Review

Karla J. McDermid*, Keelee J. Martin and Maria C. Haws

Seaweed resources of the Hawaiian Islands

https://doi.org/10.1515/bot-2018-0091
Received 4 October, 2018; accepted 15 May, 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 Hawaiʻi 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 Hawaiʻi 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: *ʻAʻohe pau ka ʻike i ka hālau hoʻokahi* (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 Hawaiʻi Island (19°35′N,

***Corresponding author: Karla J. McDermid,** Marine Science Department, University of Hawaiʻi at Hilo, 200 West Kawili St., Hilo, HI 96720, USA, e-mail: mcdermid@hawaii.edu
Keelee J. Martin: PO Box 1011, Kailua-Kona, HI 96745, USA
Maria C. Haws: Pacific Aquaculture and Coastal Resources Center, University of Hawaiʻi at Hilo, Hilo, HI 96720, USA

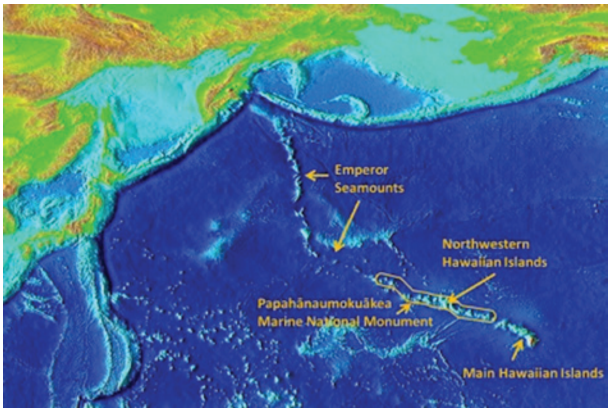

Figure 1: The Hawaiian Archipelago extends more than 3000 nautical miles from Hawaiʻi Island, the southernmost of the Main Hawaiian Islands, to Meiji Seamount, in the Emperor Seamounts. Image credit: © US National Oceanic and Atmospheric Administration.

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 Hawaiʻi 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 Hawaiʻi sits upon the Hawaiian Hotspot, and the most recent eruption started on May 3, 2018, and released 100 m^3 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), Hawaiʻi Island north to Niʻihau, 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 Hawaiʻi Island, and flows along the MHI until it shifts to a westward flowing current northwest of the island of Kauaʻi. 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

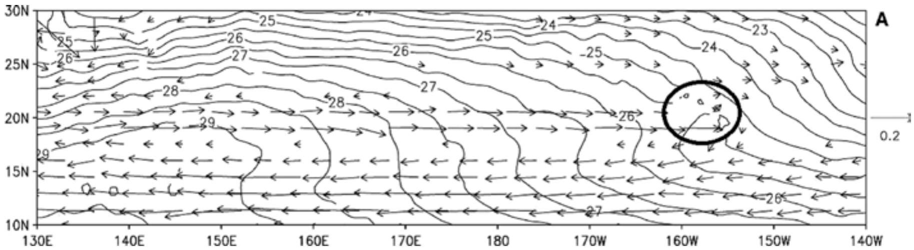

Figure 3: Current vectors in m s^{-1} at 37.5 m deep averaged for 1992–1998.
The Hawaiian Lee Countercurrent flows eastward toward the Hawaiian Islands at 19N. Arrows show current speed and direction and contours show ocean temperature (°C). The Main Hawaiian Islands are circled. Image credit: © Xie et al. (2001).

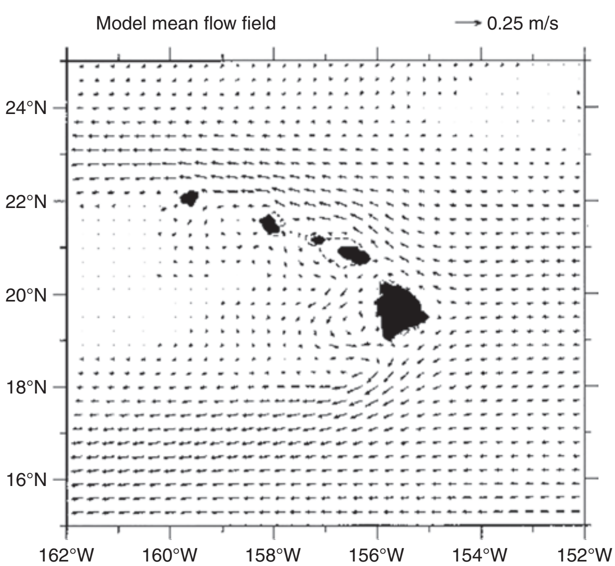

Figure 4: Average annual sea surface layer flows in the Main Hawaiian Islands.
The North Hawaiian Ridge Current flows along the northeast coasts of the islands from 19°N to 22°N. Dashed contours show 200-m isobaths; model shows areas shallower than 200 m as land. Image credit: © Qiu et al. (1997).

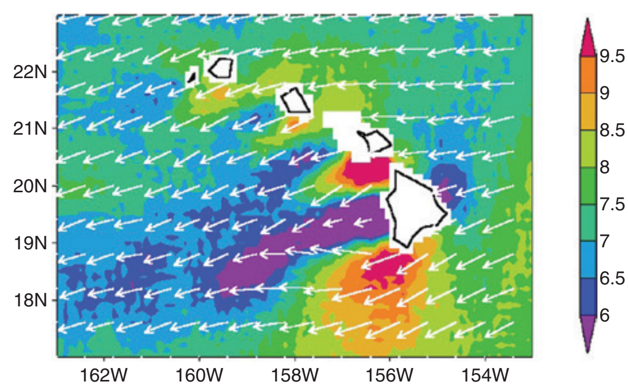

Figure 5: Northeasterly trade winds around the Main Hawaiian Islands blowing right to left.
Vectors and wind speeds (m s^{-1}) measured by the SeaWinds sensor aboard QuikSCAT satellite, Aug. 1999. Image credit: © Xie et al. (2001).

range from 25–28°C in the MHI and 19–26°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 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 phytogeographic 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 *Akalaphycus* 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 *lapaʻau* (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 (*hoʻoponopono*), 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 *ʻaumakua* 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	*Asparagopsis taxiformis* Delile	*kohu* or *līpehe*	Supreme	Intertidal to shallow subtidal	Soak overnight, pound, salt, roll into a ball, use in *po-ke*
Rhodophyta	*Ahnfeltiopsis concinna* J. Agardh	*ʻakiʻaki*	Nibbles, bite-bite	Basalt rocks in the intertidal	Chop well, bake in *imu* (underground oven)
Rhodophyta	*Gracilaria coronopifolia* J. Agardh	*manauea*	Erect branches	Ranges from tidepools in mid-intertidal to the shallow subtidal (up to 4 m) and eroded limestone	Chop, use in *po-ke*, or salt for later use
Rhodophyta	*Gracilaria parvispora* I.A. Abbott	*manauea*	Erect branches	Preference for sandy areas overlying rock with moderate water motion	Chop, use in *po-ke*, or salt for later use
Rhodophyta	*Grateloupia filicina* (J.V. Lamouroux) C. Agardh	*huluhuluwaena* or *pakeleawaʻa*	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	*Halymenia hawaiiana* Hernández-Kantún *et* A.R. Sherwood	*lepe-o-Hina*	Fringe or shawl of the goddess *Hina*	Grows on subtidal rocks up to 10 m	Rinse, chop, and salt; eaten with stew or blanched then pickled with vinegar
Rhodophyta	*Laurencia dotyi* Saito	*līpeʻepeʻe*	Hidden	Intertidal; found on eroded coral and basalt in holes or along margins of shallow pools	Chop and eaten with raw fish
Rhodophyta	*Laurencia nidifica* J. Agardh	*māneoneo*	Ticklish, peppery	Low intertidal to shallow subtidal; found on eroded coral and basalt	Rinse and salt; used as a relish
Rhodophyta	*Laurencia succisa* A.B. Cribb	*līpeʻepeʻe*	Hidden	Found on eroded coral and basalt tidepools	Chop and eaten with raw fish
Rhodophyta	*Pyropia vietnamensis* (Tanaka *et* Pham-Hoàng Ho) J.E. Sutherland *et* Monotillamaensis	*paheʻe*	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	*Codium edule* P.C. Silva	*wāwaeʻiole*	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	*Codium reediae* P.C. Silva	*aʻulaʻula*	Red fragrance	Found on coral rubble in shallow subtidal; can appear in drift	Chop or pound, use with fish stew, or in "salad"
Chlorophyta	*Ulva lactuca* Linnaeus	*pālahalaha*	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 *limu*; used as an adornment in traditional hula attire

Table 1: (continued)

Phylum	Species	Hawaiian name	Meaning	Habitat	Uses
Chlorophyta	*Ulva prolifera* (O.F. Müller) J. Agardh	*ʻeleʻele*	Black	Sandy rocks in intertidal; concrete pilings and breakwaters; brackish water	Rinse in freshwater, drain, salt. Prepared *ʻeleʻele* is favored for its strong flavor for stews and with soft, raw fish
Ochrophyta Class Phaeophyceae	*Dictyopteris australis* Sonder	*līpoa*	*Limu* 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	*Dictyopteris plagiogramma* Montagne	*līpoa*	*Limu* that is gathered from the deep	Low intertidal reaching 80 m; on rocks and epiphytically on *Sargassum* spp.	Chop or pound, and salt, usually eaten with fish or meat
Ochrophyta Class Phaeophyceae	*Sargassum aquifolium* (Turner) C. Agardh	*kala*	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

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 Hawaiʻi-based company (Noh Foods), but ironically contains dried macroalgae produced in California. Current per capita rates of *limu* consumption in Hawaiʻi have not been scientifically analyzed. A survey of 180 high school students on Oʻahu 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 hawaiiana* 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, Burreson 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* (Kützing) K.L. Vinogradova ex Scagel et al. and *Chaetomorpha antennina* (Bory) Kützing, 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, Hawaiʻi, to film the species "in the wild." Recently, *Asparagopsis taxiformis* in Hawaiʻi 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 Hawaiʻi 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 Oʻahu 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 Oʻahu 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)
Asparagopsis taxiformis (*kohu*)	Salted	$4.50–9.00	$12.00–15.00	$25.00–27.00
Codium spp. (*wāwaeʻiole*)	Fresh	$0.79–1.29	$2.00	–
Caulerpa racemosa (Forsskål) J. Agardh (sea grapes)	Fresh	$0.89–1.19	$1.95–2.95	–
Dictyopteris spp. (*līpoa*)	Salted	$3.79–4.75	–	–
Gracilaria spp. (*manauea*)	Fresh	$1.10–1.59	$2.95–3.95	$5.00–6.79
Grateloupia filicina (*huluhuluwaena*)	Salted	$2.00–3.00	–	–
Halymenia spp. (*lepe-o-Hina*)	Fresh	$1.25	–	–
Ulva prolifera (*ʻeleʻele*)	Salted	$2.09–3.59	–	–
Eucheuma spinosum 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.

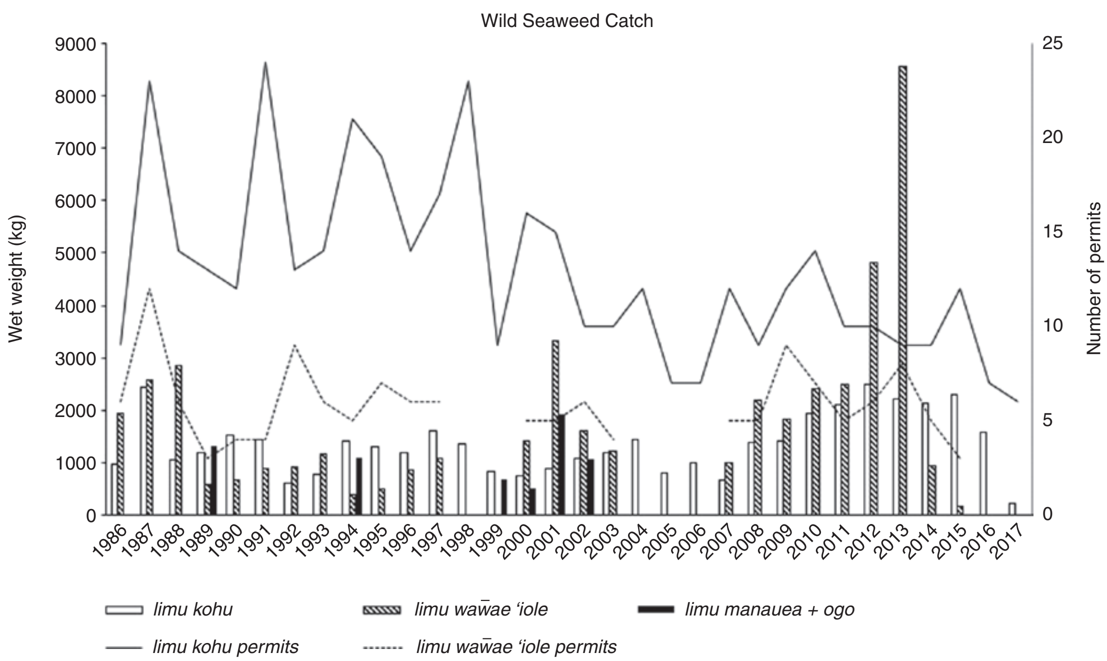

Figure 6: Annual wild-harvest of three edible Hawaiian species from 1986 through 2017 statewide and total number of permits issued by Hawaiʻi State Department of Land and Natural Resources (DLNR).
Data for *limu kohu* (*Asparagopsis taxiformis*), *limu wāwaeʻiole* (*Codium* spp.), and *limu manauea + 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 Hawaiʻi, 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 Hawaiʻi 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 Hawaiʻi 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 Kauaʻi, Maui, Oʻahu, and Hawaiʻi 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 Hawaiʻi 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 Oʻahu, 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 Kuaʻaina Hanauna Hou, a non-profit, community economic development organization – now defunct – was established in 1991 to help the local, native Hawaiian community on Molokaʻi 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 Kuaʻaina 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 Kuaʻaina 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 Kuaʻaina 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 Molokaʻi sold for US$7 kg^{-1} (US$2.20 kg^{-1} more than other seaweeds on the market), and sales of Molokaʻi *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 Oʻahu, plus about 70 kg of bottled Molokaʻi Pickled *Ogo*, Molokaʻi *Limu* Salsa, and Molokaʻi Kukui Nut Relish (Kojima 2000).

Several aquaculture experiments were conducted on Molokaʻi in conjunction with Ke Kuaʻaina 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 Kuaʻaina 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 Kuaʻaina 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 Kuaʻaina 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 Kuaʻaina 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 Waiʻanae High School on the west coast of Oʻahu 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. Waiʻanae 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 Waiʻanae 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 Waikīkī Aquarium in Honolulu, Oʻahu, 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* Kützing. At the Mokupāpapa Discovery Center in Hilo, Hawaiʻi, *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 Hawaiʻi 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 dulse (*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 Hawaiʻi at Hilo.
Image credit: © Karla McDermid.

Hawaiʻi Authority (NELHA) on the west coast of Hawaiʻi 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 Hawaiʻi 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 Hawaiʻi cultivates *Gracilaria parvispora*, *Ulva* spp., *Agardhiella* sp., and *Halymenia hawaiiana* in tumble culture to feed juvenile, native sea urchins (*Tripneustes gratilla* Linnaeus, 1758 or collector urchins or *hāwaʻe*) as part of a large-scale sea urchin hatchery opened in 2010 at the Ānuenue Fisheries Research Center in Honolulu, Oʻahu. 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 Kāneʻohe 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. hawaiiana* 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. hawaiiana* is not preferred by the urchins; *Agardhiella* sp. is consumed readily only by some urchin cohorts; and *H. hawaiiana* 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 ʻeleʻele*) 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 Oʻahu, *Gracilaria salicornia* is cultivated by a private, non-profit organization, Paepae o Heʻeia that restored and now maintains an 800-year old, 35.6 ha (=88 acre) brackish water Heʻeia Fishpond, whose lava and coral rock walls are built on the fringing reef along the shore of Kāneʻohe Bay. Between 2004 and 2012, Paepae o Heʻeia 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 Heʻeia 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 Liliʻuokalani at the turn of the 19th century. The story has been part of local oral folklore for generations (Fortner 1978, Abbott 1996): Queen Liliʻuokalani transplanted her favorite *limu huluhuluwaena* or *pakeleawaʻa* (*Grateloupia filicina*) to the reef in front of her Waikīkī house in Honolulu, Oʻahu. An article in the Honolulu newspaper *Ka Naʻi Aupuni* announced the following:

> This communication is being conveyed to all who swim or fish in the sea at Hamohamo in Waikīkī Kai, Honolulu, Oʻahu, that Queen Liliʻuokalani makes known these restrictions: the *pakeleawaʻa* seaweed is not to be harvested, also the *huluhuluwaena* seaweed, *ʻopihi* shellfish, *ālealea* shellfish, *ʻina* sea urchins, *hāʻukeʻuke* sea urchins and *pīpipi* 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 Molokaʻi and from Kauaʻi too, and from Waialua, Oʻahu 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 līpoa* is not explainable” (Abbott 1996); “when I was little, *limu* was all over…so plentiful. Today, *ʻaʻoh*e – 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 Hawaiʻi 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 ʻEwa Beach on Oʻahu was established by the state (Hawaiʻi Revised Statues § 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 Hawaiʻi 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 Oʻahu 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 Oʻahu. 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).

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

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. 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 Molokaʻi, 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 Hawaiʻi 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 Oʻahu, Molokaʻi, Maui, and Hawaiʻi

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

Species	When	Introduction location	How introduced	Concerns	Distribution; effects
Acanthophora spicifera (M. Vahl) Børgesen; "prickly seaweed"	1950s	Pearl Harbor and Waikīkī, Oʻahu	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
Avrainvillea amadelpha (Montagne) A. Gepp *et* E.S. Gepp; "leather mudweed"	Early 1980s	Oʻahu	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
Eucheuma denticulatum (N.L. Burman) Collins *et* Hervey; "smothering seaweed"	1974	Kāneʻohe Bay, Oʻahu	Introduced for carrageenan mariculture	Fast growth rate; spreads by fragmentation; outcompetes native algae and coral; no native predators in Hawaiʻi	Coral to algal-dominated ecosystem shift; habitat loss effect on recreational and commercial fisheries
Gracilaria salicornia (C. Agardh) E.Y. Dawson; "gorilla ogo"	1971	Initially found on Hawaiʻi Island; later intentionally brought to Oʻahu	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 Waikīkī; common on much of south shore of Molokaʻi Shared among farmers
Gracilaria tikvahiae McLachlan	1987	Makapuʻu, Oʻahu	Brought from Florida for mariculture to lessen harvest pressure on *G. parvispora*	Released through seawater discharge from Oceanic Institute where it was introduced	
Hypnea musciformis (Wulfen) J.L. Lamouroux; "hook weed"	1974	Kāneʻohe Bay, Oʻahu	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 Hawaiʻi and Kahoʻolawe; found at Maro Reef and Necker Island in NWHI
Hydropuntia perplexa (K. Bryne *et* Zuccarello) Conklin, O'Doherty *et* Sherwood	Unknown	Oʻahu	Possibly introduced with *A. spicifera* as a cryptic species	Was thought to be a species of *Gracilaria* until DNA analysis in 2014; no initial records of introduction	East and south Oʻahu shores
Kappaphycus alvarezii (Doty) Doty ex P.C. Silva; "elkhorn sea moss"	1979	Kāneʻohe Bay, Oʻahu	Experimental aquaculture studies	Fast growth rate; spreads by fragmentation; outcompetes native algae and coral	Kāneʻohe Bay and Kaʻaʻawa, Oʻahu
Kappaphycus striatum (F. Schmitz) Doty ex P.C. Silva	1979	Kāneʻohe Bay, Oʻahu	Experimental aquaculture studies	Fast growth rate; spreads by fragmentation; outcompetes native algae and coral	Kāneʻohe Bay, Oʻahu

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 Hawaiʻi at Mānoa professors and students, in collaboration with Waikīkī 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 Waikīkī Aquarium are collected, sorted, weighed and taken to the Honolulu Zoo's compost pile (Waikīkī 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 Hawaiʻi at Mānoa 2007). One non-profit group, Mālama Maunalua, 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 Hawaiʻi Coral Reef Initiative and funded invasive seaweed control via a variety of partnerships among the Hawaiʻi DLNR, the University of Hawaiʻi, The Nature Conservancy, the National Fish and Wildlife Foundation, Hawaiʻi 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 (*Tripneustes 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 Kāneʻohe 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 Hawaiʻi 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 Hawaiʻi 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, Hawaiʻi Island, $\delta^{15}N$ 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 Kauaʻi, 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 Oʻahu, Maui, and Hawaiʻi 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 Kāneʻohe Bay, Oʻahu, 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 pCO_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, Kuaʻāina Ulu ʻAuamo partnered with the ʻEwa Limu Project in an initiative to “gather the gatherers” (Kuaʻāina Ulu ʻAuamo 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 Oʻahu (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*), *ʻeleʻele* (*Ulva prolifera*), and *manauea* (*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 Lānaʻi are working on habitat restoration and education. Waiheʻe Limu Restoration, on Maui, is focused on restoring Hawaiʻi's native *limu* to maintain a healthy marine ecosystem and to help perpetuate traditional Hawaiian cultural practices (Waiheʻe Limu Restoration 2015). School students meet with the Waiheʻe Limu Restoration team at various sites to enhance their knowledge of Hawaiian history, marine biology, social science, and math through *limu* restoration. The Lānaʻi 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 Hawaiʻi, 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 Hawaiʻi 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 Hawaiʻi.

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 (Kuaʻāina Ulu ʻAuamo), Skippy Hau and Ryan Okano (Hawaiʻi Department of Land and Natural Resources), Dave Cohen (Ānuenue Fisheries Research Center), Bernabé Santelices (Pontificia Universidad Católica de Chile), Dana Hoppe (Waiʻanae High School), David Littrell (Pacific Aquaculture and Coastal Resources Center), Michael Caban (Mokupāpapa Discovery Center), Liz Xu (Hawaiʻi Department of Agriculture, Aquaculture & Livestock Support Services), Gwen Lentes (Waikiki Aquarium), Lisa Vollbrecht and Neil Sims (Kampachi Farms, LLC.), Keliʻi Kotubetey (Paepae O Heʻeia), Pila Wilson and Larry Kimura (Ka Haka ʻUla O Keʻelikōlani, College of Hawaiian Language, University of Hawaiʻi at Hilo), and Parker M. Smith (Hawaii Preparatory Academy).

References

Abaya, L.M., T.N. Wiegner, S.L. Colbert, J.P. Beets, K.M. Carlson, K.L. Kramer, R. Most and C.S. Couch. 2018. A multi-indicator approach for identifying shoreline sewage pollution hotspots adjacent to coral reefs. *Mar. Pollut. Bull. 129*: 70–80.

Abbott, I.A. 1978. The uses of seaweed as food in Hawaiʻi. *Econ. Bot. 32*: 409–412.

Abbott, I.A. 1988. Food and food products from seaweeds. *In:* (C.A. Lembi and J.R. Waaland, eds) *Algae and human affairs*. Cambridge University Press, Cambridge. pp. 135–147.

Abbott, I.A. 1996. *Limu: an ethnobotanical study of some Hawaiian seaweed*. 4th edition. Pacific Tropical Botanical Garden, Lawai. p. 39.

Abbott, I.A. 1999. *Marine red algae of the Hawaiian Islands*. Bishop Museum Press, Honolulu, Hawaiʻi. p. 477.

Abbott, I.A. and J.M. Huisman. 2003. New species, observations, and a list of new records of brown algae (Phaeophyceae) from the Hawaiian Islands. *Phycol. Res. 51*: 173–185.

Abbott, I.A. and J.M. Huisman. 2004. *Marine green and brown algae of the Hawaiian Islands*. Bishop Museum Press, Honolulu. p. 259.

Advanced Research Projects Agency-Energy, U.S. Department of Energy. Kampachi Farms, Blue Fields: Single Point Mooring Array for High-Yield Macroalgae Culture. https://www.arpa-e.energy.gov/?q=slick-sheet-project/single-point-mooring-array-macroalgae (accessed 01 July 2018).

Amato, D.W., J.M. Bishop, C.R. Glenn, H. Dulai and C.M. Smith. 2016. Impact of submarine groundwater discharge on marine water quality and reef biota of Maui. *PLoS One 11*: e0165825.

Arthur, K.E. and G.H. Balazs. 2008. A comparison of immature green turtle (*Chelonia mydas*) diets among seven sites in the main Hawaiian Islands. *Pac. Sci. 62*: 205–217.

Bakutis, B. 1999. Maui ban on commercial harvest saved *limu*. *Honolulu Advertiser*. 22 July 1999.

Blunt, J., J. Buckingham and M. Munro. 2012. Taxonomy and marine natural products research. *In:* (E. Fattorusso, W.H. Gerwick and O. Taglialatela-Scafati, eds) *Handbook of marine natural products.* Springer Netherlands, New York. p. 1452.

Burreson, B.J., R.E. Moore and P.P. Roller. 1976. Volatile halogen compounds in the alga *Asparagopsis taxiformis* (Rhodophyta). *J. Agric. Food Chem. 24*: 856–861.

Cardozo, K.H.M., T. Guaratini, M.P. Barros, V.R. Falcao, A.P. Tonon, N.P. Lopes, S. Campos, M.A. Torres, A.O. Souza, P. Colepicolo and E. Pinto. 2007. Review: metabolites from algae with economical impact. *Comp. Biochem. Physiol. C Toxicol. Pharmacol. 146*: 60–78.

Carter, J.O. 1906. Hoolaha Hookapu! *Ka Naʻi Aupuni*, Volume I, Number 102, 26 March 1906 translated by Larry Kimura, University of Hawaiʻi at Hilo.

Center for Tropical and Subtropical Aquaculture. 1996. *Gracilaria Gall Syndrome*. Center for Tropical and Subtropical Aquaculture Publication 194. http://www.ctsa.org/files/publications/CTSA_1246316728639809882881.pdf (accessed 31 July 2018).

Clark, B.R., M. Mizobe, J.L.M. Kaluhiwa, J. Leong and R.P. Borris. 2018. Chemical and genetic differences between Hawaiian lineages of the alga *Asparagopsis taxiformis*. *J. Appl. Phycol. 30*: 2549–2559.

Conklin, K.Y. and A.R. Sherwood. 2012. Molecular and morphological variation of the red alga *Spyridia filamentosa* (Ceramiales, Rhodophyta) in the Hawaiian Archipelago. *Phycologia. 51*: 347–357.

Conklin, K.Y., D.C. O'Doherty and A.R. Sherwood. 2014. *Hydropuntia perplexa*, n. comb. (Gracilariaceae, Rhodophyta), first record of the genus in Hawaiʻi. *Pac. Sci. 68*: 421–434.

Dennis, K. 2007. Regional notes. *Center for Tropical and Subtropical Aquaculture Publication. 18*: 1–6.

Department of Land and Natural Resources. 1990. *Report to the governor, 1989–1990*. State of Hawaiʻi, Honolulu. p. 120.

Department of Land and Natural Resources. 1994. *Report to the governor, 1993–1994*. State of Hawaiʻi, Honolulu. p. 96.

Department of Land and Natural Resources. 2001. *Report to the governor, 1999–2001*. State of Hawaiʻi, Honolulu. pp. 99–103.

Department of Land and Natural Resources. 2002. *Report to the governor, 2002*. State of Hawaiʻi, Honolulu.

Department of Land and Natural Resources, Division of Aquatic Resources. 2003. State of Hawaiʻi Aquatic Invasive Species Management Plan Final Version-September 2003. p. 205.

Department of Land and Natural Resources, Division of Aquatic Resources. 2009. Aquatic Invasive Species Summary Report 2008–2009. http://dlnr.hawaii.gov/ais/files/2014/02/AIS-Annual-Report-2008-2009.pdf (accessed 01 August 2018).

Department of Land and Natural Resources, Division of Aquatic Resources. 2018a. Fishing regulations: marine invertebrates and *limu*. http://dlnr.hawaii.gov/dar/fishing/fishing-regulations/marine-invertebrates/ (accessed 01 July 2018).

Department of Land and Natural Resources, Division of Aquatic Resources. 2018b. Invasive algae. https://dlnr.hawaii.gov/ais/invasivealgae/ (accessed 01 July 2018).

Department of Land and Natural Resources, Division of Aquatic Resources. 2018c. Invasive algae: super sucker. https://dlnr.hawaii.gov/ais/invasivealgae/supersucker/ (accessed 06 August 2018).

Department of Land and Natural Resources, Division of Aquatic Resources. 2018d. Invasive algae: sea urchin hatchery. https://dlnr.hawaii.gov/ais/invasivealgae/supersucker/ (accessed 06 August 2018).

Derse, E., K.L. Knee, S.D. Wankel, C. Kendall, C.J. Berg and A. Paytan. 2007. Identifying sources of nitrogen to Hanalei Bay, Kauaʻi, utilizing the nitrogen isotope signature of macroalgae. *Environ. Sci. Technol. 41*: 5217–5223.

Doty, M.S. 1961. *Acanthophora*, a possible invader for the marine flora of Hawaiʻi. *Pac. Sci. 15*: 547–552.

Doty, M.S. and G. Aguilar-Santos. 1966. Caulerpicin, a toxic constituent of *Caulerpa*. *Nature (London) 211*: 990.

Dudley, B.D., R.F. Hughes and R. Ostertag. 2014. Groundwater availability mediates the ecosystem effects of an invasion of *Prosopis pallida*. *Ecol. Appl. 24*: 1954–1971.

Erickson, K.E. 1983. (Chapter 4) Constituents of Laurencia. *In:* (P.J. Scheuer, ed) *Marine natural products: chemical and biological perspectives, vol. 5.* Academic Press, New York, pp. 131–258.

Fenical, W. 1982. Natural products: chemistry in the marine environment. *Science 215*: 923–928.

Fortner, H.J. 1978. *The limu eater, a cookbook of Hawaiian seaweed.* Sea Grant Miscellaneous Report University of Hawaiʻi- Sea Grant-MR-79-01, UH Sea Grant College Program, Honolulu. p. 102.

Friedlander, A., G. Aeby, E. Brown, A. Clark, S. Coles, S. Dollar, C. Hunter, P. Jokiel, J. Smith, B. Walsh, I. Williams and W. Wiltse. 2008. The state of coral reef ecosystems of the Main Hawaiian Islands. *In:* (J. Waddell, ed) *The state of coral reef ecosystems of the United States and Pacific freely associated states.* NOAA Technical Memorandum NOS 584 NCCOS 11. NOAA/NCCOS Center for Coastal Monitoring. pp. 222–269.

Glenn, E.P. and M.S. Doty. 1990. Growth of the seaweeds *Kappaphycus alvarezii*, *K. striatum* and *Eucheuma denticulatum* as affected by environment in Hawaiʻi. *Aquaculture 84*: 245–255.

Grigg, R.W. 1988. Paleoceanography of coral reefs in the Hawaiian-Emperor Chain. *Science 240*: 1737–1743.

Grigg, R.W. 2014. *Archipelago: the origin and discovery of the Hawaiian Islands*. Island Heritage Publishing, Waipahu. p. 111.

Hart, G.M. 2012. *Gathering, consumption and antioxidant potential of culturally significant seaweeds on Oʻahu Island, Hawaiʻi.* Master's thesis Botanical Sciences. University of Hawaiʻi at Mānoa, p. 129.

Hart, K.M. 2016. *Responses of native Hawaiian calcifying macroalgae to naturally occurring ocean acidification conditions.* Master's thesis Tropical Conservation Biology and Environmental Science, University of Hawaiʻi at Hilo, p. 50.

Hart, G.M., T. Ticktin, D. Kelman, A.D. Wright and N. Tabandera. 2014. Contemporary gathering practice and antioxidant benefit of wild seaweeds in Hawaiʻi. *Econ. Bot. 68*: 30–43.

Haskins, H. 2018. The undersea gardeners: love a reef, plant *limu*. *Hana Hou! Magazine*. 21(4) August/September, pp. 34–43. https://hanahou.com/archives (accessed 01 August 2018).

Hiraishi, K. 2017. In Maunalua, a fight against invasive seaweed. Hawaiʻi Public Radio. 11 Sept. 2017. http://www.hawaiipublicradio.org/post/maunalua-fight-against-invasive-seaweed.

Hiraishi, K. 2018a. Cultivating a future for Hawaiian seaweeds. Hawaiʻi Public Radio. 11 April 2018. http://www.hawaiipublicradio.org/post/cultivating-future-hawaiian-seaweed.

Hiraishi, K. 2018b. Restoring the bounty of seaweed in Waimānalo. Hawaiʻi Public Radio. 23 July 2018. http://www.hpr2.org/post/restoring-bounty-seaweed-waimanalo.

Huisman, J.M., A.R. Sherwood and I.A. Abbott. 2003. Morphology, reproduction, and the 18 S rRNA gene sequence of *Pihiella liagoraciphila* gen. et sp. nov., (Rhodophyta), the so-called 'monosporangial discs' associated with members of the Liagoraceae (Rhodophyta), and proposal of the Pihiellales ord. nov. *J. Phycol. 39*: 978–987.

Huisman, J.M., I.A. Abbott and A.R. Sherwood. 2004a. Large subunit rDNA gene sequences and reproductive morphology reveal *Stenopeltis* as a member of the Liagoraceae (Nemaliales, Rhodophyta), with a description of *Akalaphycus* gen. nov. *Eur. J. Phycol. 39*: 257–272.

Huisman, J.M., I.A. Abbott and A.R. Sherwood. 2004b. The Liagoraceae (Nemaliales, Rhodophyta) of the Hawaiian Islands III: the genus *Ganonema*, with a description of *Ganonema yoshizakii* sp. nov. *Phycologia. 43*: 296–310.

Huisman, J.M., A.R. Sherwood and I.A. Abbott. 2004c. Studies of Hawaiian Galaxauraceae (Nemaliales, Rhodophyta): large subunit rDNA gene sequences support conspecificity of *Galaxaura rugosa* and *G. subverticillata*. *Crypto. Algol. 25*: 337–352.

Huisman, J.M., I.A. Abbott and C.M. Smith. 2007. *Hawaiian reef plants.* University of Hawaiʻi Sea Grant College Program, Honolulu. p. 264.

Jensen, M.N. 2004. Cultivating edible seaweed in Hawaii: new technique helps local farmers. *Arizona Land and People 49*: 12–13.

Johnson, E.E. and T.N. Wiegner. 2014. Surface water metabolism potential in ground-water-fed coastal waters of Hawaii Island, USA. *Estuaries and Coasts 37*: 712–723.

Juvik, S.P. and J.O. Juvik (eds). 1998. *Atlas of Hawaiʻi*. 3rd edition. University of Hawaiʻi Press, Honolulu. p. 333.

Kamakaala, S. and S. Sakoda. 2017. Community-based fishery area program ORMP management priority #10. Presentation by the Division of Aquatic Resources, Hawaiʻi Department of Land and Natural Resources. http://files.hawaii.gov/dbedt/op/czm/ormp/working_group/meeting_presentations/wg_presentation_20171207_SakodaKamakaala.pdf (accessed 25 September 2018).

Kamemoto, G. 2014. A love for *limu*. *Ka Wai Ola 31*: 12–13.

Kelman, D., E.K. Posner, K.J. McDermid, N.K. Tabandera, P.R. Wright and A.D. Wright. 2012. Antioxidant activity of Hawaiian marine algae. *Mar. Drugs 10*: 403–416.

Kennedy, M. 2018. *Surf and turf: to reduce gas emissions from cows, scientists look to the ocean. All things considered.* National Public Radio. 03 July 2018.

Kikuchi, W.K. 1976. Prehistoric Hawaiian fishponds. *Science 193*: 295–299.

Kinley, R.D., M.J. Vucko, L. Machado and N.W. Tomkins. 2016. *In vitro* evaluation of the antimethanogenic potency and effects on fermentation of individual and combinations of marine macroalgae. *Am. J. Plant Sci. 7*: 2038–2054.

Kobashi, F. and S.P. Xie. 2008. The North Pacific Subtropical Countercurrent: mystery current with a history. *Int. Pac. Res. Center Climate 8*: 10–13.

Kojima, C.T. 2000. Limu. Honolulu Star Bulletin, 29 June 2000.

Kuaʻāina Ulu ʻAuamo. 2014. The *limu hui*. http://kuahawaii.org/limu-hui/ (accessed 10 August 2018).

Lapointe, B.E. and B.J. Bedford. 2011. Stormwater nutrient inputs favor growth of non-native macroalgae (Rhodophyta) on Oʻahu, Hawaiian Islands. *Harmful Algae 10*: 310–318.

Machado, L., M. Magnusson, N.A. Paul, R. Kinley, R. de Nys and N. Tomkins. 2016. Identification of bioactivities from the red seaweed *Asparagopsis taxiformis* that promote antimethanogenic activity *in vitro. J. Appl. Phycol. 28*: 1117–3126.

Marshall, K.L.E. and R.L. Vogt. 1998. Illness associated with eating seaweed, Hawaii, 1994. *West. J. Med. 169*: 293–295.

Martin, K.J. 2017. *Protein kinase inhibition and antioxidant activity of selected Hawaiian seaweeds.* Undergraduate thesis, University of Hawaiʻi at Hilo, Hilo, Hawaiʻi.

McDermid, K.J. and I.A. Abbott. 2006. Deep subtidal marine plants from the Northwestern Hawaiian Islands: new perspectives on biogeography. *Atoll Res. Bull. 543*: 525–532.

McDermid, K.J. and B. Stuercke. 2003. Nutritional composition of edible Hawaiian seaweeds. *J. Appl. Phycol. 15*: 512–524.

McDermid, K.J., B. Stuercke and O.J. Haleakala. 2005. Total dietary fiber content in Hawaiian marine algae. *Bot. Mar. 48*: 437–440.

Mencher, F.M. and S.A. Katase. 1988. Growth of *nori (Porphyra tenera)* in an experimental ocean thermal energy conversion system at the Natural Energy Laboratory of Hawaiʻi. *In:* (A.W. Fast and K.Y. Tanoue, eds) *OTEC aquaculture in Hawaiʻi.* University of Hawaiʻi-Sea Grant- MR-89-01, UH Sea Grant College Program, Honolulu. pp. 70–83.

Mencher, F.M., R.B. Spencer, J.W. Woessner, S.A. Katase and D.K. Barclay. 1983. Growth of *nori (Porphyra tenera)* in an experimental OTEC-aquaculture system in Hawaiʻi. *J. World Mari. Soc. 14*: 458–470.

Moore, R.E. 1977. Volatile compounds from marine algae. *Acc. Chem. Res. 10*: 40–47.

Moore, R.E. 1981. Toxins from marine blue-green algae. *In*: (W.W. Carmichael and W.W., eds) *The water environment – algal toxins and health.* Plenum Press, New York. pp. 15–24.

Murugan, K. and V.V. Iyer. 2013. Differential growth inhibition of cancer cell lines and antioxidant activity of extracts of red, brown, and green marine algae. *In Vitro Cell. Dev. Biol. Anim. 49*: 324–334.

Nagler, P.L., E.P. Glenn, S.G. Nelson and S. Napoleon. 2003. Effects of fertilization treatment and stocking density on the growth and production of the economic seaweed *Gracilaria parvispora* (Rhodophyta) in cage culture at Molokaʻi, Hawaiʻi. *Aquaculture 219*: 379–392.

NASA, Earth Observatory. 1999. Hawaiian Islands' Wake. https://earthobservatory.nasa.gov/images/1518 (accessed 01 August 2018).

NASA, Visible Earth. 2003. A catalog of NASA images and animations of our home planet: Hawaiʻi. https://visibleearth.nasa.gov/view.php?id=66578 (accessed 01 August 2018).

Nelson, S.G, E.P. Glenn, J. Conn, D. Moore, T. Walsh and M. Akutagawa. 2001. Cultivation of *Gracilaria parvispora* (Rhodophyta) in shrimp-farm effluent ditches and floating cages in Hawaiʻi: a two-phase polyculture system. *Aquaculture 193*: 239–248.

Nelson, S.G., E.P. Glenn, D. Moore and B. Ambrose. 2009. Growth and distribution of the macroalgae *Gracilaria salicornia* and *G. parvispora* (Rhodophyta) established from aquaculture introductions at Molokaʻi, Hawaiʻi. *Pac. Sci. 63*: 383–396.

NOAA National Centers for Coastal Ocean Science. 2016. Seaweed "super sucker" – helping restore Hawaiʻi's Kāneʻohe Bay. https://coastalscience.noaa.gov/news/nccos-funded-seaweed-super-sucker-gets-partial-credit-restoring-hawaiis-kaneohe-bay/ (accessed 01 August 2018).

O'Kelly, C.K., A. Kurihara, T.C. Shipley and A.R. Sherwood. 2010. Molecular assessment of *Ulva* spp. (Ulvophyceae, Chlorophyta) in the Hawaiian Islands. *J. Phycol. 46*: 728–735.

Oki, D.S. 1999. Geohydrology and numerical simulation of the groundwater flow system of Kona, Island of Hawaii. U.S. Geological Survey Water-Resources Investigations Report 99–4070.

Paepae o He'eia. 2018. Growing seafood for our community one *pōhaku* at a time. http://paepaeoheeia.org/ (accessed 29 September 2018).

Paytan, A., G.G. Shellenbarger, J. Street, M.E. Gonneea, K. Davis, M.B. Young and W.S. Moore. 2006. Submarine groundwater discharge: an important source of new inorganic nitrogen to coral reef ecosystems. *Limnol. Oceanogr. 51*: 343–334.

Qiu, B., D.A. Koh, C. Lumpkin and P. Flament. 1997. Existence and formation mechanism of the North Hawaiian Ridge Current. *J. Phys. Oceanogr. 27*: 431–444.

Reed, M. 1907. *The economic seaweeds of Hawai'i and their food value.* Annual report of the Hawai'i Agricultural Experimental Station, Honolulu, Hawai'i. pp. 61–88.

Rindi, F., A. Soler-Vila and M.D. Guiry. 2011. Taxonomy of marine macroalgae used as sources of bioactive compounds. *In:* (M. Hayes, ed) *Marine bioactive compounds: sources, characterization, and applications, chapter 1.* Springer Science + Business Media, LLC, Berlin/Heidelberg. p. 232.

Rodgers, K.S. and E.F. Cox. 1999. The rate of spread of the introduced Rhodophytes, *Kappaphycus alvarezii*, *Kappaphycus striatum*, and *Gracilaria salicornia* and their present distributions in Kāne'ohe Bay, O'ahu, Hawai'i. *Pac. Sci. 53*: 232–241.

Rodgers, K.S., Jokiel, E.K. Brown, S. Hau and R. Sparks. 2015. Over a decade of change in a spatial and temporal dynamics of Hawaiian coral reef communities. *Pac. Sci. 69*: 1–13.

Russell, D.J. and G.H. Balazs. 2000. *Identification manual for dietary vegetation of the Hawaiian green turtle Chelonia mydas.* NOAA Tech. Memo. NOAA-TM NMFS-SWFSC-294.

Russell, D.J. and G.H. Balazs. 2009. Dietary shifts by green turtles (*Chelonia mydas*) in the Kāne'ohe Bay region of the Hawaiian Islands: a 28-year study. *Pac. Sci. 63*: 181–192.

Ryder, E., S. Nelson, E. Glenn, P. Nagler, S. Napolean and K. Fitzsimmons. 2004a. Review: production of *Gracilaria parvispora* in two-phase polyculture systems in relation to nutrient requirements and uptake. *Bul. Fish Res. Agen. 1*: 71–76.

Ryder, E., S.G. Nelson, C. McKeon, E.P. Glenn, K. Fitzsimmons and S. Napoleon. 2004b. Effect of water motion on the cultivation of the economic seaweed *Gracilaria parvispora* (Rhodophyta) on Moloka'i, Hawai'i. *Aquaculture 238*: 207–219.

Schaffelke, B., J.E. Smith and C.L. Hewitt. 2006. Introduced macroalgae – a growing concern. *J. Appl. Phycol. 18*: 529–541.

Shannon, E. and N. Abu-Ghannam. 2016. Antibacterial derivatives of marine algae: an overview of pharmacological mechanisms and applications: a review. *Mar. Drugs 14*: 1–23.

Sherwood, A.R., A. Kurihara, K.Y. Conklin, T. Sauvage and G.G. Presting. 2010. The Hawaiian Rhodophyta Biodiversity Survey (2006–2010): a summary of principal findings. *BMC Plant Biol. 10*: 258–286.

Smith, S.V. 1981. Responses of Kaneohe Bay, Hawaii, to relaxation of sewage stress. *In:* (B.J. Neilson and L.E. Cronon, eds) *International Conference on the Effects of Nutrient Enrichment in Estuaries*, 29 May 1979, Williamsburg, VA (USA). pp. 391–412.

Smith, J.E., C.L. Hunter and C.M. Smith. 2002. Distribution and reproductive characteristics of nonindigenous and invasive marine algae in the Hawaiian Islands. *Pac. Sci. 56*: 299–315.

Smith, J.E., C.L. Hunter, E.J. Conklin, R. Most, T. Sauvage, C. Squair and C.M. Smith. 2004. Ecology of invasive red alga *Gracilaria salicornia* (Rhodophyta) on O'ahu, Hawai'i. *Pac. Sci. 58*: 325–343.

Spalding, H.L., K.Y. Conklin, C.M. Smith, C.J. O'Kelly and A.R. Sherwood. 2016. New *Ulvaceae* (Ulvophyceae, Chlorophyta) from mesophotic ecosystems across the Hawaiian Archipelago. *J. Phycol. 52*: 40–45.

Stimson, J. and S.T. Larned. 2000. Nitrogen efflux from the sediments of a subtropical bay and the potential contribution to macroalgal nutrient requirements. *J. Exp. Mar. Biol. Ecol. 252*: 159–180.

Street, J.H., K.L. Knee, E.E. Grossman and A. Paytan. 2008. Submarine groundwater discharge and nutrient addition to the coastal zone and coral reefs of leeward Hawaii. *Mar. Chem. 109*: 355–376.

United Nations. 2015. Sustainable development goals. https://www.un.org/sustainabledevelopment/development-agenda/ (accessed 17 August 2018).

United States Environmental Protection Agency (USEPA). 2013. Cesspools in Hawaii. http://www.epa.gov/region9/water/groundwater/uic-hicesspools.html (accessed 22 September 2014).

University of Hawai'i at Mānoa. 2007. Super sucker junior is the state's latest tool in the battle against alien algae. https://manoa.hawaii.edu/news/article.php?aId=1740 (accessed 01 August 2018).

van den Hoek, C. 1984. World-wide latitudinal and longitudinal seaweed distribution patterns and their possible causes, as illustrated by the distribution of Rhodophytan genera. *Helgol. Meeresunters. 38*: 153–214.

Van Houtan, K.S., S.K. Hargrove and G.H. Balazs. 2010. Land use, macroalgae, and a tumor-forming disease in marine turtles. *PLoS One 5*: e12900.

Van Houtan, K.S., C.M. Smith, M.L. Dailer and M. Kawachi. 2014. Eutrophication and the dietary promotion of sea turtle tumors. *PeerJ 2*: e602.

Vermeij, M.A., M.L. Dailer, S.M. Walsh, M.K. Donovan and C.M. Smith. 2010. The effects of trophic interactions and spatial competition on algal community composition on Hawaiian coral reefs. *Mar. Ecol. 31*: 291–299.

Veillerobe, Y.J.-P. 2004. *Sea surface temperature variability in the Northwestern Hawaiian Islands region.* Thesis Global Environmental Science, University of Hawai'i at Mānoa, p. 77.

Verbruggen, H., O. De Clerck, A.D.R. N'yeurt, H. Spalding and P.S. Vroom. 2006. Phylogeny and taxonomy of *Halimeda incrassata*, including descriptions of *H. kanaloana* and *H. heteromorpha* spp. nov. (Bryopsidales, Chlorophyta). *Eur. J. Phycol 41*: 337–362.

Vijayavel, K. and J.A. Martinez. 2010. *In vitro* antioxidant and antimicrobial activities of two Hawaiian marine *limu*: *Ulva fasciata* (Chlorophyta) and *Gracilaria salicornia* (Rhodophyta). *J. Med. Food 13*: 1494–1499.

Vucko, M.J., M. Magnusson, R.D. Kinley, C. Villart and R. de Nys. 2017. The effects of processing on the *in vitro* antimethanogenic capacity and concentration of secondary metabolites of *Asparagopsis taxiformis*. *J. Appl. Phycol. 29*: 1577–1586.

Wagner, D., A. Barkman, H.L. Spalding, B. Calcinai and S.L. Godwin. 2016. *A photographic guide to the benthic flora and fauna from mesophotic coral ecosystems in the Papahānaumokuākea Marine National Monument*. Marine Sanctuaries Conservation Series ONMS-16-04. U.S. Depart-

ment of Commerce, NOAA, Office of National Marine Sanctuaries, Silver Spring. p. 86.
Waiheʻe Limu Restoration. 2015. Restoring native Hawaiian *limu*. https://www.waiheelimu.org/ (accessed 15 July 2018).
Waikīkī Aquarium. 2018. Invasive algae cleanups. University of Hawaiʻi. http://www.waikikiaquarium.org/conservation/projects/invasive-algae-cleanups/ (accessed 01 July 2018).
Walsh, C.T. 2014. *Re-attachment and transplantation of native Hawaiian macroalgae: a potential tool for reef management and alien algae mitigation.* Master's thesis Tropical Conservation Biology and Environmental Science, University of Hawaiʻi at Hilo, p. 48.
Walsh, W., R. Sparks, C. Barnett, C. Couch, S. Cotton and D. White. 2010. *Long-term monitoring of coral reefs of the main Hawaiian Islands*. Final Report. Hawaii Department of Land and Natural Resources. NOAA Coral Reef Conservation Program. Report No.: NA06NOS4260113. https://dlnr.hawaii.gov/dar/files/2014/04/NOAA_2013_WHi_-Mon_-Rep.pdf (accessed 25 September 2018).
Whittier, R. and A. El-Kadi. 2014. Human health and environmental risk of on-site sewage disposal systems for the Hawaiian Islands of Kauaʻi, Molokaʻi, Maui and Hawaiʻi. http://health.hawaii.gov/wastewater/files/2015/09/OSDS_NI.pdf (accessed 25 September 2018).
Wiegner, T.N., A.U. Mokiao-Lee and E.E. Johnson. 2016. Identifying nitrogen sources to thermal tide pools in Kapoho, Hawaiʻi, U.S.A., using a multi-stable isotope approach. *Mar. Pollut. Bull. 103*: 63–71.
Wiejerman, M., R. Most, K. Wong and S. Beavers. 2008. Attempt to control the invasive red alga *Acanthophora spicifera* (Rhodophyta: Ceramiales) in a Hawaiian fishpond: an assessment of removal techniques and management options. *Pac. Sci. 62*: 517–532.
Williams, S.L. and J.E. Smith. 2007. A global review of the distribution, taxonomy, and impacts of introduced seaweeds. *Annu. Rev. Ecol. Evol. Syst. 38*: 327–359.
Work, T.M., M. Ackermann, J.W. Casey, M. Chaloupka, L.H. Herbst, J.M. Lynch and B.A. Stacy. 2014. The story of invasive algae, arginine, and turtle tumors does not make sense. *PeerJ PrePrints2*: e539v.
Xie, S.P., W.T. Liu, Q. Liu and M. Nonaka. 2001. Far-reaching effects of the Hawaiian Islands on the Pacific ocean-atmosphere system. *Science 20*: 2057–2060.
Ziegler, A.C. 2002. *Hawaiian natural history, ecology, and evolution*. University of Hawaiʻi Press, Honolulu. p. 512.

Bionotes

Karla J. McDermid
Marine Science Department, University of Hawaiʻi at Hilo, 200 West Kawili St., Hilo, HI 96720, USA,
mcdermid@hawaii.edu

Karla J. McDermid came to the Hawaiian Islands in 1982 as a graduate student to work on *Laurencia* species with Dr. Izzie Abbott, and she never left. Now a Professor of Marine Science at the University of Hawaiʻi at Hilo, Karla teaches and encourages young scientists to study Hawaiian seaweeds.

Keelee J. Martin
PO Box 1011, Kailua-Kona, HI 96745, USA

Keelee J. Martin was born and raised in Kailua-Kona, Hawaiʻi. In 2017, she graduated with a BS in Marine Science from the University of Hawaiʻi at Hilo. Her research experience includes antioxidant and kinase inhibition activity in Hawaiian seaweeds and research diving to assess coral health. She currently lives in Kailua-Kona and works as a seaweed aquaculturist.

Maria C. Haws
Pacific Aquaculture and Coastal Resources Center, University of Hawaiʻi at Hilo, Hilo, HI 96720, USA

Maria C. Haws is an Associate Professor of Aquaculture and the Director of the Pacific Aquaculture and Coastal Resource Center (PACRC) at the University of Hawaiʻi at Hilo. Her research interests focus on invertebrate and plant aquaculture.

Graphical abstract

Karla J. McDermid, Keelee J. Martin and Maria C. Haws

Seaweed resources of the Hawaiian Islands

https://doi.org/10.1515/bot-2018-0091
Botanica Marina 2019; x(x): xxx–xxx

Review: Wild-harvest of seaweeds in the Hawaiian Islands has fluctuated wildly during the last 30 years. Cultivation of *Gracilaria* spp. attempted to fill the void. Today, many people work to preserve cultural knowledge, re-plant the reefs, and remove invasive algal species.

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