Review

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Seaweed resources of the Hawaiian Islands

<https://doi.org/10.1515/bot-2018-0091>

Received 4 October, 2018; accepted 15 May, 2019; online first 25 June, 2019

Abstract: Up-to-date information about the unique marine flora of the Hawaiian Islands – its environment, uses, cultivation, conservation, and threats – comes from many sources, and is compiled here for the first time. The seaweed resources of the Hawaiian Islands are taxonomically diverse, biogeographically intriguing, ecologically complex, culturally significant, and economically valuable. Macroalgae, historically and today, are critical components of the marine ecosystem, as well as the diet and culture of people living in the islands. Some Hawaiian seaweeds are known to contain valuable bioactive compounds that have potential medical and pharmaceutical applications. Cultivation of Hawaiian seaweeds is carried out in tanks, ponds, and along the shoreline, both commercially and by “back-yard” farmers. Several community groups are actively working to preserve cultural knowledge, to re-plant the reefs, and to remove invasive algal species. The seaweed resources of Hawai‘i are cherished, but are at risk. The future of seaweed cultivation, maintenance and revitalization of native populations, and preservation of cultural knowledge relies on the collaborative efforts of all stakeholders.

Keywords: aquaculture; conservation; invasive species; *limu*; marine macroalgae.

Introduction

The seaweed resources of the Hawaiian Islands are taxonomically diverse, biogeographically intriguing, ecologically complex, culturally significant, and economically valuable. The residents of Hawai‘i are equally diverse, and most people have ties to cultures in which seaweeds play major roles. When you ask people in the Hawaiian Islands if they eat seaweeds, the usual answer is “yes” – in *sushi*

rolls, in salads, in stews, with raw fish, or even in cakes and custards. Real seaweed connoisseurs will tell you what species they have in the refrigerator; for some it is *Gracilaria* or *Asparagopsis*; for others it is *Pyropia* or *Ulva*. The story of seaweed resources in the Hawaiian Islands is influenced by the geographic isolation of the islands, their dynamic volcanic development, and the deep tradition of human use of marine macroalgae that can be traced to the early Polynesian inhabitants of the islands. Numerous phycologists have made important contributions to the taxonomy of the Hawaiian marine flora: Charles Gaudichaud-Beaupré, Joseph F. Rock, Minnie Reed, Marie Neal, W.A. Setchell, Paul Galtsoff, G.F. Papenfuss, Max Doty, George Hollenberg, Gerry Kraft, Bernabé Santelices, Mitchell Hoyle, Lynn Hodgson, Bill Magruder, John Huisman, and most notably Isabella A. Abbott. The current state of our seaweed resources is impacted by over-harvesting, urban development, human population growth, invasive seaweed species, and climate change. Many reef restoration workers believe that the primary cause of the decline of native seaweed species is the reduction of freshwater flows into coastal waters. The future of Hawaiian seaweed resources – their utilization and their preservation – may take new directions as people look to the sea for sustainable sources of nutritious food as outlined in the 17 Sustainable Development Goals of the 2030 Agenda for Sustainable Development adopted in 2015 by 193 countries of the United Nations General Assembly (United Nations 2015). We followed the old Hawaiian saying: *‘A’ohe pau ka ‘ike i ka hālau ho’okahi* (not all knowledge is learned in one house or one learns from many sources), and gathered information for this paper from peer-reviewed publications, books, newspapers, magazines, radio broadcasts, government technical reports, websites, unpublished data, and in-depth personal interviews. The objectives of this report are to consolidate the current understanding of Hawaiian seaweed resources and to motivate people to increase the depth and breadth of our knowledge of these resources.

Marine environment of the Hawaiian Islands

The Hawaiian Island Archipelago (Figure 1) extends more than 3000 nautical miles from Hawai‘i Island (19°35’N,

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Figure 1: The Hawaiian Archipelago extends more than 3000 nautical miles from Hawai'i Island, the southernmost of the Main Hawaiian Islands, to Meiji Seamount, in the Emperor Seamounts. Image credit: © US National Oceanic and Atmospheric Administration.

Figure 2: True-color Terra MODIS (moderate resolution imaging spectrometer) image from May 27, 2003 reveals wind patterns around the Main Hawaiian Islands that create surface waves. The calmest waters are seen in the brightest silver gradient, like the leeward southwest shores of Hawai'i and Maui. Image credit: © Jacques Descloitres, MODIS Rapid Response Team NASA/GSFC (NASA, Visible Earth 2003).

155°23'W) to Meiji Seamount (53°11'N, 164°29'E), and is the oldest, most remote, and longest chain of islands, atolls, volcanos, guyots (tablemounts), and seamounts in the world. Seventy million years ago, the Hawaiian Hotspot erupted under the Pacific Plate, and formed Meiji, the oldest known Hawaiian island, now a drowned guyot (Grigg 2014). Movement of the plate carried Meiji north and westward, and continuing volcanic activity at the hotspot formed an isolated string of over 100 volcanos (Grigg 1988), whose nearest neighbor is Johnston Atoll over 600 km to the southwest, and whose closest continental land mass is over 5000 km away. As the Pacific Plate moves farther away from the hotspot, toward the northwest at about 8 cm year⁻¹, the older islands slowly subside and erode, forming atolls, which eventually sink below the waves. Today, the island of Hawai'i sits upon the Hawaiian Hotspot, and the most recent eruption started on May 3, 2018, and released 100 m³ s⁻¹ of lava for several weeks from "Fissure 8" to the sea (USGS, personal communication 2018).

The geology of the Hawaiian Archipelago is the story of millions of years of successive lava eruptions, island growth, reef development, and island degeneration, which has yielded a vast variety of marine environments. The older atolls have lagoons encircled by fringing reefs with limestone islets; the younger islands have basalt coastlines. Locations on a single island can differ in age, wind exposure, and local sea conditions (Figure 2), resulting in coastlines with rocky substratum, beaches of basaltic or calcareous sediments, steep sea cliffs, eroded karst, or fine-grained mud flats (Juvik and Juvik 1998). This variety of geological features creates many different aquatic environments, including brackish anchialine ponds, tide pools, intertidal zones, estuaries, and shallow

and deep subtidal habitats (Juvik and Juvik 1998). Additionally, traditional Hawaiian fishponds, some of which date back as early as the 14th century, are a major human-made feature that contribute to the story of seaweeds in the Hawaiian Islands (Kikuchi 1976). Seaweeds can be found in all of these habitats.

The Main Hawaiian Islands (MHI), Hawai'i Island north to Ni'ihau, and the Northwestern Hawaiian Islands (NWHI), Nihoa to Kure Atoll, lie in the center of the subtropical gyre in the North Pacific Ocean bounded by four major currents: the North Pacific Drift, the California Current, the North Pacific Equatorial Current, and the Kuroshio Current. Two currents flow eastward toward the Hawaiian Archipelago: the weak North Pacific Subtropical Countercurrent at about 20°N (Kobashi and Xie 2008, Grigg 2014), and the subsurface Hawaiian Lee Countercurrent (Figure 3) located at 19°N (Xie et al. 2001). The North Hawaiian Ridge Current (Figure 4) flows along the northeast coasts of the Hawaiian Islands. This boundary current has an average speed of 0.10–0.15 m s⁻² and a width of 100 km (Qiu et al. 1997). Drifter data show that the North Hawaiian Ridge Current is the northern branch of a westward moving interior flow, which bifurcates east of Hawai'i Island, and flows along the MHI until it shifts to a westward flowing current northwest of the island of Kaua'i. These patterns of circulation probably have changed little in 34 million years (Grigg 1988, 2014).

The waters surrounding the Hawaiian Islands are oligotrophic and sea surface temperatures typically

Figure 3: Current vectors in m s^{-1} at 37.5 m deep averaged for 1992–1998.

The Hawaiian Lee Countercurrent flows eastward toward the Hawaiian Islands at 19°N. Arrows show current speed and direction and contours show ocean temperature ($^{\circ}\text{C}$). The Main Hawaiian Islands are circled. Image credit: © Xie et al. (2001).

Figure 4: Average annual sea surface layer flows in the Main Hawaiian Islands.

The North Hawaiian Ridge Current flows along the northeast coasts of the islands from 19°N to 22°N. Dashed contours show 200-m isobaths; model shows areas shallower than 200 m as land. Image credit: © Qiu et al. (1997).

range from 25–28 $^{\circ}\text{C}$ in the MHI and 19–26 $^{\circ}\text{C}$ in the NWHI (Juvik and Juvik 1998, Veillerobe 2004). The prevailing tradewinds blow from the northeast (Figure 5). The islands are subject to North Pacific storms, which track from west to east in winter. June to November is hurricane and tropical storm season when tropical cyclones formed near Mexico spin toward the Hawaiian Islands. The Hawaiian Islands experience semidiurnal tides with maximum amplitude of about 100 cm, which create a narrow intertidal zone for Hawaiian seaweeds. High surf or wind-driven waves easily overwhelm low tides, and impact intertidal and shallow subtidal seaweed communities along Hawaiian shorelines. Numerous streams and springs provide freshwater input to the coastal zone, especially on the windward sides of the Hawaiian Islands. On leeward coasts of several islands, submarine groundwater

Figure 5: Northeasterly trade winds around the Main Hawaiian Islands blowing right to left.

Vectors and wind speeds (m s^{-1}) measured by the SeaWinds sensor aboard QuikSCAT satellite, Aug. 1999. Image credit: © Xie et al. (2001).

discharge is the predominant source of freshwater and nutrients to nearshore waters because the permeable basalt limits the formation of streams and surface water runoff (Oki 1999, Johnson and Wiegner 2014).

Marine flora of the Hawaiian Islands

There are over 522 species of marine algae reported from the Hawaiian Islands, including over 345 species in the phylum Rhodophyta, 107 species in Chlorophyta, and 62 species in Ochrophyta, class Phaeophyceae (Abbott 1999, Abbott and Huisman 2004). Marine macroalgae are crucial components of Hawaiian marine ecosystems, as nutrient recyclers, reef-consolidators, and food for herbivorous fish, invertebrates, and green turtles, the largest marine grazer in the archipelago (Russell and Balazs 2000, Arthur and Balazs 2008, Russell and Balazs 2009). Ziegler (2002) estimated marine macroalgal endemism at 15% (found only in the Hawaiian Islands) and 83% indigenous (native, but also found elsewhere). More recently, Huisman et al. (2007) opined that 150 species are endemic to the Hawaiian Islands, and

Sherwood et al. (2010) gave an estimate of 19.5% endemism for the Hawaiian marine algal flora. The geographic isolation of the Hawaiian Archipelago makes its seaweed biogeography somewhat of an enigma. The archipelago is considered part of the tropical Indo-West Pacific phyto-geographic region (van den Hoek 1984); however, the NWHI host a mixture of characteristic tropical species, plus cold-temperate species (e.g. *Desmarestia ligulata* (Stackhouse) J.V. Lamouroux), endemic species (e.g. *Codium hawaiiense* P.C. Silva & M.E. Chacana), and species with disjunct distributions (e.g. *Nereia intricata* Yamada) (Abbott and Huisman 2003, McDermid and Abbott 2006). Recently, at mesophotic depths (50–90 m deep) in the Hawaiian Archipelago, new taxa of green macroalgae: *Halimeda* J.V. Lamouroux, *Ulva* Linnaeus, and *Umbraulva* E.H. Bae & I.K. Lee (Verbruggen et al. 2006, Spalding et al. 2016) have been reported; but close to 40, intriguing, yet-to-be-described reds, greens, and browns have been collected (see Wagner et al. 2016 for photographs). Modern DNA analyses have provided evidence for taxonomic revision of Hawaiian members of *Akalahy-cus* Huisman, I.A. Abbott & A.R. Sherwood, *Galaxaura* J.V. Lamouroux, *Ganonema* K.-C. Fan & Yung-C. Wang, *Liagora* J.V. Lamouroux, *Stenopeltis* Itono & Yoshizaki, and *Ulva* (Huisman et al. 2004a,b,c, O’Kelly et al. 2010); new species, e.g. *Pihiella liagoraciphila* Huisman, I.A. Abbott & A.R. Sherwood (Huisman et al. 2003); cryptic species, previously unreported in the Hawaiian Islands, e.g. *Hydropuntia perplexa* (Conklin et al. 2014); and multiple genetic lineages of well-known, native species, i.e. *Spyridia filamentosa* (Wulfen) Harvey (Conklin and Sherwood 2012) and *Asparagopsis taxiformis* (Clark et al. 2018), which suggest multiple arrivals/colonization events of these species. Clearly, there are lifetimes of work to be done on the taxonomy, physiology, reproduction, and ecology of Hawaiian seaweeds!

Past uses of Hawaiian seaweeds

In the Hawaiian Islands prior to Western contact (pre 1779), *limu* (Hawaiian word for a plant growing in a wet place) was a regular part of the diet and accompanied most meals. At least 63 species of *limu* were utilized by Hawaiians, of which only 29 species can be identified by both their Hawaiian and scientific names (Abbott 1996); of those about half were commonly eaten (Table 1). Traditionally, Hawaiians mixed a variety of seaweeds with raw and cooked fish, shellfish, raw dog liver, and cooked meat. *Limu* was also a relish to eat with *poi* (cooked, mashed taro) (Abbott 1996). Seaweeds were the people’s spices and served as their vegetables (Reed 1907, Fortner

1978). Seaweeds, through their collection and preparation, provided a special niche for Hawaiian women, who, until the introduction of Christianity (circa 1819) and the fall of the *kapu* (taboo) system, were forbidden to eat many other nutritious food items, including pork, coconuts, turtles, most varieties of bananas, and several species of fish (Abbott 1978). Knowledge about *limu* was passed from mother to daughter. Nutritionally, seaweeds were probably essential in the traditional Hawaiian diet because the *limu* may have contributed vitamins and important elements not found in the three primary food items: fish, taro, and breadfruit. Hawaiian seaweeds may have also provided measurable amounts of protein and dietary fiber (McDermid and Stuercke 2003, McDermid et al. 2005).

Seaweeds were also important to Hawaiian culture in medicine, rituals, legends, and in commerce as a valuable item of exchange between coastal and upland families (Abbott 1978). Many different kinds of *limu* were used by *lapa’au* (healing) practitioners to treat a wide range of ailments: small cuts and scrapes, asthma, thrush, miscarriage, sprains, and alimentary problems (Fortner 1978, Abbott 1996). *Limu kala* (*Sargassum aquifolium*, formerly *Sargassum echinocarpum*) was used in adornment for dancers, healing ceremonies, and purification ceremonies for the mourners of a dead relative (Fortner 1978). In conflict resolution or forgiveness ceremonies (*ho’oponopono*), still practiced today, participants each eat a blade of *S. aquifolium* to mark the end of the ceremony and the release of the interpersonal tensions (Abbott 1996). *Ulva lactuca* (*limu pālahalaha*) was present in many legends and was a sacred seaweed for Hawaiian families whose *’aumakua* or family deity was the shark (Abbott 1996).

Present uses of Hawaiian seaweeds

Today, as in the past, Hawaiian species of macroalgae are consumed daily, but now by people of many diverse ethnic backgrounds: Hawaiian, European, Japanese, Korean, Filipino, and others (McDermid and Stuercke 2003). In 1996, 18 seaweed species were in use, seven of which could be found in fish markets (Abbott 1996); however, in 2018, only two genera are regularly for sale: *Gracilaria* Greville, which is favored by all ethnic groups, and *Asparagopsis* Montagne, which is used sparingly as a relish because of its powerful flavor and its exorbitant cost. *Gracilaria* or *ogo* (the Japanese name) is used for fresh food, especially *po-ke*, which is cubes of raw fish, tuna or marlin or other fish, mixed with chopped seaweed. “The success of many a cocktail party has depended on the availability and the

Table 1: Commonly eaten edible species identified with both Hawaiian and scientific nomenclature (Abbott 1978, 1996, 1999, Abbott and Huisman 2004).

Phylum	Species	Hawaiian name	Meaning	Habitat	Uses
Rhodophyta	<i>Asparagopsis taxiformis</i> Delile	<i>kohu</i> or <i>līpehe</i>	Supreme	Intertidal to shallow subtidal	Soak overnight, pound, salt, roll into a ball, use in <i>po-ke</i>
Rhodophyta	<i>Ahnfeltiopsis concinna</i> J. Agardh	<i>ʻakiʻaki</i>	Nibbles, bite-bite	Basalt rocks in the intertidal	Chop well, bake in <i>imu</i> (underground oven)
Rhodophyta	<i>Gracilaria coronopifolia</i> J. Agardh	<i>manauea</i>	Erect branches	Ranges from tidepools in mid-intertidal to the shallow subtidal (up to 4 m) and eroded limestone	Chop, use in <i>po-ke</i> , or salt for later use
Rhodophyta	<i>Gracilaria parvispora</i> I.A. Abbott	None ^a	None	Preference for sandy areas overlying rock with moderate water motion	Chop, use in <i>po-ke</i> , or salt for later use
Rhodophyta	<i>Grateloupia filicina</i> (J.V. Lamouroux) C. Agardh	<i>huluhuluwaena</i> or <i>pakeleawaʻa</i>	Pubic hair	Preference for rocks lightly overlain by sand; low intertidal to shallow subtidal; also found in patches where freshwater streams or springs meet the sea	Finely chopped and lightly salted; eaten with liver, fish, beef, or octopus
Rhodophyta	<i>Halymenia hawaiiiana</i> Hernández-Kantún et A.R. Sherwood	<i>lepe-o-Hina</i>	Fringe or shawl of the goddess <i>Hina</i>	Grows on subtidal rocks up to 10 m	Rinse, chop, and salt; eaten with stew or blanched then pickled with vinegar
Rhodophyta	<i>Laurencia dotyi</i> Saito	<i>līpeʻepeʻe</i>	Hidden	Intertidal; found on eroded coral and basalt in holes or along margins of shallow pools	Chop and eaten with raw fish
Rhodophyta	<i>Laurencia nidifica</i> J. Agardh	<i>māneoneo</i>	Ticklish, peppery	Low intertidal to shallow subtidal; found on eroded coral and basalt	Rinse and salt; used as a relish
Rhodophyta	<i>Laurencia succisa</i> A.B. Cribb	<i>līpeʻepeʻe</i>	Hidden	Found on eroded coral and basalt tidepools	Chop and eaten with raw fish
Rhodophyta	<i>Pyropia vietnamensis</i> (Tanaka et Pham-Hoàng Ho) J.E. Sutherland et Monotillamaensis	<i>paheʻe</i>	Slippery	Grows on smooth basalt boulders in high intertidal; occasionally found in shaded cracks with high wave action	Rinse in seawater, cut in small pieces, salt, and let stand for a few hours; eaten with delicately flavored raw fish
Chlorophyta	<i>Codium edule</i> P.C. Silva	<i>wāwaeʻiole</i>	Rat's foot	Shallow water, reef flats, boulders; up to 20 m in subtidal	Chop or pound, use with fish stew, or in "salad"
Chlorophyta	<i>Codium reediae</i> P.C. Silva	<i>aʻulaʻula</i>	Red fragrance	Found on coral rubble in shallow subtidal; can appear in drift	Chop or pound, use with fish stew, or in "salad"
Chlorophyta	<i>Ulva lactuca</i> Linnaeus	<i>pālāhalaha</i>	Spread out	Both brackish and marine environments; found on various substrata in intertidal, sometimes epiphytic, can appear in drift; subtidal to 5 m	Chop into pieces, mix with other <i>limu</i> ; used as an adornment in traditional hula attire

Table 1: (continued)

Phylum	Species	Hawaiian name	Meaning	Habitat	Uses
Chlorophyta	<i>Ulva prolifera</i> (O.F. Müller) J. Agardh	'ele'ele	Black	Sandy rocks in intertidal; concrete pilings and breakwaters; brackish water	Rinse in freshwater, drain, salt. Prepared 'ele'ele is favored for its strong flavor for stews and with soft, raw fish
Ochrophyta Class Phaeophyceae	<i>Dictyopteris australis</i> Sonder	<i>lipoa</i>	<i>Limu</i> that is gathered from the deep	Low intertidal pools and channels reaching 50 m; common on windward coasts or areas with moderate currents and waves	Traditionally eaten heavily salted and preserved
Ochrophyta Class Phaeophyceae	<i>Dictyopteris plagiogramma</i> Montagne	<i>lipoa</i>	<i>Limu</i> that is gathered from the deep	Low intertidal reaching 80 m; on rocks and epiphytically on <i>Sargassum</i> spp.	Chop or pound, and salt, usually eaten with fish or meat
Ochrophyta Class Phaeophyceae	<i>Sargassum aquifolium</i> (Turner) C. Agardh	<i>kala</i>	To forgive	Mid intertidal up to 22 m; abundant in rocky intertidal with moderate to high wave action; reef flats	Finely chop young blades, use in stuffing, soups, or deep fry blades whole

^aThe name used in the islands is *ogo* (derived from the Japanese name "ogonori").

[Correction added on 15 August, 2019 after online publication: In Table 1, column 3, line 4 the Hawaiian name "manauea" was replaced]

freshness of this dish" (Abbott 1978). *Gracilaria* is also sold as pickled *ogo*, such as *ogo namasu* (Japanese style), and *ogo kim chee* (Korean preparation). "Prepared *limu* is a most acceptable gift to take when visiting, whether prepared in Hawaiian, Japanese, Korean or Filipino ways" (Abbott 1978). *Po-ke* has recently become popular on a global basis, which could perhaps spur increased interest in Hawaiian macroalgal species. Currently a dried seaweed and salt mixture for *po-ke* preparation is marketed by a Hawai'i-based company (Noh Foods), but ironically contains dried macroalgae produced in California. Current per capita rates of *limu* consumption in Hawai'i have not been scientifically analyzed. A survey of 180 high school students on O'ahu found that an average of three meals or snacks per week contained seaweed, with more being consumed by students of Hawaiian descent (Hart 2012).

In 2003, 22 edible Hawaiian macroalgae were analyzed for protein, lipid, carbohydrate, ash, caloric, mineral, and vitamin content (McDermid and Stuercke 2003). The red species, *Halymenia hawaiiiana* and *Pyropia vietnamensis* had the highest protein content based on dry weight, 21.2% and 16.5%, respectively. *Pyropia vietnamensis* had the highest content of β -carotene (Vitamin A) with 430 IU per gram dry weight. Vitamin A was the only vitamin that was consistently measured in detectable quantities in all species. Edible Hawaiian seaweeds are appealing and appetizing to people, not only because of nutritional value, but also because of their crisp texture, vivid colors, pungent odors, and spicy flavors. More of these native Hawaiian species that are not currently in cultivation should be considered for aquaculture endeavors.

Potential future uses of Hawaiian seaweeds

Many Hawaiian seaweeds are well-known for their secondary metabolites and diverse natural products (Doty and Aguilar-Santos 1966, Bureson et al. 1976, Moore 1977, Fenical 1982, Erickson 1983). Marine macroalgae often produce bioactive compounds as chemical defenses against bacterial infections, excessive UV radiation, predators, and epiphytes (Cardozo et al. 2007, Rindi et al. 2011, Shannon and Abu-Ghannam 2016). Bioactive compounds have been identified among all three main phyla of marine macroalgae (Blunt et al. 2012), but only a handful of studies have assessed bioactive properties and biomedical uses of Hawaiian seaweeds.

Some seaweeds produce antioxidants, which neutralize reactive oxygen species by electron donation

(Murugan and Iyer 2013). Kelman et al. (2012) reported antioxidant activity in Hawaiian species from all three phyla. The highest antioxidant power was measured in a brown species, *Turbinaria ornata* (Turner) J. Agardh, followed by two green species, *Gayralia oxysperma* (Kützinger) K.L. Vinogradova ex Scagel et al. and *Chaetomorpha antennina* (Bory) Kützinger, and a red, *Polysiphonia howei* Hollenberg (Kelman et al. 2012). Hart (2012) measured high antioxidant power in Hawaiian *Ulva flexuosa* Wulfen, followed by *Dictyota acutiloba* J. Agardh, *Martensia fragilis* Harvey, and *Codium edule*. Martin (2017, unpublished) tested eight species for antioxidant activity. *Amansia glomerata* C. Agardh, *Chnoospora minima* (Hering) Papenfuss, and *Halimeda macroloba* Decaisne had the highest antioxidant potentials; *A. glomerata*'s antioxidant value was higher than that of the control, ascorbic acid (Vitamin C).

Hawaiian seaweeds have other potential uses that remain to be developed. Antibacterial activity of Hawaiian seaweeds is present in *Ulva fasciata* Delile and *Gracilaria salicornia* (Vijayavel and Martinez 2010). *Ahnfeltiopsis concinna* is an important ingredient in a facial mask sold by Algenist® Skincare, who came to Hilo, Hawai'i, to film the species "in the wild." Recently, *Asparagopsis taxiformis* in Hawai'i has generated much interest because results from *in vitro* studies in Australia (Kinley et al. 2016, Machado et al. 2016, Vucko et al. 2017), trials with artificial rumens, and experiments with live dairy cows at the University of California, Davis (Kennedy 2018) demonstrated potent anti-methanogenic activity in *A. taxiformis* and its natural products. Methane gas in cattle burps and flatulence are a major contributor to greenhouse gases worldwide. Researchers at the University of Hawai'i at Hilo have received several requests for unrealistically large amounts of fresh Hawaiian *A. taxiformis* for experiments and aquaculture ventures. *Asparagopsis taxiformis* is a multiphyletic species with genetically identifiable lineages worldwide (Clark et al. 2018). Three *A. taxiformis* lineages were distinguished from O'ahu Island, based on mitochondrial sequencing and metabolite analysis. One *A. taxiformis* lineage contained several halogenated metabolites characteristic of only that lineage (Clark et al. 2018).

The cultivation of Hawaiian macroalgae may become a valuable tool for water quality remediation, especially in areas in the Hawaiian Islands that are impacted by organic nutrient runoff from human waste and agriculture. The potential also exists to use macroalgal species to mitigate ocean acidification impacts. Currently plans are being made by the O'ahu Waterkeeper Alliance and two of the authors (Haws and McDermid) to initiate trials

utilizing macroalgae for these purposes. Undoubtedly, as additional avenues of macroalgal research develop, new uses for Hawaiian seaweeds will arise.

Wild-harvest of Hawaiian seaweeds

Gathering seaweeds in the Hawaiian Islands is not just about collecting a food source, but is also a way for people to "connect with place," and to observe details about the seaweeds' growth, reproduction, and seasonality (Hart 2012). The connection that seaweed collecting creates among people is cherished: "Whole families from grandparents to their small grandchildren are often seen at favored *limu* places, gathering a variety of edible seaweeds, exchanging greetings and recipes with others, and enjoying a day in the sunshine" (Abbott 1978, p. 410). In 1976, approximately 36,000 kg of fresh *limu* were gathered by families for their own use; another 36,000 kg fresh weight of two species of wild *Gracilaria*, and 11,340 kg fresh weight of other Hawaiian seaweed species were sold in markets (Abbott 1978). A variety of wild-harvested seaweeds were once common in local markets, but species availability has diminished. At least eight wild-harvested species were sold in 1976; four species were available in 1985; only two are found in 2018 with significant price increases (Table 2). Probably the most favored and expensive (Abbott 1999) species available for purchase is *Asparagopsis taxiformis* (*limu kohu*), which currently sells for US\$25.00–27.00 lb⁻¹ fresh weight (=US\$55–60 kg⁻¹). In 1986, the State Division of Aquatic Resources (DAR) began recording the annual harvest of three species of seaweeds and the number of permits issued for the collection of *A. taxiformis* and *Codium* spp. (Figure 6). "Wild catch" and the number of collecting permits have fluctuated wildly during the last 30 years, but show a general decline in recent years. Cultivation of native and introduced species of *Gracilaria* has attempted to fill the void caused by lack of wild-harvested seaweeds.

The first and only report of seaweed toxicity in the Hawaiian Islands was made in 1994, when people consumed wild-harvested *Gracilaria coronopifolia* from Maui in early September and experienced burning sensations in the mouth and throat and/or serious gastrointestinal illness (Marshall and Vogt 1998). Assays of the seaweed from the picnic and from the original harvest site contained debromoaplysiatoxin and aplysiatoxin, two toxins known to be produced by the cyanobacterium, *Lyngbya majuscula* Harvey ex Gomont (Moore 1981). Marshall and Vogt (1998) concluded that the

Table 2: Market price for species in Hawaiian markets.

Species	Preparation	Price in 1976 (USD lb ⁻¹)	Price in 1985 (USD lb ⁻¹)	Price in 2018 (USD lb ⁻¹)
<i>Asparagopsis taxiformis</i> (kohu)	Salted	\$4.50–9.00	\$12.00–15.00	\$25.00–27.00
<i>Codium</i> spp. (wāwae'iole)	Fresh	\$0.79–1.29	\$2.00	–
<i>Caulerpa racemosa</i> (Forsskål) J. Agardh (sea grapes)	Fresh	\$0.89–1.19	\$1.95–2.95	–
<i>Dictyopteris</i> spp. (lipoa)	Salted	\$3.79–4.75	–	–
<i>Gracilaria</i> spp. (manauea)	Fresh	\$1.10–1.59	\$2.95–3.95	\$5.00–6.79
<i>Grateloupia filicina</i> (huluhuluwaena)	Salted	\$2.00–3.00	–	–
<i>Halymenia</i> spp. (lepe-o-Hina)	Fresh	\$1.25	–	–
<i>Ulva prolifera</i> ('ele'ele)	Salted	\$2.09–3.59	–	–
<i>Eucheuma spinosum</i> J. Agardh (introduced)	Fresh	\$0.79–0.99	–	–

Data are from Fortner (1978), Abbott (1988), and a local Hilo grocery store in August 2018. To convert prices from USD lb⁻¹ to USD kg⁻¹, divide values by 0.45.

Figure 6: Annual wild-harvest of three edible Hawaiian species from 1986 through 2017 statewide and total number of permits issued by Hawai'i State Department of Land and Natural Resources (DLNR).

Data for *limu kohu* (*Asparagopsis taxiformis*), *limu wāwae'iole* (*Codium* spp.), and *limu manauea + ogo* (*Gracilaria* spp.) were obtained from the Division of Aquatic Resources (DAR) (R. Okano, personal comm. 2018) and from DLNR reports (1990, 1994, 2001, 2002). DLNR *Gracilaria* data from 1989 only include the first 6 months of the year.

toxins possibly came from the blue-green epiphytes they observed on the *G. coronopifolia* samples!

Commercial cultivation of seaweeds in the Hawaiian Islands

Only two commercial seaweed farms are currently operating in the state of Hawai'i, down from three *Gracilaria*

farms recorded in 1989 (DLNR 1990). One of the limitations to seaweed culture in the state is the short shelf-life, which often prevents export to distant, external markets.

Royal Hawaiian Sea Farms Inc. started on the west coast of Hawai'i Island in 1987, and is the longest-running seaweed aquaculture business in the Hawaiian Islands. Initial experimentation involved cultivation of *Pyropia tenera* (Kjellman) N. Kikuchi, M. Miyata, M.S. Hwang & H.G. Choi and *Pyropia yezoensis* (Ueda) M.S. Hwang & H.G. Choi (Mencher et al. 1983, Mencher and Katase

Figure 7: *Gracilaria coronopifolia* is grown in large tanks at Royal Hawaiian Sea Farms Inc. on Hawai'i Island.

Image credit: © Steve Katase.

1988), and then the farm switched to *Gracilaria* spp. and *Codium reediae*. Royal Hawaiian Sea Farms once cultivated *Gracilaria tikvahiae*; but Steve Katase, owner of the farm, says he now grows the Hawaiian endemic, *Gracilaria coronopifolia*, and two other varieties of *Gracilaria* in tumble culture with a mix of nearshore surface seawater (24–28°C) and cold (4–6°C), nutrient-rich seawater, pumped from a depth of 914 m off Keāhole Point. One to two US tons (=0.9–1.8 metric tons) of *Gracilaria* (Figure 7) are harvested weekly and sold to supermarkets and fish markets on Kaua'i, Maui, O'ahu, and Hawai'i Island, as well as shipped to California, Washington, and Nevada. During his 31 years of farming seaweeds, Steve Katase has survived long days in the hot Kona sun, ubiquitous diatom blooms, *Gracilaria* Gall Syndrome causing twisted witch's broom-branching in the late 1990s (Center for Tropical and Subtropical Aquaculture 1996), poor growth during unusually rainy years, and fluctuations in customer tastes and demand. Katase describes seaweed aquaculture in Hawai'i as a "fragile business." His goal is someday to pass on this business to someone interested in growing seaweed and carrying on the tradition of eating fresh local *limu* – "it's important and healthy."

The other commercial seaweed farm, Marine AgriFuture LLC, now operating as Olakai Inc., was founded in 2006 on the north shore of O'ahu, at the site of a previous seaweed farm operated by Rick Spencer and Fred Mencher. Dr. Wenhao Sun uses a "sustainable ecosystem approach" in ponds (1 m deep, 1.5 m wide, and 33 m long) to cultivate the vascular plant, "Sea Asparagus" (pickleweed or *Salicornia* sp.), and several types of *Gracilaria* with the brand names "Kahuku brown ogo," "Robusta," and "Red Ogo." Olakai currently harvests twice a week and produces approximately 1134 kg week⁻¹ of seaweed. The Kahuku brown ogo is fast growing, very crunchy and succulent, and can be refrigerated to extend its shelf-life. The Robusta is slower growing. Olakai sells fresh seaweed to seafood distributors,

supermarkets, farmers' markets, grocery stores, and restaurants. Pickled ogo is sold for US\$8 in 8 oz (237 ml) jars. Dried Kahuku brown ogo is sold to the mainland US and reportedly regains its crunchiness after rehydration.

Ke Kua'aina Hanauna Hou, a non-profit, community economic development organization – now defunct – was established in 1991 to help the local, native Hawaiian community on Moloka'i develop ways for individuals or groups to earn an income while maintaining their land-use traditions and stewardship of natural resources. In 1992, University of Arizona researchers partnered with Ke Kua'aina Hanauna Hou to implement a community-based system for culturing *Gracilaria*. The collaboration was a response to declines in local, wild seaweed resources, the commercial value of *Gracilaria parvispora*, the traditional usage of *limu* in Hawaiian culture, and the need to re-establish *Gracilaria* on the reef. Ke Kua'aina Hanauna Hou provided the start-up support for growers, and then later purchased the harvested seaweed. The project incorporated a hatchery, which produced spore-coated substrata and sporelings for distribution to outplant on the reef or in polyculture with fish and shrimp, a cage-culture farm for grow-out, and a processing facility (Ryder et al. 2004a). Farmers planting and harvesting *G. parvispora* in leased coastal fishponds, received US\$1.75 to US\$2.75 lb⁻¹ (=US\$3.86–6.06 kg⁻¹) for the ogo (Kojima 2000). In 1999, total sales of *G. parvispora* or "long ogo" or "*limu loa*" by Ke Kua'aina Hanauna Hou were 10,670 kg with a wholesale market value of approximately US\$75,000. By combining ogo culture with shrimp and fish culture, production increased substantially. Long ogo grown on Moloka'i sold for US\$7 kg⁻¹ (US\$2.20 kg⁻¹ more than other seaweeds on the market), and sales of Moloka'i ogo were approximately US\$250,000 in 1999 (Ryder et al. 2004a). In 2000, about 360 to 410 kg of seaweed a week were sold to O'ahu, plus about 70 kg of bottled Moloka'i Pickled Ogo, Moloka'i *Limu Salsa*, and Moloka'i Kukui Nut Relish (Kojima 2000).

Several aquaculture experiments were conducted on Moloka'i in conjunction with Ke Kua'aina Hanauna Hou using *Gracilaria parvispora* grown in floating cages. Algal thalli fertilized with shrimp effluent had significantly higher growth rates (8.8–10.4% day⁻¹) than thalli fertilized with inorganic fertilizer (4.6% day⁻¹) (Nelson et al. 2001). Nagler et al. (2003) pulse-fertilized *G. parvispora* thalli in tanks with either mullet and milkfish effluent or inorganic ammonium compounds for 1 week, then transferred them to a nutrient-limited seawater lagoon to assess growth rates and changes in nitrogen content. Rapid growth rates (8–10% day⁻¹) were observed for 2 weeks after transfer, but growth stopped after 21 days when stored nitrogen was depleted. Ideal stocking density, based on growth

rates, was 2 kg m⁻³. *Gracilaria* in tanks showed relative growth rates of 2.8–8.9% day⁻¹ with water velocities as high as 13.7 cm s⁻¹; in shallow lagoons with water velocities ranging from 3.6–11.6 cm s⁻¹, relative growth rates were 0.02–10.3% day⁻¹ (Ryder et al. 2004b).

Ke Kua‘aina Hanauna Hou’s business model was to grow *Gracilaria* and provide free seed stock to families who either owned fishponds or had access to fishponds. According to the business plan and a handshake deal, the families could use that *limu* for their own consumption or give it away to family and friends, but they could not sell their *limu* except to Ke Kua‘aina Hanauna Hou, which then shipped the *Gracilaria* to a distributor in Honolulu (Jensen 2004). The business plan worked for a few years, until an individual decided to sell directly to the distributor. The collapse of the business model caused Ke Kua‘aina Hanauna Hou to discontinue operations. The project with such good intentions, a desirable and marketable product, proven success, and scientific support, has been left idle for about 15 years. Now Ke Kua‘aina Hanauna Hou wants to re-start *limu* growing operations, not for commercial sale, but for education and habitat restoration purposes. *Limu* education resumed in summer 2018 with a visit by a group of 25 high school students (Wally Ito, Limu Hui, 2018, pers. comm.).

A semi-commercial seaweed aquaculture endeavor was begun in 1990 at Wai‘anae High School on the west coast of O‘ahu with a saltwater well (Dana Hoppe, 2018, pers. comm.). Science students participate in the maintenance of the facility, raising the seaweeds, and running the small-scale business. Wai‘anae High School was grandfathered into the Environmental Protection Agency (EPA) water standards, and their effluent water empties into the storm drain system and ends up in a canal that runs through the high school campus. Because Wai‘anae receives so little rainfall, the canal was filled with the tank effluent, which created a saltwater “ecosystem.” Some of the seaweed raised in the tanks escaped and filled the canal with *ogo* (*Gracilaria coronopifolia* and *Gracilaria parvispora*). For many years, the students used the canal as their seedstock pond and transferred thalli to round tanks of various sizes. The classes sold fresh seaweed and pickled seaweed to the nearby community. At peak production, the students grew about 1800–2300 kg of seaweed per year. The funds raised, ranging from US\$2000 to US\$10,000 at peak production, have been used to support field trips. Some worried that the students’ *ogo* farm unfairly competed with commercial seaweed growers because the high school did not need to pay for farm employees or utilities or land use. Due to climate change, siltation, and introduction of invasive species, the seedstock canal has been compromised and it no longer is a reliable source for

seaweed. In 2017–2018, sales were very limited because the seaweed was needed for student science projects. The teacher has recently received two grants to bio-remediate the canal and try to create a seedstock pond at the high school facility, so that production can resume and again generate funds for the program.

Other seaweed cultivation efforts in the Hawaiian Islands

Seaweeds, not for human consumption, are grown at several facilities, both public and private operations. The Waikiki Aquarium in Honolulu, O‘ahu, uses seaweed for a “little bit of everything”: fish, turtle, and invertebrate food, nutrient removal, and decoration. The aquarists have used *Gracilaria*, *Caulerpa* J.V. Lamouroux, *Codium* Stackhouse, *Ulva*, and *Chaetomorpha* Kützting. At the Mokupāpapa Discovery Center in Hilo, Hawai‘i, *Caulerpa lentillifera* J. Agardh is utilized to strip nutrients from the seawater in the recirculation system for a large fish aquarium. The Four Seasons Resort has *Gracilaria* growing in their fishponds. The Pacific Aquaculture and Coastal Resources Center of the University of Hawai‘i at Hilo currently cultivates *Gracilaria parvispora*, *Gracilaria coronopifolia*, and *C. lentillifera* (Figure 8), and has used *Asparagopsis taxiformis* and *Codium edule* in growth trials (Haws, 2018, personal comm.). Large-scale cultivation of a patented strain of dulce (*Devaleraea mollis* (Setchell et N.L. Gardner) G.W. Saunders, C.J. Jackson et Salomaki occurs at the Big Island Abalone Corporation at the Natural Energy Laboratory of

Figure 8: *Caulerpa lentillifera* is cultivated at the Pacific Aquaculture and Coastal Resources Center of the University of Hawai‘i at Hilo.

Image credit: © Karla McDermid.

Hawai'i Authority (NELHA) on the west coast of Hawai'i Island. This seaweed, originally imported from the Pacific coast of the US, is not grown for commercial sale, but to provide live, fresh food for premium Ezo abalone (*Haliotis discus hannai* Ino, 1953), which are native to Japan (Dennis 2007). Big Island Abalone Corporation farms over 2 million abalone and over 30 large circulating tanks of dulse on about 4 ha (=10 acres) using a constant supply of cold, deep seawater and warm, surface seawater. Big Island Abalone Corporation started as a business in 1998 and became a commercial entity in 2001. Kampachi Farms, a small research company based at NELHA, is working to develop an offshore mariculture array on the west side of Hawai'i Island. Their Blue Fields Project plans to use a single point mooring as attachment and deep seawater as a source of nutrients for the array. Kampachi Farms is conducting a series of land-based tank trials using native and/or endemic Hawaiian species. Their aim is to produce enough biomass to be a source of food for humans and animals, and as material for biofuels (Advanced Research Projects Agency-Energy U.S. Department of Energy 2018).

The State of Hawai'i cultivates *Gracilaria parvispora*, *Ulva* spp., *Agardhiella* sp., and *Halymenia hawaiiiana* in tumble culture to feed juvenile, native sea urchins (*Tripneustes gratilla* Linnaeus, 1758 or collector urchins or *hāwa'e*) as part of a large-scale sea urchin hatchery opened in 2010 at the Ānuenue Fisheries Research Center in Honolulu, O'ahu. The urchins are raised from eggs and sperm spawned on site and grown up to 15 mm diameter, at which time they are released into Kāne'ohe Bay to control invasive, non-native seaweeds, e.g. *Kappaphycus* Doty. During initial growth experiments in 2010, 20–40 kg month⁻¹ of the seaweeds were produced. From 2011–2015, *Ulva* was used primarily as a settlement cue for urchin larvae. Combined production of *G. parvispora*, *Agardhiella* sp., and *H. hawaiiiana* was 60–110 kg month⁻¹ in 2011–2013. Average combined seaweed production rose to 110 kg month⁻¹ between July 2013 and June 2018, with greatest harvest biomass in summer months (up to 351 kg month⁻¹). The farm manager, Dave Cohen, reported small problems with his farmed species: *Ulva* spp. tends to fall apart; *H. hawaiiiana* is not preferred by the urchins; *Agardhiella* sp. is consumed readily only by some urchin cohorts; and *H. hawaiiiana* changes morphology from large foliose blades in downwelling silos to thin branches with pointy apices in open tanks with high light levels. *Sargassum* sp. has also been used as a settlement cue, but attempts to grow and reproduce *Sargassum* sp. have not been very successful. Ānuenue Fisheries Research Center also has some *Grateloupia filicina* (*limu huluhuluwaena*), and *Ulva prolifera* (*limu 'ele'ele*) in culture in partnership with The

Limu Hui, a community group focused on reef restoration (see Conservation Issues and Responses below).

Also on the island of O'ahu, *Gracilaria salicornia* is cultivated by a private, non-profit organization, Paepae o He'eia that restored and now maintains an 800-year old, 35.6 ha (=88 acre) brackish water He'eia Fishpond, whose lava and coral rock walls are built on the fringing reef along the shore of Kāne'ohe Bay. Between 2004 and 2012, Paepae o He'eia removed, by hand, 45.4 metric tonnes of *Kappaphycus*, *Acanthophora spicifera*, and *G. salicornia*, and gave it to farmers to use as fertilizer (Paepae o He'eia 2018).

Despite the importance of Hawaiian seaweeds as human food sources, marine animal fodder, reef restoration tools, and cultural icons, the future of cultivation of Hawaiian seaweeds is in jeopardy with so few growers and so few species in cultivation. More research and development of techniques to cultivate native species are urgently needed.

Conservation issues and government responses

The first documented seaweed cultivation and conservation efforts in the Hawaiian Islands are credited to Queen Lili'uokalani at the turn of the 19th century. The story has been part of local oral folklore for generations (Fortner 1978, Abbott 1996): Queen Lili'uokalani transplanted her favorite *limu huluhuluwaena* or *pakeleawa'a* (*Grateloupia filicina*) to the reef in front of her Waikiki house in Honolulu, O'ahu. An article in the Honolulu newspaper *Ka Na'i Aupuni* announced the following:

This communication is being conveyed to all who swim or fish in the sea at Hamohamo in Waikiki Kai, Honolulu, O'ahu, that Queen Lili'uokalani makes known these restrictions: the *pakeleawa'a* seaweed is not to be harvested, also the *huluhuluwaena* seaweed, 'opihi shellfish, ālealea shellfish, 'ina sea urchins, hā'uke'uke sea urchins and pipipi shellfish, in the area fronting the royal compound. It was her own royal hands that planted and caused to multiply all of these items that have been listed above, and whoever goes to collect this sea life that is now placed under regulation will be arrested and fined according to the law. All of these marine life forms were propagated by the Queen, some were brought from Hilo, some from Lahaina, some from Moloka'i and from Kaua'i too, and from Waialua, O'ahu as well. (Carter 1906).

In recent years, long-time residents in the Hawaiian Islands have noticed changes in the distribution and abundance of populations of native seaweeds, especially edible species: “the disappearance of subtidal beds... of *limu lipoa* is not explainable” (Abbott 1996); “when I was little, *limu* was all over...so plentiful. Today, 'a'ohe – no

more nothing” (Hiraishi 2018b). “It’s been about 5 years that *limu* populations crashed. We do not see *Codium*, *Caulerpa*, *Sargassum*, or *Dictyopteris* like before. The *limu* do not wash up on the beach as they used to. I miss my *huluhuluwaena* along the beach road. Our shorelines have changed” (S. Hau, personal comm. 2018).

Gracilaria coronopifolia was and still is so popular to eat, that overharvesting led to declines in wild populations in the 1970s–1980s. This decline was the impetus for legislative action to protect *Gracilaria* and regulate its harvest. The State of Hawai‘i prohibits collection of *Gracilaria* with the holdfast and when the thallus has “reproductive nodes” (cystocarps). Bag limit regulations are also outlined: for home consumption, one person is allowed one pound per day. For commercial purposes, one marine licensee is allowed 10 pounds (4 kg) per day (excluding the island of Maui where no commercial take is permitted) (DLNR, DAR 2018a). This regulation has been criticized for not adequately protecting *Gracilaria* beds (Bakutis 1999) because it promotes commercial harvest with a greater bag limit. Some Maui residents attribute their relatively plentiful wild *Gracilaria* to the ban on commercial harvest on that island (Bakutis 1999), but no scientific comparative study has been conducted. In 2011, a *limu* management area at ‘Ewa Beach on O‘ahu was established by the state (Hawai‘i Revised Statutes § 188–22.8); a person, including a person with a commercial fishing license, may hand-pick a maximum of one pound (0.45 kg) for all types of *limu* combined in the *limu* management area from 6:00 a.m. to 6:00 p.m., only during the months of July, November, and December of each year. However, any person exercising native Hawaiian gathering rights and traditional cultural practices is exempt from this regulation. This effort is one of many conservation efforts in Hawai‘i that aim to restore more local and indigenous control over the use of natural resources (Kamakaala and Sakoda 2017).

Hart et al. (2014) enlisted fifty-five high school students from four public schools on O‘ahu to interview community members about *limu* gathering. Of those interviewed, 30 adults were knowledgeable *limu* gatherers, and all stated there was either a “decline” (76%) or a “serious decline” (24%) in wild seaweed abundance on O‘ahu. Some interviewees defined the declines in terms of individual species, while others noted reduced quality in size, cleanliness, or taste. Interviewees also classified what they believed to be potential causes of macroalgal decline (Table 3).

Twenty macroalgal species (Table 4) have been introduced since the 1950s, either intentionally for aquaculture or food, or accidentally on boat hulls, to the Hawaiian Islands (Doty 1961, Glenn and Doty 1990, Conklin et al.

Table 3: Survey results for perceived causes of macroalgal decline in the Hawaiian Islands (Hart et al. 2014).

Factor implicated in decline	Number of interviewees who mentioned this factor
“Over-picking” (gathering more than you need or gathering to sell)	17
Pollution	7
Development	6
More people gathering	6
Improper harvest technique	4
Climate change	2
Invasive species	2
Unspecified degradation	4
Not sure/don’t know	5

2014). Most of these species became naturalized and expanded their distribution from the original point of introduction, and are now considered alien, invasive seaweeds (Rodgers and Cox 1999, Smith et al. 2002) that compete with native species, contribute to the decline of reef health, and sometimes pile up on beaches. Invasions of non-native algal species are a major driver of coastal ecosystem change worldwide (Schaffelke et al. 2006, Williams and Smith 2007). In the Hawaiian Islands, the non-native red algal species of particular concern are *Eucheuma denticulatum*, *Kappaphycus alvarezii*, *Gracilaria salicornia*, and *Hypnea musciformis*. Smith et al. (2004) were concerned about *G. salicornia* because of its reproduction via fragmentation, fast growth rates, rapid dispersal, broad physical tolerances, and low consumption by herbivores. In surveys along the south shore of Moloka‘i, Nelson et al. (2009) reported up to 475 g dry weight m⁻² of *G. salicornia* growing in dense beds in the silty zone within 50 m of shore, and concluded that the seaweed would eventually spread farther along the coast. In the Hawaiian Islands, blooms of non-native macroalgae have become increasingly problematic (Lapointe and Bedford 2011), facilitated by anthropogenic nutrients in storm water runoff and overfished herbivorous fish and urchin populations (Friedlander et al. 2008). A multi-faceted approach is needed to eradicate and/or control these algal species and prevent their further spread.

The State of Hawai‘i developed an Aquatic Invasive Species Management Plan in 2003 that is currently being implemented (DLNR 2003). The objective of this plan is multi-agency collaboration to prevent further introductions, reduce the spread of alien species, respond to introductions with control and/or eradication methodologies, educate the public, and modify current aquatic invasive species policy. Efforts on O‘ahu, Moloka‘i, Maui, and Hawai‘i

Table 4: Invasive, alien species of macroalgae in Hawai'i (Rodgers and Cox 1999, DLNR 2009, Conklin et al. 2014, DLNR 2018b).

Species	When	Introduction location	How introduced	Concerns	Distribution; effects
<i>Acanthophora spicifera</i> (M. Vahl) Børgesen; "prickly seaweed"	1950s	Pearl Harbor and Waikiki, O'ahu	Likely entered on hull of military fuel barge from Guam	Fast growth rate; spreads by fragmentation, can reproduce sexually; not prone to desiccation	Coral to algal-dominated ecosystem shift; habitat loss effect on recreational and commercial fisheries; found on all MHI
<i>Avrainvillea amadelpha</i> (Montagne) A. Gepp et E.S. Gepp; "leather mudweed"	Early 1980s	O'ahu	Unknown	Fast growth rate; spreads by fragmentation; outcompetes sea grasses that feed marine species; traps sediments and mud that can create an anoxic layer	Coral to algal-dominated ecosystem shift; habitat loss effect on recreational and commercial fisheries
<i>Eucheuma denticulatum</i> (N.L. Burman) Collins et Herve; "smothering seaweed"	1974	Kāne'ōhe Bay, O'ahu	Introduced for carrageenan mariculture	Fast growth rate; spreads by fragmentation; outcompetes native algae and coral; no native predators in Hawai'i	Coral to algal-dominated ecosystem shift; habitat loss effect on recreational and commercial fisheries
<i>Gracilaria salicornia</i> (C. Agardh) E.Y. Dawson; "gorilla ogo"	1971	Initially found on Hawai'i Island; later intentionally brought to O'ahu	Aquaculture	Fast growth rate; spreads by fragmentation; outcompetes native algae and coral	Coral to algal-dominated ecosystem shift; habitat loss effect on recreational and commercial fisheries; benthic community structure and species diversity significantly altered in Waikiki; common on much of south shore of Moloka'i Shared among farmers
<i>Gracilaria tikvahiae</i> McLachlan	1987	Makapu'u, O'ahu	Brought from Florida for mariculture to lessen harvest pressure on <i>G. parvispora</i>	Released through seawater discharge from Oceanic Institute where it was introduced	
<i>Hypnea musciformis</i> (Wulfen) J.L. Lamouroux; "hook weed"	1974	Kāne'ōhe Bay, O'ahu	Brought from Florida for kappa-carrageenan mariculture	Fast growth rate; spreads by fragmentation; forms large mats that wash ashore and decompose, decreasing property value and beach use	Coral to algal-dominated ecosystem shift; habitat loss effect on recreational and commercial fisheries; found on all MHI islands except Hawai'i and Kaho'olawe; found at Maro Reef and Necker Island in NWHI
<i>Hydropuntia perplexa</i> (K. Byrne et Zuccarello) Conklin, O'Doherty et Sherwood	Unknown	O'ahu	Possibly introduced with <i>A. spicifera</i> as a cryptic species	Was thought to be a species of <i>Gracilaria</i> until DNA analysis in 2014; no initial records of introduction	East and south O'ahu shores
<i>Kappaphycus alvarezii</i> (Doty) Doty ex P.C. Silva; "elkhorn sea moss"	1979	Kāne'ōhe Bay, O'ahu	Experimental aquaculture studies	Fast growth rate; spreads by fragmentation; outcompetes native algae and coral	Kāne'ōhe Bay and Ka'a'awa, O'ahu
<i>Kappaphycus striatum</i> (F. Schmitz) Doty ex P.C. Silva	1979	Kāne'ōhe Bay, O'ahu	Experimental aquaculture studies	Fast growth rate; spreads by fragmentation; outcompetes native algae and coral	Kāne'ōhe Bay, O'ahu

MHI, Main Hawaiian Islands; NWHI, Northwestern Hawaiian Islands.

Island to control the biomass and spread of invasive marine algae have used a variety of procedures to kill, remove, or control invasive populations. Since 2002, University of Hawai'i at Mānoa professors and students, in collaboration with Waikiki Aquarium and Outrigger Hotels, have carried out a community-based project to remove alien species, to educate the public, and to reconnect people to the reef. Once or twice a year, with over 500 people per year involved, alien species on the reef in front of Waikiki Aquarium are collected, sorted, weighed and taken to the Honolulu Zoo's compost pile (Waikiki Aquarium 2018). Community-based volunteer clean-ups throughout the state have resulted in more than 100 US tons (=90.7 metric tonnes) of invasive algae removed by 2000 volunteers through more than 20 events held since 2003 (University of Hawai'i at Mānoa 2007). One non-profit group, Mālama Maunaloa, organizes community *huki* (pulling) events during which more than 50 residents spend the morning knee-deep in the water pulling invasive leather mudweed or *Avrainvillea amadelpha* (Hiraishi 2017).

From 1998–2014, the National Centers for Coastal Ocean Science supported the Hawai'i Coral Reef Initiative and funded invasive seaweed control via a variety of partnerships among the Hawai'i DLNR, the University of Hawai'i, The Nature Conservancy, the National Fish and Wildlife Foundation, Hawai'i Invasive Species Council, the National Sea Grant Program, and the US Fish and Wildlife Service. In 2006, a modified gold dredging barge with a 40-horsepower engine running on biodiesel with a Venturi vacuum system was developed and named "The Super Sucker." Divers feed seaweed into a long hose attached to the pump that sucks the thalli onto a sorting table. Local farmers receive the bagged seaweed to use as fertilizer. The Super Sucker's operations can remove 363 kg of seaweed per hour. The Super Sucker Junior, a smaller, more mobile, 5 m by 2.5 m barge, propelled by a 25-horsepower engine and equipped with two four-horsepower pumps capable of siphoning 300 l of water per minute, was deployed in 2007 (UH Mānoa 2007). The construction cost of Super Sucker Junior was approximately US\$50,000, with an additional US\$150,000 per year needed to operate and maintain the system. In 2012, the Super Sucker, Super Sucker Junior, and an additional Mini-Sucker removed over 589,000 kg of invasive algae; in 2013, over 40,000 kg of algae were removed (DLNR, DAR 2018c). These removal numbers reflect effort more than algal abundance or distribution. Weather days, engine maintenance issues, urchins available for outplant, and experimental removal protocols may have contributed to the lower harvest in 2013 (Justin Goggins, HI State DLNR Aquatic Invasive Species Coordinator, 2019, pers. comm.).

Accelerated growth rates and simple life history strategies of some invasive species allow rapid re-establishment and dominance of these species after mitigation efforts (Smith et al. 2004, Wiejerman et al. 2008). The State developed a plan to breed native herbivorous sea urchins (*Triploneustes gratilla* or collector urchins) and release the young urchins on reefs after Super Sucker efforts (DLNR, DAR 2018d). Although no completely successful eradications have been documented, The Nature Conservancy reported that some populations of invasive macroalgae disappeared from Kāne'ohe Bay by 2015 after Super Sucker vacuuming and sea urchin release (NOAA National Centers for Coastal Ocean Science 2016). Field experiments in 2014 demonstrated that *Eucheuma denticulatum* and *Gracilaria salicornia* declines in abundance, which began in 2008 in the bay, were the result of grazing by native herbivores, probably fishes, as well as high summer water temperatures in 2014 and 2015 (John Stimson, UHM, 2019, pers. comm.). The State has not made any large-scale effort to replant or replenish coastal areas with native Hawaiian algal species representative of pre-invaded algal assemblages. Theoretically, if various native species of significant size and high growth rate are replanted into coastal zones affected by invasive algae, the dominance of the non-natives will be challenged by the out-planted natives. Replanting or restoration of native species has been hampered by lack of methods to produce most species in captivity and the means by which to assure successful transplantation, although preliminary research (Walsh 2014) suggests that this could be accomplished with some species.

Water resources and macroalgae

Water resources can impact macroalgal populations. One issue of concern in the Hawaiian Islands is the reduction in freshwater flows caused by stream diversion for crop irrigation, and the spread of deep-rooted non-native plants, i.e. *mesquite* trees (*kiawe* in Hawaiian or *Prosopis pallida* (Humb. & Bonpl. ex Willd.) Kunth), which draw down groundwater in coastal areas (Dudley et al. 2014). Submarine groundwater discharge is recognized as an important source of freshwater and nutrients to coastal waters and coral reefs (Paytan et al. 2006, Street et al. 2008). At two sites on leeward Hawai'i Island, primary production in surface water was significantly higher within groundwater plumes (Johnson and Wiegner 2014). Several species of Hawaiian macroalgae, e.g. *Grateloupia filicina*, *Gracilaria coronopifolia*, and *Ulva prolifera* are most commonly found in shallow nearshore areas where there is

some freshwater input (Abbott 1999, Abbott and Huisman 2004). Stakeholders have cited reduction of freshwater flows at multiple sites as a credible cause of the reduced macroalgal presence and abundance (Wally Ito, Limu Hui, 2018, pers. comm.).

A second problem, the contamination of coastal waters by input of terrestrial pollutants, has received even more attention. Human sewage is of particular concern because Hawai'i has more cesspools (110,000) than any other state (USEPA 2013; Whittier and El-Kadi 2014). The rapid flow and widespread input of nutrients and bacteria from cesspools are exacerbated by the porous nature of volcanic soils. At Puakō Bay, Hawai'i Island, $\delta^{15}\text{N}$ values in macroalgae were traced to inputs of sewage, rather than to agriculture (Wiegner et al. 2016, Abaya et al. 2018). However, on Maui and Kaua'i, fertilizer carried by subterranean groundwater provided the most nitrogen in the nearshore waters (Derse et al. 2007, Amato et al. 2016). Proximity to sugarcane fields and waste water injection wells on Maui resulted in higher biomass for three species: *Ulva* spp., *Hypnea musciformis*, and *Acanthophora spicifera*, and lower benthic species diversity (Amato et al. 2016). Nitrogenous pollution has been implicated as a causal factor in phase shifts from coral-dominated to macroalgal- or turf-dominated ecosystems in waters off O'ahu, Maui, and Hawai'i Island (Smith 1981, Walsh et al. 2010, Rodgers et al. 2015). However, Vermeij et al. (2010) pointed out that on Maui, trophic interactions and spatial competition – rather than human impact – may have caused increased turf and macroalgal abundance compared to corals. Ecological impacts of nutrient enrichment, may extend to other organisms, such as sea turtles. Van Houtan et al. (2010, 2014) investigated prevalence and possible causes of a tumor-forming disease in green turtles (*Chelonia mydas* Linnaeus, 1758), and suggested that in chronically eutrophic Hawaiian coastal waters, increased consumption of invasive seaweeds could be a factor because these seaweeds store excess nitrogen as arginine, a possible metabolic promoter of the herpes virus in turtles. These findings were refuted by Work et al. (2014), who argued that the article by Van Houtan et al. (2014) had procedural flaws and did not provide compelling evidence of a link among seaweeds, arginine, and turtle tumors.

Removing obvious sources of nutrients may not solve all problems associated with increased macroalgal biomass or the presence of invasive species. Stimson and Larned (2000) described the history of a native seaweed, *Dictyosphaeria cavernosa* (Forsskål) Børgesen, in relation to changes in nutrient availability. When sewage outfalls were diverted in Kāne'ohe Bay, O'ahu, abundance of the prolific *D. cavernosa* declined; however, the decrease in total macroalgal

abundance did not continue. Two invasive species, *Gracilaria salicornia* and *Kappaphycus striatum*, continued to spread throughout the bay. Stimson and Larned (2000) hypothesized that dissolved inorganic nitrogen in the sediments continued to supply sufficient nitrogen to support growth of these species. Thus, impacts from pollution may have persistent effects on macroalgal populations.

Ocean acidification is an impending conservation issue for the seaweeds of the Hawaiian Islands. Four native aragonite-producing macroalgae, *Halimeda macroloba*, *Padina australis* Hauck, *Dichotomaria marginata* (J. Ellis & Solander) Lamarck, and *Galaxaura rugosa* (J. Ellis & Solander) J.V. Lamouroux, showed a greater change in percent CaCO_3 content at an experimental transplant site, than at the corresponding control sites (Hart 2016). The experimental site had high $p\text{CO}_2$, low pH, and low aragonite saturation. Results suggested that ocean acidification has the potential to shift nearshore macroalgal community structure and to reduce biodiversity in the Hawaiian Islands.

Community responses to conservation issues

Small, local organizations have started working on their own to replant native species and conserve traditional *limu* gathering knowledge. In 2014, at the request of elders who gather and care for native Hawaiian *limu* around the islands, Kua'āina Ulu 'Auamo partnered with the 'Ewa Limu Project in an initiative to “gather the gatherers” (Kua'āina Ulu 'Auamo 2014). Over 30 traditional *limu* practitioners representing six Hawaiian Islands came together for 4 days of learning, knowledge sharing, and discussion. This community-based group, now known as The Limu Hui, is concerned about the loss of traditional Hawaiian knowledge of *limu*, the break in the connection between people and *limu*, the decline in the health of reefs, and the changes in *limu* abundance in urbanized areas (Hiraishi 2018a). Wally Ito, the group's leader, says, “When people stop going to the shore to pick *limu*, then they lose interest in *limu* and the sea.” The Limu Hui hopes to shift the focus from eradication of alien species to habitat restoration, to share cultural knowledge (names, uses, preparations), and to preserve traditional uses of *limu*. The group works with schools and communities to out-plant braided raffia cordage with fragments of *Gracilaria parvispora*, and *Grateloupia filicina* which Mr. Ito propagates at the Ānuenue Fisheries Research Center on O'ahu (Haskins 2018, Hiraishi 2018b). The Limu Hui hosts an annual gathering to bring together people interested in *limu* to raise awareness of the importance of

limu to the environment and to pass on knowledge of *limu*, held primarily by elders in rural, sometimes remote communities. The ability to maintain traditional *limu* practices and pass on *limu* knowledge is hampered by the decreasing abundance of a resource that was once plentiful. Urban development, improper harvesting, alien species, and climate change affect *limu* around the islands. Mr. Ito also pointed out that the loss of freshwater springs nearshore may have reduced abundance of *pālahalaha* (*Ulva lactuca*), *huluhuluwaena* (*Grateloupia filicina*), ‘ele‘ele (*Ulva prolifera*), and *manaua* (*Gracilaria coronopifolia*). As gatherers and keepers of the traditional usage of *limu* slowly age and die, so does their knowledge.

Other community organizations based on the islands of Maui and Lāna‘i are working on habitat restoration and education. Waihe‘e Limu Restoration, on Maui, is focused on restoring Hawai‘i’s native *limu* to maintain a healthy marine ecosystem and to help perpetuate traditional Hawaiian cultural practices (Waihe‘e Limu Restoration 2015). School students meet with the Waihe‘e Limu Restoration team at various sites to enhance their knowledge of Hawaiian history, marine biology, social science, and math through *limu* restoration. The Lāna‘i Limu Restoration Project began as a backyard project in 2011, growing *Gracilaria parvispora* in 208-l drums (Kamemoto 2014). In 2014, the program shifted to tying *G. parvispora* and *Grateloupia filicina* to stones and placing them in 6 m by 6 m pens on the reef. A proposal to expand to eight tanks on land with solar-powered generators, sea water pumps, and an educational facility, all for conservation, not commercial production, remains on hold.

Conclusions

In the last 20 years in Hawai‘i, declining wild seaweed resources, dwindling commercial ventures, and diminished traditional knowledge are tangible issues. *Limu* collecting areas are now kept as secret as fishing holes. The factors that may limit seaweed mariculture in Hawai‘i include the oligotrophic surface waters, pollution at some sites, the numerous permits required, the limited availability of information about growth requirements for native species suitable for commercial applications, and the lack of large kelp-sized species. The future of cultivated species, native seaweed populations, and cultural knowledge of *limu* in the Hawaiian Islands are intertwined with the exponentially increasing demands on a finite resource. More university researchers, government natural resources agencies, seaweed farmers, elected officials, high school teachers, community members, and *limu*

enthusiasts need to work together to support, to encourage, and to respect each other’s knowledge and efforts to grow seaweeds, to re-plant seaweeds, and to cherish the rich diversity of seaweeds in Hawai‘i.

Acknowledgments: Many thanks to all those who so generously provided facts, unpublished data, personal insights, and encouragement: Steve Katase (Royal Hawaiian Sea Farms), Wenhao Sun (Olakai Inc.), Wally Ito and Brenda Asuncion (Kua‘āina Ulu ‘Auamo), Skippy Hau and Ryan Okano (Hawai‘i Department of Land and Natural Resources), Dave Cohen (Ānuenue Fisheries Research Center), Bernabé Santelices (Pontificia Universidad Católica de Chile), Dana Hoppe (Wai‘anae High School), David Littrell (Pacific Aquaculture and Coastal Resources Center), Michael Caban (Mokupāpapa Discovery Center), Liz Xu (Hawai‘i Department of Agriculture, Aquaculture & Livestock Support Services), Gwen Lentes (Waikiki Aquarium), Lisa Vollbrecht and Neil Sims (Kampachi Farms, LLC.), Keli‘i Kotubetey (Paepae O He‘eia), Pila Wilson and Larry Kimura (Ka Haka ‘Ula O Ke‘elikōlani, College of Hawaiian Language, University of Hawai‘i at Hilo), and Parker M. Smith (Hawaii Preparatory Academy).

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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 will be guest-edited by Alan T. Critchley, Anicia Hurtado, Leonel Pereira, Melania Cornish, Danilo Largo and Nicholas Paul.

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