed cutting? The rockweed (*Ascophyllum nodosum*) industry of Maine and the Martitime Provinces. *Ann. NY Acad. Sci. 1249*: 84–103.

Seitz, R.D., H. Wennhage, U. Bergström, R.N. Lipcius and T. Ysebaert. 2014. Ecological value of coastal habitats for commercially and ecologically important species. *ICES J. Mar. Sci. 71*: 648–665.

Sharp, G.J. and J.D. Pringle. 1990. Ecological impact of marine plant harvesting in the northwest Atlantic: a review. *Hydrobiologia 204/205*: 17–24.

Sharp, G.J., R. Ugarte and R.E. Semple. 2006. The ecological impact of marine plant harvesting in the Canadian Maritimes, implications for coastal zone management. *Sci. Asia 32*: 77–86.

Smale, D.A., M.T. Burrows, P. Moore, N. O'Connor and S.J. Hawkins. 2013. Threats and knowledge gaps for ecosystem services provided by kelp forests: a northeast Atlantic perspective. *Ecol. Evol. 3*: 4016–4038.

Springer, Y.P., C.G. Hays and M.H. Carr. 2010. Towards ecosystem-based management of marine macroalgae – the bull kelp *Nereocystis luetkeana*. *Oceanogr. Mar. Biol. Ann. Rev*. *48*: 1–41.

Stagnol, D., M. Renaud and D. Davoult. 2013. Effects of commercial harvesting of intertidal macroalgae on ecosystem biodiversity and functioning. *Est. Coast. Shelf Sci. 130*: 99–110.

Stagnol, D., R. Michel and D. Davoult. 2016. Unravelling the impact of harvesting pressure on canopy-forming macroalgae. *Mar. Freshw. Res. 67*: 153–161.

Steen, H., F.E. Moy, T. Bodvin and V. Husa. 2016. Regrowth after kelp harvesting in Nord-Trøndelag, Norway. *ICES J. Mar. Sci. 73*: 2708–2720.

Subba Rao, P.V. and V.A. Mantri. 2006. Indian seaweed resources and sustainable utilization: scenario at the dawn of a new century. *Curr. Sci. 91*: 164–174.

Teagle, H., S.J. Hawkins, P.J. Moore and D.A. Smale. 2017. The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *J. Exp. Mar. Biol. Ecol. 492*: 81–98.

Tognelli, M.F., M. Fernandez and P.A. Marquet. 2009. Assessing the performance of the existing and proposed network of marine protected areas to conserve marine biodiversity in Chile. *Biol. Cons. 142*: 3147–3153.

Trono, G.C. 1999. Diversity of the seaweed flora of the Philippines and its utilization. *Hydrobiologia 398/399*: 1–6.

Ugarte, R.A., G. Sharp and B. Moore. 2006. Changes in the brown seaweed *Ascophyllum nodosum* (L.) Le Jol. morphology and biomass produced by cutter rake harvests in southern New Brunswick, Canada. *J. Appl. Phycol. 18*: 351–359.

Ugarte, R., J.S. Craigie and A.T. Critchley. 2010. Fucoid flora of the rocky intertidal of the Canadian Maritimes: implications for the future with rapid climate change. *In*: (Isreal, A., R. Einav, J. Seckbach, eds) *Seaweeds and their role in globally changing environments*. Springer, Dordrecht. pp. 73–90.

UNEP. 2011. Taking steps toward marine and coastal ecosystem-based management – an introductory guide. United Nations Environment Program, Regional Seas Reports and Studies 189.

Vásquez, J.A., N. Piaget and J.M.A. Vega. 2012. The *Lessonia nigrescens* fishery in northern Chile: "how you harvest is more important than how much you harvest". *J. Appl. Phycol. 24*: 417–426.

Vea, J. and E. Ask. 2011. Creating a sustainable commercial harvest of *Laminaria hyperborea*, in Norway. *J. Appl. Phycol. 23*: 489–494.
Vega, J.M.A., B.R. Broitman and J.A. Vásquez. 2014. Monitoring the sustainability of *Lessonia nigrescens* (Laminariales, Phaeophyceae) in northern Chile under strong harvest pressure. *J. Appl. Phycol. 26*: 791–801.
Vetter, E.W. and P.K. Dayton. 1999. Organic enrichment by macrophyte detritus, and abundance patterns of megafaunal populations in submarine canyons. *Mar. Ecol. Prog. Ser. 186*: 137–148.
Waage-Nielsen, E., H. Christie and E. Rinde. 2003. Short-term dispersal of kelp fauna to cleared (kelp-harvested) areas. *Hydrobiologia 503*: 77–91.
Wernberg, T., S. Bennett, R.C. Babcock, T. de Bettignies, K. Cure, M. Depczynski, F. Dufois, J. Fromont, C.J. Fulton, R.K. Hovey, E.S. Harvey, T.H. Holmes, G.A. Kendrick, B. Radford, J. Santana-Garcon, B.J. Saunders, D.A. Smale, M.S. Thomsen, C.A. Tuckett, F. Tuya, M.A. Vanderklift and S. Wilson. 2016. Climate-driven regime shift of a temperate marine ecosystem. *Science 353*: 169–172.
Werner, A. and S. Kraan. 2004. Review of the potential mechanization of kelp harvesting in Ireland. Marine Environment and Health Series 17. Marine Institute 2004.
Wilson, K.L., M.A. Skinner and H.K. Lotze. 2019. Projected 21st century distribution of canopy-forming seaweeds in the Northwest Atlantic with climate change. *Div. Distr. 25*: 582–602.
Worm, B. and H.K. Lotze. 2006. Effects of eutrophication, grazing, and algal blooms on rocky shores. *Limnol. Oceanogr. 51*: 569–579.
Worm, B. and H.K. Lotze. 2016. Marine biodiversity and climate change. *In*: (T. Letcher, ed) *Climate and global change: observed impacts on Planet Earth*. 2nd edition. Elsevier, Amsterdam, The Netherlands. pp. 195–212.
Worm, B., R. Hilborn, J.K. Baum, T.A. Branch, J.S. Collie, C. Costello, M.J. Fogarty, E.A. Fulton, J.A. Hutchings, S. Jennings, O.P. Jensen, H.K. Lotze, P.A. Mace, T.R. McClanahan, C. Minto, S.R. Palumbi, A.M. Parma, D. Ricard, A.A. Rosenberg, R. Watson and D. Zeller. 2009. Rebuilding global fisheries. *Science 325*: 578–585.
Zemke-White, W.L. and M. Ohno. 1999. World seaweed utilization: End of century summary. *J. Appl. Phycol. 11*: 369–376.
Zemke-White, W.L., S.R. Speed and D.J. McClary. 2005. Beach-cast seaweed: a review. New Zealand Fisheries Assessment Report 2005/44. pp. 47.

Supplementary Material: The online version of this article offers supplementary material (https://doi.org/10.1515/bot-2019-0027).
Article note: This article is part of the special issue series of *Botanica Marina: Seaweed resources of the world: a 2020 vision*, which has started publication in *Botanica Marina* 2019, vol. 62, issue 3. The series is guest-edited by Alan T. Critchley, Anicia Hurtado, Leonel Pereira, Melania Cornish, Danilo Largo and Nicholas Paul.

Bionotes

Heike K. Lotze
Department of Biology, Dalhousie University, 1355 Oxford Street, PO BOX 15000, Halifax, NS, B3H 4R2, Canada
hlotze@dal.ca.
https://orcid.org/0000-0001-6258-1304

Heike K. Lotze is a Professor of Marine Ecology at Dalhousie University in Halifax, Canada and Canada Research Chair in Marine Renewable Resource (2006–2016). Ever since her first research project on seaweeds, Heike's research has focused on human-induced changes in marine populations, communities and ecosystems, and how we can improve management and conservation to sustain the structure and functions of marine ecosystems and the services they provide for human well-being.

Inka Milewski
Department of Biology, Dalhousie University, 1355 Oxford Street, PO BOX 15000, Halifax, NS, B3H 4R2, Canada

Inka Milewski is a Research Associate at Dalhousie University in Halifax, Canada and has been a Science Advisor for several non-governmental organizations in Canada for over 20 years. Her research is focused on quantifying the effects of pollution, nutrient loading, habitat alteration, fisheries, and aquaculture on marine ecosystems with a goal to inform policy and the public on resource management and conservation issues.

Julia Fast
Department of Biology, Dalhousie University, 1355 Oxford Street, PO BOX 15000, Halifax, NS, B3H 4R2, Canada

Julia Fast is currently completing her Bachelor of Science with a double major in Biology and Environmental Science at Dalhousie University in Nova Scotia, Canada. Julia is broadly interested in the effects of humans on marine ecosystems and species, and has been a Research Assistant in Heike Lotze's lab working on the management of seaweed harvesting around the world and the impacts of nutrient loading on coastal ecosystems.

Lauren Kay
Department of Biology, Dalhousie University, 1355 Oxford Street, PO BOX 15000, Halifax, NS, B3H 4R2, Canada

Lauren Kay graduated with a MSc in Marine Biology from Dalhousie University in Halifax, Canada in 2015. Both her undergraduate and graduate research projects focused on rockweed habitats along the Canadian shoreline, including the effects of nutrient loading, harvesting and climate change on rockweed growth and survival as well as canopy and community structure. She currently lives in Montreal and is studying Medicine at McGill University.

Boris Worm
Department of Biology, Dalhousie University, 1355 Oxford Street, PO BOX 15000, Halifax, NS, B3H 4R2, Canada

Boris Worm is a Killam Research Professor of Marine Conservation Biology at Dalhousie University in Halifax, Canada. His work focuses on documenting and understanding changes in marine biodiversity, as well as finding science-based solutions for marine conservation and management at regional and global scales.