

ECOLOGICAL IMPACTS AND INTERACTIONS OF THE INTRODUCED  
RED ALGA, *KAPPAPHYCUS STRIATUM*, IN KANE'OHE BAY, O'AHU

A THESIS SUBMITTED TO THE GRADUATE DIVISION OF THE  
UNIVERSITY OF HAWAII IN PARTIAL FULFILLMENT OF THE  
REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

IN

BOTANICAL SCIENCES  
(BOTANY - ECOLOGY, EVOLUTION AND CONSERVATION BIOLOGY)

MAY 2000

by

Monica May Lon Woo


Thesis Committee:

Celia M. Smith, Chairperson  
John S. Stimson  
Curt C. Daehler

We certify that we have read this thesis and that, in our opinion, it is satisfactory in scope and quality as a thesis for the degree of Master of Science in Botanical Sciences (Botany - Ecology, Evolution and Conservation Biology).

THESIS COMMITTEE

  
\_\_\_\_\_  
Chairperson

  
\_\_\_\_\_

  
\_\_\_\_\_

## Abstract

The introduction of *Kappaphycus striatum* to Kane'ohē Bay, O'ahu, in the early 1970's has been followed by its spread and establishment in many parts of the Bay. The abundance and apparent overgrowth of *K. striatum* on live coral in certain areas of the Bay has raised the concern of management. To assess the factors that may control the distribution of *K. striatum*, a study was undertaken to establish minimum fragment size that could function as propagules, caged growth potential and grazing intensities at sites of varying *K. striatum* abundance were evaluated. Determination of *K. striatum* impact on live coral was monitored by a time series photography study. Vegetative propagation through fragmentation is an effective dispersal mechanism that has most likely contributed to the spread and establishment of *K. striatum*. Fragments weighing 0.05 g were capable of net growth in the field, suggesting that fragments created by physical disturbance can be carried by waves and currents to new locations where they can possibly establish. The growth potential study indicates that *K. striatum* is capable of net growth in all sites surveyed, suggesting that environmental differences across the Bay are not limiting its establishment. Results of the grazing intensity study suggest that herbivory does play an important role in preventing the establishment of *K. striatum* in areas where *K. striatum* is absent. No definitive explanations can be given for the abundance of *K. striatum* in certain areas. Through the time series photography study, overgrowth of *K. striatum* on live coral was observed within a one-year period. Results from these studies suggest that the spread of *K. striatum* is relatively slow in comparison

to other algal invasions, but will continue to spread with the present herbivory levels and environmental conditions.

## TABLE OF CONTENTS

Abstract .....	iii
List of Tables.....	vii
List of Figures.....	viii
Chapter I: Literature Review.....	1
Introduction .....	1
Study site: Kane'ohu Bay.....	2
<i>Kappaphycus</i> and <i>Eucheuma</i> complex.....	3
Marine invasion ecology .....	7
Mechanisms of marine invasions .....	8
Patterns and processes of marine invasions .....	9
Ecological consequences of marine invasions .....	10
Algal invasions.....	12
Vegetative propagation via fragmentation .....	13
Herbivory on coral reefs.....	16
Herbivores in the tropical reef environment .....	16
Algal defenses .....	17
Effects of herbivory.....	18
Herbivory and introduced species.....	22
Herbivory and the <i>Kappaphycus</i> and <i>Eucheuma</i> complex.....	23
Aspects of Research .....	24

Chapter II: Ecological Impacts and Interactions of the Introduced Red Alga, <i>Kappaphycus striatum</i> in Kane'ohē Bay, O'ahu.....	25
Abstract .....	25
Introduction .....	26
Materials and Methods .....	32
Field survey .....	32
Growth potential across the Bay, herbivory and seasonal growth .....	33
Percent cover .....	36
Survival and growth of fragments .....	37
Coral and algal interaction .....	37
Results .....	38
Growth potential across the Bay .....	38
Grazing intensity .....	39
Seasonality of growth rates and herbivory .....	40
Twenty four hour surveys .....	40
Fragmentation.....	41
Changes in percent cover .....	41
Coral and algal interaction .....	42
Discussion .....	42
References .....	71

## LIST OF TABLES

<u>Table</u>	<u>Page</u>
1 Location and description of sites chosen during field survey that were used for predator exclosure and growth potential studies.....	53
2 Statistical summary of repeated measures ANOVA of caged growth rates and sites with time as a repeated measure.....	54
3 Statistical summary of ANOVA of a weighted regression with clod card diffusion as the predictor and caged growth rates as the response.....	57
4 Statistical summary of repeated measures ANOVA of grazing intensity and sites with time as a repeated measure.....	59
5 Statistical summary of repeated measures ANOVA of caged growth rates and grazing intensity at 3 sites over one year with time as a repeated measure .....	64

## LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1 Distribution of <i>Kappaphycus</i> species within Kane'ohē Bay as surveyed in 1996. Reproduced from Rodgers and Cox (1999) .....	51
2 Map of nine study sites in Kane'ohē Bay, O'ahu, used for caged growth and grazing intensity studies .....	52
3 Growth rates of caged <i>K. striatum</i> at sites 1 to 5 from February to October .....	55
4 Growth rates of caged <i>K. striatum</i> at sites 5 to 9 from April to July .....	56
5 Scatterplot of clod card diffusion factor versus caged growth rate at 9 study sites .....	58
6 Average grazing intensities calculated by averaging differences between paired caged and uncaged growth rates at sites 1 to 5 from February to October .....	60
7 Average grazing intensities calculated by averaging differences between paired caged and uncaged growth rates at sites 5 to 7 from April to July .....	61
8 Average grazing intensities calculated by averaging differences between paired caged and uncaged growth rates at sites 8 and 9 from April to July .....	62
9 Average caged growth rates over one year at the back reef, reef #29 and Coconut .....	63
10 Average grazing intensities calculated by averaging differences between paired caged and uncaged growth rates at the back reef, reef #29 and Coconut .....	65
11 Average initial and final weights of fragments assayed in mesh cages placed on rubble .....	66
12 Average initial and final weights of fragments assayed in sand .....	67



13 Change in *K. striatum* percent cover at two sites over one year ..... 68

14 Photographs taken from the time series photography study in the back  
reef area of Kane'ohē Bay..... 69

15 Photographs taken from the time series photography study in the back  
reef area of Kane'ohē Bay..... 70

# CHAPTER 1

## LITERATURE REVIEW

### INTRODUCTION

The recent observation of *Kappaphycus striatum* dominance on the reefs in Kane'ohē Bay has become a cause of concern for resource management. Since its introduction in the early 1970's from the Philippines, there has been relatively little documentation of the locations of the original plantings or the specific species of *Kappaphycus* and *Eucheuma* spp. that were planted. A study conducted by Dennis Russell documents the early history of the *Kappaphycus* and *Eucheuma* spp. establishment and dispersal in the bay from 1974 to 1976 (Russell 1981). An additional study that compared the growth of *Kappaphycus alvarezii*, *Kappaphycus striatum* and *Eucheuma denticulatum* was conducted by Glenn and Doty from 1976 to 1977 in a pen culture on the north reef of Coconut Island (Glenn and Doty 1990). More recently, a tow-board survey of the distribution of *Kappaphycus* spp. in Kane'ohē Bay was conducted in 1996 by Rodgers and Cox (1999).

The patterns and processes of this and many algal invasions remain poorly understood. The goal of this review is to provide background information on Kane'ohē Bay and the *Kappaphycus* and *Eucheuma* spp., as well as examine where the state of the field of marine invasions lies at this time. In addition, an exploration of the factors that may have influenced the success of *K. striatum* in Kane'ohē Bay, such as herbivory and fragmentation, will be discussed.

## STUDY SITE: KANE'OHE BAY

Kane'ohe Bay is the most well-studied and largest enclosed body of water in the state of Hawaii, stretching 13 km in length and 4 km in width and encompassing 11,000 acres (57,000,000 m<sup>2</sup>) of submerged lands (Smith et al. 1981). The bay is composed of a variety of different habitats, many of which have been substantially altered through the past 100 years of shore-based agriculture, urban development, military, science and commercialism (Rodgers and Cox 1999). Roughly 90% of the South Bay, 70% of the Central Bay and 5% of the North Bay have been altered. The bay has two major channels, with most of the water entering across an extensive barrier reef area. Water circulation time takes place within 2-3 weeks (State of Hawaii, DLNR, 1998).

There are an estimated 50 linear miles of streams, which at one time flowed into the bay. Twenty-five percent have been channelized and 43% have been diverted. The shoreline stretches approximately 20 linear miles, 58% of which have been modified by seawalls, docks, fishponds and dredging/filling activities. Originally, 28 to 30 fishponds bordered the bay. Twenty-one have been filled in and two have been converted to marinas (State of Hawaii, DLNR, 1998).

Kane'ohe Bay is one of the only locations in the United States where all three coral reef types can be found. The fringing reef is located adjacent to the shoreline and is estimated to consist of 12 million m<sup>2</sup> of reef area. Patch reefs are isolated patches of coral that represent a complete, self-contained ecosystem. There are 60 patch reefs in the bay consisting of 2.5 million m<sup>2</sup> of reef material. An offshore barrier reef complex forms a protective barrier for Kane'ohe Bay and encompasses an area of 22 million m<sup>2</sup>. The barrier reef depth ranges from 40 to 110 feet and consists of a fore reef area as well as an

extensive back reef area that is composed of reef flat, coral communities, seagrass and algae beds and two emergent sand bars (State of Hawaii, DLNR, 1998).

Kane'ohe Bay has the largest urban population in close proximity to living reefs in the Pacific, and as a result, faces many anthropogenic influences. The introduction of pollutants such as lead, Chlordane and Dieldrin (both insecticides), DDT, Heptachlor and PCB's as well as sedimentation, aquarium collection, overfishing, commercial activities, and alien species have all led to the substantial alteration of the bay. Additional problems include terrigenous sediments, diversion and channelization of streams, changes in the watershed and riparian environment and 25 years of sewage discharge that ended in 1977 (Rodgers and Cox 1999). The board of the Department of Land and Natural Resources has focused conservation efforts in Kane'ohe Bay and an action plan has been formed in an effort to design a means to conserve the natural resources (State of Hawaii, DLNR, 1998).

#### ***KAPPAPHYCUS AND EUCHEUMA SPP.***

The systematics of *Eucheuma* and *Kappaphycus* spp. are far from satisfactory because of the large size, indeterminate growth, phenotypic variability and apparently infrequent sexual reproduction of these organisms. Because individuals can reach up to 5 to 10 kg in wet weight with bulky fronds extending a meter or more in length, typically only small portions are preserved for taxonomic investigation. Many important features of reproductive morphology and post-fertilization development are poorly known (Lluisma and Ragan 1995). Initial attempts were made by Doty and Norris (1985) to organize the taxonomy of *Eucheuma* and *Kappaphycus* spp. according to carrageenan

type and morphological characters. Several reinvestigations have taken place since that time resulting in the reorganization of the systematics. The existence of three species, *Kappaphycus striatum*, *Kappaphycus alvarezii*, and *Eucheuma denticulatum* were known to have been introduced in Kane'ohe Bay (Russell 1983).

*Eucheuma* and *Kappaphycus* spp. are economically important seaweed genera for carrageenan extraction in tropical areas. *E. denticulatum* and *K. alvarezii* account for over 90% of all seaweed exports from the Philippines and 70% of the world's supply of semirefined carrageenan (Llana 1991). *Eucheuma* cultivation in the Philippines began in 1969-1970, using strains of *K. alvarezii* and *E. denticulatum* known as 'tambalang' and 'spinosum', respectively (Lim and Porse 1981). As the demand for carrageenan increased worldwide, *Kappaphycus* and *Eucheuma* spp. cultivation has been promoted in Indonesia since 1985 (Ohno et al. 1996), as well as in Tanzania in 1989 (Mshigeni 1992, Lirasan and Twide 1993). Recent attempts to cultivate *K. alvarezii* have also been made in Vietnam (Ohno et al. 1996).

The commercial importance of *Kappaphycus* and *Eucheuma* spp., because of their high carrageenan content, has led to several studies that have attempted to determine optimal growth conditions (Glenn and Doty 1990, Ask 1994, Dawes et al., 1994, Ohno et al. 1996). Although locations and conditions varied among the studies, growth rates remained fairly constant among studies (4 to 5% day<sup>-1</sup>). A study by Glenn and Doty (1990) that examined *K. alvarezii*, *K. striatum* and *E. denticulatum* in Kane'ohe Bay demonstrated that growth rates tended to be independent of season, with the exception of *K. alvarezii* growing 15% faster in summer than in winter and spring. The correlations between growth rate and environmental variables were low. The study suggested a range

of conditions under which the three species can be productive: temperature maxima of 24 to 30° C and minima of 21 to 22° C, nitrogen levels of 2 to 4  $\mu\text{M}$ , phosphate levels of 0.5 to 1.0  $\mu\text{M}$ . The degree of water motion was not correlated with growth rate, but rather the direction of wind driving water across the thalli. Downstream thalli appeared unhealthy and exhibited half the growth rate of upstream thalli. When trade winds reversed direction, upstream thalli showed reduced growth rates.

The central Pacific species of *Eucheuma* appear to be sublittoral species (Doty 1973) which are adapted to growing under high light and temperature regimes. Using uniform cylinders one cm in length removed three to five cm from a branch tip, photosynthetic rates of *K. alvarezii* ( $2685 \mu\text{l O}_2 \text{ g dry wt.}^{-1} \text{ h}^{-1}$ ), *K. striatum* ( $2031 \mu\text{l O}_2 \text{ g dry wt.}^{-1} \text{ h}^{-1}$ ) and *E. denticulatum* ( $2107 \mu\text{l O}_2 \text{ g dry wt.}^{-1} \text{ h}^{-1}$ ) as well as respiration rates ( $484 \mu\text{l O}_2 \text{ g dry wt.}^{-1} \text{ h}^{-1}$ ,  $471 \mu\text{l O}_2 \text{ g dry wt.}^{-1} \text{ h}^{-1}$ ,  $630 \mu\text{l O}_2 \text{ g dry wt.}^{-1} \text{ h}^{-1}$  respectively) were determined by Doty and Glenn (1981) under laboratory conditions using a Gilson Warburg Apparatus. Maximum rates of photosynthesis for all three species occurred at 30° C, while inhibition was observed at 35 to 40° C. Respiration rates peaked at 25° and 40° C. Light saturation of photosynthesis occurred at approximately 1200 ft-candles with a compensation point at 50 to 100 ft-candles at 24° C for all three species.

An additional study by Dawes (1989) demonstrated by use of photosynthesis versus irradiance measurements that *K. alvarezii* showed very limited ability to acclimate to temperature changes. A loss in photosynthesis rate after exposure to 18° C occurred either abruptly or gradually, and the alga showed only a very limited ability to acclimate to 22° C. Dawes (1992) also examined irradiance acclimation of *K. alvarezii* and *E. denticulatum*. Three forms of both species were compared. *E. denticulatum* showed

genetic differentiation among strains in photosynthetic responses to increasing irradiances and levels of chlorophyll *a* and phycoerythrin, producing sun-type and shade-type responses in four cultivars. In contrast, *K. alvarezii* showed phenotypic plasticity with no apparent separation into sun or shade responses or any pattern in pigment levels. The results of the study suggest that there was ecotypic differentiation to irradiances by forms of *E. denticulatum*, but not forms of *K. alvarezii*. The photosynthetic efficiency differed for the red and green forms of *E. denticulatum*, but not for *K. alvarezii*, which indicates that pigment levels in ecotypes of *K. alvarezii* may not always be linked to productivity.

A study conducted by Larned (1995) provides the first data for nutrient requirements of *Kappaphycus alvarezii* in Kane'ohē Bay. Results of nutrient enrichment experiments indicate that nitrogen availability limits the growth rates of *Kappaphycus alvarezii* in a laboratory culture system. Thalli supplied with ammonium-enriched seawater grew at significantly higher rates than thalli in unenriched ambient water column seawater or phosphate-enriched seawater. It was also demonstrated that ammonium and nitrate+nitrite concentrations within mats of *Kappaphycus alvarezii* were significantly higher than concentrations in the water column above the mats. Examination of the dissolved inorganic nitrogen concentrations in the microenvironments associated with mat-forming species in the field and manipulation of DIN concentrations in the laboratory suggest that nitrogen is very likely to limit the growth of *K. alvarezii* in the field and that its morphology allows for exclusive use of sediment nitrogen.

## MARINE INVASION ECOLOGY

The U.S. Congressional Office of Technology Assessment estimates that there is a minimum of 4,500 non-indigenous species (NIS) known to be established in the United States, which represents two to eight percent of the taxonomic groups examined. Approximately 15% of these NIS are believed to be species that have caused both ecological and/or economic impacts (Ruiz et al. 1997). Recently, NIS in the marine environment have received more attention, and it has been realized and accepted that NIS are a potent force of ecological change on local, regional and global scales (Cohen and Carlton 1996, Ruiz et al. 1997). Of additional concern are the increased frequencies of marine invasions at the close of the 20<sup>th</sup> century (Carlton 1989, Carlton 1996).

Arrival, settlement, expansion and persistence (Mollison 1986) are the four steps of a species introduction. The arrival of a species does not necessarily imply its establishment. There have been several examples of species that have been introduced, but apparently have not naturalized (Gruet et al. 1976). The settlement phase involves the build-up of populations of individuals *in situ*, in the new region. If the species is able to survive the variation of the physical, chemical and biotic factors of the area, the species is considered naturalized (Ribera and Boudouresque 1995). Once naturalization has taken place, the species spread more widely, thus beginning the expansion phase (Ribera and Boudouresque 1995). Expansion may occur either naturally or with human assistance (Ribera 1994). Following the expansion, is the persistence phase, which is characterized by either a decline followed by stabilization at a lower level than the maximum reached during the expansion phase or by a plateau close to the maximum attained (Ribera and Boudouresque 1995).



### Mechanisms of Marine Invasions

Long distance introduction of marine organisms has been well known for more than a century. The most obvious vector is international shipping, either as a result of the transport of fouling organisms attached to the hull or by the discharge of ballast water (Rueness 1989). The movement of ballast waters appears to be the single largest source of NIS transfer around the world (Carlton et al. 1985, Ruiz et al. 1997). Stored in dedicated ballast tanks or cargo holds, the ballast water of ships is used for vessel trim, stability and maneuverability (Hutchings 1992). Unfiltered water taken aboard may contain any planktonic organisms in the water column which can be transferred thousands of miles, released into a non-native habitat, and possibly settle, establish and reproduce (Carlton and Geller 1993). An additional mode of introduction is the importation of commercially important species in mariculture, such as oysters. As a consequence of deliberate transplantation, accidental introductions of various algae have taken place. The algae may have been growing as germlings attached to oyster shells or even possibly used as packing material for shipments. The introduction of *Sargassum muticum* to Europe is believed to have occurred by this mechanism (Rueness 1989).

A problem associated with marine invasions is the difficulty in tracing the source of the introduction. Most known invasions, however, have occurred in or near ports with international shipping traffic and appear linked to ballast water as the most plausible source (Carlton and Geller 1993, Ruiz et al. 1997). A single ship can carry > 150,000 metric tons of ballast water that is usually taken from plankton-rich bays and estuaries (Carlton 1985). A study conducted by Carlton and Geller (1993) found that ballast water from 159 ships arriving in Oregon containing ballast water from 25 ports in Japan had 16

animal and 3 protist phyla and 3 plant divisions. Acting as a nonselective dispersal mechanism, ballast water release raises many questions about the natural geographic distributions of marine species, forcing scientists to reconsider if a species is native or non-native. This is especially confounding in disciplines where systematics and taxonomy is not well-established.

### Patterns and Processes of Marine Invasions

A current question is why do marine invasions occur when they do? Although organisms have been transferred for decades through various mechanisms, why are we seeing evidence of bivalve and algal invasions now and not several decades earlier? What allows certain invasions to succeed while others fail? Current focus is on the donor region, the specific site at which a given species interfaces with a transport mechanism, and on the recipient region, the specific site where a species is initially released (Carlton 1996). In addition, inoculation events and the mechanism of dispersal are also being closely examined.

Changes in donor regions are believed to be an important factor in understanding the processes of marine invasions. Environmental changes may lead to population increases of resident species, allowing more individuals to be available to interface with a transport mechanism. This may also allow regional species not present in the donor region to expand their ranges into the donor area to interface with the transport mechanism (Carlton 1996). The increase of the clam, *Theora lubrica* in the polluted waters of the Inland Sea of Japan was correlated with its increase in the San Francisco Bay (Carlton 1996). In addition, the availability of new donor regions also can influence the possibility of invasion. Species are able to jump from port to port, contingent upon its

establishment in the previous donor region. Such is the case with the Laurentian Great Lakes, which are now exporters of the Eurasian zebra mussel, *Dreissena polymorpha* (Carlton 1996).

Environmental changes in the recipient region can also play a role in the establishment of NIS. Physical changes due to natural processes or from human-mediated causes could lead to changes in minimum habitat size or in disturbance states. In addition, changes in salinity and temperature, increases or decreases in pollution, changes in water flow as well as many other factors could influence the potential invasibility of a particular region (Carlton 1996). The concept of invasion windows was coined by Johnstone (1989) and further explored by Crawley (1989), both emphasizing the idea that it is an interaction of many factors which may allow a species to become established.

Inoculation events as well as dispersal vectors may also play a role in determining invasion success. Inoculation events occur when large numbers of a species are transported and subsequently released. A large vessel may transport and release millions of larvae and release them into a new habitat (Carlton 1996). To further complicate this phenomena, increase in the dispersal vector (more ballast water being released), increase in vector speed (faster ships), as well as an improvement in vector quality (use of tanks to hold only ballast water and not petroleum) can all contribute to the increased survival and dispersal of marine organisms (Carlton 1996).

#### Ecological Consequences of Marine Invasions

The ecological impacts of NIS, such as molluscs, bryozoans, crabs, ctenophores and vascular plants have been documented in marine and estuarine habitats around the

world (Ruiz et al. 1997). The most studied examples have come from NIS that have become dominant in a community. The well-studied *Dreissena polymorpha*, an introduced bivalve in the Great Lakes, fundamentally changed the community structure and function, replacing other benthic organisms, filtering plankton communities from overlying waters, and effecting food web structure, nutrient dynamics and sedimentation rates (Carlton et al. 1990, MacIsaac 1996).

Invasions can also have an impact on biodiversity at many different levels (Ruiz et al. 1997). Invasions can initially increase local species number or species richness (Peet 1974). However, through strong direct or indirect effects, this could lead to reduced species richness and/or a decrease in the abundance or “evenness” of remaining species (Drake 1991, Ruiz et al. 1997). In addition, invasions may decrease variation in species composition among communities, increasing homogeneity by adding common (exotic) species or by removing unique or endemic species (Harrison 1993). Spatial patterns of diversity above the species level may also be influenced by invaders, although the best way to measure these effects is currently being debated (Gaston 1996). Additionally, invasions may alter genetic diversity both within and among populations, resulting from increased gene flow and differential success of particular genotypes (Ruiz et al. 1997).

Clearly, studies of the patterns and processes of marine invasions are needed in order for us to more clearly understand the long and short-term effects of marine invasions. At present, very few marine extinctions have been recorded compared to terrestrial systems, with none of them being related to invasions (Carlton 1993). However, many other ecological consequences can result as previously discussed.

Current questions being proposed are how to identify species that will invade, when will an invasion take place, where will it invade and what will happen after it invades.

Although answers to each of these questions will aid in increasing our understanding of invasion biology in the marine environment, it seems as though with the spatial and temporal variation that is especially present in marine systems, that the development of models will be difficult. At present, we know how marine invasions are taking place and we know what can result from them. Continued empirical studies are still needed, but more emphasis should be placed on developing strategies for prevention in order to avert future invasions.

### **ALGAL INVASIONS**

Studies of algal invasions are lacking in comparison to other introduced marine organisms, such as barnacles and crabs. In some regions of the world, comprehensive inventories of the marine flora are too recent to confidently determine if a species was introduced without the risk of high error (Ribera and Boudouresque 1995). It is therefore difficult to provide an accurate record of marine algal introductions because information is available only for a few specific regions. Sixty-one macrophyte species are believed to have invaded the Mediterranean, 28 along the Atlantic coast, and approximately 11 in Southern Australia. Species, probability of introduction, and probable origin are summarized by Ribera and Boudouresque (1995). In addition, 21 species of macroalgae were probably introduced to New Zealand (Adams 1994), 18 species have been introduced to Hawaii (Russell 1992), and two species in Brazil (Oliviera 1984).

Of the 18 algal invasions that have been recognized in Hawaii, the invasions by three are considered highly successful (Russell 1992). *Acanthophora spicifera* was accidentally introduced in the early 1950's (Doty 1961) to Pearl Harbor and/or Waikiki, possibly from Guam (Russell 1992). It has since spread to the 5 main islands and is well-established on all the Hawaiian islands except Hawaii. *Hypnea musciformis*, another successful invasive species, was intentionally introduced from Florida to Kane'ohe Bay in 1974 (Abbott 1987). It spread rapidly throughout Kaneohe Bay after a lag phase of approximately 3 years. Apparently because it can float as drift and even attach itself to other algae, it spread rapidly through the islands. *H. musciformis* has become an important issue for land managers in Maui, as several tons of the algae wash up on to beaches weekly in West Maui. *Gracilaria salicornia*, an intentional introduction to O'ahu, has also been highly successful in Hawaii, and is prolific especially in Kane'ohe Bay and Waikiki (Russell 1992).

#### VEGETATIVE PROPAGATION VIA FRAGMENTATION

The most well-studied example of an algal invasion is the introduction of *Caulerpa taxifolia* to the Mediterranean. The rapid dispersal and expansion of *C. taxifolia*, spreading at a rate of  $50 \text{ km yr}^{-1}$ , is a dramatic illustration of the efficacy of propagation via fragmentation (Meinesz et al. 1993). Vegetative propagation has been a successful means of reproduction in the aquaculture industry (Glenn and Doty 1990), but few studies have documented the ecological ramifications of reproduction through fragmentation. The ability to fragment, disperse and establish is typical of many weedy, invasive species, yet few studies have been conducted to quantify these processes.

The ability to reproduce via fragmentation has been recognized in tropical marine species, such as *Acanthophora spicifera* (Kilar and McLachlan 1986), *Hypnea musciformis* (Russell and Balazs 1994) and *Kappaphycus striatum* (Glenn and Doty 1990), all known as invasive, weedy species on Oahu. No information is available on fragmentation capabilities of other weedy species, such as *Gracilaria salicornia* (introduced) and *Dictyosphaeria cavernosa* (unknown origin). Vegetative propagation through fragmentation could be an important ecological advantage, playing a significant role in the dynamics, recruitment and productivity of a population.

Several factors affect fragmentation success, but these factors have only recently been addressed (Walters and Smith 1994, Smith and Walters 1999). In ecological contexts, successful fragmentation is influenced by factors such as fragment size, fragment re-attachment, dispersal capabilities of fragments, fragmentation potential (force required to produce fragments) and causes of fragmentation in the field. Despite the relevance of these factors as related to fragmentation success, they have remained largely unstudied. Increasing our knowledge of these components not only will expand our understanding of reef dynamics and interactions, but also will allow for effective management strategies to be developed for species that spread by vegetative fragments.

Once fragmentation ability has been established, factors affecting fragmentation success should then be examined. Determination of minimum viable fragment size becomes an important component as fragments are effective propagules, capable of dispersing to previously uninhabited environments. Estimation of minimum viable fragment size, flow regimes and fragment sinking rates will then allow for predictions of dispersal range for species known to reproduce only vegetatively. Determination and

comparison of viable fragment sinking rates among species may not only explain current distributions, but also predict future patterns of dispersal. An additional factor to be considered is the amount of time required for attachment. Algae have a variety of mechanisms that allow for attachment, such as holdfasts, rhizoids and coalescence. Once attachment has occurred in an appropriate area, the possibility of falling out of the photic zone becomes much less, and the probability of successful establishment much higher. For many algae such as *Hypnea musciformis*, however, numerous opportunities exist for establishment, as the alga is capable of growing epiphytically on other algae or unattached as drift (Russell and Balazs 1994).

The force required to produce fragments will vary among algal tissue, morphology and structure (Pennings and Paul 1992). Grazing and water motion most commonly cause tissue damage (Denny et al. 1989, Pennings and Paul 1992). In order to obtain a more precise idea of how readily fragments can be produced, the force required to incur breakage can be quantified. Wave energy exposes algae to forces such as tension, compression and shear. Assessment and comparison of plant flexure, plant strength and plant elasticity allows quantification of mechanical properties from which estimates of fragment production in the field may be possible. In addition, it would also be valuable to examine the location and type of tissue damage imposed on the algae in the field. Determination of the probability of fragment success upon arrival to a previously uninhabited area would also give be useful in developing management strategies and estimating patterns of dispersal.



## HERBIVORY ON CORAL REEFS

Coral reef communities are examples of diverse species assemblages in marine systems, that their maintenance has been the subject of much debate (Connell and Orias 1964, MacArthur 1965, Pianka 1966, Menge and Sutherland 1976). The influence of herbivory on reef community structure has drawn much interest (Stephenson and Searles 1960, Randall 1961, Wanders 1977, Ogden and Lobel 1978, Sammarco 1982, Lewis 1985, Lewis and Wainwright 1986).

Tropical reef algal communities, unlike the temperate subtidal, are characterized by a prevalence of calcified crustose algae and filamentous turf and relatively less macroalgae in comparison to temperate systems (Lubchenco and Gaines 1982). Many studies report the distributions of tropical algae to be patchy, with species distributed in particular regions such as deep sand plains (Dahl 1973, Hay 1981a), intertidal reef flats (Littler and Doty 1975, Hay 1981b, Hay et al. 1983), or to vast shallow subtidal areas (Tsuda 1972, Wanders 1976, Adey et al. 1977, Conner and Adey 1977, Morrissey 1980). Historically, many studies were conducted in the Caribbean, and cannot accurately represent all tropical reef systems. Methods of determining the presence and absence of algae are not well-developed across disciplines which may limit generalizations.

### Herbivores in the tropical reef environment

Coral reefs also contain diverse and abundant herbivore assemblages, including microcrustaceans, molluscs, echinoids and fishes (Hiatt and Strasburg 1960, Ogden and Lobel 1978). Studies have demonstrated the profound influence of herbivores on the structure of coral reef communities (Stephenson and Searles 1960, Randall 1961, Wanders 1977, Ogden and Lobel 1978). Herbivorous fishes in the families *Acanthuridae*

(surgeonfishes) and *Scaridae* (parrotfishes) and urchins are important components, both ecologically and evolutionarily, of the herbivore guild on many tropical reefs (Randall 1965, Wanders 1977, Steneck 1983, Hay 1984, Lewis 1985, Lewis and Wainwright 1985, Duffy and Hay 1990). Studies have demonstrated marked spatial variation in abundance within the herbivore guild, with acanthurids predominant in shallow habitats and scarid fishes dominant in deeper habitats (Bouchon-Novaro and Harmlin-Vivien 1981, Randall 1963, Barlow 1975, Bradbury and Goeden 1974, Lewis and Wainwright 1985). It has been suggested that physical habitat characteristics, such as topographic complexity, may determine local distributions of reef fish populations (Hiatt and Strasburg 1960, Randall 1963, Luckhurst and Luckhurst 1978). A study by Lewis and Wainwright (1985), however, suggests that spatial distributions of scarids and acanthurids may be determined by complex interactions of several factors, including proximity to shelter, predator abundance, density of territorial competitors as well as local availability of food resources.

#### Algal Defenses

Seaweeds possess a variety of adaptations and defenses against herbivores. A strategy utilized by some seaweeds is to escape from herbivores spatially. Habitats and microhabitats where herbivores are not active, such as holes and cracks or shallow sand plains and reef flats can provide a refuge for some algae (Hay 1990). Additionally, associations with unpalatable algae or life history traits that coincide with low herbivore activity may allow for the seaweed to escape herbivory (Lubchenco and Cubit 1980, Hay 1986). In tropical regions, where herbivores are mobile and abundant year-round, many seaweeds escape herbivory through chemical and morphological defenses. Seaweeds

produce a large number of secondary metabolites, including terpenes, acetogenins, aromatic compounds, and phlorotannin polyphenolics (Faulkner 1984, Hay 1990). In addition to deterring herbivores, these compounds may also aid in resisting pathogens and fouling organisms (Wahl 1989). Plants may contain a variety of secondary metabolites to deter a wide range of herbivores. Some are capable of allocating these defenses to parts of the plant that are especially susceptible to herbivory (Hay et al. 1988, Duffy and Hay 1990). Some seaweeds adjust their morphology to intense grazing pressure by forming short, tightly packed turfs that significantly reduce losses to herbivory (Hay 1981b). In summary, seaweeds may exhibit combinations of structural, chemical, morphological defenses and life history traits to deter herbivores.

#### Effects of Herbivory

The effects of herbivory on species composition in reef community organization has been the focus of several studies (Lewis 1986, Morrisson 1988, Hackney et al. 1989, McClanahan et al. 1996, Hixon and Brostoff 1996, McCook 1997). One of the early investigations evaluated reductions in grazing intensity of adult acanthurids and scarids (Lewis 1986). Rapid and dramatic shifts in benthic community structure followed, as portions of coral colonies were overgrown and subsequently killed by macroalgae. In addition, total macroalgal abundance significantly increased with a decrease in algal turf, crustose coralline algae and coral abundance. The study suggests that herbivorous fish grazing appears to maintain a tropical benthic assemblage dominated by algal turfs and crustose coralline algae by reducing abundance of macroalgal species with superior overgrowth abilities. The study also demonstrated that spatial variation in herbivore grazing may act to maintain different benthic species assemblages under fundamentally

distinct selective regimes. Shallow habitats that supported dense stands of macroalgal species were found to represent spatial refuges from herbivores with locally lower densities of acanthurids and scarids, while the spur and groove formations in a back reef habitat led to dominance by algal turfs and crustose corallines.

Hackney et al. (1989) explored the relationship between macroalgae and herbivores further by taking into account the morphology and physiology of the macroalgae, algal turfs and crustose corallines. His model predicts that benthic algal community structure is primarily controlled by herbivore grazing pressure and that characteristic adaptations arise from the persistence of different assemblages of algal species under different grazing regimes. This would result in different zones of shallow reefs supporting algal groups with characteristic morphologies, rates of productivity and standing crop. The investment of resources to maintain a particular morphological or physiological adaptation will result in a reduction of energy available for maximizing photosynthetic efficiency or supporting alternate adaptations (Littler and Littler 1980, Hay 1981b, Hay et al. 1983, Hackney 1989). As a result, adaptations that may increase fitness in high grazing intensity areas may be inappropriate in low grazing intensity habitats. Alternative adaptations that increase competitive ability or responses to physical stresses, such as desiccation, may increase algal fitness in such habitats (Hackney et al. 1989). According to the model, crustose algae are able to persist in high grazing intensity habitats due to their resistant morphology, but have low primary productivity rates per unit area and per unit biomass. The presence of macroalgae is low to absent in high grazing intensity areas, but macroalgae can have very high primary productivity rates per unit area. The adaptations of these macroalgae include the ability

to maintain upright morphology. Turfs persist in moderate to high grazing intensity areas with high primary productivity rates per unit area and very high productivity rates per unit biomass. Its high surface area to volume ratio result in high growth rates. Although this model is based on morphological and physiological rationales, it remains simplistic as it does not address issues of great diversity within any one category of algae, their palatability, grazer preference and nutrient acquisition strategies.

A more recent study conducted by Hixon and Brostoff (1996) examines the relationship between herbivory and succession in coral reef environments. The study suggests that within habitats, herbivorous fishes may enhance local algal diversity by causing between-patch differences in algal species composition and also by maintaining high local diversity within one kind of patch, such as damselfish territories. Differential grazing can cause different successional trajectories leading to algal assemblages of very different species composition. Herbivorous fishes are therefore capable of maintaining the diversity of tropical benthic algae at three scales: between habitats, between patches, and within patches. The ability of herbivorous fishes to differentially affect succession of benthic algae over small spatial scales may partially explain the maintenance of high species diversity on coral reefs.

McCook (1997) examined the effects of herbivory on zonation of *Sargassum* spp. A combination of transplants and herbivore exclusion was used to explore the influences of herbivory, physiological tolerance limits and recruitment and dispersal in regulating the distribution and abundance of *Sargassum* spp. The study focused on the absence of *Sargassum* spp in the coral zone. Herbivory may be the major cause of zonation patterns, but the importance of this factor varied between and within reefs. Further, recruitment to

the coral zone was very low and was not affected significantly by herbivores. This suggests that *Sargassum* distribution is determined by scale-dependent interactions between recruitment, dispersal and herbivory.

Although there are many studies which document the importance of herbivory in determining algal abundance and distribution, very few consider the influence of factors such as nutrient availability and water motion. Nutrients are available to plants via remineralization of organic biomass, fixation of atmospheric nitrogen and diffusion (Hatcher 1990). Larned (1998) found that inorganic nitrogen limited the growth rates of 8 out of 9 macroalgal species in a laboratory nutrient enrichment experiment, demonstrating the important role of nutrient availability in the water column at low water flow rates. In addition to the ability to avoid damage by herbivores, algae must also be able to effectively acquire nutrients. Physical factors, such as water motion, therefore become an important component as the boundary layer thickness surrounding the algae can strongly influence the diffusion of nutrients down a concentration gradient to sites of nutrient uptake (Hatcher 1990). The relative dominance model developed by Littler and Littler (1980) considers nutrient levels and herbivore activity as the two major factors that control the relative dominance of various groups of benthic algae. Herbivory is considered the principal control on algal biomass and species group, while nutrients set the upper limits to biomass and species group. It is therefore necessary to approach questions of algal abundance and distribution from a multi-faceted perspective, rather than focusing solely on one factor.

It is also important to consider the mesograzers as part of the herbivores on reefs. Mesograzers are animals such as amphipods, copepods, tanaids, polychaetes and small

gastropods, that depend on seaweed for both food and shelter (Brostoff 1988) Algal species composition was only slightly altered by mesograzers. Few species showed any response to the removal of natural populations of mesograzers. Mesograzers do reduce the standing crop of epiphytic species on a particular host and alter species composition, resulting in epiphyte flora consisting of microscopic algae. Brostoff (1988) concluded that epiphytes have no great adverse effects on their host thalli, which conflicts with the findings of Brawley and Adey (1981) and D'Antonio (1985). This could be due to the fact that the former study was conducted in a tropical environment in contrast to other studies in temperate environments. Hay and Fenical (1988) reports that mesograzzer populations are usually kept at low densities by predators, usually having little obvious effect on most seaweeds. The types of effects can vary widely, however, among mesograzzer species.

#### Herbivory and Introduced Species

Studies examining the relationship between herbivory and introduced algal species exist for only a few algal species. Information on the role of herbivory by resident species in determining the success of introduced species is rare. Ribera and Boudouresque (1995) report that *Caulerpa taxifolia* is strongly avoided (in summer) by the native Northwestern Mediterranean herbivorous sea urchin *Paracentrotus lividus*. Trowbridge (1995) examined herbivory of the introduced *Codium fragile* ssp. *tomentosoides* along the New Zealand coast and concluded that the diverse assemblage of intertidal herbivores exerted little grazing pressure on *C. fragile*. Additionally, a similar study by Prince and LeBlanc (1992) examined herbivory of introduced *C. fragile* ssp. *tomentosoides* off the coast of Maine and found that the algae was not preferred by the

native sea urchin, *Strongylocentrotus droebachiensis*, contributing to its success and continued spread.

Herbivory and *Kappaphycus/Eucheuma* spp.

There are few studies that have documented herbivory on *Kappaphycus/Eucheuma* spp. A study conducted by Russell (1983) demonstrated the consumption of *Kappaphycus/Eucheuma* spp. by *Acanthurus triostegus sandvicencis* and *Zebrasoma flavescens*, common reef fishes, through gut sampling. The study also demonstrated that herbivorous fishes appeared to selectively graze on the smaller branches of the thalli. In holding pen trials, 40 *Acanthurus dussumieri* consumed 51 g from a 515 g thallus in 3.5 hours, as determined from growth rates of caged and uncaged thalli were compared. Fishes reduced the growth rate at 0.5 m by 50% and at 2.0 m by 80%. Brostoff (1988) showed that mesograzers do not significantly affect the relative abundances of *Eucheuma/Kappahycus*, spp. but do affect the amount of epiphytes, as discussed above. The similarity of *Eucheuma/Kappaphycus* spp. abundance between samples with and without mesograzers suggest that epiphytes have no great adverse effects on their host thalli.

The influence of herbivory on the abundance of macroalgae on tropical reefs is well-documented. The nature of the interactions and mechanisms between herbivores and algae, however, are quite complex and are only beginning to be understood. Additionally, many studies have neglected to consider other factors, such as nutrient availability and acquisition and water motion as additional components that determine algal abundance and distribution. Previous studies suggest that herbivory may play an important role in the distribution and abundance of *K. striatum* in Kane'ohē Bay. Few



studies, however, have documented the effects of herbivory on the distribution and abundance of introduced algae. These studies could increase our understanding of the underlying mechanisms that allow successful invasions to take place as well as aid in forming effective management strategies.

## ASPECTS OF RESEARCH

With our limited understanding of marine invasions and especially algal invasions, studies that broaden our knowledge of the patterns, processes and mechanisms that lead to invasion success are crucial. The introduction of *Kappaphycus striatum* to Kane'ohe Bay provides a unique opportunity to examine some of the factors that may play a role in determining the abundance and distribution of an invasive alga. The dynamics of the spread of introduced algae are poorly understood, and the characteristics of a community that allow for the successful establishment of marine algae are largely unknown. Little is known of the ecology of *K. striatum* in the field. The objective of this study is to investigate the effects of herbivory as well as determine possible impacts, seasonal patterns of growth, minimum fragment size and growth rate potential of *K. striatum* across the Bay. Through this study in Kane'ohe Bay, I hope to answer the following questions: (1) Does high grazing pressure limit the distribution of *K. striatum*, (2) Does low grazing pressure lead to *K. striatum* abundance, (3) Does *K. striatum* have the potential for growth across the Bay, (4) What is the minimum fragment size capable of regrowth into an adult plant, (5) Does *K. striatum* exhibit seasonal growth patterns, (6) Is *K. striatum* overgrowing live coral, (6) Is the benthic cover of *K. striatum* increasing.

## Chapter II

# ECOLOGICAL IMPACTS AND INTERACTIONS OF THE INTRODUCED RED ALGA, *KAPPAPHYCUS STRIATUM*, TO KANE'OHE BAY, O'AHU

### Abstract

The introduction of *Kappaphycus striatum* to Kane'ohe Bay, O'ahu, in the early 1970's has been followed by its spread and establishment in many parts of the Bay. The abundance and apparent overgrowth of *K. striatum* on live coral in certain areas of the Bay has raised the concern of management. To assess the factors that may control the distribution of *K. striatum*, a study was undertaken to establish minimum fragment size that could function as propagules. Caged growth potential and grazing intensities at sites of varying *K. striatum* abundance were also evaluated. Determination of *K. striatum* impact on live coral was monitored by a time series photography study. Vegetative propagation through fragmentation is an effective dispersal mechanism that has most likely contributed to the spread and establishment of *K. striatum*. Fragments weighing 0.05 g were capable of net growth in the field, suggesting that fragments created by physical disturbance can be carried by waves and currents to new locations where they can possibly establish. The growth potential study indicates that *K. striatum* is capable of net growth in all sites surveyed, suggesting that environmental differences across the Bay are not limiting its establishment. Results of the grazing intensity study suggest that herbivory does play an important role in preventing the establishment of *K. striatum* in areas where *K. striatum* is absent. No definitive explanations can be given for the abundance of *K. striatum* in certain areas. Through the time series photography study,

overgrowth of *K. striatum* on live coral was observed within a one-year period. Results from these studies suggest that the spread of *K. striatum* is relatively slow in comparison to other algal invasions, but will continue to spread with the present herbivory levels and environmental conditions.

## INTRODUCTION

The study of the establishment of invasive species is an important component of our efforts to preserve biodiversity and to minimize environmental degradation. The invasion of marine and estuarine systems by non-native species has become a widely recognized phenomenon that continues to take place around the world (Grosholz and Ruiz 1995). Studies of biological invasions have documented substantial alteration of pre-existing communities through the displacement of native species by predation, hybridization or competitive interactions (Lodge 1993, Ricciardi et al. 1995). In comparison to the extensive literature that documents invasions of terrestrial and freshwater habitats, relatively little is known of the history or impact of marine invasions (Lodge 1993). Quantitative studies and long-term experiments to distinguish the effects of an introduction on populations and communities from the effect of other types of variation in the marine environment have only recently begun to emerge.

Three macroalgal species, *Eucheuma denticulatum*, *Kappaphycus alvarezii* and *Kappaphycus striatum*, were introduced to the fringing reef area at the Hawaii Institute of Marine Biology on Coconut Island in the 1970's. The introductions took place as part of aquaculture studies motivated by the increasing commercial value of the carrageenan found in the cell wall component of these species. Russell (1981) documented the

establishment and dispersal of *Kappaphycus* and *Eucheuma* spp. in Kane'ohē Bay from 1974 to 1976. The systematics of *Eucheuma* and *Kappaphycus* are far from satisfactory because of the large size, indeterminate growth, phenotypic variability and apparently infrequent sexual reproduction of these organisms. Thus, the complex of species will be referred to as *Kappaphycus* spp. unless otherwise specified. These seaweeds were planted in several locations, particularly nets and wire holding pens in the center of the northwestern fringing reef bordering Coconut Island. Even without additional attention, the populations of *Kappaphycus* spp. grew rapidly, alarming the public. This led to an initial cleanup effort to remove a portion of the mixed *Kappaphycus* spp. population from the fringing reef of Coconut Island (Russell 1981). Although the population of *Kappaphycus* spp. on Coconut Island has diminished to near absence, contrary to the predictions of Russell (1981), *Kappaphycus* spp. have spread from Coconut Island to reefs across the Bay. His study proposed that vegetative fragments capable of regenerating into adult thalli would be unable to cross the channel because of rapid rates of sinking by fragments and because deeper water was unsuitable for its growth. A more recent study by Rodgers and Cox (1999) documented the distribution of *Kappaphycus* spp. from the southern to the northern portions of the Bay and also estimated the rate of spread since its introduction (Figure 1). Growth rates across the Bay and effects of herbivory were not examined by Rodgers and Cox (1999). The spread, current high levels of abundance in some parts of Kane'ohē Bay and apparent overgrowth on coral of *Kappaphycus striatum* has raised the concern with Department of Land and Natural Resources, State of Hawaii.

There are several factors that may contribute to the success of *K. striatum* in Kane'ohē Bay. Dispersal capabilities allow for small or possibly even large pieces to be carried by currents to new areas and possibly establish. Williamson and Brown (1986) proposed that a strong capacity for dispersal is a major characteristic of species likely to successfully invade. The success of *Caulerpa taxifolia* and *Codium fragile* ssp. *tomentosoides*, species that rapidly dispersed upon introduction, is evidence that this factor influences invasion success (Ribera and Bourdouresque 1995, Trowbridge 1995). Further, the dramatic spread of these species in the waters of the Mediterranean and the east coast of the United States respectively, is sustained by their rapid growth, asexual reproduction as well as their broad tolerance to physiological conditions (Ribera and Bourdouresque 1995, Trowbridge 1995). Likewise, these studies would suggest that the ability of *K. striatum* to reproduce asexually by fragmentation has contributed to its success in Kane'ohē Bay. Additionally, in productive areas, *Kappaphycus* spp. exhibit high growth rates, doubling their size in 15 to 30 days (Azanza-Corrales et al. 1982, Rodgers and Cox 1999). Because of these high growth rates, *K. striatum* appears to be capable of producing vegetative fragments at a high rate (Russell 1981), having growth rates of 4 to 5% day<sup>-1</sup> (Russell 1983, Glenn and Doty 1989).

The absence of natural enemies has also been proposed as a factor influencing invasion success (Williamson and Brown 1986). Information on the role of herbivory by resident species in determining the success of introduced species is rare. Ribera and Bourdouresque (1995) report that *Caulerpa taxifolia* is strongly avoided (in summer) by the native Northwestern Mediterranean herbivorous sea urchin *Paracentrotus lividus*. Trowbridge (1995) examined herbivory of the introduced *Codium fragile* ssp.

*tomentosoides* along the New Zealand coast and concluded that the diverse assemblage of intertidal herbivores exerted little grazing pressure on *C. fragile*. Additionally, a similar study by Prince and LeBlanc (1992) examined herbivory of introduced *C. fragile* ssp. *tometosoides* off the coast of Maine and found that the algae was not preferred by the native sea urchin, *Strongylocentrotus droebachiensis*, contributing to the alga's success and continued spread.

It has been hypothesized that novel secondary metabolites in introduced species may contribute to their success due to the "chemical jump" that would be required of native herbivores (Orians 1984). Although this has not been tested in marine algae, the influence of palatability on herbivory has been demonstrated in several experiments (Duffy and Hay 1990, Prince and LeBlanc 1992, Trowbridge 1995). Tropical algae produce a large number of secondary metabolites, including terpenes, aromatic compounds, acetogenins, and phlorotannin polyphenolics (Faulkner 1984, Hay and Fenical 1988, Duffy and Hay 1990). The presence of secondary metabolites varies considerably among species and the effects of the metabolites can differ according to the type of herbivore (Duffy and Hay 1990). This would suggest that the presence of effective chemical defenses and overall palatability can play an important role in determining the success of a species in an introduced habitat.

A primary concern for management is that *K. striatum* appears to be overgrowing coral in several areas. Coral reefs are well-known for their diversity and commercial value, especially in relation to the fishing and tourism industries. Examples of dramatic shifts in reef community structure have taken place around the world that have significantly altered coral reefs (Hughes 1994). Reefs in Jamaica have been overfished

and suffered an urchin mass mortality. Without its primary herbivores, benthic algal blooms began, eventually forming extensive mats up to 10 to 15 cm deep that have prevented larval recruitment of corals (Hughes 1994). These shifts from coral to algal dominance can lead to a substantial change in ecosystem structure and function, with a significant depletion of reef fisheries (Done 1992). Possible outcomes could involve degradation in terms of the physical attractiveness of the reef and fisheries (Done 1992). Management has similar concerns of the impacts of *K. striatum* on the corals of Hawaii, as reestablishment of corals is not certain.

The patchy distribution of *K. striatum*, with very high coverage found in close proximity to areas of low coverage, has raised questions about the fine-scale factors controlling the distribution of *K. striatum*. The abundance of macroalgae is an important component of reef status (Hughes 1994), but little is known of the patterns or causes of macroalgal distributions on coral reefs (McCook 1997). Several studies have documented the effects of herbivory in reef community structure (Stephenson and Searles 1960, Randall 1961, Wanders 1977, Ogden and Lobel 1978, Sammarco 1982, Lewis and Wainwright 1985, Lewis 1986). An investigation conducted by Lewis (1986) demonstrated that when grazing intensity of adult acanthurids and scarids was experimentally reduced, rapid and dramatic shifts in benthic community structure followed. As portions of coral colonies were overgrown and subsequently killed by macroalgae, total macroalgal abundance significantly increased with a decrease in algal turf, crustose coralline algae and coral abundance. The study suggests that herbivorous fish grazing appears to maintain a tropical benthic assemblage dominated by algal turfs and crustose coralline algae by reducing abundances of macroalgal species with superior

overgrowth abilities. Additionally, fragmentation can also influence algal abundance. Russell (1981) demonstrated that when sources of algal fragments were removed, nearby algal populations declined significantly.

In addition to the well-documented effects of herbivory on algal distribution, the availability of nutrients and physical factors, such as water motion, can play important roles in determining algal distribution. Larned (1998) found that inorganic nitrogen limited the growth rates of 8 out of 9 macroalgal species, including *K. striatum*, in a laboratory nutrient enrichment experiment. Further examination in the field of the dissolved inorganic nitrogen concentrations in the microenvironments associated with mat-forming species, such as *K. striatum*, and manipulation of DIN concentrations in the laboratory, suggested that nitrogen is very likely to limit the growth of *K. striatum* in the field and that its morphology allows for exclusive use of sediment nitrogen. Thus, physical factors, such as water motion become an important component as the boundary layer thickness surrounding the algae can strongly influence the diffusion of nutrients down a concentration gradient to sites of nutrient uptake (Hatcher 1990). The relative dominance model developed by Littler and Littler (1984) considers nutrient levels and herbivore activity as the two major factors that control the relative dominance of various groups of benthic algae. Herbivory is considered the principal control on algal biomass and species group, while nutrients set the upper limits to biomass and species group.

The invasion of Kane'ohe Bay by *K. striatum* allows for several questions to be evaluated in a tropical reef setting that has substantial ecosystem information. The dynamics of the spread of introduced algae are poorly understood, and the characteristics of a community that allow for the successful establishment of marine algae are largely



unknown. Few studies have examined the role of herbivory in determining the outcome of introduced species. Additionally, little is known of the ecology of *K. striatum* in the field. The objective of this study is to investigate the effects of herbivory as well as determine possible impacts, seasonal patterns of growth, minimum fragment size and growth rate potential of *K. striatum* across the Bay. Through this study in Kane'ohu Bay, I hope to answer the following questions: (1) Does high grazing pressure limit the distribution of *K. striatum*, (2) Does low grazing pressure lead to *K. striatum* abundance, (3) Does *K. striatum* have the potential for growth across the Bay, (4) What is the minimum fragment size capable of regrowth into an adult plant, (5) Does *K. striatum* exhibit seasonal growth patterns, (6) Is *K. striatum* overgrowing live coral, (6) Is the benthic cover of *K. striatum* increasing within a site.

## MATERIALS AND METHODS

### Field survey

An initial visual survey of reefs was conducted in Kane'ohu Bay, O'ahu to find study sites that differed in abundance of *K. striatum*. Two to three reefs containing varying *K. striatum* abundance, wave energy and topography were chosen from the north, central and south portions of Kane'ohu Bay (Figure 2). Areas of low and high abundance were chosen according to the amount of *K. striatum* encountered in a 25 m transect swim along and parallel to the reef crest. In areas of low *K. striatum* abundance, *K. striatum* was either absent or only rarely found in small isolated patches. In areas of high *K. striatum* abundance, *K. striatum* could be found within 1 m<sup>2</sup> of each meter of the 25 m transect. These study sites were examined to assess both the grazing pressure of *K.*

*striatum* and its growth potential across the Bay in the absence of herbivory. Differences in water motion were determined by comparing the diffusion factors of three to four plaster of Paris clod cards placed at each site. Diffusion factors were calculated following the methods of Jokiel and Morrissey (1993). On two dates during the summer of 1999, cards were deployed for approximately 24 hours at each site. Using a weighted regression, diffusion factors were correlated with caged *K. striatum* growth rates obtained during the same summer months. Sites that contained more growth rate data during the summer were weighted more heavily than sites with only one set of summer growth rate data.

#### Growth potential across the Bay, herbivory and seasonal growth

From October 1998 to October 1999, caged and uncaged thalli of *K. striatum* were deployed to examine its growth rates and the intensity of grazing at 9 study sites (Figure 2). Growth was assessed in predator enclosure cages and grazing intensity was measured as the difference between growth inside and outside of cages. Locations and reef environments of the nine sites are summarized in Table 1. Large thalli to be used for grazing and growth field studies were collected from the back reef area and returned to the laboratory in seawater. Approximately 200 individual thalli were collected for each sampling date. Thalli with a branching morphology were selected in the field rather than thalli with a smooth mound morphology. The thalli from the field ranged in weight from 20 to 50 g and were broken into smaller pieces weighing 20 to 25 g (wet weight), approximately 8 cm in length. Thalli were dried in a salad spinner, weighed wet to the nearest 0.01 g and were randomly assigned to two levels of herbivory, caged and

uncaged. The predator enclosures were placed in the field one day after weighing. Individual caged and uncaged thalli were weighed at the start of each experimental period and reweighed after approximately five to seven days in the field.

Caged and uncaged thalli were attached to 2.5 cm vinyl coated wire mesh platforms (30 x 15 cm) using coiled, plastic coated, single strand electrical wiring. The coils were 4 cm in diameter containing 6 to 7 rings. The coil was threaded through the branches of *K. striatum* and then attached to the mesh platforms. Cages had walls, roofs and floors of 0.5 cm vinyl coated mesh. All cages were 8 x 8 x 8 cm high.

The magnitude of possible cage effects was assayed in two ways. Differences in water motion inside and outside of the cage was measured by the diffusion factor of clod cards. Clod cards were placed inside and outside of 12 cages and left on the inner reef flat of the fringing reef of Coconut Island for 24 hours. Differences between the inside and outside of cages were analyzed using a paired t test. Additionally, to determine differences in light availability and flow rate, 14 caged and uncaged thalli were placed in low flow seawater tables for approximately 6 days. Differences in growth rates were analyzed using a paired t test.

The platforms holding caged and uncaged thalli were placed on rubble terraces on the windward reef crests at eight of the sites. At the site on the back of the barrier reef, currents and waves were strong, requiring platforms to be attached to non-living reef substrate using two pieces of rebar. As many as five sites were sampled during each of the herbivory assays. Each site was sampled a minimum of five times.

Because initial weights were within a narrow range (20 to 25 g), growth rates were determined by subtracting initial weight from final weight of an individual thallus

and dividing by the number of days in the field. Very low negative values occasionally resulted due to breakage during handling in the field and were not included in the analysis if values were more than three standard deviations from the mean. Grazing intensity was determined by calculating the difference between the growth rates of a caged and an uncaged thallus from a single platform.

Differences in grazing intensity among sites were analyzed using an unbalanced two-way repeated measures ANOVA (Systat 8.0). Following the ANOVA, mean values of grazing intensity between sites of high and low *K. striatum* abundance were compared for all dates using post-hoc linear contrasts to test if low *K. striatum* sites had significantly higher grazing intensities than high abundance *K. striatum* sites. P-values were adjusted using a sequential Bonferroni method (Rice 1989).

Caged growth rates were compared using an unbalanced two-way repeated measures ANOVA to detect differences in growth potential across the Bay (Systat 8.0). Following the ANOVA, caged growth rates from the high *K. striatum* abundance sites were compared to those of the low *K. striatum* abundance sites using post-hoc linear contrasts. Mean caged growth rates between the two categories were compared for all dates to test if high *K. striatum* abundance sites had significantly higher growth rates than low *K. striatum* abundance sites. P-values were adjusted using the sequential Bonferroni method (Rice 1989).

Effects of seasonality on caged growth rates and grazing intensities were determined by comparing caged growth rates and grazing intensities at three sites over one year. Results were analyzed using an unbalanced two-way repeated measures ANOVA (Systat 8.0). Difference contrasts were performed sequentially between

sampling dates to determine if there was a significant difference among seasons. P-values were adjusted using the sequential Bonferroni method (Rice 1989).

Twenty four hour surveys were conducted in order to identify grazers of *K. striatum* in a field setting. In July 1998, two 50 m transects were surveyed in the back reef area in sites of low and high *K. striatum* abundance every hour for 24 hours. Two observers swam on either side of the transect line. The presence and interactions of herbivores with *K. striatum* within 3 m of the transect line were recorded. Each transect was swum in approximately 10 minutes. An additional survey was conducted in February 1999 on the windward fringing reef of Coconut Island. Pieces of *K. striatum* weighing approximately 50 to 60 g were attached to mesh platforms and placed parallel to the reef slope and reef flat along a 50 m transect. Four platforms were placed along each line. One observer swam along the reef slope transect and another along the reef flat transect. The presence and interactions of herbivores with *K. striatum* within 2 m of the transect were recorded every hour for 24 hours. Each transect was swum in approximately 10 minutes.

#### Percent Cover

Two sites in areas of high *K. striatum* abundance in the back reef were surveyed in order to detect changes in abundance of *K. striatum* within the area. Within the two sites, two 50 m transects were laid out along coral reef areas and 10 random points were chosen along each line. A 1 m<sup>2</sup> quadrat with 81 cross points was placed at each of the 10 randomly chosen points. The number of crosspoints that fell upon *K. striatum* was counted. Transects were conducted approximately every month for one year.

### Survival and Growth of Fragments

Thalli were collected from the field and placed in seawater tables supplied with running seawater. Small fragments were removed from larger thalli, weighed and placed in different weight categories, ranging from 0.03 g to 0.25 g in weight and 0.25 cm to 1 cm in length. Fragments were color coded according to size class by attachment of fine plastic coated wire to the plant piece. The fragments were placed in two different environments. One set of fragments was placed in a pan filled with sand covered with 0.5 cm plastic coated mesh and placed on the reef flat. The other set of fragments was placed in cages with walls, floors and roofs of 0.5 cm plastic coated mesh. Ten fragments in each size class were used. These cages were placed on the reef flat. The cages and pan were left in the field for approximately 6 days. Remaining fragments were brought back from the field and reweighed at that time. The three field trials took place in the summer of 1998 and 1999.

### Coral and Algal Interaction

To monitor the effects of algal encroachment on live coral, four photostations were constructed. Rebar was used to mark the sites and act as a camera mount. The rebar was pounded deeply into the sandy substratum to minimize changes in the photographed area through time. The camera was mounted on a platform constructed from acrylic and PVC piping that slid over the rebar. Markers were placed on the coral head to indicate where the camera frame should line up. Photographs were taken monthly.

## RESULTS

### Growth Potential across the Bay

*K. striatum* caged growth rates varied significantly among sites and across date, but there was also a significant date  $\times$  site interaction (Table 2). Analyses were performed on two sets of sites because they differed in sample dates. Areas of high abundance as indicated by asterisks in Figures 3 and 4 did not have significantly higher growth rates than sites with low abundance on any date when caged growth rates were compared in an *a posteriori* hypothesis test ( $p > 0.05$ ). At sites 1-5, growth rates were similar on most dates with the exception of June 6 where the range of growth rates among sites was comparatively much wider (Figure 3). At sites 5-9, variation in growth rates among sites was considerably larger than sites 1-5 (Figure 4). Reef #43 was not included in the analysis because it was not sampled on the April and May dates, but is included in Figure 4. Differences in growth rates among sites varies among dates within one year (Table 2).

The two clod card runs conducted in August and July at the nine sites yielded significant differences in diffusion factors among sites ( $p < 0.001$ ). Higher diffusion factors indicate relatively higher water motion among sites. A weighted linear regression of average caged growth rates during the summer months as the response variable and average diffusion factor as the predictor was significant ( $p = 0.011$ ) (Table 3) (Figure 5)

There was no significant difference in growth rates of caged and uncaged thalli when they were grown in water tables ( $t = -1.43$ ,  $n = 14$ ,  $p = 0.15$ ). Additionally,

differences in clod card diffusion factors inside and outside of cages were nonsignificant in a low flow regime ( $t = -1.42$ ,  $n = 12$ ,  $p = 0.18$ ).

### Grazing Intensity

Grazing intensity varied significantly among sites and across date (Table 4) (Figures 6 and 7). A date  $\times$  site interaction was also significant (Table 4). Reef #44 and #43 were not included in the analysis because of exceptionally high grazing intensity values on three dates. Average grazing intensities and standard errors for reefs #44 and #43 are summarized in Figure 8. Areas of abundance are indicated by an asterisk in Figures 6 and 7. To compare grazing intensities in relation to the abundance of *K. striatum*, the grazing intensities of Coconut, Checker-A and reef #3, abundance sites, were compared to grazing intensities of the back reef and reef #29, high abundance sites, in an *a posteriori* hypothesis test. The grazing intensities at the high abundance sites were significantly lower than grazing intensities at low abundance sites for all dates (Figure 6, Table 4). For the data collected on different dates, a similar hypothesis test compared grazing intensities of Checker-A and Checker-B, low abundance sites, to the grazing intensity of reef #24, a high abundance site (Table 4) (Figure 7). Grazing intensities were significantly different for all dates. In high abundance sites, low grazing intensities remained constant for all sampling dates. In low abundance sites, however, grazing intensities fluctuated considerably among sampling dates. Figure 8 demonstrates that in a single month, grazing intensities can vary within the same site.



### Seasonality of Growth Rates and Herbivory

Three sites were chosen to evaluate seasonality of caged growth and grazing intensity over a one year period. Average growth rates of caged thalli at three sites over a one year period are shown in Figure 9. Growth rates varied significantly among sites and across dates ( $p = 0.03$ ,  $p = 0.01$ ) (Table 5). The date  $\times$  site interaction was not significant ( $p = 0.12$ ). *A posteriori* difference contrasts detected a significant increase in growth rates between March and June and a decrease between September and October ( $p = 0.04$  for both contrasts), suggesting higher growth rates during the summer months. Average grazing intensities over one year at the back reef and reef #29 were low throughout the year (Figure 10). At Coconut, however, grazing intensities were higher and fluctuated considerably in comparison to the back reef and reef #29 (Figure 10). A repeated measures ANOVA yielded a significant difference among these three sites ( $p = 0.01$ ), whereas the significant difference among dates was marginal among sites ( $p = 0.07$ ) (Table 5). Difference contrasts between sampling dates for Coconut only revealed a significant increase in grazing intensity between March and June ( $p = 0.03$ ).

### Twenty four Hour Surveys

The first 24 hour survey conducted in August 1998 in the back reef area did not reveal any significant source of herbivory. The sea hare, *Stylocheilus longicaudus*, was observed in large numbers (30 to 40) on clumps of *K. striatum* during the evening hours. During daylight hours, juvenile parrotfish were commonly observed grazing on clumps of *K. striatum*. Gut analysis and quantification of herbivory were not performed. The second 24 hour survey was conducted at Coconut Island in July 1999, where previous

predator exclosure assays revealed high grazing intensities. Transects were examined every hour along the reef crest and in on the flat. No herbivores were observed grazing on *K. striatum*. Grazing scars resembling parrotfish bites have been observed, however, on uncaged thalli at Coconut Island at the end of predator exclosure assays.

### Fragmentation

Fragments of various sizes were grown in sand and mesh cages to determine minimum fragment size capable of maintaining positive growth. Fragments in the mesh cages placed on rubble significantly increased in weight in all weight classes when initial and final weights were compared in a two-sample t-test (Figure 11). For the fragments assayed in sand, classes A, B and C maintained initial weight was maintained, while weights in class D declined (Figure 12).

### Change in Percent Cover

No net change in percent cover of *K. striatum* was detected in two study sites over a one year period. Figure 13 shows the change in percent cover of *K. striatum* at two sites in the back reef area over a one year period. No change in either site is apparent when initial and final percent cover is compared. A slight increase in November and February in both sites can be seen, but the percent cover drops down to its initial levels in both sites.

### Coral and algal interaction

Photographs taken from August 1998 to August 1999 at four sites in the back reef area reveal that the algae is overgrowing live coral. The encroachment of the algae on the coral appears to be gradual, however. Considerable change in algal cover was observed within the first six months. The following six months, however, there appeared to be only minor changes in the algal cover (Figures 14 and 15).

## DISCUSSION

Abundance of an alga on tropical reefs is a function of plant growth abilities, nutrient availability and grazing pressures. Previous to this study, the ability of *K. striatum* to spread and grow in different areas of the Bay was a point of some confusion (Russell 1981). The varying environmental conditions across the Bay could possibly limit the distribution of *K. striatum* and play a role in its patchy distribution. Results from this study, however, have demonstrated that *K. striatum* is capable of net growth within cages in the south, central and northern regions of the Bay (Figures 3 and 4). Interpretation of the significant interaction between date and site in the ANOVA indicate that differences in growth rates among sites vary among dates (Table 3). The significant correlation between the diffusion factor of clod cards and caged growth rates suggests that water motion may play a role in the establishment of the algae, contrary to the findings of Glenn and Doty (1990) (Table 3) (Figure 5). Higher wave energy, which may decrease boundary layer thickness and increase nutrient uptake, was significantly correlated to higher growth rates at the sites examined. Reef #24, a site of low wave energy and low caged growth rates, however, is an area of high *K. striatum* abundance.

These results suggest that varying environmental conditions and nutrient availability underlie the distribution of *K. striatum*, and other factors such as herbivory and dispersal may be more important regulators of the alga's current distribution.

Because of the complexity of herbivory on coral reefs, it becomes difficult to draw conclusions about how much grazing pressure affects *K. striatum* distribution from this experiment alone. These complexities include factors such as proximity to shelter. Variations in reef topography can play an important role in determining the presence or absence of herbivores, and as a result, the presence or absence of algae. Although cages were continually placed on the windward reef crests of all sites, except the back reef site, we cannot generalize results to all areas of the reef. Grazing on the reef slope and crest will be distinctly different from grazing on the reef flat as distance to shelter and tidal levels vary. Additionally, the presence of other algae can further complicate interpretation of results. Placing a set of cages with *K. striatum* in an area with no algae, in an area with abundant *K. striatum* and in an area with other macroalgae could lead to very different results even if grazer abundance is constant. In an area with very little algae, grazing on the uncaged thalli may be high because of lack of alternate food sources. In areas of high *K. striatum* abundance, grazing may be low due to the large amount of *K. striatum* surrounding the uncaged thalli. Additionally, the presence of more preferred algae can influence herbivory on uncaged thalli as grazers may feed upon the more preferred food source. All of the above mentioned factors result in difficulty answering the question of grazing intensity influencing the distribution of *K. striatum* through the methods employed.

The results of this study suggest that grazing intensity, as measured through average growth rate differences between paired caged and uncaged thalli is low at sites of high *K. striatum* abundance (Figures 6 and 7). Grazing intensity values at the 3 sites, reef #29, reef #24 and the back reef, were consistently close to zero for all dates. These three sites of high *K. striatum* abundance are all located in the central Bay region. An explanation of the low grazing intensity values could be because of the presence of large amounts of *K. striatum* in the area; grazers may have not encountered the uncaged thalli. It is apparent in these sites however, that *K. striatum* is growing faster than grazers can consume it. This most likely arises from several factors such as low grazer density and lack of sea urchins in the Bay, which could possibly lead to low grazer abundance and low food preference in comparison to other algae (Stimson, unpubl. data). Grazing scars have been observed in the field at high abundance sites, such as the barrier reef site and along the reef slopes and crests of reef #29 and #24, demonstrating that grazing is taking place. Although the 24 hour survey failed to reveal a large number of grazers, grazing is evident both at the barrier reef site and areas where uncaged growth rates are low. The sea hares observed in the 24 hour survey, *Stylocheilus longicaudus*, are seasonal and their biomass is most likely too small and too episodic to exert enough grazing pressure to explain long term patterns in algal abundance. Juvenile scarids and acanthurids have been observed biting the branch tips of the algae. In areas of high abundance, continual grazing on branch tips causes smooth mounds of *K. striatum* to form over the coral. As the outermost branch tips are grazed, *K. striatum* continues to grow through the proliferation of tips in the interior of the thallus.

Sites in the southern region of the Bay had varying grazing intensities. When the grouped grazing intensities of the low cover sites, Coconut, Checker-A and reef #3, were compared to the intensities at the high cover sites, the back reef and reef #29, grazing intensities were significantly higher at the low sites for all dates. Coconut Island is a marine protected area where fishing and collection do not take place. With presumed higher grazer abundance and diversity, one would expect grazing intensity to be higher as well. This high grazing intensity may arise from the lack of alternate food sources in the area. Coconut Island was the original site of the *K. striatum* introduction and once supported a large population of *K. striatum* that has drastically declined. This lends support to the hypothesis that grazing levels can regulate the abundance of *K. striatum* in an area. At Coconut Island, uncaged growth rates were consistently equal to or below zero, suggesting that the algae would no longer establish in the presence of the current herbivore assemblage. Additional south bay sites, Checker-A and Checker-B yielded similar grazing intensity levels to Coconut Island (Figures 6 and 7). These sites are not marine protected areas, however, and also contain alternate food sources in the area. Despite these factors, grazing intensity was high on most dates and uncaged growth rates close to or below zero. This also supports the hypothesis that grazing plays an important role in the distribution of *K. striatum*. Reef #3 was inconsistent in its grazing intensity values, with 3 dates having high values and 3 dates having low. With its close proximity to Coconut Island, it would seem likely that *K. striatum* had the opportunity to invade, but has not. Positive caged growth rates indicate that *K. striatum* can survive at this site, but has not proliferated, most likely because of grazing. In all of the south Bay sites, *K. striatum* has had the opportunity to invade and spread because of their close proximity to

the source of the introduction, but has not. From the results of this study, it is reasonable to conclude that grazing plays an important role in limiting its spread and if conditions remain the same, will most likely not invade these areas.

The north Bay sites were not included in the analysis because of episodic high grazing events (Figure 8). The northern region of the Bay is the least impacted region and would be expected to contain a large, diverse grazer population and diverse habitats. Reefs #44 and #43 are very different environments. Reef #44 consistently has a large amount of macroalgae on the reef flat, including *K. striatum* as well as several native species. Reef #43 has very little macroalgae and a large amount of coral cover. Surprisingly, the first four dates on reef #44 and two dates on reef #43 revealed that very little grazing was taking place. On the last three dates, however, grazing intensities increased markedly. Uncaged thalli were grazed heavily, often weighing only 3 to 4 g upon retrieval. Grazing of this magnitude did not take place at any other site. These results suggest that grazing in the north Bay is patchy. This may possibly explain the presence of *K. striatum* on reef #44 even though grazing intensity has been demonstrated to be high. Perhaps there are invasion windows, time periods that allow for successful colonization of an area due to low grazing, which has led to its proliferation on reef #44. The exceptionally high grazing intensities at reef #43, as well as the absence of alternate food sources, may explain why *K. striatum* has not established on this reef.

The results of the seasonality study do not support the possibility that the growth rates of *K. striatum* are substantially reduced during any season of the year. There was an approximate doubling in growth rate during the summer months, with growth rates decreasing, but remaining positive throughout the rest of the year (Figure 9). The

increases in growth rate during summer months, however, may be counteracted by the possible increase in grazing intensity during the summer months (Figure 10). It is difficult to make any precise assumptions about the seasonality of grazing intensity because only one site out of the three surveyed, Coconut, demonstrated that grazing was taking place. In the barrier reef site and reef #29, both areas of high *K. striatum* abundance, grazing intensity remained close to zero for the entire year. As previously mentioned, this could arise from the presence of alternate food sources in the area. In the predator enclosure study, where grazing intensity was measured at several sites across the Bay, a similar trend was observed, where grazing intensity increased in the summer months (Figures 6 and 7).

The results of the fragmentation study aid in furthering our understanding of the dispersal and spread of *K. striatum* over the past 25 years. As Rogers and Cox (1999) estimated, *K. striatum* is spreading at a rate of  $250 \text{ m yr}^{-1}$  and has spread 6 km from its original point of introduction in 1974. Since this 1996 survey, there have been reports of *K. striatum* even further north. With fragments weighing as little as 0.05 g capable of maintaining positive growth, waves and currents can continually carry these propagules to already existing *K. striatum* populations or to new locations. Additionally, fragments may be carried via anchor snagging or other human activities that transport fragments even further. The results of the study also suggest that the fragments will be viable and rapidly grow if settling on substratum other than sand. It is also possible that large tumbleweeds of *K. striatum* may detach from substrate and disperse to new locations and possibly establish, providing an additional source of fragments. To further our understanding of *K. striatum* spread, it would be useful to estimate the number of



fragment generated from a given area over time in addition to determining sinking rates at different current speeds. Russell (1983) reports a sinking rate of  $1 \text{ cm sec}^{-1}$  with 2 mg apical tips. Additionally, assessment of the probability of fragment success within an area would be useful, as fragments may grow using residual energy reserves but may not survive long term.

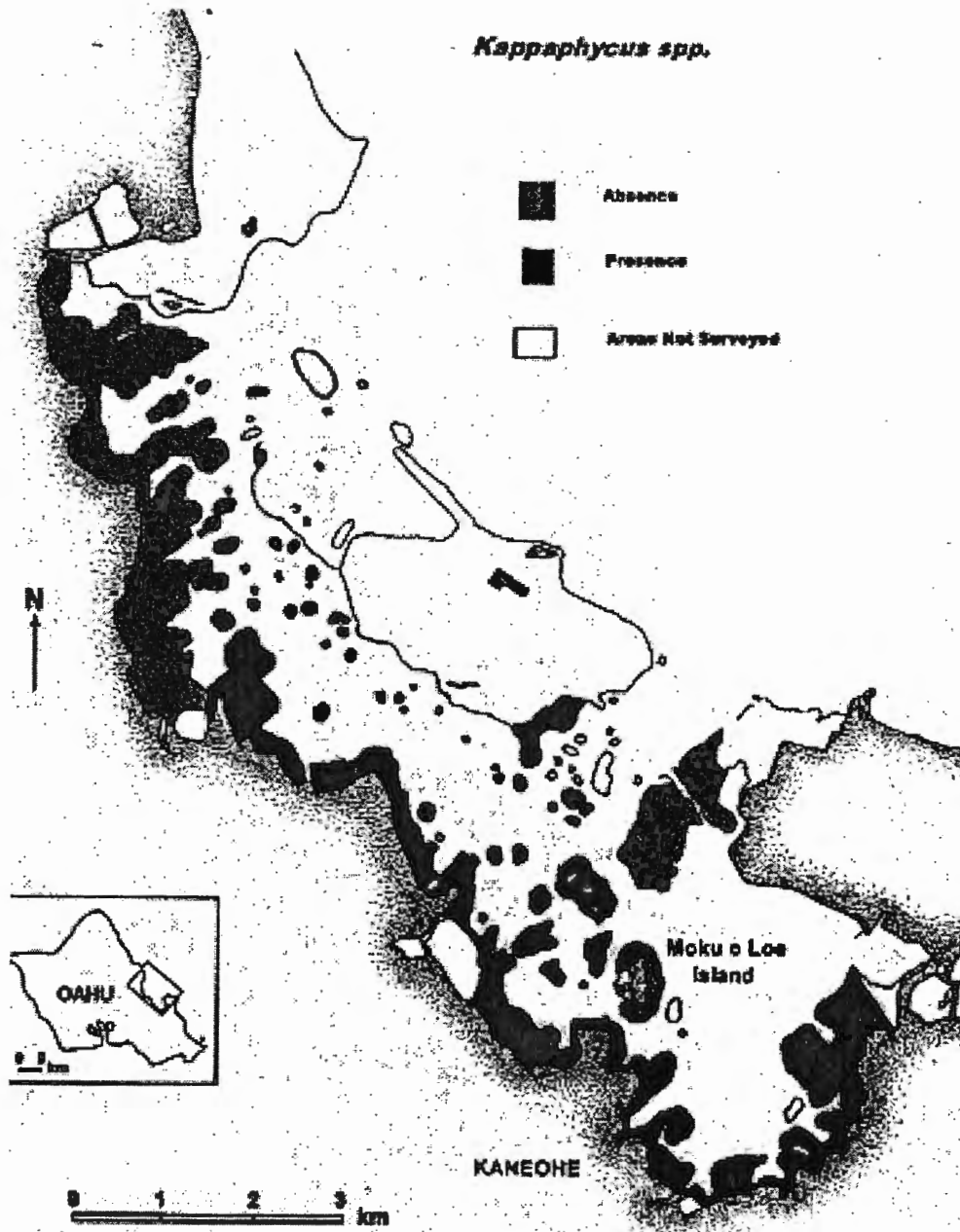
In comparison to other algal invasions that have taken place around the world, *K. striatum* has a relatively low rate of spread. *Caulerpa taxifolia* in the Mediterranean has been reported to spread up to  $53 \text{ km yr}^{-1}$ , and *Codium fragile* along the east coast of North America has been estimated to spread  $55 \text{ km yr}^{-1}$ . In the Hawaiian Islands, *Acanthopora spicifera* and *Hypnea musciformis* spread to the five main islands since their introduction (Russell 1981), whereas *K. striatum* has remained inside Kane'ohe Bay for 25 years. This may be partially related to a relatively higher sinking rate of *K. striatum* fragments in comparison to *A. spicifera* and *H. musciformis*. Estimates of percent cover over one year in the back reef area suggest that *K. striatum* cover has not increased at these sites, but this does not necessarily support the idea that the spread of *K. striatum* is relatively low. It is possible that the methods employed were not sensitive enough to detect changes in percent cover or that the population of *K. striatum* in that particular area has reached its climax. The time series photograph study in the back reef area also demonstrated that, over one year, changes in *K. striatum* cover over live coral were fairly slow.

Our understanding of the dynamics of invasions is in its infancy. The introduction and consequent invasion of *K. striatum* in Kane'ohe Bay gives us a unique opportunity to study the factors that influence invasion success. The ability of *K.*

*striatum* to adapt morphologically to various environmental conditions, such as high wave energy and grazing pressure, has likely contributed to its establishment in the Bay. In addition, asexual reproduction by fragmentation has played an important role in its dispersal and spread. Not limited by environmental conditions, the distribution of *K. striatum* appears to be in part determined by dispersal and herbivory and substrate availability. From this study, it is possible to partially explain the absence of *K. striatum* from areas of potential establishment by examining grazing intensity values. It is difficult, however, to explain the abundance of *K. striatum* in certain areas. It is apparent in these areas that growth of *K. striatum* is far surpassing grazing rates. There are no significant differences in grazer densities between sites of high and low algal abundance on one reef (Stimson, unpubl. data), which would lead to the hypothesis that the presence of alternate food sources may allow for *K. striatum* establishment. If *K. striatum* is not a heavily preferred algae, it could establish and spread in the presence of more preferred food sources, eventually forming a large population. Additionally, certain areas may be more likely to be a sink for fragments that are created at an existing source population.

The impacts of invasive species are well-documented and can result in substantial alteration of ecosystems. With our understanding of the mechanisms of marine invasions in its infancy, empirical studies that investigate the impacts and interactions of invasive species are crucial. The introduction of *K. striatum* to Kane'ohē Bay provides a unique opportunity to examine some of the factors that may play a role in determining the abundance and distribution of an invasive alga. This study demonstrates how herbivory, fragmentation and environmental conditions can be related to invasion success. As

mangers attempt to develop effective strategies for invasive species, further studies measuring nutrient dynamics and fragment success would be useful.



**Figure 1: Distribution of *Kappaphycus* species within Kane'ohe Bay as surveyed in 1996. Reproduced from Rodgers and Cox (1999).**

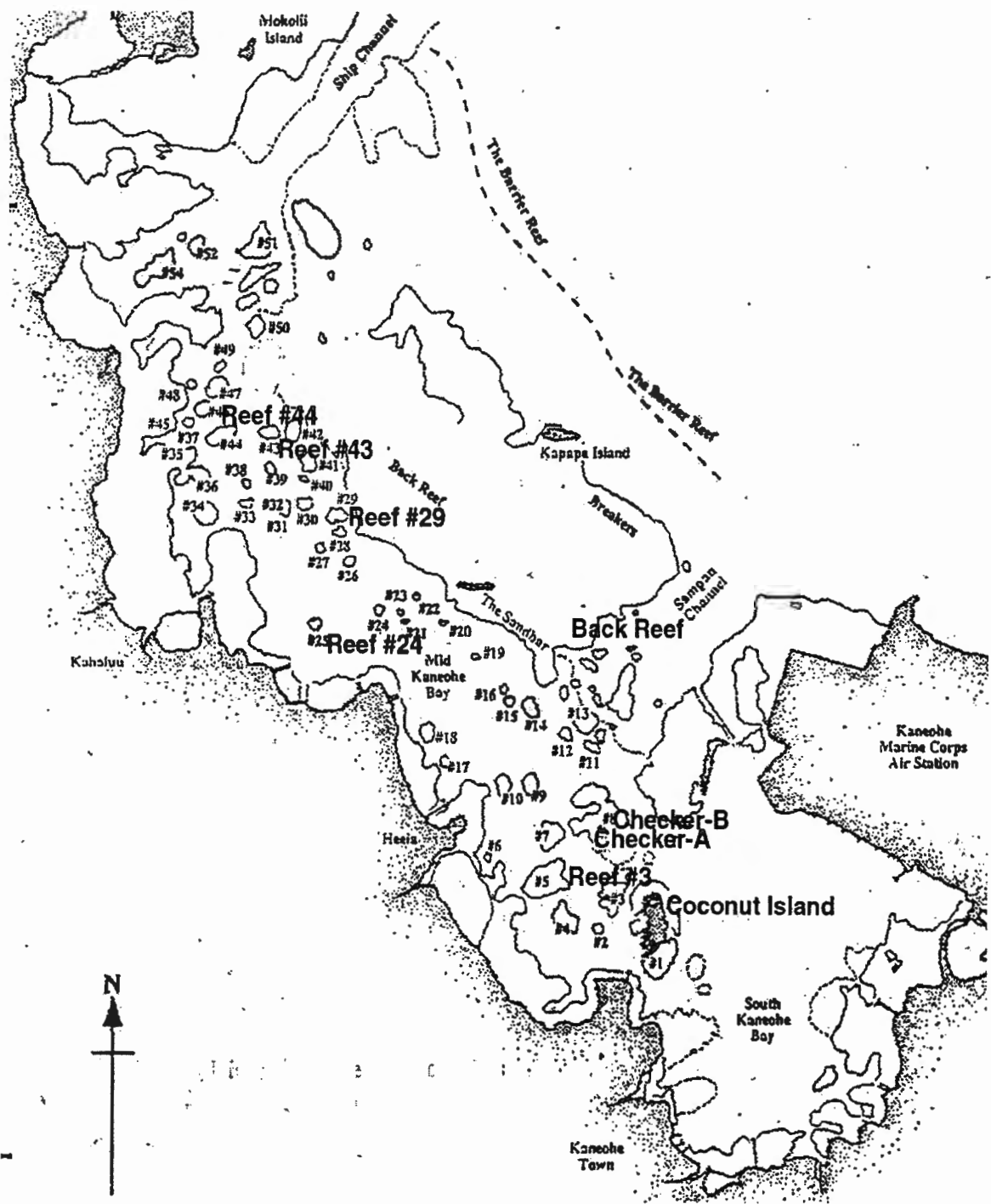


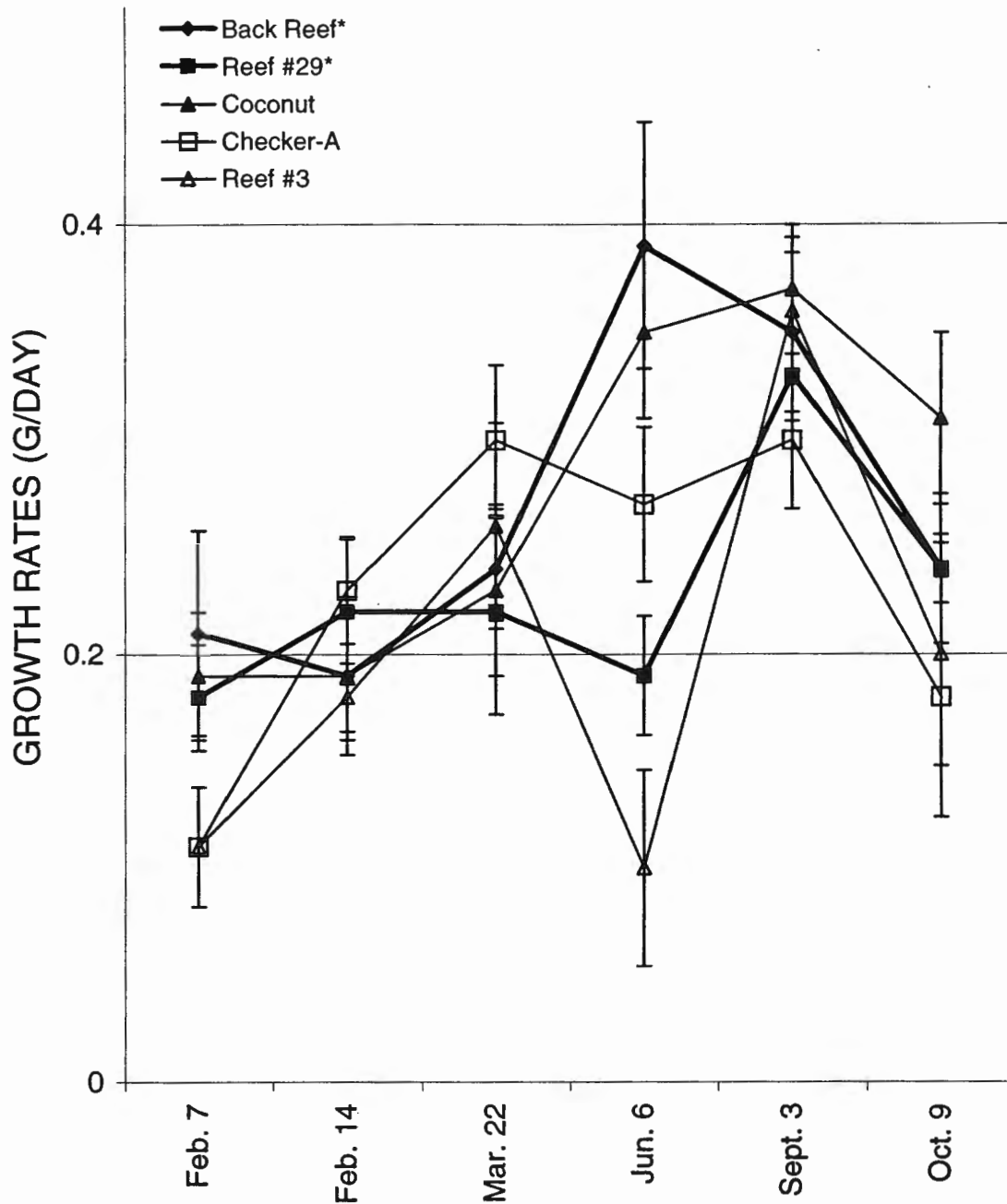
Figure 2: Map of 9 study sites in Kane'ohē Bay, O'ahu, used for caged growth and grazing intensity studies.

**Table 1: Location and description of sites chosen during field survey and used for predator enclosure assays. Dates of predator enclosure assays included.**

SITE	ENVIRONMENT/LOCATION	ALGAL ABUNDANCE AND DIVERSITY	SAMPLING DATES
COCONUT	Fringing reef, south bay	<i>K. striatum</i> absent, other macroalgae present, low diversity	Oct., Nov., Dec., Feb., Feb., Mar., Jn., Sept., Oct.
PATCH REEF #29	Mid-size patch reef, central bay	High <i>K. striatum</i> abundance, other macroalgae present, low diversity	Nov., Dec., Feb., Feb., Mar., Jn., Sept., Oct.
BACK REEF	Irregular reef topography, central bay	High <i>K. striatum</i> abundance, very little other macroalgae	Nov., Dec., Feb., Feb., Mar., Jn., Sept., Oct.
PATCH REEF #3	Mid-size patch reef, south bay	<i>K. striatum</i> absent, other macroalgae abundant on reef flat, high diversity	Feb., Feb., Mar., Jn., Sept., Oct.
CHECKER-A	Large patch reef, south bay	<i>K. striatum</i> absent, other macroalgae present on reef flat, high diversity	Feb., Feb., Mar., Apr., My, Jn., July (5), Sept., Oct.
CHECKER-B	Large patch reef, south bay	<i>K. striatum</i> absent, other macroalgae present on reef flat, high diversity	April, May, July (5)
PATCH REEF #24	Small patch reef, central bay	<i>K. striatum</i> abundant, other macroalgae abundant on reef flat and slope	April, May, July (5)
PATCH REEF #44	Large patch reef, north bay	<i>K. striatum</i> present, other macroalgae abundant on reef flat	April, May, July (5)
PATCH REEF #43	Large patch reef, north bay	<i>K. striatum</i> absent, other macroalgae absent	July (5)

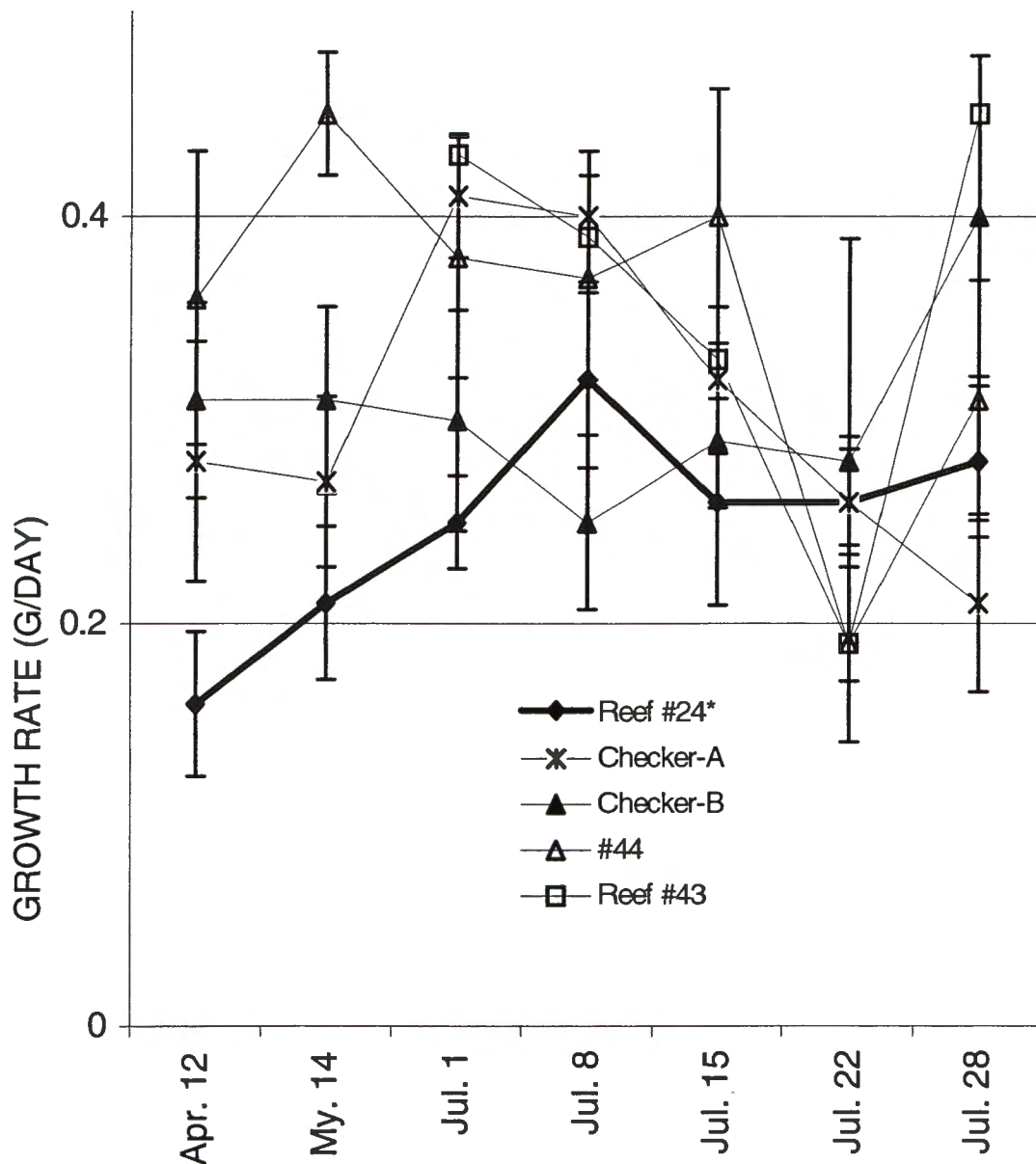
**Table 2: Repeated measures ANOVA analysis of variance: comparison of caged growth rates among sites with time as a repeated measure.**

SITES 1-5				
SOURCE	df	MS	F	p
Site	4	0.065	2.900	0.026
Time	5	0.250	13.752	0.000
Time*Site	20	0.038	2.119	0.004
Error	310	0.018		
SITES 5-8				
Site	3	3.660	21.778	0.000
Time	6	1.862	10.539	0.000
Time*Site	18	0.892	5.048	0.000
Error	270	0.117		



**Figure 3: Growth rates of caged *K. striatum* at sites 1 to 5 from February to October. Asterisk indicates sites of high *K. striatum* abundance.  $n = 12, 13, 14, 14, 14$  for back reef, reef #29, Coconut, Reef #3 and Checker respectively. Error bars indicate  $\pm$  one standard error. See Table 3 for statistical analysis.**

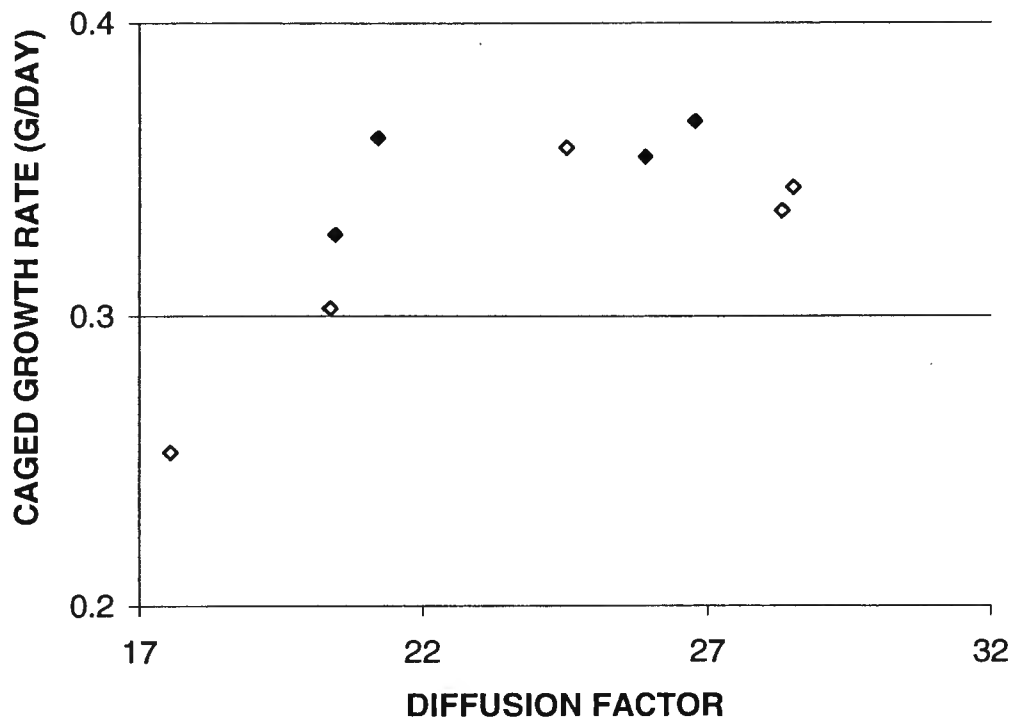




**Figure 4: Growth rates of caged *K. striatum* at sites 5-9 from April to July. Asterisk indicates site of high *K. striatum* abundance. n = 13, 13, 12, 11 for reef #24, Checker-A, Checker-B, and reef #44 respectively. Reef #43 was not included in the analysis because it was not sampled on the April and May dates. Error bars indicate +/- one standard error. For statistical analysis see table 3.**

**Table 3: Analysis of variance table of a weighted regression with clod card diffusion factor as the predictor and caged growth rate as the response. Sites with more summer caged growth rate data (sites 5 to 9) were weighted more heavily than sites only one data set of summer caged growth rates (sites 1-4).**

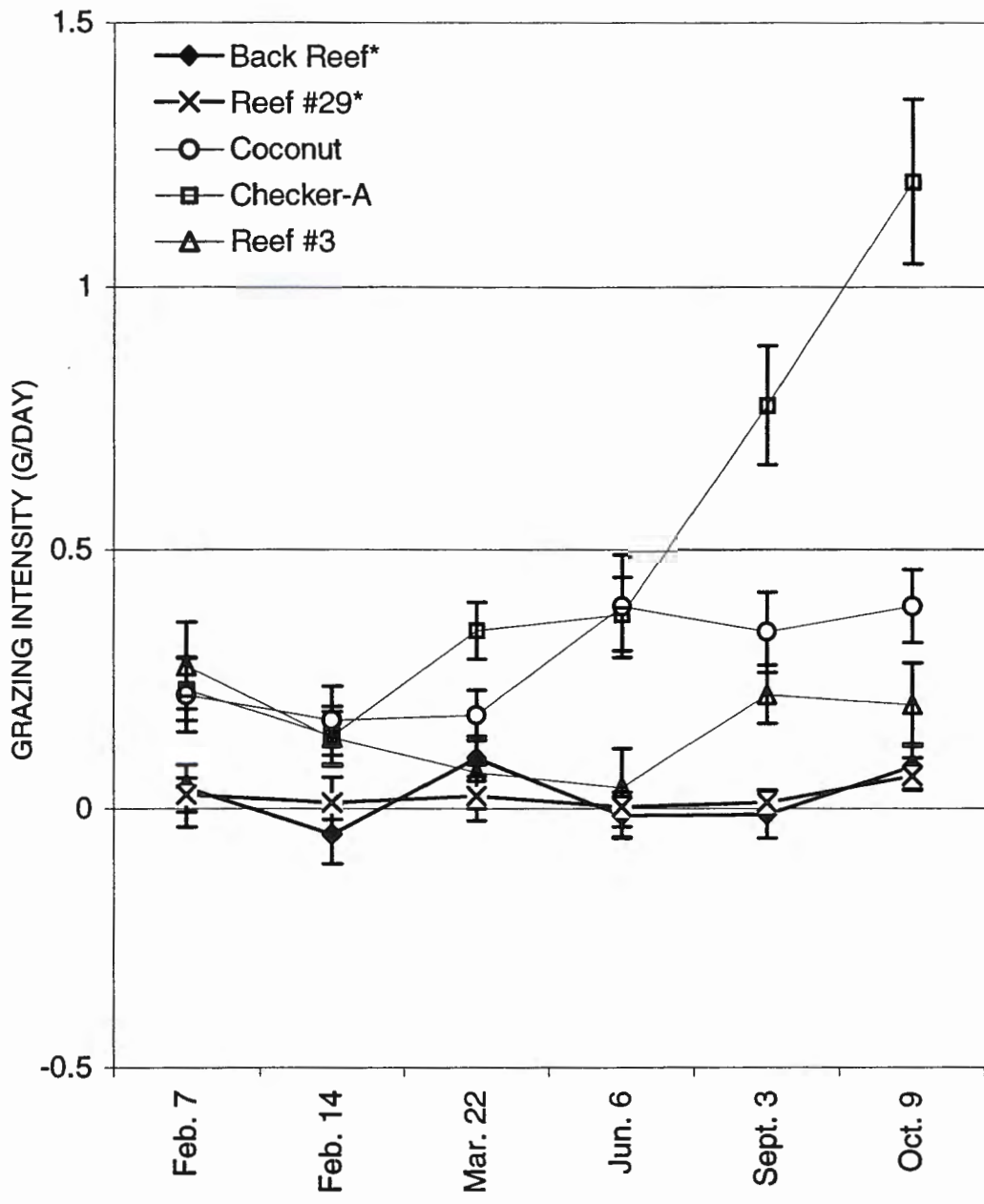
Source	SS	df	MS	F	p
Regression	0.025	1	0.025	11.593	0.011
Residual	0.015	7	0.002		



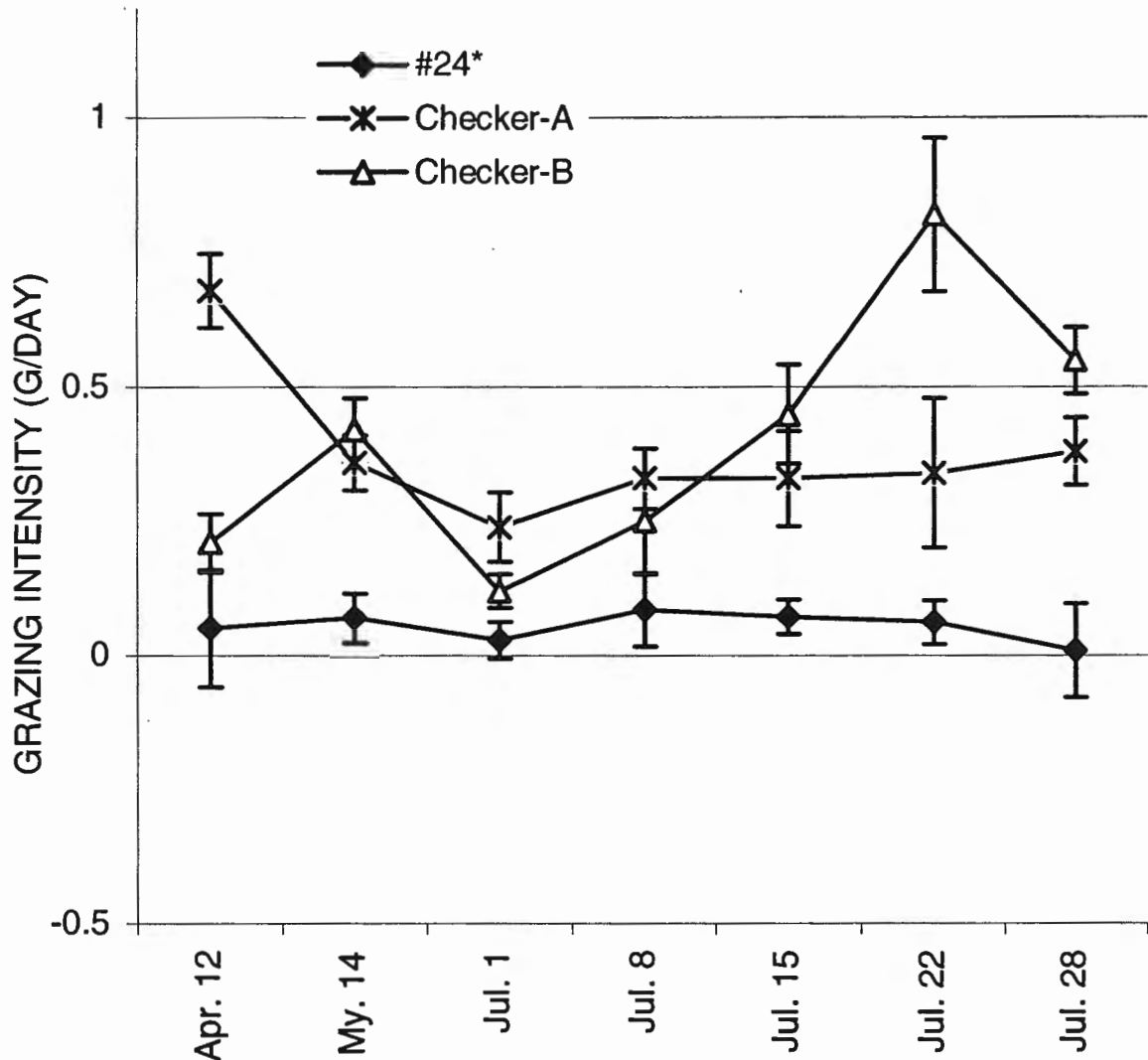
**Figure 5: Scatterplot of clod card diffusion factor versus caged summer growth rates at 9 sites. Using a weighted linear regression, a significant correlation between diffusion factor and caged growth rates was observed ( $p < 0.011$ ). Open diamonds indicate sites that were weighted more heavily because of larger numbers of sampled summer growth rates. Closed diamonds indicate sites that only contained one summer growth rate.**

**Table 4: Repeated measures analysis of variance: comparison of grazing intensities among sites with time as a repeated measure.**

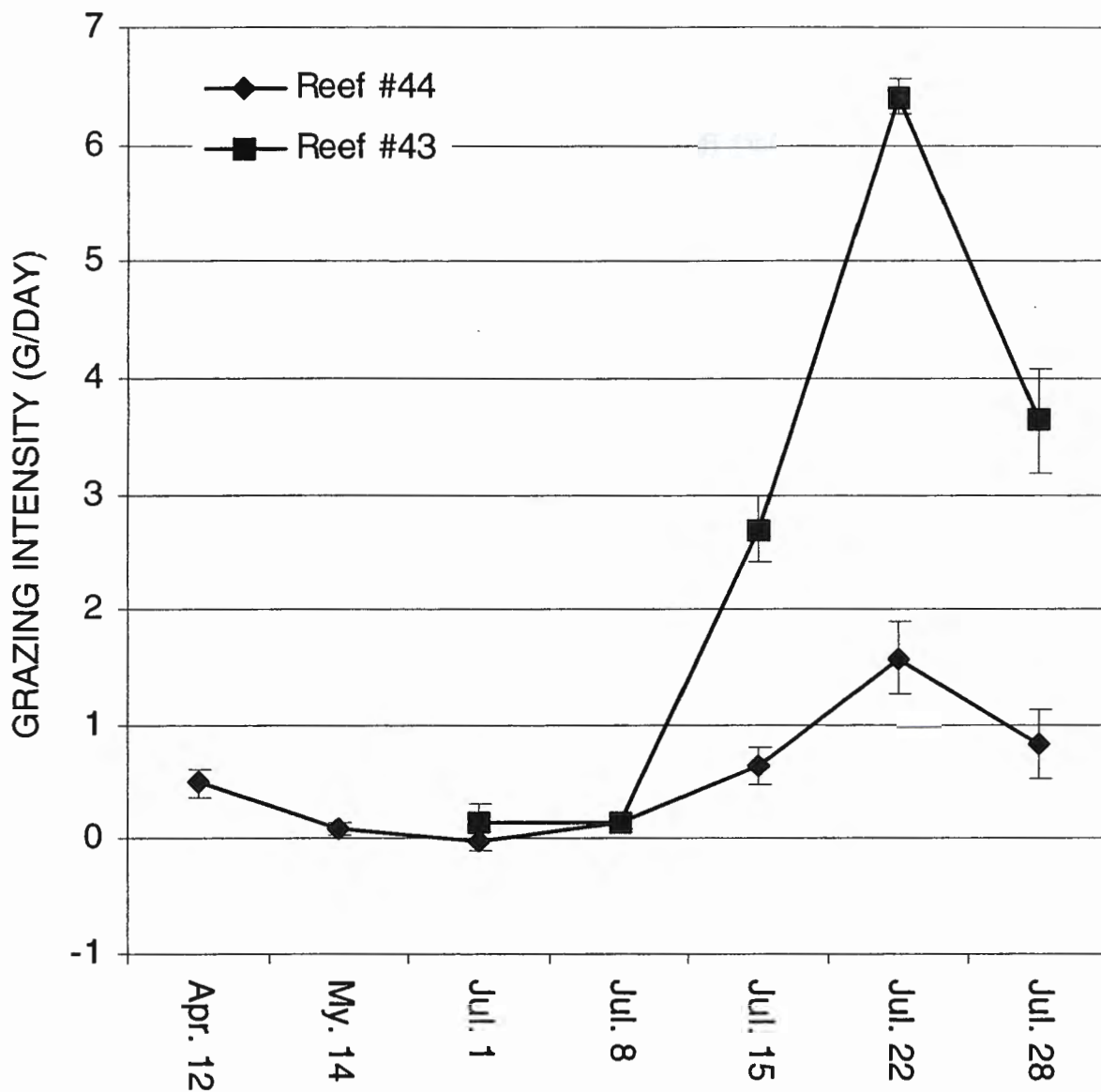
SITES 1-5				
SOURCE	df	MS	F	p
Site	4	3.107	50.014	0.000
Time	5	0.779	13.808	0.000
Time*Site	20	0.381	6.746	0.000
Error	290	0.056		
SITES 5-7				
Site	2	3.442	59.958	0.000
Time	6	0.272	3.490	0.000
Time*Site	12	0.340	4.356	0.000
Error	210	0.078		



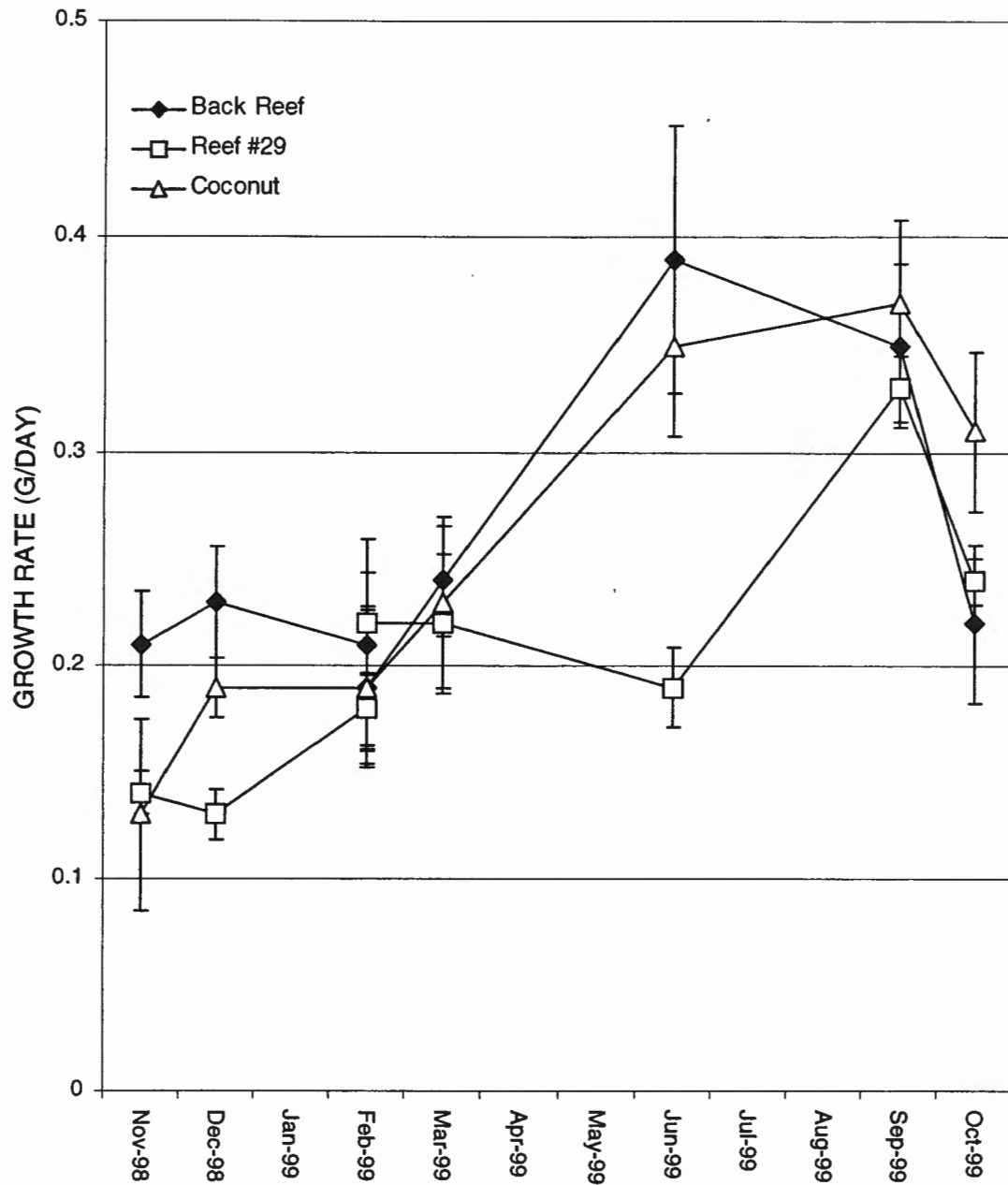
**Figure 6: Average grazing intensities calculated by averaging differences between paired caged and uncaged growth rates at sites 1-5 from February to October. Error bars indicate standard errors of the mean. Asterisks indicate sites of high *K. striatum* abundance. n =11, 13, 14, 12, 13 for the back reef, reef #29, Coconut, Checker-A, reef #3. Error bars indicate +/- one standard error. For statistical analysis see Table 3.**



**Figure 7: Average grazing intensities calculated by differences between paired caged and uncaged growth rates at sites 5-7 from April to July. Error bars indicate +/- one standard error of the mean. Asterisk indicates a site of high *K. striatum* abundance. n = 13, 13 and 12 for reef #24, Checker-A and Checker-B respectively. See Table 4 for statistical analysis.**



**Figure 8: Average grazing intensities calculated by differences between paired caged and uncaged growth rates at sites 8 and 9. Both sites are located in the North Bay and were not included in the analysis. Error bars indicate standard errors of the mean. Note scale.**

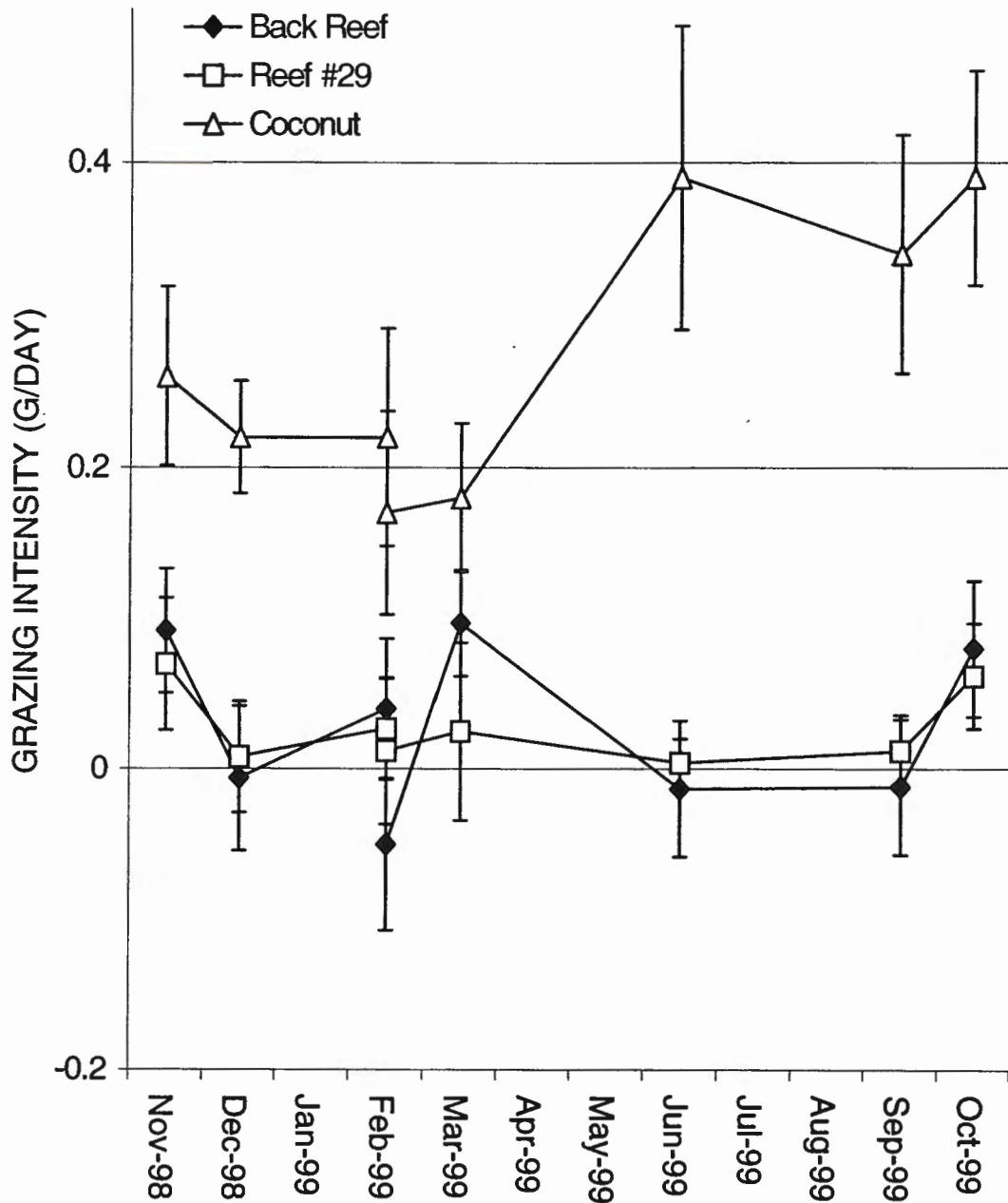


**Figure 9: Average caged growth rates over one year at the back reef, reef #29 and Coconut. Error bars indicate standard errors of the mean. A repeated measures analysis revealed significant differences among sites and dates (Table 5). Difference contrasts yielded a significant difference between March and June ( $p = 0.04$ ).**

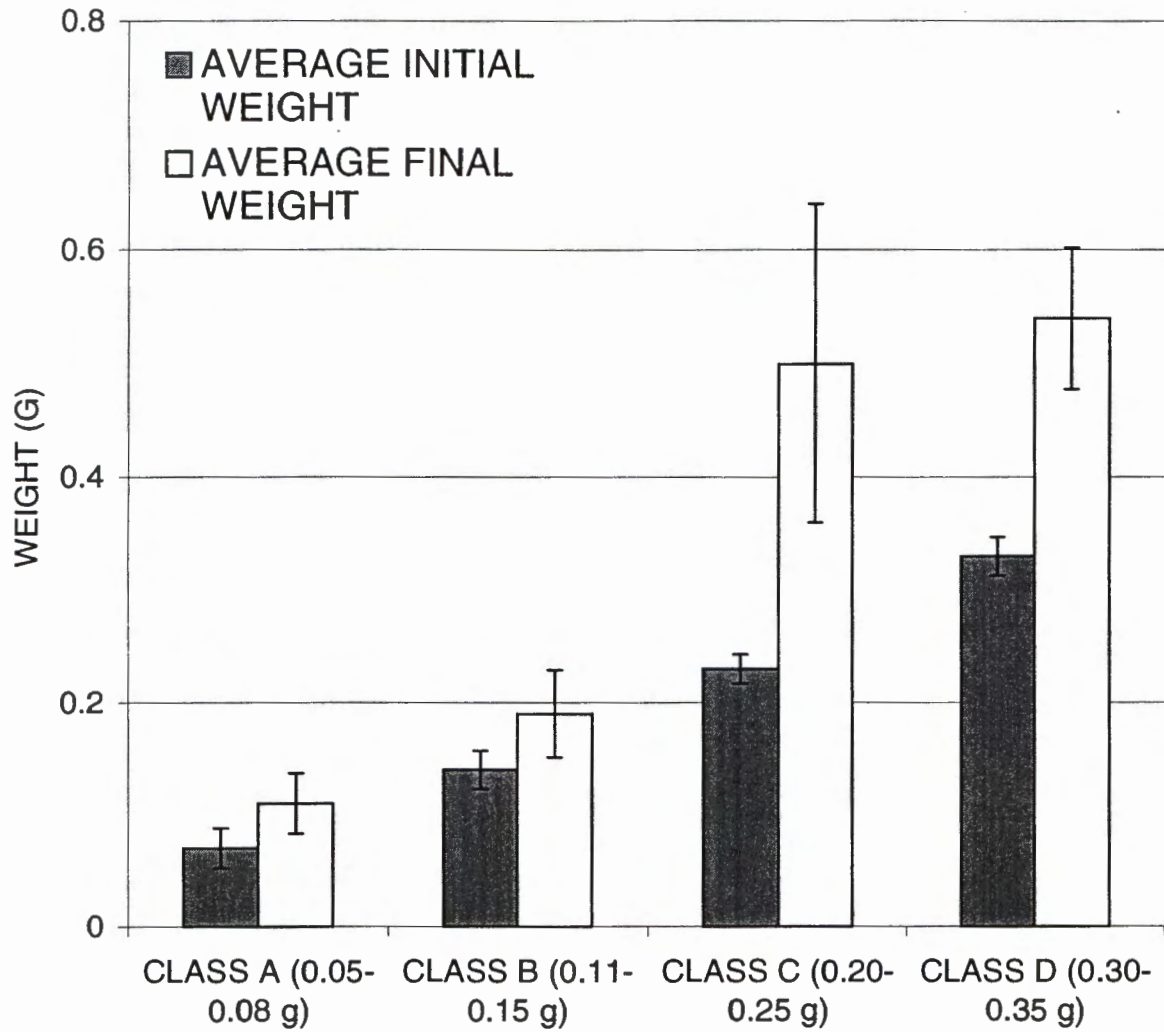


**Table 5: Repeated measures analysis of variance: comparison of caged growth rates and grazing intensities at 3 sites over one year with time as a repeated measure.**

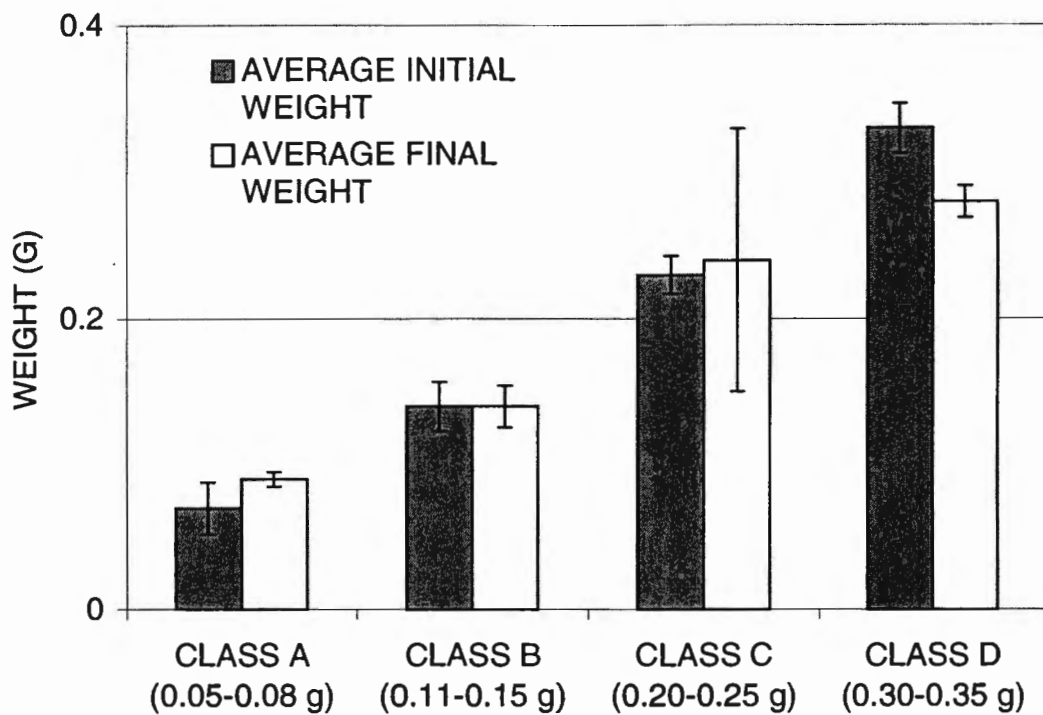
Growth Rate				
SOURCE	df	MS	F	p
Site	2	0.068	3.743	0.033
Time	7	0.173	11.404	0.000
Time*Site	14	0.022	1.467	0.124
Error	252	0.015		
Grazing Intensity				
Site	2	2.044	56.260	0.000
Time	7	0.067	4.881	0.073
Time*Site	14	0.045	1.276	0.240
Error	245	0.036		



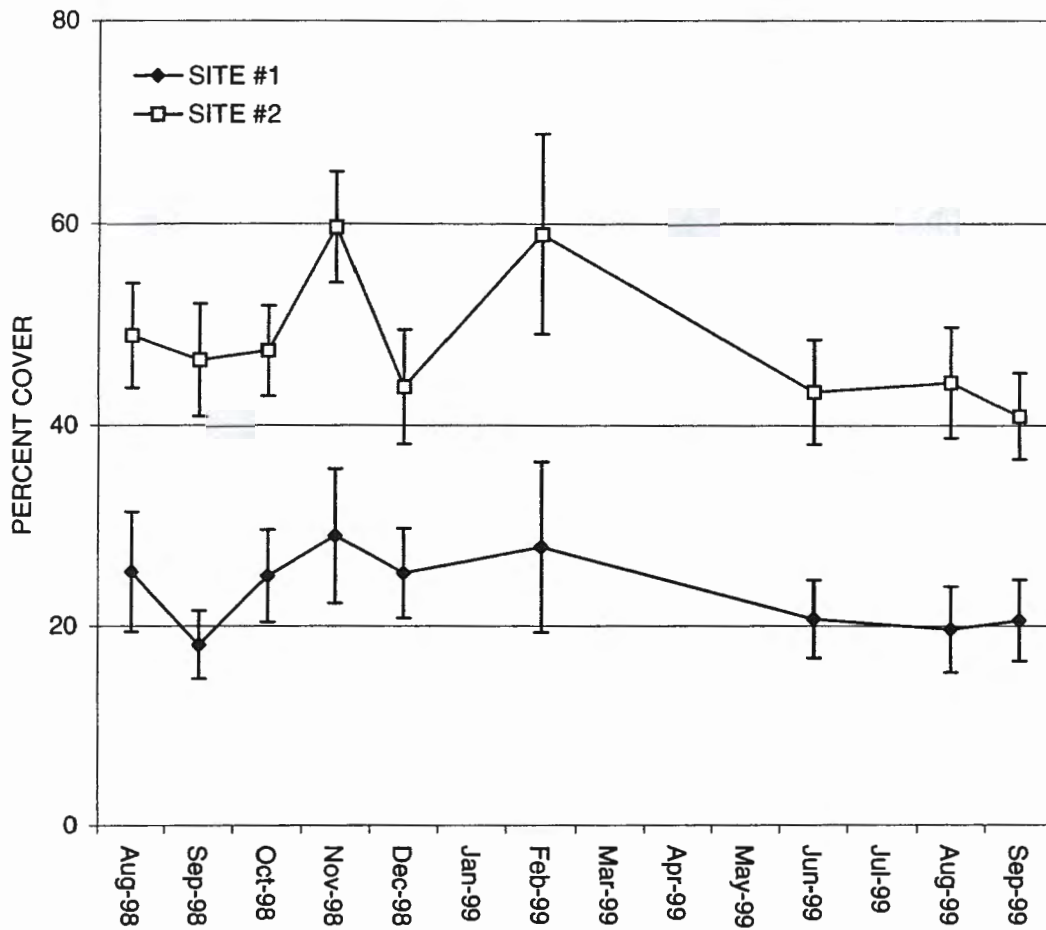
**Figure 10: Average grazing intensities calculated by differences between paired caged and uncaged growth rates. Error bars indicate standard errors of the mean. A repeated measures analysis revealed a significant difference among sites ( $p < 0.01$ ), and only a marginal significance across dates ( $p = 0.07$ ). Difference contrasts revealed a significant difference between March and June for Coconut ( $p = 0.03$ ). See table 5 for statistical analysis.**



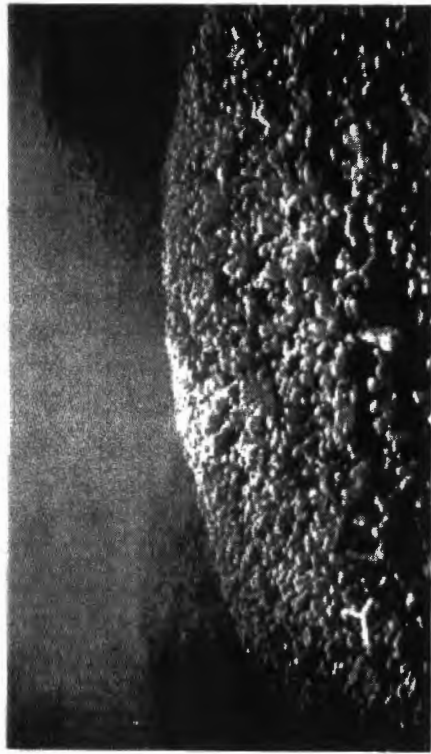
**Figure 11: Average initial and final weights of fragments assayed in mesh cages placed on rubble. A significant increase in weight was detected in a two sample t-test when initial and final weights were compared ( $p < 0.05$ ). Error bars indicate standard deviation.**



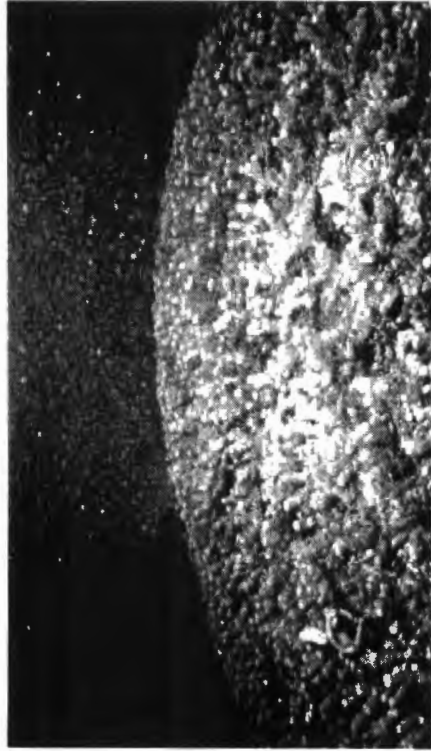
**Figure 12: Average initial and final weights of fragments assayed in sand. No significant increase in weight was detected between initial and final weights in all size classes. Error bars indicate standard deviation.**



**Figure 13: Change in *K. striatum* percent cover at two sites over one year. Error bars indicate standard error of the mean. Initial and final percent cover in both sites did not change in one year. A slight increase is apparent in November and February.**



A.



B.

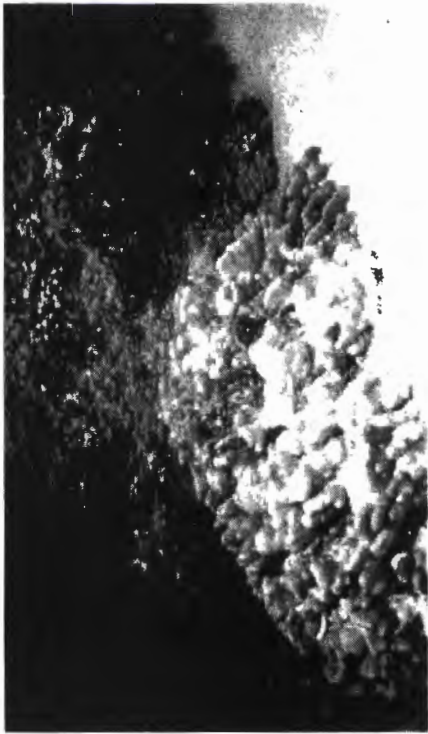


C.

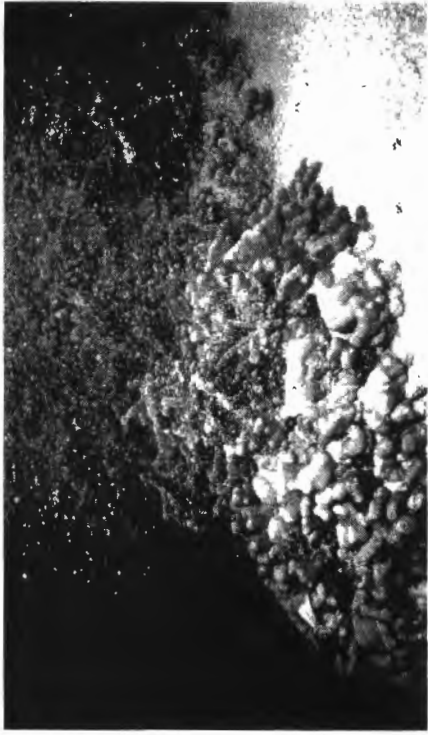


D.

**Figure 14: Photographs taken from the time series photography study in the back reef area of Kane'ohe Bay. A) Photograph taken in July 1998, B) Photograph taken in February 1999, C) Photograph taken in April 1999, D) Photograph taken in June 1999.**



A.



B.



C.



D.

**Figure 15: Photographs taken from the time series photography study in the back reef area of Kane'ohē Bay. A) Photograph taken in July 1998, B) Photograph taken in February 1999, C) Photograph taken in April 1999, D) Photograph taken in June 1999.**

## REFERENCES

- Abbott, I. A. There are aliens among the algae, too-or limu malihini. *Newsl. Hawaiian Bot. Soc.*, 26: 60-63.
- Adams, N. 1994. *Seaweeds of New Zealand. An illustrated guide.* Canterbury University Press publ., Stanford, California, pp. 827.
- Adey, W. H., Adey, P. J., Burke, R., and Kaufman, L. 1977. The Holocene reef systems of Eastern Martinique, French West Indies. *At. Res. Bull.* 218: 1-40.
- Ambrose, R. and Nelson, B. 1982. Inhibition of giant kelp recruitment by an introduced brown alga. *Bot. Mar.* 25: 265-267.
- Ananza-Corrales, Mamauag, S. S., Alfiler, E., and Orolfo, M. J. 1992. Reproduction of *Eucheuma denticulatum* (Burman) Collins and Hervey and *Kappaphycus alvarezii* (Doty) Doty farmed in Danajon Reef, Philippines. *Aquaculture.* 103: 29-34.
- Ask, E. I. 1994. A crop model for *Kappaphycus alvarezii*. Master's Thesis. University of Hawaii, Manoa.
- Barlow, G. W. 1975. On the sociobiology of four Puerto Rican parrotfishes (Scaridae). *Mar. Bio.* 33: 281-293.
- Bouchon-Navaro, Y., Harmelin-Vivien, M. 1981. Quantitative distribution of herbivorous reef fishes in the Gulf of Aqaba, Red Sea. *Mar. Bio.* 63: 79-86.
- Bradbury, R. H., Goeden, G. 1975. The partitioning of the reef slope environment by resident fishes. In, *Proc. 2<sup>nd</sup> Int. Symp. on Cor. Rf.*, Great Barrier Reef Committee, pp. 167-178.
- Brawley, S. H. and Adey, W. H. 1981. The effects of micrograzers on algal community structure in a coral reef microcosm. *Mar. Bio.* 61: 167-177.
- Brostoff, W. N. 1988. Seaweed community structure and productivity: the role of mesograzers. *Proc. 6<sup>th</sup> Int. Cor. Rf. Symp.* 2: 1-6.
- Carlton, J. T. 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: The biology of ballast water. *Oceanorg. Mar. Bio. Ann. Rev.* 23: 313-374.
- Carlton, J. T. 1989. Man's role in changing the face of the ocean: biological invasions and implications for conservation of near-shore environments. *Bio. Cons.* 3: 265-273.
- Carlton, J. T. 1993. Neoeinctions of marine invertebrates. *Amer. Zool.* 33: 499-509.



- Carlton, J. T. 1996. Pattern, Process and Prediction in Marine Invasion Ecology. *Bio. Cons.* 78: 97-106.
- Carlton, J.T., Thompson, J.K., Schemel, L.E., and Nichols, F.H. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. I. Introduction and dispersal. *Mar. Ecol. Progr. Ser.* 66: 81-94.
- Carlton, James T. and Geller J.B. 1993. Ecological roulette: the global transport and invasion of non-indigenous marine organisms. *Science.* 261: 78-82.
- Cohen, A. T. and J. T. Carlton. Nonindigenous aquatic species in a United States estuary: A case study of the biological invasions of San Francisco Bay and delta. U.S. Fish and Wildl. Serv.
- Connell, J. H. and Orias, E. 1964. The ecological regulation of species diversity. *Am. Nat.* 98: 399-414.
- Conner, J. L. and Adey, W. H. 1977. The benthic algal composition, standing crop, and productivity of a Caribbean algal ridge. *At. Res. Bull.* 211: 1-39.
- Crawley, M.J. 1989. Chance and timing in biological invasions. In *Biological invasions, a global perspective.* ed. J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmanek, and M. Williamson. John Wiley, New York. pp. 407-23.
- D'Antonio, C. 1985. Epiphytes on the rocky intertidal alga *Rhodomela laris* (Turner) C. Agardh: Negative effects on the host and food for herbivores? *J. Exp. Mar. Bio Ecol.* 86: 197-218.
- Dahl, A. L. 1973. Benthic algal ecology in a deep reef and sand habitat off Puerto Rico. *Bot. Mar.* 15: 171-175.
- Dawes, C.J., Lluisma, A.O., and Trono, G.C. 1994. Laboratory and field growth studies of commercial strains of *Eucheuma denticulatum* and *Kappaphycus alvarezii* in the Philippines. *J. Appl. Phyc.* 6: 21-24.
- Dawes, C.J. 1992. Irradiance acclimation of the cultured Philippine seaweeds, *Kappaphycus alvarezii* and *Eucheuma denticulatum*. *Bot. Mar.* 35: 189-195.
- Dawes, C.J. 1989. Temperature acclimation in cultured *Eucheuma isiforme* from Florida and *E. alvarezii* from the Philippines. *J. Appl. Phyc.* 1: 59-65.

- Denny, M., Brown, V. Carrington, E., Kraemer, G. and Miller, A. 1989. Fracture mechanics and the survival of wave-swept macroalgae. *J. Exp. Mar. Bio. Ecol.* 127: 211-228.
- Done, T. J. 1992. Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia*. 247: 121-132.
- Doty, M. S. 1961. *Acanthophora*, a possible invader of the marine flora of Hawaii. *Pac. Sci.* 15: 547-552.
- Doty, M.S. 1973. Farming the red seaweed, *Euचेuma*, for carrageenans. *Micronesia*. 9: 59-71.
- Doty, M.S. and Norris, J.N. 1985. *Euचेuma* species (Soleriaceae, Rhodophyta) that are major sources of carrageenan. In: Abbott I.A. (ed.), *Taxonomy of Economic Seaweeds. With Reference to some Pacific and Caribbean Species*. Volume I. California Sea Grant College Program. La Jolla. pp 47-61.
- Drake, J.A. 1991. Community assembly mechanics and the structure of an experimental species ensemble. *Am Nat.* 137: 1-26.
- Duffy, J. E. and Hay, M. E. 1990. Seaweed adaptations to herbivory. *Bioscience*. 40: 368-375.
- Faulkner, D. J. 1984. Marine natural products: metabolites of marine algae and herbivorous marine molluscs. *Nat. Prod. Rep.* 1: 251-280.
- Gaston, K. J. 1996. *Biodiversity: a biology of numbers and difference*. Blackwell Science Ltd., Cambridge.
- Glenn, E.P. and Doty, M.S. 1981. Photosynthesis and respiration of the tropical red seaweeds, *Euचेuma striatum* (tambalang and elkhorn varieties) and *E. denticulatum*. *Aq. Bot.* 10: 353-364.
- Glenn, E. P. and Doty, M. S. 1990. Growth of the seaweeds *Kappaphycus alvarezii*, *K. striatum*, and *Euचेuma denticulatum* as affected by environment in Hawaii. *Aquaculture*. 84: 245-255.
- Grosholz, E. D. and Ruiz, G. M. 1996. Predicting the impact of introduced marine species: lessons from the multiple invasions of the European green crab *Carcina maenas*. *Bio. Conserv.* 78: 59-66.
- Gruet, Y., Heral, M. and Robert, J. (1976). Premères observations sur l'introduction de la faune associée au naissain d'hûtres japonaises *Crassostrea gigas* (Thunberg), importé sur la côte atlantique française. *Cahiers de Biologie Marine*. 17: 173-184.

- Hackney, J. M., Carpenter, R. C., and Adey, W. H. 1989. Characteristic adaptations to grazing among algal turfs on a Caribbean coral reef. *Phycologia*. 28: 109-119.
- Harrison, S. 1993. Species diversity, spatial scale, and global change. In P.M. Kareiva, J.G. Kingsolver, and R.B. Huey (eds.) *Biotic interactions and global change*, Sinauer Associates Inc., Sunderland. pp. 388-401.
- Hatcher, B. 1990. Coral reef primary productivity: a hierarchy of pattern and process. *TREE*. 5:149-155.
- Hay, M. E. 1981a. Herbivory, algal distributions and the maintenance of between-habitat diversity on a tropical fringing reef. *Am Nat*. 118: 520-540.
- \_\_\_\_\_. 1981b. The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. *Ecology*. 62: 739-750.
- \_\_\_\_\_. 1984. Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? *Ecology*. 65: 446-454.
- \_\_\_\_\_. 1986. Associational plant defenses and the maintenance of species diversity: turning competitors into accomplices. *Am Nat*. 128: 617-641.
- Hay, M. E., Colburn, T., Downing, D. 1983. Spatial and temporal patterns of herbivory on a Caribbean fringing reef: the effects on plant distributions. *Oecologia* (Berlin). 58: 299-308
- Hay, M. E., Paul, V. J., Lewis, S. M., Gustafson, K., Tucker, J., and Trindell, R. N. 1988. Can tropical seaweeds reduce herbivory by growing at night? diel patterns of growth, nitrogen content, herbivory and chemical versus morphological defenses. *Oecologia*. 75: 233-245.
- Hay, M. E. and Fenical, W. 1988. Marine plant-herbivore interactions: the ecology of chemical defense. *Ann. Rev. Ecol. Syst.* 19: 111-145.
- Hay, M. E., Renaud, P.E. and Fenical, W. 1988b. Large mobile versus small sedentary herbivores and their resistance to seaweed chemical defenses. *Oecologia*. 75: 246-252.
- Hiatt, R. W., Strasburg, D. W. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecol. Mono.* 30: 54-127.
- Hixon, M. E. and Brostoff, W. N. 1996. Succession and herbivory: effects of differential fish grazing on Hawaiian coral-reef algae. *Ecol. Mono.* 66: 67-90.

- Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*. 265: 1547-1551.
- Hutchings, P. 1992. Ballast water introductions of exotic marine organisms into Australia. Current status and management options. *Mar. Polln. Bulln.* 25: 196-199.
- Johnstone, I.M. 1986. Plant invasion windows: a time-based classification of invasion potential. *Bio. Rev.* 61: 369-94.
- Jokiel, P. and Morrissey, J. 1993. Water motion on coral reefs: evaluation of the 'clod card' technique. *Mar. Ecol. Prog. Ser.* 93: 175-181.
- Kilar, J. and McLachlan, J. 1986. Ecological studies of the alga, *Acanthophora spicifera* (Vahl) Boerg. (Ceramiales: Rhodophyta): vegetative fragmentation. *J. Exp. Mar. Bio. Ecol.* 104: 1-21.
- Lana, E.G. 1991. Production and utilization of seaweeds in the Philippines. *Indo. Int.* 1/91: 12-17.
- Larned, S. 1998. Nitrogen- versus phosphorus-limited growth and sources of nutrients for coral reef macroalgae. *Mar. Bio.* 132: 409-421.
- Lewis, S. M. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecol. Mono.* 56: 183-200.
- Lewis, S. M. and Wainwright, P. C. 1985. Herbivore abundance and grazing intensity on a Caribbean coral reef. *J. Exp. Mar. Bio. Ecol.* 87: 215-228.
- Lim J.R., Porse, H. 1981. Breakthrough in the commercial culture of *Eucheuma spinosum* in Bohol, Philippines. In Levring T (ed.), *Proc. Tenth Int. Seaweed Symp.* Walter de Gruyter, Berlin, pp. 601-606.
- Lirasan, T. and Twide P. 1993. Farming *Eucheuma* in Zanzabar, Tanzania. *Hydrobiologia.* 260/261: 373-378.
- Littler, M. M. and Doty, M. S. 1975. Ecological components structuring the seaward edges of tropical Pacific reefs: the distribution, communities and productivity of Porolithon. *J. Ecol.* 63: 117-129.
- Littler, M. M. and Littler, D. S. 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. *Am Nat.* 116: 25-44.
- Lodge, D.M. 1993 Biological invasions: lessons for ecology. *TREE.* 8: 133-137.

- Lluisma, A. O. and Ragan, M. A. 1995. Relationships among *Eucheuma denticulatum*, *Echeuma isiforme* and *Kappaphycus alvarezii* (Gigartinales, Rhodophyta) based on nuclear ssu-rRNA gene sequences. *J. Appl Phyc.* 7: 471-477.
- Lubchenco, J. and Cubitt, J. 1980. Heteromorphic life histories of certain marine algae as adaptations to variations in herbivory. *Ecology.* 61: 676-687.
- Lubchenco, J. and Gaines, S. D. 1982. A unified approach to marine plant-herbivore interactions. II. *Biogeography. Ann. Rev. of Ecol. and Syst.* 13: 111-138.
- Luckhurst, B. E. and Luckhurst, K. 1978. Analysis of the influence of substrate variables on coral reef fish communities. *Mar. Bio.* 49: 317-323.
- MacArthur, R. H. 1965. Patterns of species diversity. *Biol. Rev. Camb. Phil. Soc.* 40: 510-530.
- MacIsaac, H.J. 1996. Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. *Amer. Zool.* 36: 287-299.
- McClanahan, T.R., Nugues, M. and Mwachireya, S. 1994. Fish and sea urchin herbivory and competition in Kenyan coral reef lagoons: the role of reef management. *J. Exp. Mar. Bio. Ecol.* 184: 237-254.
- McCook, L.J. 1997. Effects of herbivory on zonation of *Sargassum* spp. within fringing reefs of the central Great Barrier Reef. *Mar. Bio.* 129: 713-722.
- Meinesz, A., Vaugelas, J. de, Hesse, B. and Mari, X. 1993. Spread of the introduced tropical green alga *Caulerpa taxifolia* in northern Mediterranean waters. *J. App. Phyc.* 5: 141-147.
- Menge, B. A. and Sutherland, J. P. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *Am Nat.* 110: 351-369.
- Mollison, D. 1986. Modeling biological invasion: change explanation, prediction. *Phil. Trans. Roy. Soc. Lon. Ser. B*, 314: 675-693.
- Morrissey, J. 1980. Community structure and zonation of macroalgae and corals on a fringing reef of Magnetic Island (Queensland, Australia). *Aq. Bot.* 8: 91-139.
- Morrison, D. 1988. Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. *Ecology.* 69: 1367-1382.

- Mshigeni, K.E. 1992. Seaweed farming in Tanzania: A success story. In Mshigeni K.E., Bloton J.J., Critchley A.T., Kiangi G. (eds), *Proc. First Int. Workshop on Sustainable Seaweed Resource Development in Sub-Saharan Africa*. Univ. Press, pp. 221-245.
- Ohno, M, Nang, H.Q. and Hirase, S. 1996. Cultivation and carrageenan yield and quality of *Kappahycus alvarezii* in the waters of Vietnam. *J. Appl. Phyc.* 8: 431-437.
- Oliviera, E. de (1984). Algas exóticas nos mares brasileiros. *Ciência e Cultura (SanPaulo)*. 36: 801-803.
- Ogden, J. C. and Lobel. P. 1978. The role of herbivorous fishes and urchins in coral reef communities. *Environ. Bio. Fish.*, 3: 49-63.
- Orians, G. H. 1984. Site characteristics favoring invasions. *Ecology of Biological Invasions of North America and Hawaii* (eds H.A. Mooney and J. A. Drake). pp. 133-148. Springer-Verlag, New York.
- Peet, R. K. 1974. The measurement of species diversity. *Ann. Rev. Ecol. Syst.* 5: 285-308.
- Pennings, S. and Paul, V. 1992. Effect of plant toughness, calcification, and chemistry on herbivory by *Dolabella auricularia*. *Ecology*. 73: 1606-1619.
- Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. *Am Nat.* 100: 33-46.
- Prince, J. S. and LeBlanc, W. G. 1992. Comparative feeding preference of *Strongylocentrotus droebachiensis* (Echinoidea) for the invasive seaweed *Codium fragile* ssp. *tomentosoides* (Chlorophyceae) and four other seaweeds. *Mar. Bio.* 113: 159-163.
- Randall, J. E. 1961. Overgrazing of algae by herbivorous marine fishes. *Ecology*. 42: 812.
- Randall, J. E. 1963. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. *Carib. J. Sci.* 3: 31-47.
- Randall, J. E. 1965. Grazing effect on seagrasses by herbivorous marine fishes. *Ecology*. 42: 812.
- Ricciardi, A., Whoriskey, F.G., and Rasmussen, J.B. 1995. Impact of the *Dreissena* invasion on native unionid bivalves in the upper St. Lawrence. *Can. J. Fish. Aq. Sci.* 53: 1434-1444.

- Ribera, M. 1994. Les macrophytes marins introduits en Méditerranée: biogéographie. In: *Introduced species in European coastal waters* (Bourdouresque, C. F., Briand, F. and Nolan, C. eds), European Commission publs., Luxembourg. pp. 37-41.
- Ribera, M. and Boudouresque, C. 1995. Introduced marine plants, with special reference to macroalgae: mechanisms and impact. *Prog. Phyc. Res.* 11: 188-268.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution.* 43: 223-225.
- Rodgers, S. K. and Cox, E. F. 1999. Rate of spread of Introduced Rhodophytes *Kappaphycus alvarezii*, *Kappaphycus striatum*, and *Gracilaria salicornia* and their current distributions in Kane'ohe Bay, O'ahu, Hawai'i. *Pac. Sci.* 53: 232-241.
- Rueness, Jan. 1989. *Sargassum muticum* and other introduced Japanese macroalgae: biological pollution of European coasts. *Mar. Polln. Bulln.* 20: 173-176.
- Ruiz, Gregory M., Carlton, James, T., Grosholz, Edwin D., and Hines, Anson H. 1997. Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent and consequences. *Amer. Zool.* 37: 621-632.
- Russell, D. J. 1981. The introduction and establishment of *Acanthophora spicifera* (Vahl) Boerg. and *Eucheuma striatum* Schmitz in Hawaii. Ph.D. dissertation. University of Hawaii at Manoa. pp. 7-11, 71-82.
- Russell, D. J. 1983. The ecology of the imported red seaweed *Eucheuma striatum* Schmitz on Coconut Island, Oahu, Hawaii. *Pac. Sci.* 27: 87-102.
- Russell, D. 1992. The ecological invasion of Hawaiian reefs by two marine red algae, *Acanthophora spicifera* (Vahl) Boerg. and *Hypnea musciformis* (Wulfen). *J. Ag. ICES Mar. Sci. Symp.*, 194: 110-125.
- Russell, D. and Balazs, G. 1992. Colonization by the alien marine alga *Hypnea musciformis* (Wulfen) J. Ag. (Rhodophyta: Gigartinales) in the Hawaiian Islands and its utilization by the green turtle, *Chelonia mydas* L. *Aq. Bot.* 1994: 53-60.
- Sammarco, P. W. 1982. Effects of grazing by *Diadema antillarum* Philippi (Echinodermata: Echinoidea) on algal diversity and community structure. *J. Exp. Mar. Bio. Ecol.* 65: 83-105.
- Smith, C. and Walters, L. in review. Fragmentation as a strategy for *Caulerpa* species: Implications for population structure and management of an invasive weed. *Mar. Ecol. (Pubblicazioni della Stazione zoologica di Napoli)*

- Smith, S. V., Kimmerer, W. J., Laws, E. A., Brock, R. E., and Walsh, T. W. 1981. Kaneohe Bay sewage diversion experiment: Perspectives on ecosystem responses to nutritional perturbation. *Pac. Sci.* 35: 279-402.
- State of Hawaii, Department of Land and Natural Resources: Division of Aquatic Resources. (1998) Administrative study. Kane'ohe Bay.
- Steneck, R. S. 1983. Escalating herbivory and resulting adaptive trends in calcareous algal crusts. *Paleobiology.* 9: 44-61.
- Stephenson, W. and Searles, R. B. 1960. Experimental studies on the ecology of intertidal environments at Heron Island I. Exclusion of fish from beach rock. *Austr. J. Mar. Fresh. Res.* 2: 241-267.
- Trowbridge, C. D. (1995). Establishment of the green alga *Codium fragile* ssp. *tomentosoides* on New Zealand rocky shores: current distribution and invertebrate grazers. *J. Écol.* 83: 949-965.
- Tsuda, R. T. 1972. Morphological, zonal, and seasonal studies of two species of *Sargassum* on the reefs of Guam. *Proc. 7<sup>th</sup> Int. Seaw. Symp.* pp. 40-44.
- Wahl, M. 1989. Marine epibiosis. I. Fouling and antifouling: some basic aspects. *Mar. Ecol. Prog. Ser.* 58: 175-189.
- Walters, L. and Smith, C. 1994. Rapid rhizoid production in *Halimeda discoidea* Decainse (Chlorophyta, Caulerpales) fragments: a mechanism for survival after separation from adult thalli. *J. Exp. Mar. Biol. Ecol.* 175: 105-120.
- Wanders, J. B. W. 1976. The role of benthic algae in the shallow reef of Curacao (Netherlands Antilles) II. Primary productivity of the *Sargassum* beds on the north-east coast submarine plateau. *Aq. Bot.* 2: 327-335.
- Wanders, J. B. W. 1977. The role of benthic algae in the shallow reef of Curacao. III. The significance of grazing. *Aq. Bot.* 3: 357-390.
- Williamson, M. H. and Brown, K. C. (1986). The analysis and modelling of British invasions. *Phil. Trans. Roy. Soc. Lon., Ser. B,* 314: 505-522.