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Rate of Spread of Introduced Rhodophytes *Kappaphycus alvarezii*, *Kappaphycus striatum*, and *Gracilaria salicornia* and Their Current Distributions in Kāne'ohe Bay, O'ahu, Hawai'i[1]

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ABSTRACT: Spread of the introduced macroalgae *Kappaphycus alvarezii* (Doty), *Kappaphycus striatum* Schmitz, and *Gracilaria salicornia* C. Ag. was measured on reefs in Kāne'ohe Bay, O'ahu, Hawai'i. The red algae *Kappaphycus alvarezii* and *Gracilaria salicornia* were introduced to specific sites in Kāne'ohe Bay in the 1970s. Since that time their distributions have increased, and the algae have spread through the bay. To assess the current extent of these algae in the bay and determine their rate of spread, we performed surveys with a manta towboard. In addition, abundance of these species was determined by detailed reef transects in the central bay in three habitats: barrier reef, patch reef, and fringing reef. All three species have become well established. These algae were found in all areas of Kāne'ohe Bay. Distributions are not uniform within the central bay. Abundance of *Kappaphycus* spp. was highest on patch reefs in shallow water. *Gracilaria salicornia* was most abundant on the fringing reef. *Kappaphycus alvarezii* and *K. striatum* have spread 6 km from their points of introduction in 1974, an average rate of spread of approximately 250 m yr^{-1}. *Gracilaria salicornia* has spread over 5 km since its introduction in 1978, an average rate of spread of approximately 280 m yr^{-1}. High abundance of these introduced species appears to be associated with moderate water motion.

SINCE 1950 AT LEAST 18 species of macroalgae have been introduced and become established on the island of O'ahu, Hawai'i. Commercial, experimental, and accidental introductions have resulted in the establishment of alien species from several South Pacific locations, Florida, California, and Japan (Russell 1992). Between 1970 and 1978, 10 algal species were introduced in Kāne'ohe Bay (Eldredge 1994). *Gracilaria salicornia* C. Ag. was first introduced in September 1978 in Kāne'ohe Bay. *Kappaphycus alvarezii* (Doty) (formerly *Eucheuma striatum*) was introduced from the Philippines into Honolulu Harbor in 1974 and transplanted to several locations on the northwestern reef bordering Moku o Lo'e in Kāne'ohe Bay in September 1974 (Russell 1983). *Kappaphycus striatum* Schmitz (formerly a variety of *Eucheuma striatum*) was introduced to Kāne'ohe Bay sometime between 1970 and 1976.

Kappaphycus alvarezii lacks a sexual reproductive cycle and reproduces through vegetative fragmentation. Russell (1981) hypothesized that this characteristic would prevent its dispersal to new areas because *K. alvarezii* did not survive in deep water, and thalli did not appear to cross channels or dredged reef areas. Russell also concluded that *K. alvarezii* is noncompetitive with indigenous algae because it inhabits sand-covered grooves on the reef edge where native species are not abundant. The distribution of *K. alvarezii* in Kāne'ohe Bay has not been documented since 1978 (Russell 1983).

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Studies of *Kappaphycus* spp. (Glenn and Doty 1989, 1992) at Moku o Lo'e found that water motion was the environmental factor that had the most influence on growth rates of these species. Maximum growth rates were found at the highest water motion in those studies, 15 cm sec^{-1}, with 81–98% of the variation in growth rates attributable to water motion.

This survey assessed the current distributions of *Kappaphycus* spp. and *Gracilaria salicornia* throughout Kāne'ohe Bay. Additional intensive transect surveys were done in the central bay to estimate the abundance of these introduced species in zones representing fringing, patch, and barrier reef habitats. During these intensive surveys we also measured water motion.

MATERIALS AND METHODS

Study Site

Kāne'ohe Bay is the largest embayment in the state of Hawai'i and the most extensively studied (e.g., Smith et al. 1981, Evans et al. 1986, Hunter and Evans 1995, Laws and Allen 1996). Anthropogenic influences affecting Kāne'ohe Bay include erosional runoff of terrigenous sediments, diversion and channelization of streams, changes in the watershed and riparian environments, and 25 yr of sewage effluent discharge that ended in 1977.

Three reef types are found in Kāne'ohe Bay: fringing reefs, patch reefs, and the barrier reef (Smith et al. 1973). The tops of the fringing reefs are generally in water less than 1 m in depth. A steep dropoff then extends from approximately 1 m to the floor of the lagoon, which has a mean depth of 10 m. The reef slope supports a diverse fish community and relatively high coral cover. Seventy-nine patch reefs are located within Kāne'ohe Bay, ranging from 21 to 850 m in diameter. The upper slopes of these patch reefs display the highest coral cover. The barrier reef complex is 2 km wide and 5 km long, with a back reef flat of less than 1 to 2 m depth. Two dredged channels intersect the north and south ends of the barrier reef.

Geographic Extent of Species Distributions

To detect the presence or absence of *Kappaphycus* spp. and *G. salicornia*, a systematic survey of all accessible areas within Kāne'ohe Bay was undertaken in the summer of 1996 using a manta towboard, which is effective in monitoring broad-scale changes in benthic communities. The observer was towed parallel to the reef to allow for maximum visibility of the reef slope and outer reef flat, the habitat these algae occupy. A constant towing speed was maintained between 1 and 2 knots (0.5 and 1 m sec^{-1}) for a standardized tow of 5 min. Tow direction was standardized with clockwise tows around patch reefs and south to north tows along the fringing reef. Visibility was recorded every 10 tows using horizontal secchi disk distance. The inner reef flats were assessed with snorkel, every 500 m along the fringing reef and diagonal swims across the larger patch reefs.

There are both advantages and disadvantages to the manta towboard technique (English et al. 1994). Advantages include efficiency in appraisal of sites to assess their representativeness of large areas. Distribution and abundance of benthic organisms can be estimated in a relatively short time at remote locations. Surveys can be conducted rapidly with this method when covering large distances. However, tow boarding is not suited for areas of limited visibility or deep water, and organisms may be overlooked.

Detailed Surveys of Representative Central Bay Transects

Based on observations from manta towing, the central bay was selected to assess algal abundance at four fringing, three patch, and four barrier reef sites. At each site, except the barrier reef sites, stations were located at each of two depths: shallow (< 1 m) and deep (3 m). These two depths were selected to investigate the statement that abundance of *Kappaphycus* spp. is low in deeper waters (Russell 1983). All barrier reef stations were less than 1 m depth. At patch reef sites, stations were established on both leeward and windward reef slopes and across the tops of the patch reefs. During May–September 1996, coverage of macroalgae, coral, and substratum type was determined visually along three 25-m transects at each station. Transects were placed haphazardly along each depth gradient and coverage assessed using a 1-m^2 quadrat placed at 15 randomly chosen points along each transect. At each station, water motion was measured using plaster of paris clod cards (Jokiel and Morrissey 1993). On six dates, two cards were deployed for 24 hr at each station except at the barrier reef where cards remained for only 12 hr because of higher water motion.

RESULTS

Geographic Extent

Gracilaria salicornia was found to have spread over 5 km since its original introduction in September 1978 at Moku o Lo'e (Figure 1). *Gracilaria salicornia* had a distribution that was not uniform throughout the south bay (Figure 2). It was absent from one patch reef and the southeastern end of the barrier reef. It was found in parts of the central bay and extends into the north bay. It occurred in low abundance on the barrier reef and higher abundance on the fringing and patch reefs.

Kappaphycus spp. have also spread throughout Kāne'ohe Bay (Figure 3). From the point of origin on the northwest reef bordering Moku o Lo'e, they have extended their ranges toward the south bay and well into the central bay. *Kappaphycus* spp. have spread at least 5.7 km from the point of original introduction on Moku o Lo'e in September 1974 (Glenn and Doty 1992). Distributions were not uniform on the barrier reef. *Kappaphycus* spp. now occur in low abundance in the north bay as well.

Detailed Surveys of Representative Central Bay Transects

Distribution of these introduced species is patchy throughout the central bay. The highest abundance of *Kappaphycus striatum* and *K. alvarezii* occurred on patch reef sites at depths <1 m (Table 1). *Gracilaria salicornia* had highest abundance on the barrier and fringing reef sites less than 1 m in depth and did not occur at the patch reef sites on these transects (Table 1). *Dictyosphaeria cavernosa*, another common macroalgal species in the bay, occurred in highest abundance at deep patch reef stations followed by deep fringing reef stations and shallow patch reef stations. Other species of macroalgae were most abundant at the barrier reef sites.

Abundances of the introduced species were highest at sites with shallow depth and moderate water motion ($6 < DF < 14$) (Figure 4). At the barrier reef stations with high water motion ($DF > 14$), abundances of the introduced species were low. Likewise, at patch reef stations with low water motion ($DF < 6$), abundances were low.

DISCUSSION

Kappaphycus spp. and *Gracilaria salicornia* have spread throughout Kāne'ohe Bay. These species are nearly cosmopolitan in the south bay and central bay. Although they currently occur in low abundance in the north bay and the barrier reef, they have spread into these regions and their abundance may continue to increase. High growth rates, effective propagation, and morphological plasticity can accelerate the spread of introduced species into new areas (Carpenter 1990). *Kappaphycus* spp. exhibit high growth rates. In productive areas, algae can double their size in 15–30 days or less (Azanza-Corrales et al. 1992). In Hawai'i, *Kappaphycus alvarezii* has a year-round 5% average daily growth rate (Russell 1983). *Kappaphycus* spp. have an effective means of propagation via vegetative regeneration (Azanza-Corrales et al. 1992), although reproductive plants are rare. Vegetative fragmentation is an effective means of dispersal of other invading algal species into new areas (Mshigeni 1978, Kilar and McLachlan 1986, Meinesz et al. 1993, Davis et al. 1997). With these characteristics of high growth rates and vegeta-

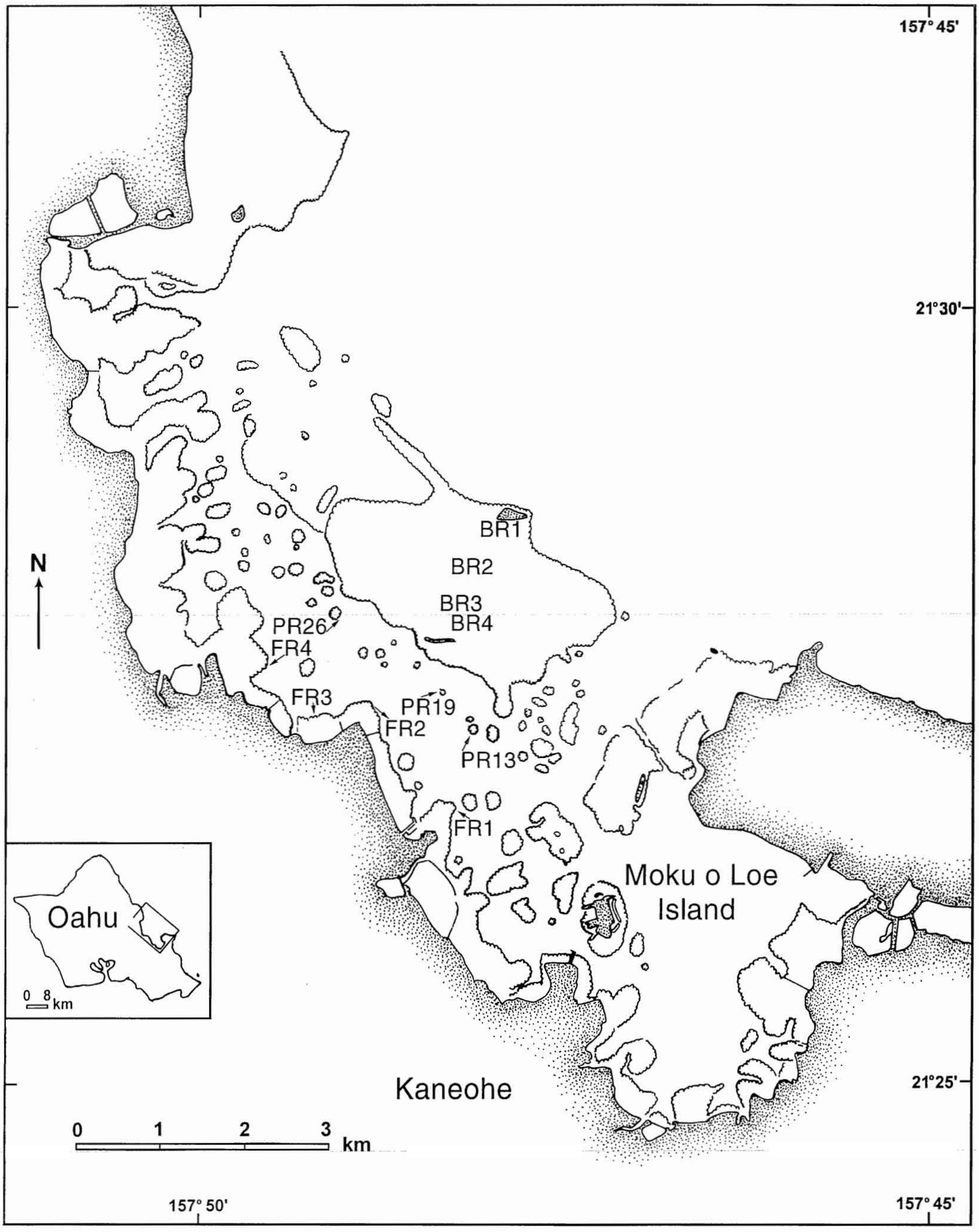

FIGURE 1. Map of Kāne'ohe Bay, O'ahu, Hawai'i. Locations of survey transects are indicated. Abbreviations are as follows: BR, barrier reef; FR, fringing reef; PR, patch reef.

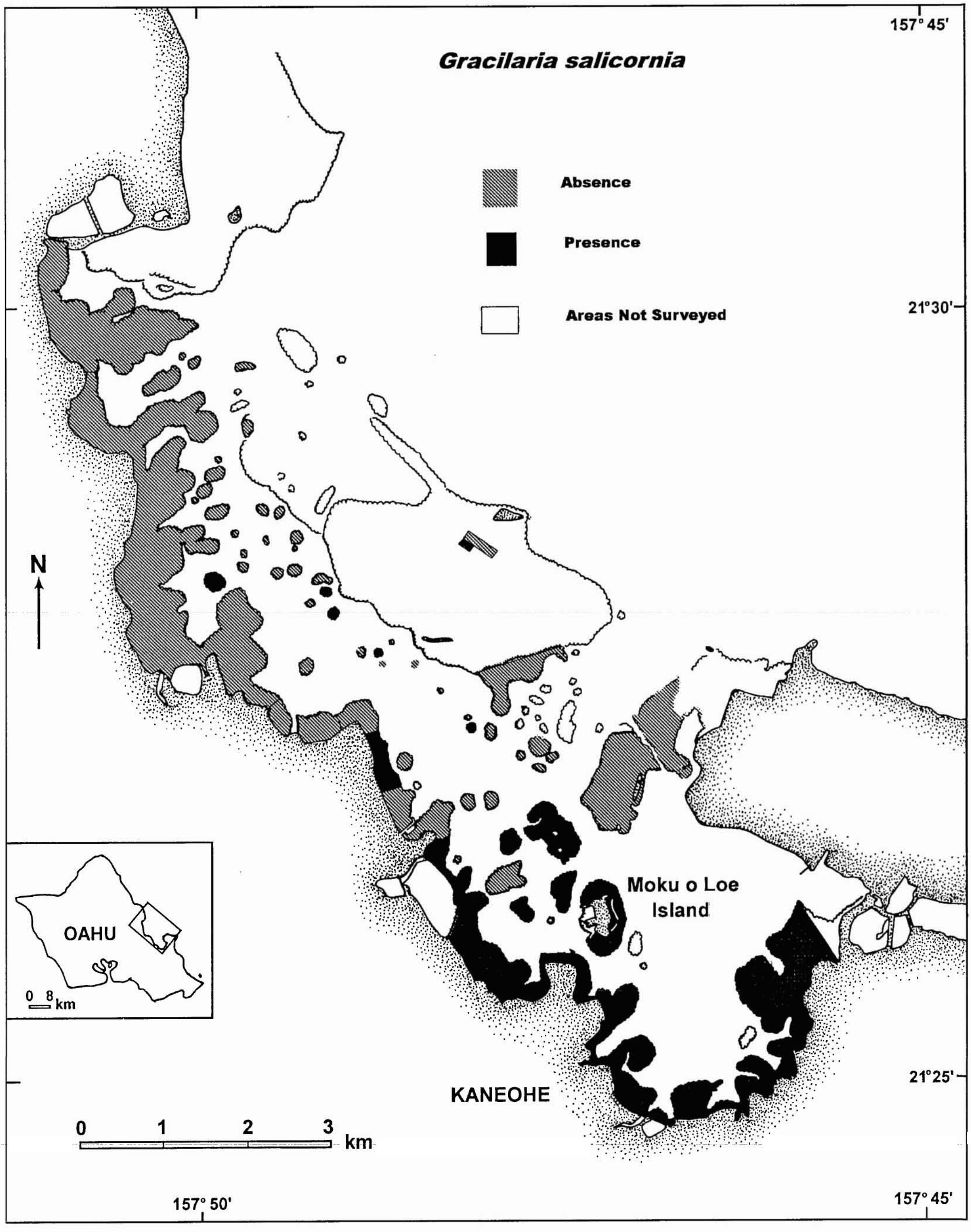

FIGURE 2. Distribution of *Gracilaria salicornia* within Kāne'ohe Bay.

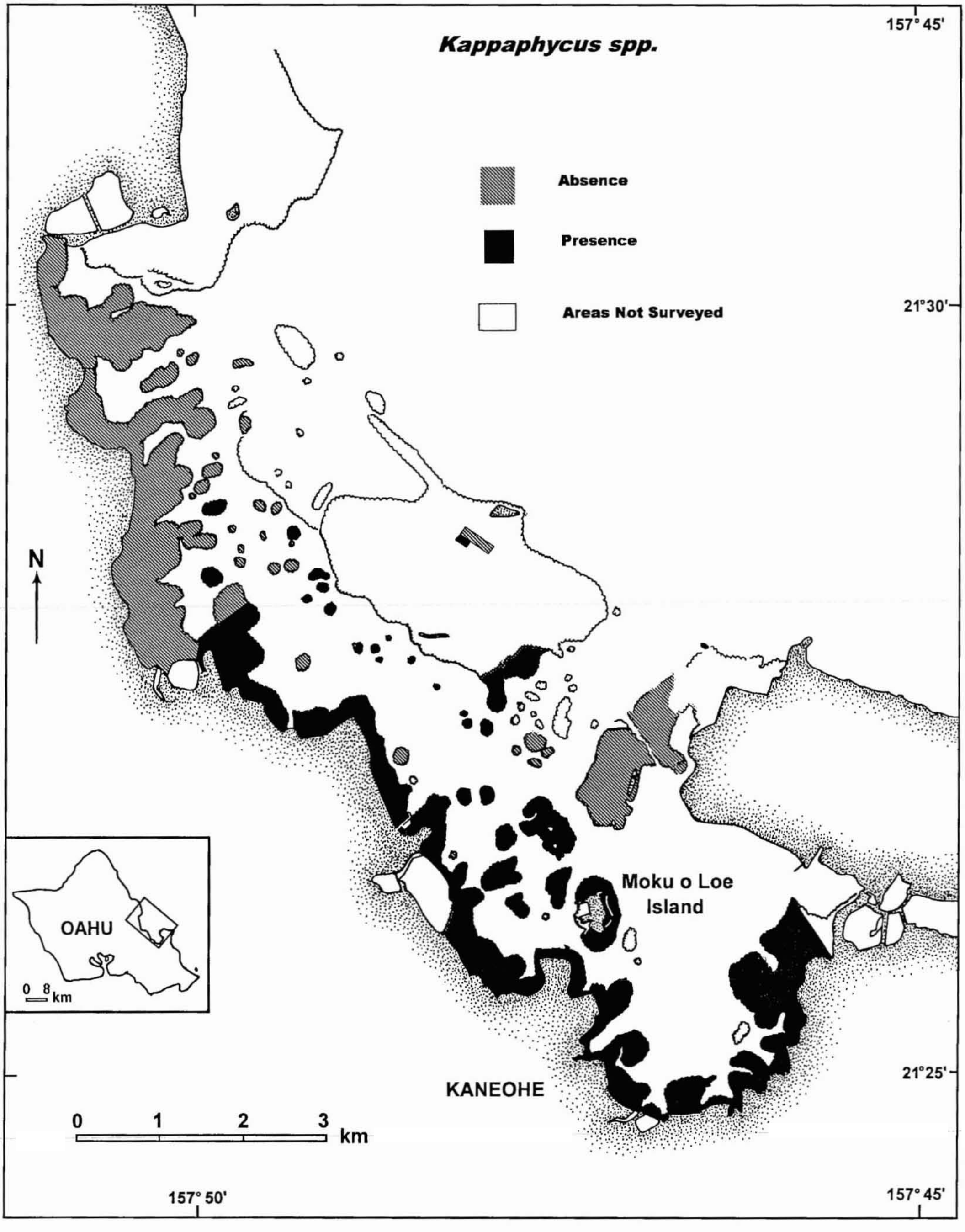

FIGURE 3. Distribution of *Kappaphycus* species within Kāne'ohe Bay.

TABLE 1

MEAN PERCENTAGE COVERAGE (±SE) OF ALGAL SPECIES, CORAL, AND SUBSTRATE TYPES IN THREE HABITAT TYPES AND TWO DEPTHS IN THE CENTRAL BASIN OF KĀNE'OHE BAY

SITE[a]	DEPTH (m)	NO. OF STATIONS[b]	% *Kappaphycus alvarezii*	% *Kappaphycus striatum*	% *Gracilaria salicornia*	% *Dictyosphaeria cavernosa*	% OTHER MACRO-ALGAE	% CORAL	% ROCK	% SAND	% SILT	DIFFUSION FACTOR
BR	1	4	0.02 ± 0.02	1.96 ± 1.92	0.98 ± 0.98	0.75 ± 0.18	50.7 ± 11.7	1.43 ± 0.96	24.0 ± 4.49	16.4 ± 3.81	0.00	15.2 ± 2.74 $n = 20$
PR	1	9	0.22 ± 0.12	4.59 ± 2.06	0.00	17.6 ± 4.33	10.2 ± 4.13	16.7 ± 3.59	37.39 ± 4.81	14.5 ± 6.48	0.00	10.6 ± 0.57 $n = 54$
PR	3	6	0.01 ± 0.01	0.87 ± 0.62	0.00	40.0 ± 4.55	0.70 ± 0.81	5.79 ± 2.40	35.5 ± 4.34	0.00	10.0 ± 3.10	5.10 ± 0.56 $n = 36$
FR	1	4	0.06 ± 0.02	0.01 ± 0.01	2.01 ± 1.27	3.13 ± 2.61	10.7 ± 1.25	10.6 ± 7.41	35.4 ± 2.03	41.6 ± 8.49	0.00	10.3 ± 0.79 $n = 24$
FR	3	4	0.00	0.00	0.00	27.2 ± 10.2	0.00	28.1 ± 4.52	28.9 ± 3.22	5.40 ± 3.13	14.0 ± 5.25	3.60 ± 0.39 $n = 24$

[a] BR, barrier reef; PR, patch reef; FR, fringing reef.
[b] $n = 3$ transects per station.

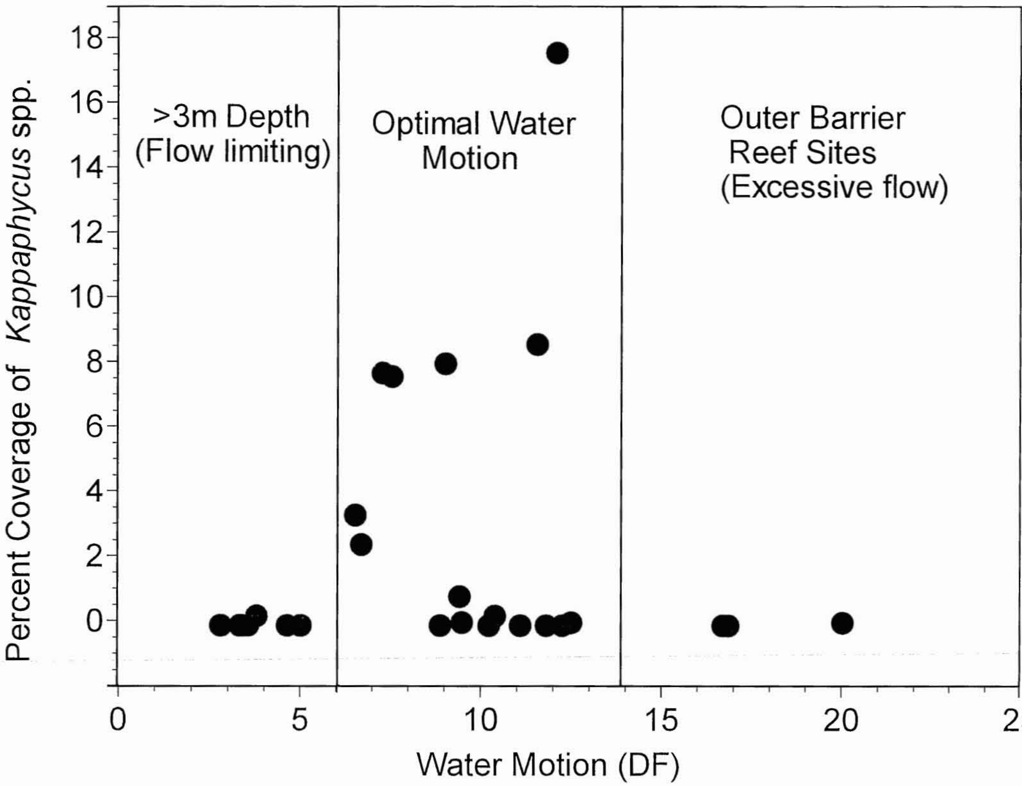

FIGURE 4. Percentage coverage of *Kappaphycus* species on transects as related to water motion (DF).

tive fragmentation, the distributions of *Kappaphycus* spp. and *Gracilaria salicornia* will probably continue to expand. Other introduced rhodophytes have successfully spread throughout the Hawaiian Islands. *Acanthophora spicifera* was introduced into Pearl Harbor and/or Waikīkī around 1950 and has become widely established through vegetative fragmentation on all the main Hawaiian Islands (Russell 1992). *Hypnea musciformis* was introduced into Kāne'ohe Bay in 1973 and, after a 3-yr lag, was found throughout the bay (Russell 1992).

Kappaphycus spp. and *Gracilaria salicornia* demonstrate the potential to spread throughout Hawai'i. *Kappaphycus* spp. were introduced at five stations on the shallow north reef flat of Moku o Lo'e in 1974 (Glenn and Doty 1992). Using a maximum range extension of 5.7 km in 1996, we estimate the rate of spread as 260 m yr^{-1}. *Gracilaria salicornia* was introduced to Moku o Lo'e in 1978 (Russell 1992), and therefore the rate of spread was estimated at 280 m yr^{-1}. These estimates of the rate of spread are at the low end of published data for other introduced species. Davis et al. (1997) reported 300 m yr^{-1} spread for *Caulerpa scalpelliformis* in Botany Bay, New South Wales. Meinesz et al. (1993) reported a spread of *Caulerpa taxifolia* of 53 km yr^{-1} in the Mediterranean. The spread of *Codium fragile* along the east coast of North America was estimated to be 55 km yr^{-1} (Carlton and Scanlon 1985).

The ranges of introduced *Kappaphycus* and *Gracilaria* species have extended well beyond Moku o Lo'e, contrary to the prior suggestion that physical and biological limitations would prevent their spread (Russell

1982). We propose that these species will continue to spread throughout Kāne'ohe Bay in areas within the optimal range of water motion (Figure 4). Increased water flow or wave action may limit the distribution of macroalgal species by removing the thallus from the substrate (Conover 1968). Low water motion can limit the rate of advection of nutrients to algal tissues (Larned 1998). Other factors, such as grazing, may also affect the distributions of these species.

Kappaphycus alvarezii fragments were found on the beach at Kualoa located at the far northwestern end of Kāne'ohe Bay, a distance of 2 km from its farthest documented distribution on reefs. Kahana Bay is located 3.2 km northwest of Kāne'ohe Bay and may be the next area colonized by these species. This sheltered bay provides suitable substrata and other physical factors conducive to growth of these invasive species.

Ecological invasions can advance rapidly and have negative effects on marine ecosystems. Knowledge of the effects these species have on the environment, how they spread, and the physical, biological, and chemical factors that influence their distribution will assist in predicting the impact invasive species have on indigenous species and aid in the conservation and management of reefs.

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