Distribution and Reproductive Characteristics of Nonindigenous and Invasive Marine Algae in the Hawaiian Islands[1]

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Abstract: Quantitative and qualitative surveys were conducted on five of the main Hawaiian Islands to determine the current distribution of nonindigenous algae and to assess the level of impact that these algal species pose to Hawai‘i's marine ecosystems. Maps were generated to examine the spread of these organisms from initial sites of introduction and to assimilate information regarding habitat characteristics that appear to make some sites more susceptible to invasion than others. Blooms of native invasive algae were also documented when encountered. The potential for vegetative propagation via fragmentation was examined experimentally as a mode of reproduction for four of the most common species of nonindigenous algae in Hawai‘i. This research has demonstrated that each of these algal species currently has a distinctive distribution and reproductive strategies appear to vary among species. More research is needed to further understand the competitive strategies and unique ecological characteristics that allow these nonindigenous species to become highly successful in the Hawaiian Islands.

Healthy coral reef ecosystems are often dominated by reef-building corals and coralline algae, with macroalgae and algal turfs typically restricted to areas of reefs that are relatively less accessible to herbivores. On reefs subjected to anthropogenic disturbances such as increased terrestrial nutrients or the removal of grazers, however, algal growth rates may exceed grazing rates and result in overgrowth of corals and other benthic invertebrates (Hatcher and Larkum 1983, Littler and Littler 1984, Steven and Larkum 1993, Smith et al. 2001, Stimson et al. 2001). The long-term consequences of these phase shifts from coral to algal dominance may include the loss of biodiversity, a decrease in the intrinsic value of the reef, changes in the community structure of the reef fishes dependent upon corals for habitat and shelter, and erosion of the physical structure of the reef (Hughes 1994). Phase shifts involving both indigenous and nonindigenous algae have been documented in Hawai‘i but have not been thoroughly studied. Thus, documenting the nature and characteristics of these problems before invasive algal species become ecological dominants on Hawai‘i's reefs is crucial.

Blooms of both indigenous and nonindigenous marine algae have become common in the Hawaiian Islands over the last several decades (Russell 1987, 1992, Stimson et al. 1996, Rodgers and Cox 1998). In tropical regions, blooms of indigenous algae have often been tied to reductions in grazing intensity and increases in anthropogenically derived nutrient levels (Miller et al. 1999, McClanahan et al. 2001, McCook et al. 2001, Smith et al. 2001, Stimson et al. 2001, Thacker et al. 2001). However, the mechanisms driving the

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abundance and success of nonindigenous algae worldwide remain unclear and may be the result of a number of interacting factors.

The introduction of nonindigenous algae in the marine environment has been, and continues to be, a devastating issue in relation to the health and stability of nearshore ecosystems. The introduction and impacts of nonindigenous algae such as *Caulerpa taxifolia* (Vahl) C. Agardh in the Mediterranean, *Codium fragile* (Sur.) Hariot subsp. *tomentosoides* (van Goor) Silva in New England and New Zealand, *Sargassum muticum* (Yendo) Fensholt in Europe and Mexico, and *Undaria pinnatifida* (Harvey) Suringar in Australia, New Zealand, and Europe have been widely documented (Hanisak 1980, Carlton and Scanlon 1985, Espinoza 1990, Meinesz et al. 1993, Trowbridge 1995, Bellan-Santini et al. 1996, Critchley et al. 1997, Ferrer et al. 1997, Andrew and Viejo 1998, Campbell and Burridge 1998, Curiel et al. 1998, Karlsson and Loo 1999, Stuart et al. 1999, Schaffelke et al. 2000). In the Tropics, nonindigenous marine plants pose threats to both coral-dominated habitats and sea grass beds and have the potential to reduce biodiversity and substantially alter the structure of reef ecosystems (Maragos et al. 1996, Critchley et al. 1997, Den Hartog 1997).

The success of these nonindigenous algae may be the result of a variety of factors including chemical or physical defense from herbivory and diverse physiological characteristics that lead to rapid growth rates (Borowitzka 1981, Duffy and Hay 1990, Holmlund et al. 1990, Hay et al. 1994, Bolser and Hay 1996, Hay 1997, Paul 1997). Native species of algae also have the potential to become "invasive," leading to massive blooms and ecological dominance as was seen with *Dictyosphaeria cavernosa* (Forsskål) Boergesen in Kāne'ohe Bay (Smith et al. 1981, Hunter and Evans 1995, Stimson et al. 1996, 2001), *Cladophora sericea* (Hudson) Kuetzing on Maui (Hodgson 1994), and *Turbinaria ornata* (Turner) J. Agardh in Tahiti (Stiger and Payri 1999).

At least 19 species of macroalgae have been introduced to O'ahu, Hawai'i, since 1950, and five of these have become successful (Table 1). Some of these plants were brought to Hawai'i from Florida or the Philippines purposely for commercial aquaculture projects that were later abandoned (Russell 1992). Another species was unintentionally introduced after a heavily fouled ship originating in Guam arrived in Hawai'i (Doty 1961). However, the origin and source of many other apparently introduced algae remain unknown (Doty 1961, Brostoff 1989). The most likely vector of transport is through ship fouling and/or ballast water because many of these nonindigenous algae were first collected in or around harbors and gradually dispersed to neighboring areas. However, there is little information on the current distribution patterns of these plants throughout the Hawaiian Islands. To determine if these nonindigenous algae (or invasive indigenous species) are indeed posing threats to Hawai'i's marine resources, we need to first document their current distribution and evaluate their abundance in relation to particular habitats. Information regarding the distribution of nonindigenous algae can then provide insights into the possible mechanisms of dispersal.

Fragmentation or vegetative propagation is a common mode of reproduction in the marine environment and may be an important mechanism for algal propagation (Smith and Walters 1999). From an ecological perspective, the ability to fragment readily, disperse widely before recruitment, and successfully attach in short periods of time are all likely to be important characteristics of invasive species that bloom frequently. For species that do fragment, knowing the smallest size that is viable sets important criteria for cleanup and mitigation activities.

The success of both nonindigenous algae and indigenous invasive algae in coastal environments may be the result of a wide range of physiological, ecological, and reproductive characteristics. Each species may have a unique approach, or they may all use similar strategies to become ecological dominants. The goals of this study were to determine the distribution, relative abundance, and reproductive characteristics of the five most successful nonindigenous algae in the main Hawaiian Islands and to document other invasive species blooms when encountered.

TABLE 1

Updated List of Successful Macroalgae Introduced to Oʻahu Since 1950 (Russell 1992)

Species	Oʻahu locale	Date	Origin	Success	Product Value?	Competition?
Acanthophora spicifera	Pearl Harbor and/or Waikīkī	After 1950	Guam	Highly successful	None	*Laurencia* spp.
Avrainvillea amadelpha	Koko Head, Kahe Pt.	After 1981	West Pacific?	Highly successful	None	*Halophila hawaiiana*
Gracilaria salicornia	Waikīkī and Kāneʻohe Bay	April 1971, September 1978	Big Island (Hawaiʻi)	Highly successful	Agar	Many reef spp.
Hypnea musciformis	Kāneʻohe Bay	January 1974	Florida	Highly successful	Kappa carrageenan	Many reef spp.
Kappaphycus spp.	Honolulu Harbor and Kāneʻohe Bay	September 1974 to late 1976	Philippines	Successful	Kappa carrageenan	Many reef spp.

MATERIALS AND METHODS

Ecological Surveys

The species of nonindigenous algae documented in this study along with their relevant ecological characteristics are presented in Table 1. Before conducting field surveys, a database at the Bernice P. Bishop Museum, Honolulu, Hawaiʻi, was summarized to tabulate existing information from voucher specimens collected from around the state.

Baseline surveys were conducted around the islands of Hawaiʻi, Maui, Molokaʻi, Oʻahu, and Kauaʻi to map the current distribution and/or appearance of nonindigenous and indigenous invasive macroalgae throughout the main Hawaiian Islands. These surveys were semiquantitative and provided descriptive data for each survey site, including relative abundance of algal species ranked on a scale of 0–10 (0, not present; 10, 100% cover), habitat type (e.g., sand, lava bench, coral, rock, artificial substrate), date, temperature, salinity, Global Positioning System (GPS) coordinates, dominant herbivore community characteristics, depth, and any other relevant information. All surveys were conducted by snorkel and were primarily focused in depths of less than 3 m. At each site, a general survey and reconnaissance of the area were conducted for approximately 1 hr. At that time, approximately five 0.25-m^2 quadrants were placed haphazardly throughout the shallow subtidal and intertidal regions to assess nonindigenous algae species abundances. As many shorelines as possible were surveyed; the total number of sites surveyed per island was dependent upon accessibility and environmental conditions. A total of 14 sites was surveyed on Hawaiʻi Island, 13 sites on Kauaʻi, 15 sites on Maui, 15 sites on Molokaʻi, and 20 sites on Oʻahu.

Voucher specimens of algae were deposited at the Bernice P. Bishop Museum for future reference. Following each of the surveys, alien species distributions and relative abundance were plotted using ArcView GIS (Geographic Information Systems) maps for each of the islands. These maps were then compared with those generated from the historical data compiled from the Bishop Museum's database. This information highlights which of the alien species have been most successful at dispersing between islands and where blooms currently exist.

In Kāneʻohe Bay, Oʻahu, the site where several species of alien algae were initially introduced into the state, quantitative surveys were conducted so that future changes could be monitored more precisely. For these surveys, two 30-m transect lines were positioned on the reef crest perpendicular to the shoreline and ran across habitats from the reef crest to the reef flat. The abundance of all species of algae and benthic invertebrates was estimated using percentage cover in ten 0.25-m^2 quadrants positioned randomly along each transect.

Reproductive Biology of Nonindigenous Algae

The ability of four of the most common nonindigenous algae species, *Acanthophora spicifera* (Vahl) Boergesen, *Avrainvillea amadelpha* (Montagne) Gepp & Gepp, *Gracilaria salicornia* (C. Agardh) Dawson, and *Hypnea musciformis*, to reproduce via fragmentation or cloning was examined both in the field and at the Waikīkī Aquarium. Several individuals of each species were collected in the field from Kahala Reef, O'ahu, and were transported in seawater to the Waikīkī Aquarium. Individuals were cut into four size classes (0.5, 1.0, 2.0, and 4.0 cm long [field component] or 0.5, 1.0, 2.0, and 3.0 cm long [Waikīkī Aquarium]) using razor blades and calipers. Apical regions of all species were used except for *A. amadelpha*, in which the subterranean portion was considered to be more regenerative than the upright portion (Littler and Littler 1999). Fragments were weighed and randomly placed into 4 by 5 by 5 cm compartments in clear plastic boxes. The lids of these boxes were modified to incorporate fine screen mesh that allowed water flow into and out of the compartments but prevented fragments from escaping. Six replicates (separate boxes) of each species and size combination were used.

For the field component of this experiment, boxes were weighted with two 0.9-kg (2-lb) lead weights. They were placed on the reef flat in the Waikīkī Marine Life Conservation District (MLCD) at a depth of approximately 1 m on 6 May 2000. Boxes were left in the field for 1 week and were then brought into the laboratory and all fragments were reweighed. Boxes were then returned to the reef but were not subsequently recovered due to a large south swell that apparently dislodged and removed them from the experimental area. The same experiment was then repeated at the Waikīkī Aquarium in outdoor tanks with natural lighting and flowing unfiltered seawater to ensure successful completion of the experiment. Fragment boxes were dusted daily to remove fine particulate matter from the mesh screen that may have shaded the samples. Fragments were weighed weekly for 1 month.

Data generated in fragmentation studies were plotted as percentage increase in weight (total new weight minus initial weight divided by initial weight). Data were analyzed using a two-way analysis of variance (ANOVA) with time and size as factors (both fixed) for each species. To determine which size fragments grew the most in relation to their initial weight, Tukey's multiple comparisons were used to test for differences in growth between the four size classes.

In addition to the fragmentation studies, searches were made for sexually reproductive individuals during field surveys and in collected samples.

RESULTS

Ecological Surveys

Results of field surveys are presented in detail on the Alien and Invasive Algae in Hawai'i website developed as part of this research project (http://www.botany.hawaii.edu/HCRI/default.htm).

Numbers of voucher specimens deposited in the Bishop Museum database before and during this study are shown for each island in Table 2. Historically the greatest number of nonindigenous algae specimens was collected on the island of O'ahu. Other areas such as West Maui, which had been known in the past to have problems with alien species, lacked adequate documentation. Data summarized in Table 2 also highlight islands where new nonindigenous algae records were documented. For example, new records were set for *Hypnea musciformis* on Kaua'i and Moloka'i, and *Avrainvillea amadelpha* was located on Kaua'i, the first observation of this species beyond O'ahu. This information provided a historical record and a starting point from which to monitor the spread of each of these species.

Sites surveyed during this study are shown in Figure 1. Summary information for each of these sites including site number, name, island, total number, and abundance of nonindigenous algae species, and the relative abundance of each nonindigenous algae species is presented in Table 3. The island of

TABLE 2

Number of Voucher Specimens for Each Alien Species Deposited in the Bishop Museum Before This Study (Bishop) and as Part of This Study

Island	Study	*Acanthophora spicifera*	*Avrainvillea amadelpha*	*Eucheuma* sp.	*Gracilaria salicornia*	*Hypnea musciformis*	*Kappaphycus* spp.
Hawai‘i	Bishop	4	0	0	4	1	0
	This study	2	0	0	2	0	0
Maui	Bishop	13	0	0	0	1	0
	This study	12	0	0	0	10	0
Moloka‘i	Bishop	7	0	0	0	0	0
	This study	9	0	0	**1**	**5**	0
Lāna‘i	Bishop	2	0	0	0	0	0
	This study	ns	ns	ns	ns	ns	ns
Kaho‘olawe	Bishop	0	0	0	0	0	0
	This study	ns	ns	ns	ns	ns	ns
O‘ahu	Bishop	61	5	14	18	34	46
	This study	18	1	0	8	8	9
Kaua‘i	Bishop	22	0	0	0	0	0
	This study	8	**1**	0	0	**2**	0

Note: This information highlights where alien species were collected from islands that they had not previously been collected from before (in bold). ns, not surveyed.

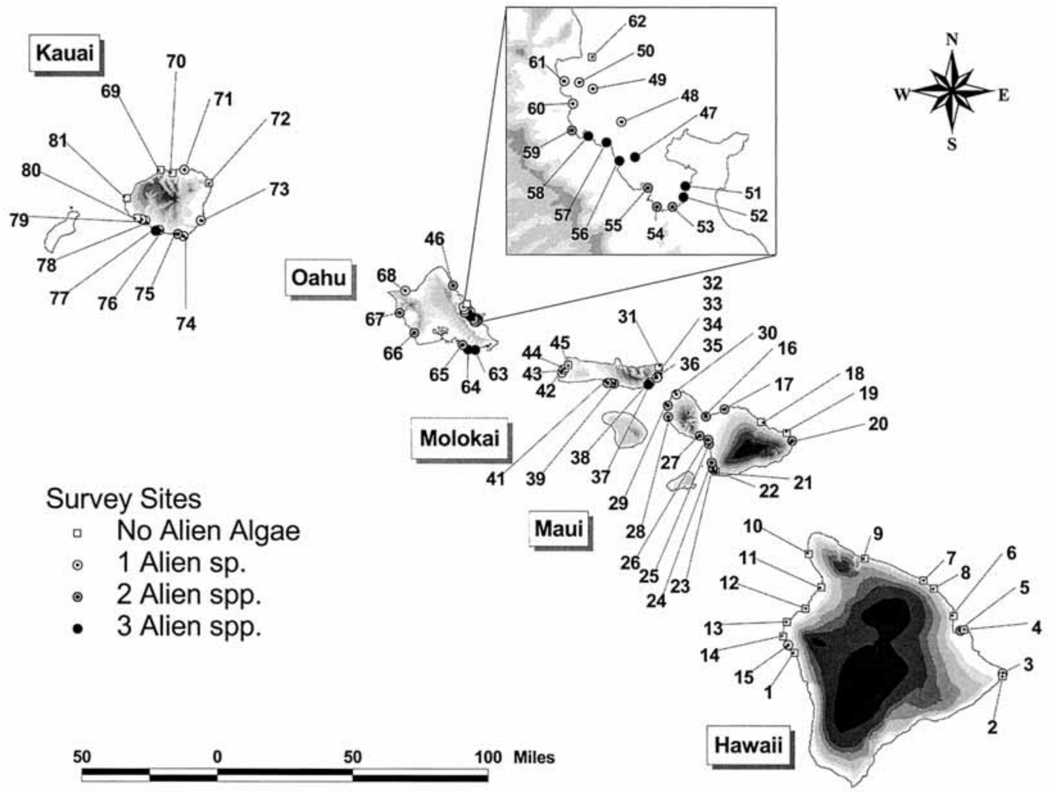

FIGURE 1. Map of all sites surveyed for nonindigenous algae in the main Hawaiian Islands. Each number represents a particular site and corresponds to the appropriate entry in Table 3. Symbols represent the number of nonindigenous algae species present.

TABLE 3

List of All Sites Surveyed for Nonindigenous Algae on the Five Main Hawaiian Islands

Site No.	Site Name	Island	No. of Nonindigenous Algae Species	Relative Abundance of Nonindigenous Algae (% Cover)	*Acanthophora spicifera*	*Gracilaria salicornia*	*Hypnea musciformis*	*Kappaphycus* spp.	*Avrainvillea amadelpha*
1	Kailua Harbor	Hawai‘i	0	0	0	0	0	0	0
2	Vacationland	Hawai‘i	0	0	0	0	0	0	0
3	Kapoho	Hawai‘i	1	20	0	2	0	0	0
4	Leleiwi	Hawai‘i	0	0	0	0	0	0	0
5	Onekahakaha	Hawai‘i	2	70	2	5	0	0	0
6	Pepe‘ekeo	Hawai‘i	0	0	0	0	0	0	0
7	Hakalau	Hawai‘i	0	0	0	0	0	0	0
8	Laupāhoehoe	Hawai‘i	0	0	0	0	0	0	0
9	Waipi‘o Valley	Hawai‘i	0	0	0	0	0	0	0
10	Māhukona	Hawai‘i	0	0	0	0	0	0	0
11	Puakō	Hawai‘i	0	0	0	0	0	0	0
12	Kīholo	Hawai‘i	0	0	0	0	0	0	0
13	Makalawena	Hawai‘i	0	0	0	0	0	0	0
14	Keāhole	Hawai‘i	0	0	0	0	0	0	0
15	Honokohau Harbor	Hawai‘i	1	10	1	0	0	0	0
16	Kahului Harbor	Maui	2	40	1	0	3	0	0
17	Kū‘au	Maui	2	40	2	0	2	0	0
18	Ke‘anae	Maui	0	0	0	0	0	0	0
19	Wai‘anapanapa	Maui	0	0	0	0	0	0	0
20	Hāna Harbor	Maui	2	20	1	0	1	0	0
21	La Pérouse Bay	Maui	0	0	0	0	0	0	0
22	Kanahena Bay	Maui	1	10	1	0	0	0	0
23	‘Āhihi tide pools	Maui	2	30	1	0	2	0	0
24	Wailea	Maui	2	30	2	0	1	0	0
25	Kīhei Beach	Maui	2	40	2	0	2	0	0
26	Kīhei residential	Maui	2	70	2	0	5	0	0
27	Mā‘alaea	Maui	2	90	1	0	8	0	0
28	Lahaina	Maui	2	30	2	0	1	0	0
29	Honokōwai	Maui	2	50	1	0	4	0	0
30	Honolua	Maui	1	10	1	0	0	0	0
31	Hālawa Valley	Moloka‘i	0	0	0	0	0	0	0
32	Kalaekapu	Moloka‘i	0	0	0	0	0	0	0
33	Pōhakuloa	Moloka‘i	0	0	0	0	0	0	0
34	Kūmimi	Moloka‘i	0	0	0	0	0	0	0
35	Kūmimi Point	Moloka‘i	1	10	1	0	0	0	0
36	Palalupi	Moloka‘i	1	20	2	0	0	0	0

37	Kūpeke	Molokaʻi	2	40	3	0	1	0	0
38	Pūkoʻo	Molokaʻi	3	60	1	4	1	0	0
39	Hotel Molokaʻi	Molokaʻi	2	30	2	0	1	0	0
40	Molokaʻi Shores	Molokaʻi	2	40	3	0	1	0	0
41	Kaunakakai Harbor	Molokaʻi	2	40	3	0	1	0	0
42	Poʻolau	Molokaʻi	1	20	2	0	0	0	0
43	Puʻu Koaʻe	Molokaʻi	1	10	1	0	0	0	0
44	Pāpōhaku Beach-south	Molokaʻi	0	0	0	0	0	0	0
45	Pāpōhaku Beach-north	Molokaʻi	0	0	0	0	0	0	0
46	Hauʻula	Oʻahu	2	0	0	0	0	0	0
47	Patch reef #14	Oʻahu	3	30	1	0	1	1	0
48	Patch reef #29	Oʻahu	1	50	0	0	0	5	0
49	Patch reef #44	Oʻahu	1	20	0	0	0	2	0
50	Patch reef #54	Oʻahu	1	10	1	0	0	0	0
51	South bay #1	Oʻahu	3	60	1	4	0	1	0
52	South bay #2	Oʻahu	3	70	2	4	0	1	0
53	South bay #3	Oʻahu	2	40	1	3	0	0	0
54	South bay #4	Oʻahu	2	60	1	5	0	0	0
55	Coconut Island boat dock	Oʻahu	2	60	2	4	0	0	0
56	Central bay #1	Oʻahu	3	40	2	1	0	1	0
57	Central bay #2	Oʻahu	3	60	1	4	0	1	0
58	Central bay #3	Oʻahu	3	40	1	2	0	1	0
59	North bay #1	Oʻahu	2	40	2	2	0	0	0
60	North bay #2	Oʻahu	1	10	0	1	0	0	0
61	North bay #3	Oʻahu	1	10	0	0	0	1	0
62	Kualoa	Oʻahu	0	0	0	0	0	0	0
63	Kahala Beach	Oʻahu	3	30	2	0	1	0	3
64	Waikīkī Natatorium	Oʻahu	3	90	2	6	1	0	0
65	Ala Moana	Oʻahu	2	60	5	0	1	0	0
66	Kahe Point	Oʻahu	2	20	0	0	1	0	2
67	Mākaha	Oʻahu	2	10	0	0	1	0	0
68	Mokulēʻia	Kauaʻi	1	10	1	0	0	0	0
69	Hāʻena	Kauaʻi	0	0	0	0	0	0	0
70	Hanalei Bay	Kauaʻi	0	0	0	0	0	0	0
71	ʻAnini Beach	Kauaʻi	1	40	4	0	0	0	0
72	Anahola	Kauaʻi	0	0	0	0	0	0	0
73	Nāwiliwili Harbor	Kauaʻi	1	20	2	0	0	0	0
74	Poʻipū Beach	Kauaʻi	1	20	2	0	0	0	0
75	Prince Kūhiō Beach	Kauaʻi	3	40	2	0	1	0	1
76	Port Allen Harbor	Kauaʻi	1	30	3	0	0	0	0
77	Salt Pond Beach	Kauaʻi	2	50	3	0	2	0	0
78	Kīkīaola	Kauaʻi	1	20	2	0	0	0	0
79	Kīkīaola Harbor	Kauaʻi	1	30	3	0	0	0	0
80	ʻŌʻōmanō Point	Kauaʻi	0	0	0	0	0	0	0
81	Polihale Beach	Kauaʻi	0	0	0	0	0	0	0

Note: Site numbers correspond to numbers plotted in Figure 1. The relative abundance of each of the individual species ranked on a scale of 0 (not present) to 10 (100% cover) is given.

O‘ahu appears to be most heavily impacted by nonindigenous algae, and it is common there to find up to three nonindigenous algae species at any given site. Several sites on the island of O‘ahu also had greater than 50% cover of nonindigenous algae. West Maui is another area that is heavily impacted by nonindigenous algae; specifically *Hypnea musciformis* was found occupying up to 80% cover in some areas. As a general trend, the south and southwestern shores of all islands excluding Hawai‘i are most impacted by nonindigenous algae. The island of Hawai‘i is the least impacted of the main islands; there *Gracilaria salicornia* and *Acanthophora spicifera* are the only nonindigenous algae species present, at two locations per species.

Quantitative surveys were conducted in Kāne‘ohe Bay, O‘ahu, and the relative abundance and distribution of total alien algae (all species combined), the invasive alga *Dictyosphaeria cavernosa*, and hard coral at all sites surveyed in the bay are presented in Figure 2. Detailed results and photographs of Kāne‘ohe Bay sites are displayed on the website. Nonindigenous algae were most abundant in southern Kāne‘ohe Bay and appeared to be negatively associated with hard coral abundance. *Dictyosphaeria cavernosa* was more common at the central and north-bay sites than in the south bay, and hard coral abundance increased along a south-to-north gradient. Results obtained from different patch reefs throughout the bay seem to be highly variable and did not show any clear trends.

Blooms of indigenous invasive species were observed on the island of Maui and in Kāne‘ohe Bay, O‘ahu. The green alga *Ulva fasciata* Delile appeared in high abundance in Kahului Harbor and in North Kīhei on the island of Maui. Another green alga, *Cladophora sericea*, was blooming from northern Lahaina to Honokōwai in the north/west region of Maui. Several species were found to be invasive within Kāne‘ohe Bay, including *Dictyosphaeria cavernosa* and other nonindigenous algae as shown in Figure 2.

Reproductive Biology of Alien Algae

In field experiments (Figure 3), *H. musciformis* showed the greatest potential for fragmentation in all size classes, with the highest success in the smallest fragments. This species has “apical hooks” at the tips of its branches that attach or anchor the alga onto other macroalgae and any other available substrate. The smallest fragments were generated from these apical hooks and showed up to a 200% increase in weight over 1 week. When this species is ripped from the substrate, these hooks are likely to be left behind to regrow. Other species examined showed lesser potential for vegetative propagation as a successful means of asexual reproduction (Figure 3).

Fragmentation studies conducted at the Waikīkī Aquarium produced results similar to those obtained in the field (Figure 4). Again, the smallest fragments of *H. musciformis* showed the largest increase in weight during the study period. Fragments of *G. salicornia* also showed significantly high growth rates for all size classes examined. *Acanthophora spicifera* initially showed positive growth in most size classes but began showing signs of decomposition toward the end of the experiment. The cylindrical branches of this species are covered with large, bumpy spines and despite continual dusting of sediment from experimental boxes, these spines tended to trap fine sediment. Eventually, most fragments began to decline in health as a result of sediment burial. Most of the fragments of *A. amadelpha* showed very little growth during the experimental interval. The largest size class for this species showed more growth relative to initial weight than any of the other sizes examined.

Results of the two-factor ANOVA showed that time was significant (Table 4) for all four species, indicating that even though fragments were growing throughout the experiment, the greatest increase in growth occurred during the first week of the experiment. This pattern was most likely the result of a gradual decline in health due to sedimentation and decreased metabolism associated with low water motion. Fragment size was also significant for all species except for *A. spicifera*. For both *H. musciformis* and *G. salicornia* the smallest (0.5 cm) fragments grew the most. Pieces of tissue as small as 0.5 cm are viable as propagules. For *A. amadelpha* the largest fragments were the most successful. This

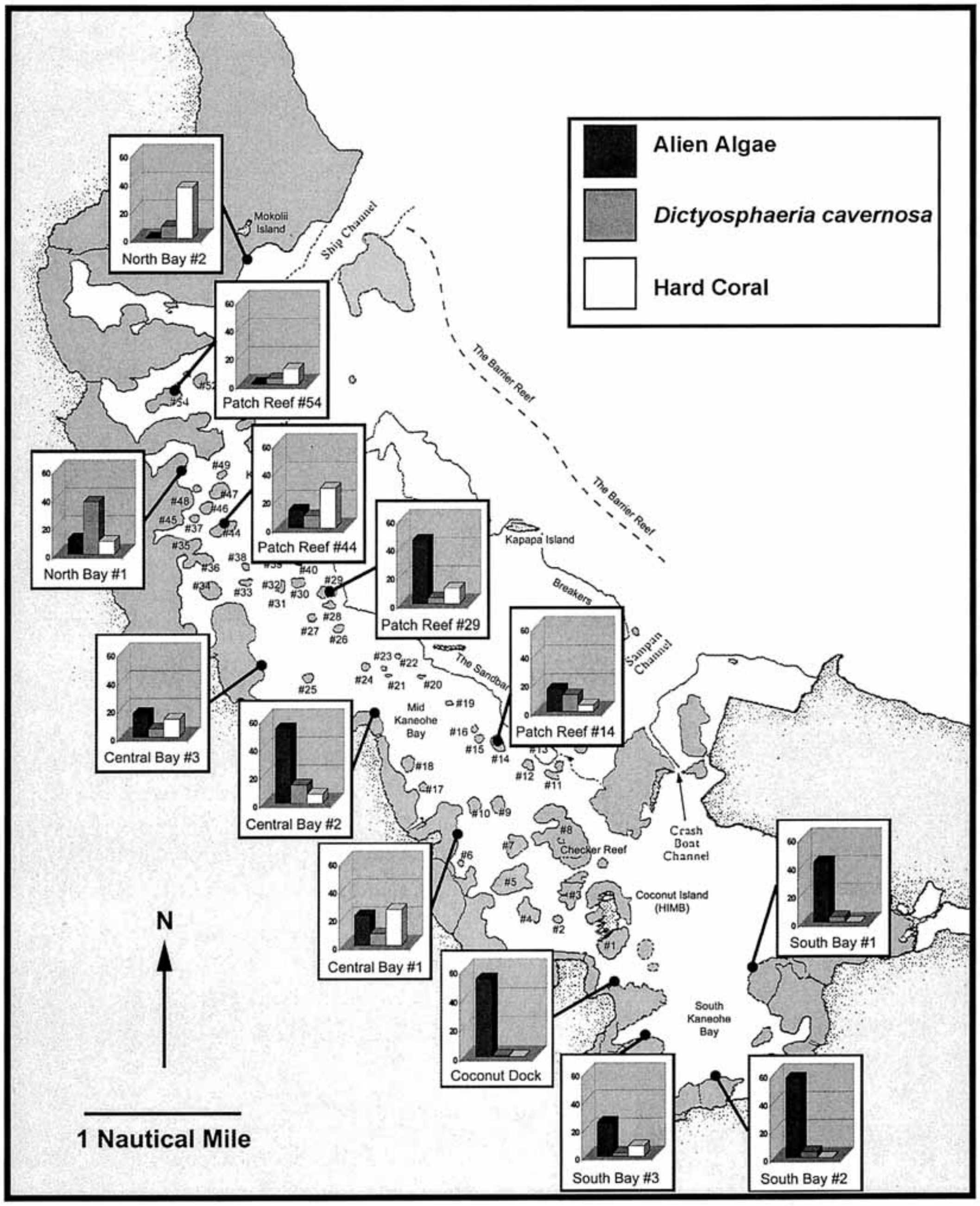

Figure 2. Map showing the distribution and abundance of hard coral, nonindigenous algae, and indigenous invasive algae within Kāne‘ohe Bay, O‘ahu. Graphs show the mean percentage cover of each benthic category (nonindigenous algae, all species; invasive algae, *Dictyosphaeria cavernosa;* hard coral, all species) recorded in 10 randomly placed quadrants along each of two replicate 30-m transect lines at each site surveyed.

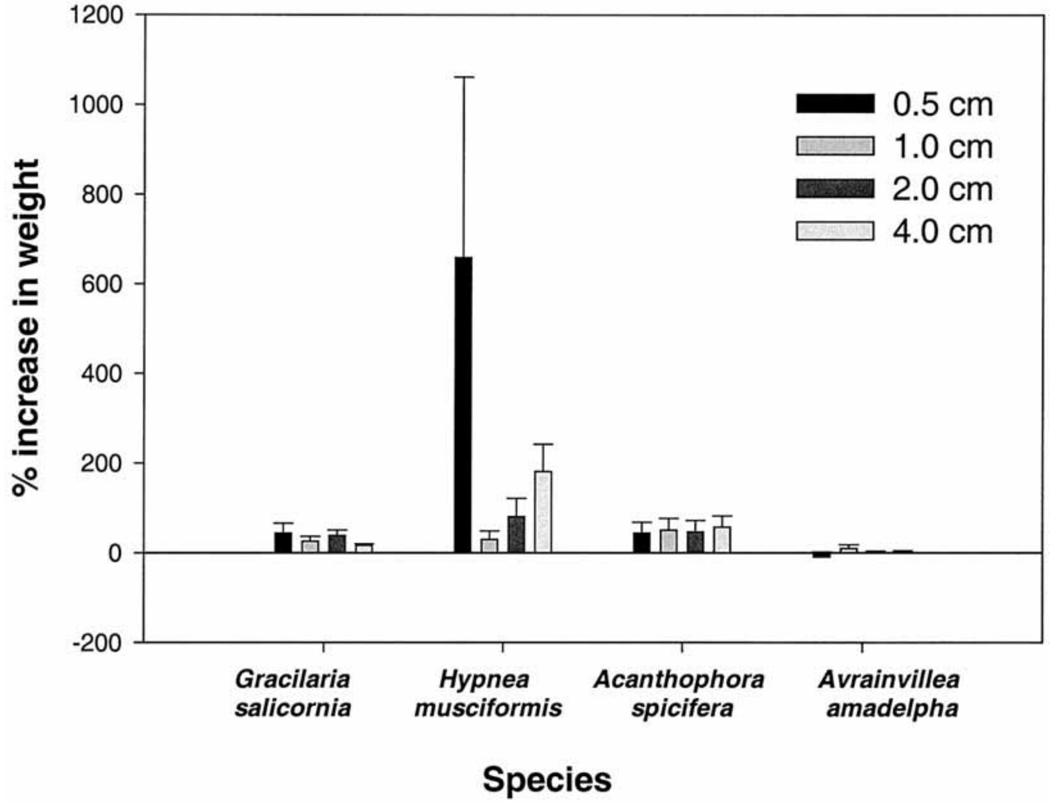

FIGURE 3. Graph of results from the field fragmentation study showing the mean percentage increase in growth of fragments of different sizes generated from four alien species of algae over a 7-day period. Values are the mean of six replicate samples per species size combination. Bars are ±1 SE of the mean.

species appeared to be able to regrow from fragments 3 cm or greater in size.

Before this study, sexual reproduction had not been observed in the field for any of the species of algae introduced to Hawai'i. During the field surveys, sexually reproductive individuals of *A. spicifera* were collected on all islands except Hawai'i. Individuals of this species were also observed on the hulls of ships on O'ahu, Maui, Moloka'i, and Kaua'i. None of the other nonindigenous algae was fertile when collected or observed in the field.

The Five Most Common Alien Algae Species in Hawai'i

Information obtained during this study can be used to define areas that may be more susceptible to invasion than others. However, based on the diversity in ecological strategies observed for each of these alien species, it is difficult to make any specific predictions. In the broadest context, sites with low topographic complexity, low herbivore abundance, and high terrestrial nutrient input seem to be most at risk. As different levels of each of these factors are considered, the issue becomes more complex. Information generated during this study for the five most common species of alien algae in Hawai'i is summarized here.

Acanthophora spicifera

DISTRIBUTION IN HAWAI'I. *Acanthophora spicifera* was initially unintentionally introduced to Pearl Harbor on the island of O'ahu in 1952 from a barge originating in

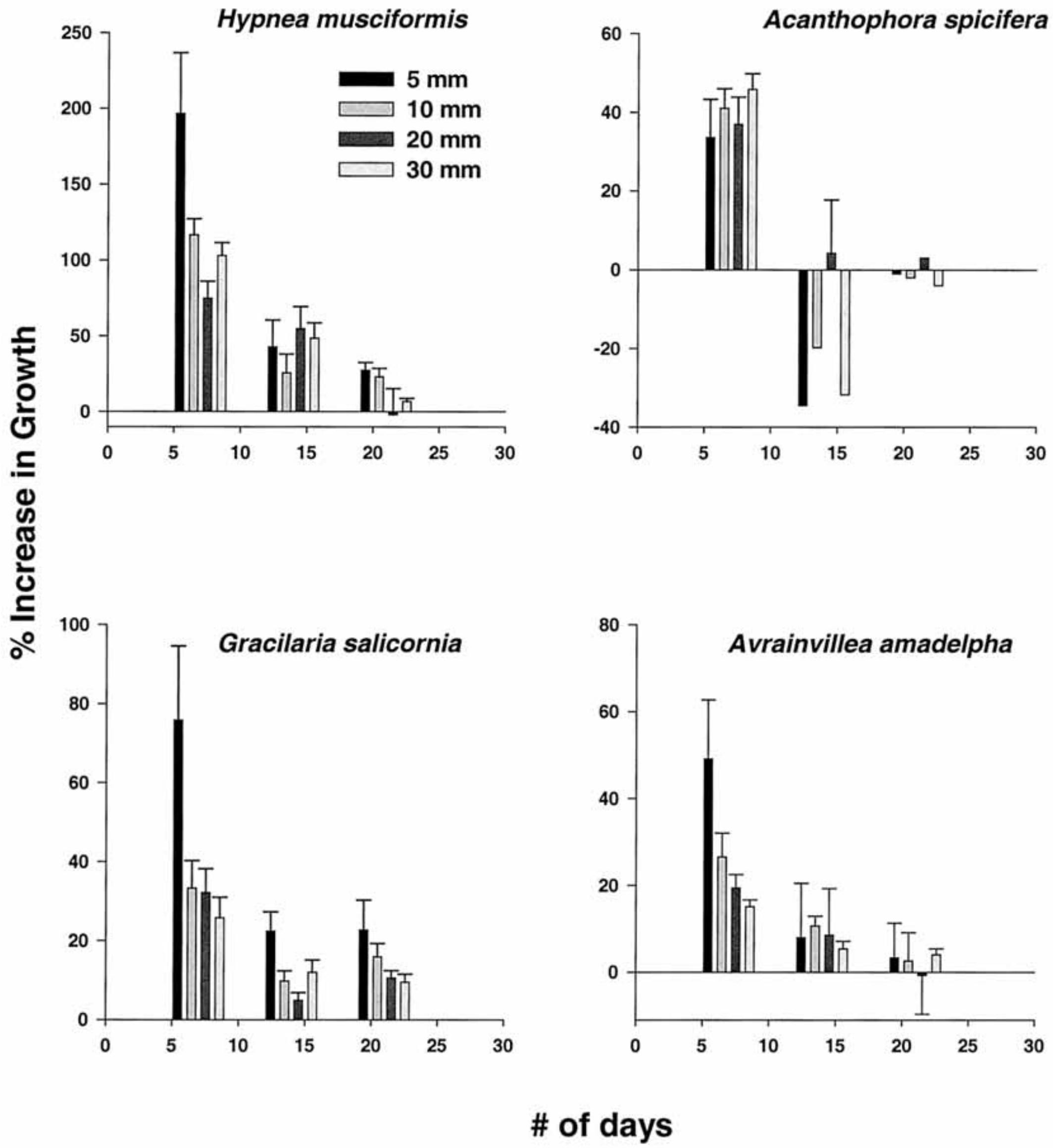

FIGURE 4. Graphs of results from the Waikīkī Aquarium fragmentation study. Each graph shows the mean percentage increase in growth of fragments of different sizes generated from four alien species of algae. Measurements were made every 7 days for 1 month. Values are the mean of six replicate samples per species size combination. Bars are ±1 SE of the mean.

Guam. Based on field surveys conducted during this study, *A. spicifera* is the most common nonindigenous algal species in Hawai'i. This species was found on every island surveyed, and its distribution was fairly uniform around all coastlines except for the island of Hawai'i. This organism appears to have radiated in all directions from the initial site of introduction. It is most common in intertidal regions and in semiprotected tide pools, where it may escape spatially from herbivory. This species was commonly observed fouling ship hulls in

TABLE 4

Results of the Two-Way ANOVA for the Waikīkī Aquarium Fragmentation Study

	Time		Size		
Species	*F*	*P*	*F*	*P*	Significant Size (cm)
Acanthophora spicifera	23.3	<0.0001	0.59	0.623	ns
Avrainvillea amadelpha	14.86	<0.0001	2.64	0.050	3.0
Gracilaria salicornia	22.91	<0.0001	5.38	0.002	0.5
Hypnea musciformis	38.95	<0.0001	3.28	0.026	0.5

Note: Factors (time and size) were both treated as fixed variables. Significant size refers to the size class that showed the largest increase in growth during the experiment as determined by Tukey's multiple comparisons. ns, not significant.

harbors throughout the state during field surveys. Although this plant was a common component of the marine flora and is clearly displacing native species in Hawai'i, it does not appear to form large, monospecific nuisance blooms.

REPRODUCTION. During field surveys, samples of this species were collected whenever encountered, and several tetrasporophytes and female gametophytes containing mature carpospores were found on all islands except Hawai'i. This species appears to be able to release sexual propagules at all times of the year and because of this may have greater potential for dispersal than plants that reproduce only by fragmentation. This species did also show some fragmentation potential. The broad distribution of this species may also be due in part to hull fouling and transport by small boats and vessels throughout the Islands.

Avrainvillea amadelpha

DISTRIBUTION IN HAWAI'I. *Avrainvillea amadelpha* was initially reported by Brostoff (1989); it was collected at Koko Head and Kahe Point, O'ahu, after 1981. Based on field surveys, this organism has persisted in both of these locations and has spread laterally from Koko Head to Kahala on O'ahu's south shore and from Kahe Point north on the west shore. Previous to this study *A. amadelpha* had never been found beyond O'ahu; however, we located a small population at Prince Kūhiō Beach Park on Kaua'i, suggesting that this organism is able to disperse between islands. This species inhabits soft or sandy bottom habitats where the majority of the plant biomass is subsurface. This nonindigenous alga frequently serves as a substrate for many native species of epiphytic algae and as habitat for many invertebrates. The endemic Hawaiian sea grass *Halophila hawaiiana* and *A. amadelpha* now co-occur in areas that were once *H. hawaiiana* meadows (Unabia 1984). This may prove to be a considerable conservation and management problem, and more research is needed to determine *A. amadelpha*'s ecological strategies and impacts on the native biota.

REPRODUCTION. *Avrainvillea amadelpha* showed the lowest overall potential to reproduce via fragmentation when compared with the other nonindigenous algae examined. Of all size classes studied, this species showed the highest success in the largest fragments (3 cm). Sexual reproduction was not observed in samples of *A. amadelpha* collected from O'ahu populations. However, identification of reproductive material for this species requires microscopic examination; it is possible that we overlooked reproductive individuals in the field. The recent finding of this species on Kaua'i suggests that it is dispersing; however, the mechanism remains unclear.

Gracilaria salicornia

DISTRIBUTION IN HAWAI'I. *Gracilaria salicornia* has an interesting history in Hawai'i. Two populations of this species were known to exist on the island of Hawai'i (in Hilo Bay and Kapoho) before 1950; the origin of these populations is unknown but may be tied to early harbor arrivals in Hilo from the Philippines. In the 1970s this species was transported intentionally from Hilo to two locations on Oʻahu (Waikīkī and Kāneʻohe Bay) for aquacultural projects that were later abandoned. Sometime in the 1980s *G. salicornia* was brought from Oʻahu to Pūkoʻo fishpond on the island of Molokaʻi (I. Abbott, pers. comm.), where the alga *Gracilaria parvispora* is being cultivated. This nonindigenous algal species currently has the most discontinuous distribution of all species examined in this study. It is now found on three islands, with no obvious continuity among locations. At most of the sites where *G. salicornia* was found, this alga was highly dominant over a distinct area. It was very common in southern Kāneʻohe Bay but was not found in the north bay. *Gracilaria salicornia* was dominant in Waikīkī in front of the Aquarium but was not present at adjacent sites such as Ala Moana Beach Park or at Kahala. It seems that, once introduced, this species may have the ability to spread within a site laterally and become locally dominant but does not have great success at dispersing larger distances between sites or islands, over this two-decade time frame.

REPRODUCTION. *Gracilaria salicornia* was able to fragment successfully in all size classes examined. These results suggest that once this species is introduced, it may be able to spread laterally within a site via vegetative growth. However, the fragments are quite heavy (mean, 0.05 g/cm ± 0.005 SE) and tend to sink rapidly, perhaps explaining why it is not as successful at spreading between sites. With physical disturbance such as wave action or trampling, these fragments likely get washed off the reef and sink out of favorable conditions (e.g., below the photic zone) before becoming established. Sexual reproduction was never observed in the field, and therefore fragmentation is most likely the primary mode of reproduction in this species. Further, Nishimura (2000) found a high degree of genetic similarity between individuals collected throughout Waikīkī. It seems likely that existing populations of this species around the state of Hawaiʻi were initially unintentionally introduced followed by secondary intentional spread. Localized dominance is then facilitated by morphology (Larned 1998), physiology (Beach et al. 1997), and fragmentation.

Hypnea musciformis

DISTRIBUTION IN HAWAIʻI. *Hypnea musciformis* was initially introduced to Kāneʻohe Bay, Oʻahu, in 1974 as part of an aquaculture project that was later abandoned. This organism is the second most common nonindigenous algal species in Hawaiʻi. *Hypnea musciformis* has not yet spread to all of the islands and was not as abundant or as evenly distributed as *A. spicifera* but is clearly becoming more common. It is common on the islands of Oʻahu and Maui but only appears to be blooming at discrete locations. *Hypnea musciformis*, when abundant, usually co-occurs with *Ulva fasciata*, a known weedy species in a genus known to require high nutrient flux for growth (Larned 1998). Therefore, the mechanisms that influence bloom formation in this species may be related to land use activities and nutrient input. It is surprising that *H. musciformis* was not common in Kāneʻohe Bay, the site of initial introduction, occurring at only 1 out of 15 bay survey sites in fairly low abundance (Figure 1).

REPRODUCTION. Although *H. musciformis* was not observed to reproduce via sexual reproduction in Hawaiʻi during this study, it is able to propagate vegetatively in all size classes examined, with the greatest success observed in the smallest fragments. As mentioned previously, the tips of the branches of this species are inflated and have characteristic "hooks." These hooks twine tightly around axes of other plants. Once the epiphytic biomass of *H. musciformis* reaches a certain size or weight, wave action or other physical disturbance may crop the majority of the *Hypnea* off the host plant, leaving the "hooks" behind. Our fragmentation study showed that these hooks can increase in weight up to 200% in a week, thereby rapidly propagating this species. In addition to the hooks, drift biomass that is ripped up can also disperse to new locations. It appears that fragmentation is the primary mode of reproduction in this species; however, the genetic basis for this remains to be tested.

Kappaphycus spp.

DISTRIBUTION IN HAWAI'I. At least two species of *Kappaphycus* were intentionally introduced with state permits into Kāne'ohe Bay, O'ahu, for aquaculture in the 1970s. Some 30 yr later, during this study, this genus was still found only in and around Kāne'ohe Bay and had a very patchy distribution within the bay itself. It was most common on patch reefs but could also be found in variable abundance on the fringing reefs from the south up to the most northerly site surveyed as well as on the back reef (Woo 1999). *Kappaphycus* appears to have spread uniformly from its initial site of introduction at Coconut Island and has become heavily dominant on some patch reefs in the bay. In some areas this organism is clearly competitively dominant, occupying up to 80% of the substrate. Because of its large stature, *Kappaphycus* also appears to be competing with coral and may be able to overgrow live coral colonies. Once established in an area, this nonindigenous alga may be able to spread laterally but, like *G. salicornia*, does not appear to be able to spread long distances or between islands.

REPRODUCTION. *Kappaphycus* in Hawai'i is most likely several (at least two species) taxonomic entities that have a great deal of morphological plasticity. Female gametophytes are needed to identify these plants to species; *Kappaphycus* was not observed to be reproductive during this study. Although *Kappaphycus* may not be reproducing sexually in Hawai'i, it is clearly successful at vegetative propagation. This mode of reproduction was not examined in this study due to extensive work conducted previously by Woo (1999). That research showed that *Kappaphycus* regrew in the field from fragments as small as 0.5 cm. This method of reproduction is most likely the primary mode of propagation for *Kappaphycus* spp. in Hawai'i. It is unclear why this plant has not spread outside Kāne'ohe Bay, but is likely due to the heavy weight of fragments and the inability of the propagules to disperse long distances. As with *G. salicornia*, the fragments most likely sink out of favorable habitats or below the photic zone before becoming established.

CONCLUSIONS

This research has highlighted numerous aspects of nonindigenous algal species biology that had not previously been documented in Hawai'i. The current distribution of each nonindigenous algal species has been mapped and will serve as a basis for future monitoring and assessment of coral reefs throughout the state. Reproductive mechanisms involved in propagating and dispersing these nonindigenous algal species were examined and provide tools for developing management schemes or eradication programs. Because of the ability of many of these nonindigenous algal species to propagate vegetatively, caution is needed when developing eradication programs to avoid further dispersal. Blooms of native algal species were also encountered and preliminarily documented. Future research should examine top-down and bottom-up forcing factors that may limit or determine the ultimate growth potential for each invasive species, both indigenous and nonindigenous. Herbivore feeding preferences can be used to determine if marine protected areas or fisheries management areas will help to reduce the abundance of these species (McClanahan 1997). Finally, nutrient fluxes into reef regions and rates of uptake by these plants will contribute to our understanding of why some of these organisms bloom under certain conditions. The issues of nonindigenous and invasive algae in Hawai'i are dynamic. Each species is specialized and likely employs unique strategies that lead to ecological success in a variety of habitats. A diverse and multidisciplinary approach is needed to address management issues related to invasive species mitigation and eradication in the marine environment.

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