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THE DISTRIBUTION AND PRODUCTION OF CALCAREOUS MACROALGAE IN CARD SOUND, FLORIDA

by

Steven David Bach

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
(Botany)
in The University of Michigan
1975

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CHAPTER I

INTRODUCTION

The fact that shallow coastal waters are of great importance in terms of production of living material was emphasized in a recent summary of world plant and animal productivity (Whittaker and Likens, 1973). These authors visualized the oceans as being "relative deserts fringed with more productive waters where, in areas of upwelling and on continental shelves, nutrient availability is enhanced." This area includes the continental shelves, coastal estuaries and shallow nearshore waters, and occupies only 8 to 10 percent of the total surface area of the ocean. However, this relatively small area contributes almost 25 percent of the total 24.9×10^9 metric tons of reduced carbon estimated to be produced in the ocean each year and is from 3 to 16 times as productive as the open ocean on an areal basis (Whittaker and Likens, 1973). In recent years these productive areas have been increasingly subjected to an expanding variety of human pressures which demand their multiple use as fisheries resources, commercial waterways, outdoor recreation areas and sewage receptacles (Thayer, Wolfe and Williams, 1975).

Because the seagrasses such as Thallasia testudinum (Hydrocharitaceae) and Halodule wrightii (Potamogetonaceae) form one of the most widespread and productive benthic plant comminities in the shallow waters of the subtropical

coastal zone (Thayer, et al., 1975), it is imperative to understand their ecology so that facts will be available for proper management of these valuable natural resources. Furthermore, "seagrasses must be considered in terms of their interaction with the other sources of primary production that support the estuarine trophic structure before their significance can be fully appreciated" (Thayer, et al., 1975).

However, while a considerable amount of literature exists on seagrasses in general (McRoy and Helssfrich, in press; den Hartog, 1970; Philips, 1974) surprisingly little is known about the relative contributions and the significance of the other primary producers in seagrass communities (Thayer, et al., 1975; McRoy and Helssfrich, in press). A recently held international workshop for studies of seagrass communities (McRoy and Helssfrich, in press) summarized its recommendations concerning primary production by saying that "a review of the available literature indicates that currently, information does not exist to assess the magnitude of the formation of organic matter in seagrass meadows and its limitations either on a larger global and regional scale or on the smaller physiological and metabolic level of the individual organisms." The workshop also pointed out that "seasonal patterns both in the seagrass and associated flora and fauna exist in the temperate and tropical zones, although these patterns may be

completely different. Detailed studies on the seasonality of the physical environment, growth patterns of seagrasses and algae, reproductive cycles of the animal components and their interactions are necessary to compare the organismal assemblages of different geographical regions."

In most areas of the tropics and subtropics Thalassia testudinum Konig is the most widespread and important seagrass (den Hartog, 1970). In most Thalassia communities of Florida and the Carribean, the calcareous macroalgae Halimeda incrassata, Penicillus capitatus, Rhipocephalus phoenix and Udotea flabellum are well represented (Figure 1). However, their roles as primary producers and sediment contributors within this community have not been intensively studied. Furthermore, while some laboratory studies have been done on the growth and biology of these algae (Colinvaux, Wilbur and Watabe, 1965) little is known about their reproduction and longevity in the Thalassia community. The present study is an attempt to fill a gap in our knowledge of these areas.

1.1 STATEMENT OF HYPOTHESIS

The calcareous macroalgae Halimeda, Pencillus, Rhipocephalus and Udotea are an important group of subdominant plants which produces significant amounts of lime mud and organic matter in the Thalassia community. The nature and relative magnitude of this production must be estimated and other functions of these plants

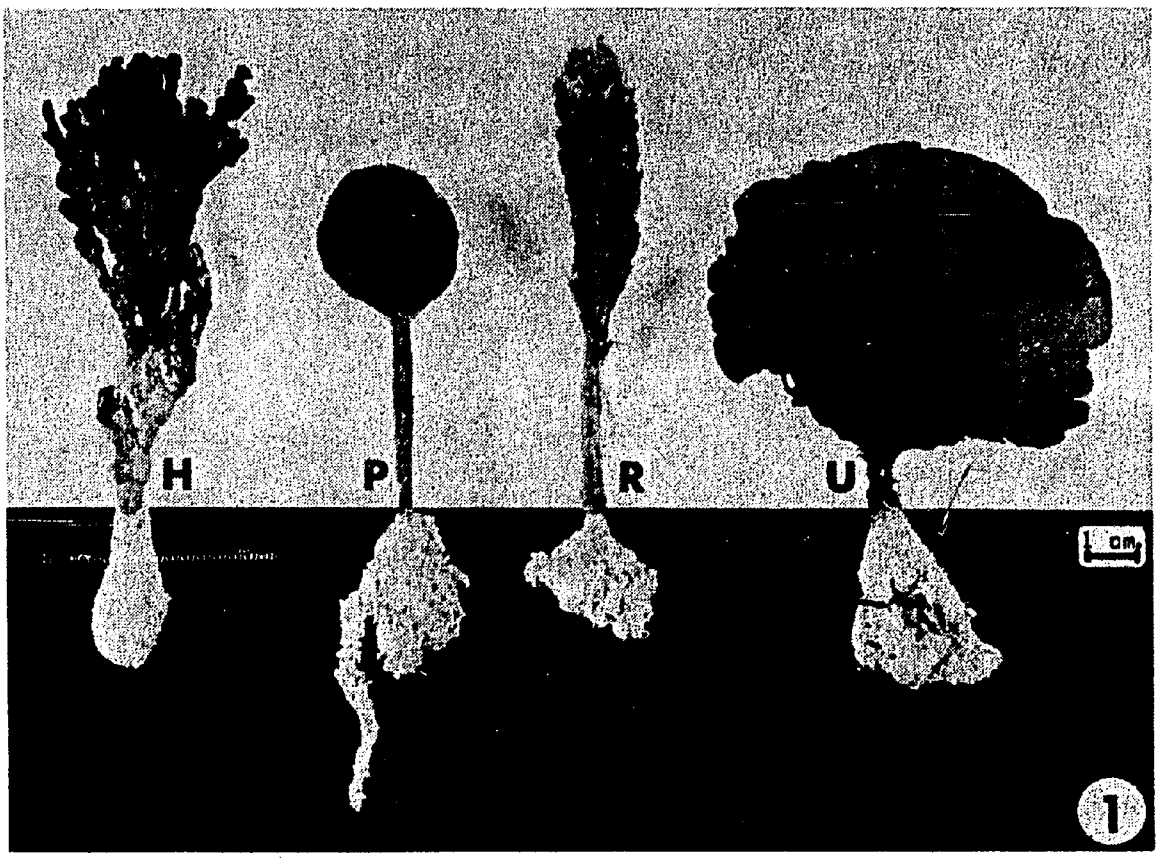


Figure 1. Halimeda incrassata (H), Penicillus capitatus (P), Rhipocephalus phoenix (R), and Udotea flabellum (U). These were the four most common calcareous macroalgae observed in Card Sound, Florida. The green part of the plant (light background) is the actively photosynthetic portion, and the plants are anchored in the substrate by the holdfast (dark background), which consists of a mass of entwined rhizoids. (photograph courtesy of Dr. D.S. Marszalek, University of Miami).

identified if the ecology of the Thalassia community is to be more thoroughly understood.

1.2 OBJECTIVES

The objectives of this study are the following:

1. To examine the spatial distribution and seasonal growth and yield of Halimeda incrassata, Halimeda monile, Penicillus capitatus, Rhipocephalus phoenix and Udotea flabellum in Card Sound, Florida.

2. To define some of the major factors that limit the standing crop, growth and yield of this group of plants in Card Sound.

3. To show the significance of this group of sub-dominant macroalgae as an ecological component of the Card Sound Thalassia community.

CHAPTER II

LITERATURE REVIEW

2.1 TAXONOMY

The following outline describes the taxonomic position of the calcareous macroalgae in the present study:

Division: Cholorophyta
Class: Chlorophyceae
Order: Siphonales
Family: Codiaceae

Early taxonomic treatments of these plants are found in the papers of Gepp and Gepp (1909, 1911), Blackman and Tansley (1902), Børgeson (1911, 1912, 1940, 1946, 1948), Oltmanns (1904), and Howe (1905, 1907, 1909). Other important taxonomic studies include those of Taylor (1928, 1950, 1960). Egerod (1952) provided a review of much of the earlier taxonomy. Today the order Siphonales is generally recognized to include all green algae that are siphonous and non-septate in the vegetative phase (Dawson, 1966; Taylor, 1960). The plants in the present study are placed in the family Codiaceae (Dawson, 1966; Taylor, 1960; Fritsch, 1956), and are characterized by a thallus of intertwined coenocytic filaments (Fritsch, 1956).

2.2 MORPHOLOGY

Descriptions of the morphology of the Codiaceae are found in Gepp and Gepp (1905, 1911), Mirande (1913),

Fritsch (1956) and Dawson (1966). Other work has been done on the morphology of calcified forms by McConnel and Colinvaux (1967). Marszalek and Small (1969) and Marszalek (1971) have examined the morphology of aragonite crystal bundles of H. incrassata, P. capitatus, R. phoenix and U. flabellum.

2.3 DESCRIPTION OF THE MAJOR SPECIES STUDIED

Halimeda incrassata: This species is characterized by a thallus which is subdivided into several branches. Each branch is composed of a chain of calcified trilobed plates (Figure 1). A compact mass of basal rhizoids holds the thallus into place in the sediment. Growth of the plant occurs by addition of individual plates to the tips of the branches. Dying plates turn white and break off from the tips of the branches and are deposited in the sediment.

Halimeda monile: This Halimeda has the same general structure as H. incrassata except that the trilobed plates of H. monile are cylindrical and the thallus is usually much shorter. Growth occurs in the same manner as H. incrassata.

Halimeda opuntia: This plant usually grows in mats attached to hard substrates. The plant thallus consists of branches of flat interconnected plates which are similar superficially to H. incrassata. Basal rhizoids attach the mat to the substrate.

Penicillus capitatus: This species consists of a single stalk which develops a large spherical cap composed of branched filaments (Figure 1). Growth consists of development and maturation of one stalk and one cap which eventually die and decay.

Rhipocephalus phoenix: This species is characterized by the distinctive tapering pointed cap (Figure 1). The filaments of the cap are joined together to form overlapping sheets. Growth follows the same pattern as P. capitatus.

Udotea flabellum: This plant consists of a large, flat, fan-shaped cap and a proportionately smaller stalk (Figure 1). The growth pattern consists of development and maturation of a single thallus as with P. capitatus.

2.4 EVOLUTION, SYSTEMATICS AND DISTRIBUTION

The Codiaceae have existed since the Cambrian and were present at that time in considerable variety (Johnson, 1961). Their abundance has increased from the Ordovician until the present, and by the Ordovician most of their basic morphological structures were established (Johnson, 1961). Halimeda is thought to have been one of the most important rock builders during the Cenozoic (Johnson, 1961; Chapman, 1906). The genus Halimeda is known from the late Cretaceous to the present, while individual species appear to have much shorter geological histories (Johnson, 1961). Penicillus first appeared in the

geological record in the Eocene (Ginsburg, 1972).

An excellent review of the systematics and geographic distribution of the genus Halimeda was done by Hillis (1959). Halimeda is the most widespread genus of these calcareous algae and is found throughout the tropics and subtropics. The distribution of Halimeda roughly follows the 25° isotherm for tropical species and the 20° isotherm for subtropical species (Hillis, 1959). On a world-wide basis, Penicillus, Udotea and Halimeda are found in both eastern and western hemispheres, but Rhipocephalus is known only in the western hemisphere (Gepp and Gepp, 1911). Halimeda incrassata (Ellis) Lamx is known in the western Atlantic from Bermuda, the Carolinas, Florida and Caribbean to Brazil (Diaz-Piferrer 1969). Penicillus capitatus Lamark is known from Bermuda, North Carolina, Florida and the Caribbean south to Argentina (Diaz-Piferrer, 1969). Rhipocephalus phoenix (Ellis and Solander) Lamx and Udotea flabellum follow this same distribution, but U. flabellum is not reported from North Carolina.

2.5 SUBSTRATE REQUIREMENTS

Substrate requirements vary between each species. H. opuntia favors rocky or sandy bottoms while H. tuna and H. scabra usually attach to stones (Soegiarto, 1972). In Curacao, Børgeson (1911) reported massive carpets of H. opuntia which excluded most other algae in sandy areas.

Species of Penicillus, Rhipocephalus and Udotea are found in a variety of habitats varying from hard rock to extremely fine sediments (Taylor, 1960). Algae in this group are noted for their ability to inhabit extremely loose unconsolidated sediments where sea-grasses are unable to develop, giving these algae a competitive advantage in these areas (Humm, 1973). In Biscayne Bay, Florida, Wanless (1969) noted that the calcareous macroalgae were more common in central areas of the bay covered by thin layers (less than 15 cm) of coarse sediment and colonized by sparse Thalassia. Thorhaug (1974b) reported that these algae were more common in central Card Sound. Margalef (1962) stated that in rubble or hard bottom areas Halimeda (no species given) plays an intermediate role in the succession of the Thalassia community, whereas Penicillus (no species given) seems to be an intermediate in shallow sediment areas. Presumably the algae produce and accumulate carbonate sediment which eventually leads to the establishment of a Thalassia community.

2.6 RELATIONSHIP TO SEDIMENT BINDING AND TRAPPING

These algae are also important in the binding and trapping of sediments in mature Thalassia communities. Bernatowicz (1952) observed that Halimeda, Penicillus and Udotea "grew in abundance" in Bermuda Thalassia beds, and that the Thalassia acted as a retainer of the

skeletal material deposited by these plants. This process helps thicken and widen Thalassia beds. Swinchatt (1965) also reported that these same algae acted in a similar manner in Florida Thalassia beds. Jindrich (1969) stated that the accumulation of carbonate sediment over Pleistocene bedrock in the Florida Keys was primarily due to the sediment trapping ability of H. opuntia and T. testudinum. He also noted that production of calcareous sediment by H. opuntia contributed to the differential buildup of Thalassia beds. Scoffin (1970) reported that the holdfast-rhizoid system of these algae made them important as sediment binders but that their abundance in Bimini Lagoon was not great enough for them to act as effective sediment traps like Laurencia and Thalassia.

2.7 CONTRIBUTION OF SEDIMENT MATERIAL

Many observations have been made which indicate that large amounts of carbonate are produced by calcareous macroalgae. For example, Alexander Agassiz (1888) noted that "immense masses of Udotea and Halimeda grow on the shallowest flats of the Florida reefs." Other qualitative observations by Howe (1907), Van Overbeek and Crist (1947) and Lang (1974) also support the idea that calcareous macroalgae are significant contributors of sediment deposited in tropical coastal waters.

Hoskin (1963) reported that Halimeda debris accounted for 35 percent of the total volume of sediment in samples from Alacran reef lagoon in the Caribbean. However, Stoddart (1969) pointed out that "Halimeda varies considerably in importance" in the formation of sediments. For example, over 80 feet of 99 percent pure Halimeda sand make up the floor of Funafuti lagoon in the Pacific (Finckh, 1904), but Emery (1956) reported that it only formed 1 percent of the sediments in Johnston lagoon. Therefore, large variations exist in the relative abundance of Halimeda in different depositional environments.

Ginsburg et al. (1963) compared the relative importance of Halimeda in sediment production in reef environments around the world. Using examples from Bikini, the Florida reef tract and the Gulf of Batabano, they hypothesized that a relationship existed between current speed and the relative abundance of various kinds of sediments. In lagoonal and back reef margins Halimeda debris is found consistently. Halimeda, they suggest, will be most abundant in areas where water movement is "intermediate between wave agitated shelf margins and restricted bays."

Stockman, Ginsburg and Shinn (1967) studied the calcium carbonate production of P. capitatus in Florida Bay and the Florida reef tract. They estimated that

3.23 g calcium carbonate/m^2/year were produced in Florida Bay and 25 g calcium carbonate/m^2/year were produced in the reef tract. Production by P. capitatus could account for 1/3 of the lime mud in Florida Bay and most of the lime mud in the reef tract. Production by Halimeda, Rhipocephalus and Udotea was not estimated. Consequently, a major gap in our knowledge of sediment deposition by these plants still exists.

Lowenstam (1955) reported that the aragonite crystals found in Abaco lime mud are similar in size and shape to the crystals of aragonite produced by the disintegration of Halimeda, Rhipocephalus, Penicillus and Udotea. Lowenstam and Epstein (1957) theorized that the oxygen isotope ratio of the Abaco lime muds was in the correct range for an algal source. However, Cloud (1962) and Purdy (1963) pointed out that there was doubt concerning the assumed temperatures and salinities used by Lowenstam and Epstein in calculating the O_2 isotope ratios.

Cloud (1962) measured the standing crop of P. capitatus and R. phoenix in a 25-m^2 area near the northwestern part of the Great Bahama Bank. He found that the plants in this single area averaged 0.3 g carbonate/thallus and that there were 1.5 thalli/m^2. Cloud (1962) questioned whether or not the biomass and turnover rate of these algae was enough to account for all the aragonite present in the Abaco Bank. Neumann and Land (in press)

reported a total average density of 20 plants/m^2 for H. incrassata, P. capitatus, R. phoenix and U. flabellum in the Bight of Abaco, Bahamas.

Using their own estimates of biomass and the turnover times given by Thorhaug (1965), Colinvaux, et al. (1965) and Stockman, et al. (1967), Neumann and Land (in press) stated that the most conservative estimate indicated that H. incrassata, P. capitatus, R. phoenix and U. flabellum could have produced 50 percent more aragonite mud than was present in the Bight of Abaco. The highest estimate by these authors gave an overproduction of 3 times the amount of sediment in the Bight. They concluded that these algae were very important in the lime mud budget of the Bahamas.

Using the data of Colinvaux, et al. (1965) and Stockman, et al. (1967), Chave, Smith and Roy (1972) estimated the amount of calcium carbonate produced by Penicillus and Halimeda as 10^4 g/m^2/year. These authors did not mention the particular species of plants being discussed, however, making it very difficult to interpret their calculations.

Doty (1969, 1970) studied the seasonal variation in standing crop of several algae in Hawaii using a stratified random sampling method. Among the benthic algae, Halimeda was the most abundant, averaging 12 g dry weight/m^2. Doty estimated that Halimeda produced from 2 to 3

generations (crops) per year and that in Hawaii it displays "pseudo-seasonality," i.e., its presence in the summer is overshadowed by other species of algae, making it appear less plentiful than it actually is.

Soegiarto (1972) estimated the carbonate production of Halimeda discoidea on a reef in Kanoehe Bay, Hawaii. On the basis of measurements of estimated life spans and standing crops he concluded that H. discoidea contributed only 3.4% of the total carbonate produced on the reef.

2.8 GROWTH RATES

There are very few detailed studies in the literature concerning growth rates of the calcareous siphonaceous macroalgae. At Funafuti Atoll in the Pacific, Finckh (1904) observed a single branch of Halimeda growing through a hole in a board used to study the growth of corals. After six weeks the branch had grown to a height of 55 mm and a width of 80 mm. This was equivalent to 14.38 g of plant material in 6 weeks, or about 0.34 g dry weight per day for this particular branch.

Colinvaux, et al. (1965) studied the growth of several genera of tropical macroalgae. They described the formation of new segments of H. discoidea in laboratory aquariums in North Carolina and Ireland. The increase in the area of a single plant at North Carolina was 28 percent in 78 days. The H. discoidea in Ireland

doubled their height in about 10 months. The growth of Halimeda was sporadic in that periods of active growth were followed by longer periods of quiescence in which no growth would occur. These observations were confirmed by Goreau (1963). In the studies of Colinvaux, et al. (1965), several plants developed segments simultaneously while other plants in the same aquarium or in other aquariums did not grow at all. On some plants all branches would die and fall off, leaving the base of the plant "seemingly alive" for months. Some of these stalks eventually produced new branches, indicating that the stalk portion can act as a perennial structure. In contrast, P. capitatus developed from a juvenile stage to an adult in 10 to 14 days, a much more rapid development time than the Halimedas (Colinvaux, et al., 1965). Several generations of P. capitatus were produced in 10 months of culture. Rhizoids connecting the parent plants with the juvenile showed that vegetative propagation had occurred.

Thorhaug (1965) studied the growth and morphology of P. capitatus in south Florida. Asexual propagation by rhizoids was observed, but sexual reproduction was never observed either in the laboratory or in the field. P. capitatus was found to have a life span of approximately 3 months. Factors affecting the spatial distribution of the plants included predation by molluscs, water depth

and current speed. Dwarf populations were found in very high current areas. The plants were most abundant in summer, growing on sandy and muddy bottoms. Growth measured in outside tanks showed the greatest increases in length in summer.

Thorhaug (1972a) also gave field and laboratory growth rates for calcareous macroalgae. Mean maturation time for P. capitatus at 22°C in an inside tank was 27 to 29 days and 19 days in a tank held at 30°C. Field observations indicate that P. capitatus matured in 19 days. These estimates were almost identical for U. flabellum. Branches of H. incrassata in the field were reported to grow from 1.1 to 1.7 cm/week. The highest growth was recorded in higher current areas.

Thermal pollution studies have also provided estimates of the life spans of calcareous macroalgae. Observations made in 1-m^2 frames at 24 stations in Card Sound and Turkey Point, Florida for 3 to 5 years (Thorhaug, 1974b)resulted in estimates of 2 to 12 generations per year for H. incrassata, P. capitatus, R. phoenix and U. flabellum. Each plant was estimated to produce from 1 to 9 offspring during its lifespan.

2.9 THERMAL LIMITS

Thorhaug, Roessler and Segar (1973) and Thorhaug (1974a) discussed various aspects of the thermal limits of these algae in south Florida. Field and laboratory

data showed that the upper lethal limit of P. capitatus is from 31° to 32°C, and 31° to 32°C for H. incrassata. These limits are based on several days exposure to the above range of temperatures.

Zieman (1970) studies the effects of a thermal effluent on the production of Thalassia and the diversity of the benthic plant community at Turkey Point, Florida. Decreases in the diversity of the algae and seagrass community were observed when the water temperature rose above 26° to 28°C. No attached benthic plants were able to survive an elevation of 4°C above the summer mean temperatures, and elevations of only 2°C above summer mean ambient caused serious effects.

2.10 ^{14}C UPTAKE STUDIES

A very limited literature exists concerning measurements of ^{14}C uptake in these algae. Bunt (1971a), in an unpublished annual report, measured the rate of ^{14}C uptake in P. capitatus and H. incrassata in Card Sound but gave the results in a qualitative way, saying that the plants showed "extremely low levels of activity." Goreau (1961), reported that carbon fixing rates for H. tuna and H. opuntia in the light were 2.5 to 4.0 times faster than rates of hermatypic corals (the actual rates for the two algae were reported as 26.39 and 50.52 µg organic cargon/mg N/hr respectively). In a later paper, Goreau (1963) gave the following carbon fixation

rates of the four most important plants considered in the present study:

plant	sample size n	incorporation rate (µg C/mg N/hr ± SD)
Halimeda incrassata	7	17.6 ± 11.75
Penicillus capitatus	10	12.5 ± 1.45
Udotea flabellum	1	11.5
Rhipocephalus phoenix	6	7.3 ± 2.59

These rates were intermediate between more rapid rates exhibited by the Rhodophycean genera Liagora and Galaxura and the slower rates exhibited by Goniolithon and Lithothamnion.

Using measurements of ^{14}C uptake in plants enclosed in clear glass jars, Larkum and Drew (1967) found that the rate of carbon fixation was limited by light somewhere between the depths of 15 and 37 m on the coast of Malta.

2.11 INTERACTION WITH ANIMALS

The interaction of calcareous algae with animals has received some attention also. In a study of the perference of certain mollusc species for different marine algae, Warmke and Almodovar (1963) showed that 72 percent of all animals collected were found on Chlorophyta. Seventy-two percent of the total Anachis

pulchella collected were found on H. opuntia. Most of the snails in the Halimeda were young and only 13.5 percent were adults. This indicated that either the snails were collected at the start of their breeding season or else that they spent the juvenile portion of their life on the algae. H. opuntia was thought to be the most important of these algae in supporting molluscs because of its commonness and the fact that it formed large thick mats which provide an excellent habitat for small animals.

Dahl (1973) showed that in Puerto Rico, H. incrassata grew in a back reef area in a dynamic relationship with sponges. By providing the sponge with a point of attachment, the alga and the sponge together produced a new type of substrate on and in which other plants and animals could live. The result was "extensive hummocks of animal and plant material interspersed with clear, current-swept sandy areas not unlike some terrestrial desert and dune communities" (Dahl, 1973).

There have been numerous studies which indicate that calcareous algae of the family Codiaceae are eaten by fish. During a saturation dive in the Tektite project (U.S. Virgin Islands), Earle (1971) placed wire cages in transects perpendicular to a coral reef in 40 to 50 feet of water. Grazing on benthic plants decreased rapidly with increasing distance from the reef. Earle

(1971) also carried out experiments of preferences of different fish for various kinds of algae. Bundles of algae were laid out near the underwater habitat for fish to graze on and the apparent grazing preferences of the fish were recorded. H. incrassata, P. capitatus, R. phoenix and U. flabellum were readily eaten by surgeonfish and parrotfish. The study pointed out that algae and seagrasses flourished in areas where fish were lacking and that feeding by herbivores took place primarily during the daylight hours. The study concluded that herbivorous fish exert "a major influence on the abundance, diversity and distribution of benthic marine plants in tropical seas." In contrast to later work by Ogden, Brown and Salesky (1973) in shallower patch reefs, Earle hypothesized that invertebrate herbivores are of "relatively small importance in tropical seas" and suggested that the plants of these regions have affected evolution of fishes because of the grazing relationship. Ogden, et al. (1973) later showed that the urchin Diadema also exerts a major effect on the plants in the around shallow Virgin Island patch reefs. Nocturnal feeding by this particular urchin was a major factor in producing the halos commonly surrounding these patch reefs. Note that these two studies were carried out in quite different environments.

Randall (1965) showed that sea chubs, parrotfish

and surgeonfish families of West Indian fishes are highly dependent on benthic plants for food, and that many reef fish depend on the benthic flora in the algal plain away from the reef. Mathieson, Fralick, Burns and Flahive (1971), in the same Tektite program, also found that grazing pressure on benthic plants was greatly reduced 30 m from the reef (a 30 m depth change was involved). Cage experiments showed an increase in the diversity and density of plant life inside enclosures placed on the reef as compared to outside. Transplantation of H. incrassata plants from the nearby Thalassia bed to the reef resulted in heavy grazing on the algae by reef fishes. It was concluded that selective grazing by fishes probably occurs and that all plants present within about 30 meters of the reef were exposed to heavy grazing.

In contrast to the above observations, Bakus (1969) stated that coral reef fish usually avoid calcareous forms of algae such as Halimeda and also other algae with tough thalli such as Turbinaria. Other data also support this view. Gut content analysis of parrotfish from Johnston Island and surgeonfish, triggerfish and puffers of Palmyra in the Pacific showed that Halimeda was insignificant in their food habits (Emery, 1956).

2.12 PHYSIOLOGY

Work on the physiology of this plant group has been

largely limited to calcification. Goreau (1961) showed that H. tuna and H. opuntia calcified 1.5 to 10 times faster than reef building corals and 20 times faster than non-reef forming corals.

In a later paper, Goreau (1963) demonstrated large variation in calcium carbonate deposition in calcareous algae which could be attributed to "growth fluctuations" in the plants themselves as previously discussed. Variations in calcification was also attributed to variation in light intensities during the course of the uptake experiments. Penicillus and Halimeda had slower calcification rates than Liagora and Galaxura, but other Rhodophytes (Lithothamnion, Goniolithon) had the lowest calcification rates. Halimeda was unique in being able to calcify faster in the dark, which perhaps accounts for its greater vertical distribution and higher carbonate content at greater depths (Bohm, 1973). This pattern was the opposite of Penicillus, Rhipocephalus and Udotea whose carbonate content decreased with depth.

Stark, Almodovar and Kraus (1969) studied the factors affecting calcification in H. opuntia and H. discoidea. H. opuntia was shown to calcify faster and have a higher percentage of $CaCO_3$ than H. discoidea. Calcification in both species was stimulated by light, and a diurnal rhythm of calcification was exhibited which paralleled chloroplast migration.

The sequence of calcification in H. discoidea was studied by Wilbur, Colinvaux and Watabe (1969). Calcification begins on the outside of the cell wall and proceeds away from the wall, filling in the extracellular spaces between the cortical utricles. Using the scanning electron microscope, Marszalek (1971) showed that the calcium carbonate crystals formed by H. incrassata, R. phoenix and U. flabellum are very similar to one another in shape and size but are distinguishable from one another by the size and shape of the crystal bundles.

Other work on calcification includes that by Bohm (1961) who demonstrated that the calcium is bound by an extracellular acidic water soluble mucoprotein. Bohm (1973) also showed that carbonate content of calcareous macroalgae varied with genus, species and depth. Halimeda was the most heavily calcified genus, Udotea the least and Rhipocephalus and Penicillus were intermediate. The maximum mineral content was Halimeda: 97% (of dry weight), Penicillus and Rhipocephalus: 60% and Udotea: 37%. Other work on the physiology of calcification can be found in Bohm (1969, 1972a, 1972b).

An important area of research on the physiology of these plants is concerned with their toxicology. For example, extracts of H. opuntia have been demonstrated to have antimicrobial activity on bacterial cultures (Oleson, Maretzki and Almodovar, 1964; Almodovar, 1964).

This alga was noted to be especially abundant on the reef, and showed no "marked seasonal variation in antimicrobial activity" in Puerto Rico. Welch (1962) reported that P. capitatus and H. monile did not display anti-fungal activity, while H. opuntia showed intermediate activity levels. Hashimoto, Fusetani and Nozawa (1972) showed that H. opuntia, H. monoloba and H. cuneata were nontoxic to mice and rabbit blood cells. The relationship of antibiotic activity of marine algae to their ecology is poorly understood at the present time and promises to be a very interesting area of research.

2.13 REPRODUCTION

Reproductive bodies have been reported in Halimeda (Gepp and Gepp, 1911; Howe, 1907; Schmitz, 1880; Feldmann, 1951; Graham,1975) and Udotea (Philips, 1957). Halimeda produces biflagellate swarmers of unknown function (Fritsch, 1956; Graham, 1975; Colinvaux et al., 1965). Hillis (1959) summarized the seasonal data on reproduction of Halimeda known to that time and concluded that no definite relationship seems to exist between the time of year and reproduction. Reproductive bodies have been reported for Penicillus, but these were shown to be epiphytic organisms (Fritsch, 1956). Sexual reproduction is unknown in Penicillus and Rhipocephalus despite the fact that many workers have looked for it (Fritsch, 1956; Thorhaug, 1965). Gametangia have been reported in Udotea

(Philips, 1957) but no swarmers have been observed.

The literature review above points out that while much general qualitative information is available, detailed information is lacking regarding the ecological role of calcareous macroalgae. Very few quantitative long term studies have been done on the standing crop, growth rates and primary production of the group in relation to the rest of the community. Research in these areas is needed if this role is to be understood.

CHAPTER III

DESCRIPTION OF THE STUDY AREA

Card Sound is a shallow coastal lagoon in the lower section of Biscayne Bay, Florida (Figure 2). It lies approximately 34 km south of Miami, and is largely removed from the effects of pollution found in certain parts of north Biscayne Bay (McNulty, 1961, 1970). The power plants at Turkey Point discharged thermal effluents into Card Sound during 1972, but the effects on the biota of the Sound were negligible since the temperature, volume and duration of the effluent were not great enough to damage the community (Roessler and Tabb, 1974; Thorhaug, 1974b;Hixon, 1975). This was due to a combination of factors including the length of the effluent canal and the choice of the site for releasing the effluent.

3.1 CLIMATE

South Florida is classified as a subtropical region. Mean monthly air temperatures for the year range from 17.8^{o}C in January to 31.6^{o}C in August. Mean annual air temperature is 24.6^{o}C. Maximal annual air temperature extremes of 1.7^{o}C and 36.7^{o}C have been reported by the Weather Bureau. Summer is considered to extend from May to October and is characterized by gentle east and southwest winds. In the winter, winds are of higher velocity and shift to the east and especially the northeast.

Figure 2. Map of the study area showing the state of Florida and the location of Card Sound, which lies in the southern part of Biscayne Bay, approximately 25 miles south of Miami.

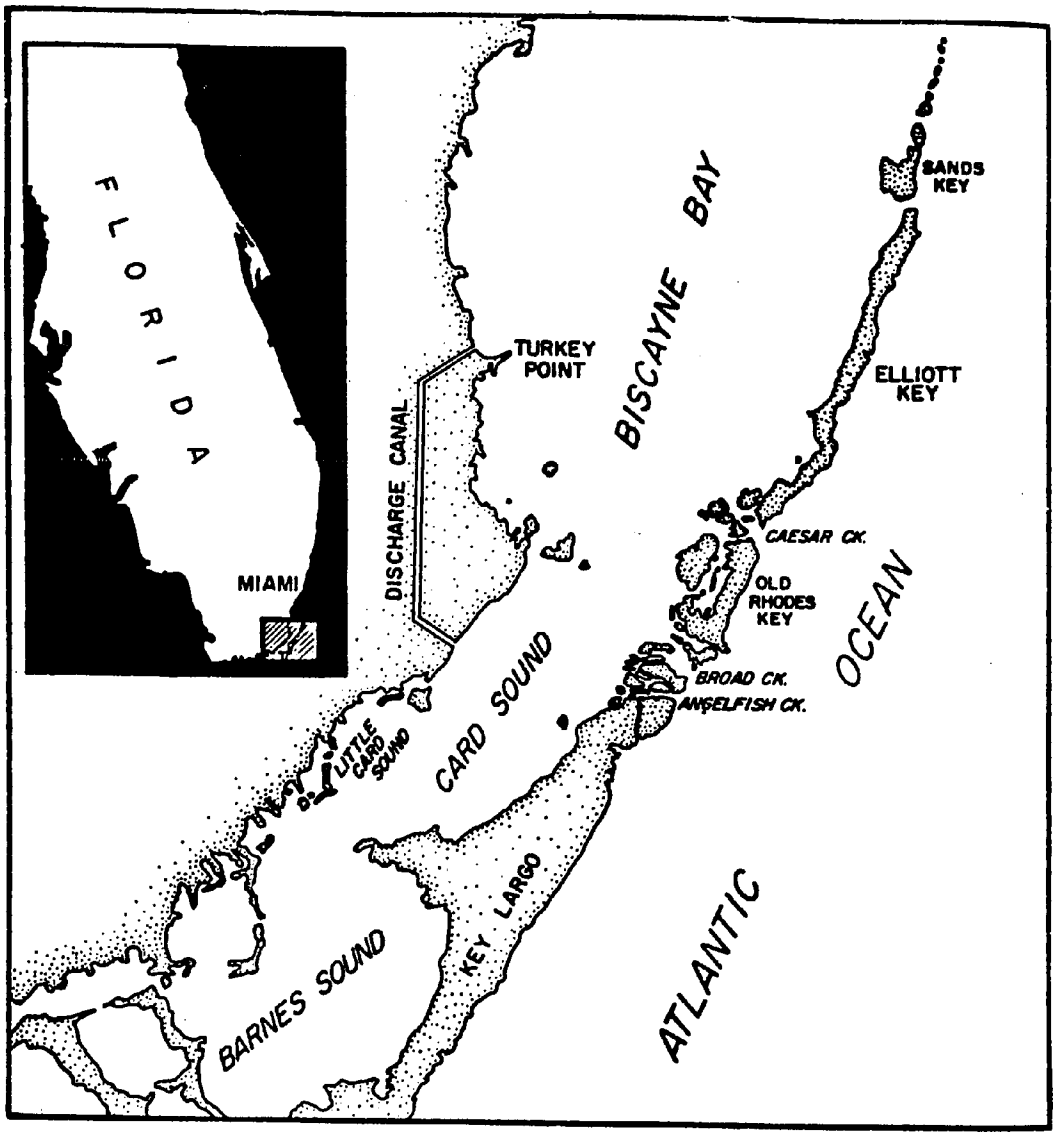

FLORIDA
MIAMI
DISCHARGE CANAL
TURKEY POINT
BISCAYNE BAY
SANDS KEY
ELLIOTT KEY
CAESAR CK.
OLD RHODES KEY
BROAD CK.
ANGELFISH CK.
OCEAN
LITTLE CARD SOUND
CARD SOUND
KEY LARGO
ATLANTIC
BARNES SOUND

Figure 2

Frequent cold fronts moving through the area in winter commonly produce northeasterly winds in excess of 20 miles per hour. Rainfall in south Florida amounts to about 50-60 inches per year, of which over 70 percent falls during the summer months. Hurricanes with winds over 75 mph affect the area about once every seven years on the average, but hurricanes passed over the Biscayne Bay area in 1964, 1965 and 1966.

3.2 AREAL GEOGRAPHY AND BATHYMETRY

Card Sound is about 8 km long by 4.9 km wide. It is separated from the rest of Biscayne Bay to the north by the Arsenicker Keys and the shoal waters of Midnight Pass and Cutter Bank (Figure 3). To the east a series of deep (8 m maximum depth) channels connect with the Atlantic Ocean through the Florida Keys. These channels include Broad and Angelfish Creeks as well as numerous smaller interconnected channels. To the south, Card Bank creates a shoal barrier between Card Sound and Little Card Sound (Figure 3). Card Sound averages less than 3 meters in depth. At the mouth of the channels on both sides of Key Largo,tidal banks have formed which rise to within less than a few inches of the surface at low tide. Cutter Bank and Card Bank also rise to within a few inches of the surface at low tide. To the east, the bottom drops to a maximum depth of 3.6 m just inside Key Largo.

Figure 3. Map of the bathymetry of Biscayne Bay and Card Sound, Florida. Dots show the locations of sediment depth determination by hand probing. Contours of water dpeth taken from hydrographic charts and topographic maps (from Wanless, 1969).

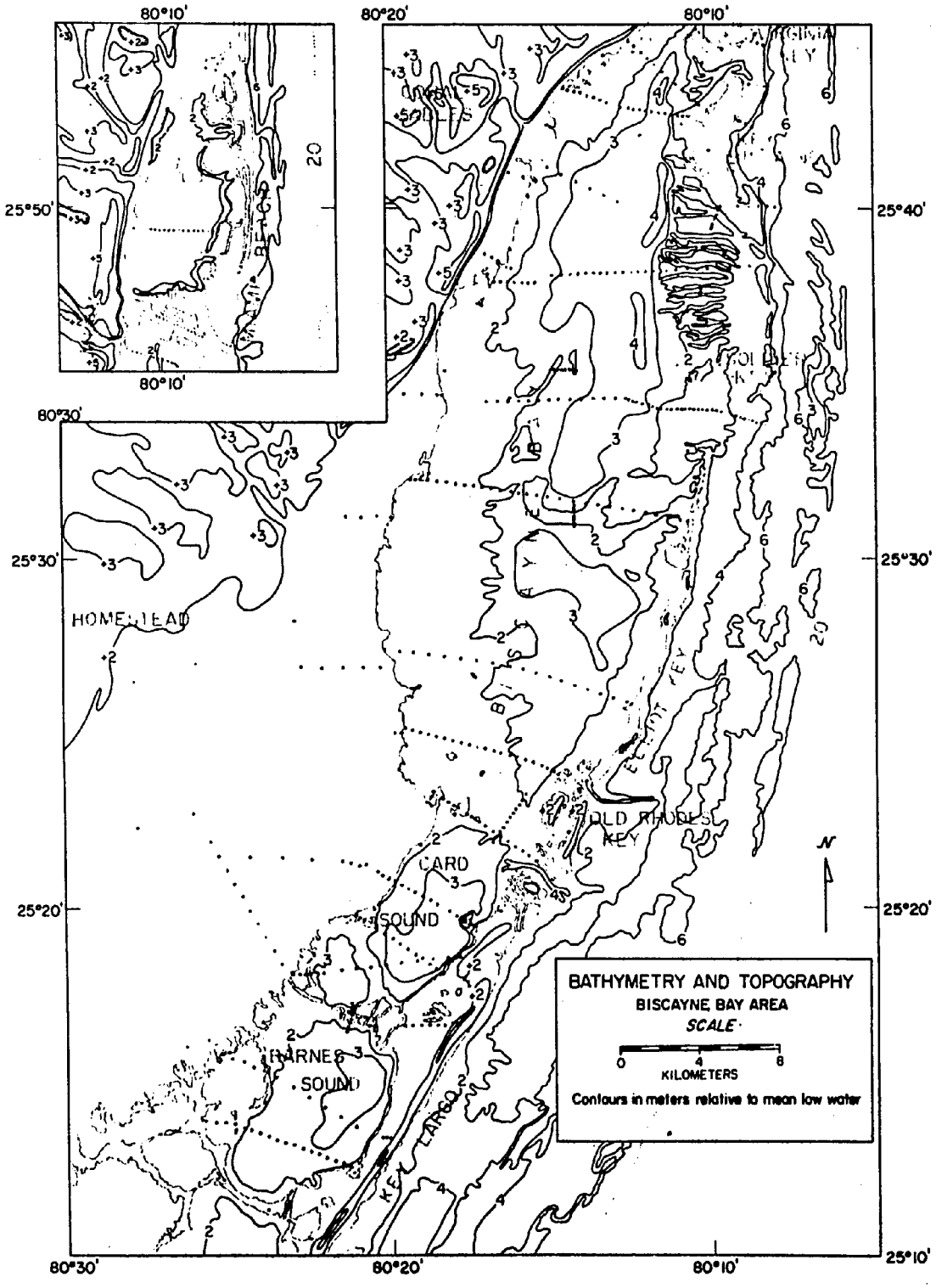

80°10'
80°20'
80°10'
25°50'
25°40'
80°30'
25°30'
25°30'
HOMESTEAD
25°20'
25°20'
CARD
SOUND
ARNES
SOUND
KEY LARGO
80°30'
80°20'
80°10'
25°10'
N
BATHYMETRY AND TOPOGRAPHY
BISCAYNE BAY AREA
SCALE
0 4 8
KILOMETERS
Contours in meters relative to mean low water

Figure 3

3.3 CIRCULATION AND EXCHANGE

In general, the patterns of circulation and exchange in Card Sound are controlled by a combination of tidal action, wind forcing of water, bottom topography and fresh water runoff. These factors all interact to produce a pattern which varies from day to day and season to season.

Fresh water enters Card Sound from numerous small streams on its western shore (Figure 2), from Key Largo and the Model Land Canal, which directs drainage off the land into Card Sound. Fresh water also enters directly from rainfall and ground water percolation. Density stratification can be intense along the western shoreline but is usually shortlived (Hela, Carpenter and McNulty, 1957) because the basin is so shallow. Intense temporary stratification due to fresh water runoff has been observed near the mouth of the Model Land Canal (Lee and Rooth, 1972). Bunt, Lee, Taylor, Rost and Lee (1971) also reported "temporary but intense haloclines sometimes involving only a few cm at the immediate water surface." Stratification due to drought and resulting higher salinities has also been observed to occur in the extreme southeastern part of Card Sound (Lee and Rooth, 1972). This results in the movement of more dense higher salinity water along the bottom towards the deeper parts of Card Sound (Lee and Rooth, 1972). Within Card Sound

itself salinities in the rainy season are generally lower closer to the western shoreline due to fresh water runoff.

Tides in Card Sound are semi-diurnal. Due to frictional damping of shoal areas in Biscayne Bay (Figure 3) and the channels connecting to the Atlantic on Key Largo, tides in Card Sound lag behind the tides at Government cut, 20 miles north, by roughly 3 hours. Mean tidal range in Card Sound is 24 cm while at the Miami harbor entrance the range in 80 cm. Tidal action within Card Sound has been separated into two types, that occurring in the interior of the sound and that occurring in the area around the Angelfish and Broad Creek channel systems (Lee and Rooth, 1972). Tidal exchange in the interior of the sound is limited to a back and forth, (NE-SW) pattern which reverses with each tide. Tidal action of this kind produces isohalines down the long axis of the sound and a salinity barrier which furhter hinders exchange. Active tidal exchange with the ocean is limited to a semi-circular area just inside Key Largo which has a radius of about 500 times the depth of the channels (Lee and Rooth, 1972). Current speeds and tidal volumes are high in the tidal creeks but are limited to the relatively small above mentioned area. Tidal currents through Anglefish and Broad Creeks reach 3.0 knots (Hela, et al., 1957). The tidal inflow through

these creeks reaches 68,000 cfs and 52,300 cfs on the outflow (Michel, 1970). Significant tidal exchange also occurs between Biscayne Bay and Card Sound. Tidal flow rates may reach 72,000 cfs across Cutter Bank on the inflowing tide and 25,500 cfs on the outflowing tide. Signifcant tidal exchange across Card Bank also occurs and amounts to an estimated 43,000 cfs of the outgoing tide and 38,500 cfs on the inflow (Riege, 1974).

Wind forcing has varied effects on circulation and exchange in Card Sound. During the winter when north and northeast winds associated with periodic cold fronts occur, an internal wind driven circulation is believed to be established in the Sound. During these periods waves are fetch limited (Lee and Rooth, 1972) to less than 1 m (because of the physical restrictions of the surrounding land and submerged tidal banks). Wind forces water down the western shoreline, setting up a counterclockwise current flow which moves water slowly south. Wind action also mixes the water vertically and horizontally, moving it into the tidal inlets where it can then exchange directly with the ocean. This has the effect of reducing the flushing time of the Sound (Lee and Rooth, 1972).

Superimposed on these separate patterns of tidal, wind, and topographically produced water movement is the combination of wind with tidal effects. Morril and Olsen

(1955) reported that winds of over 20 mph may possibly cancel out some tidal currents in Biscayne Bay. Lee and Rooth (1972) distinguished patterns of tidal flow in terms of windy and calm periods. By measuring the salinity distribution in Card Sound they were able to detail several patterns of interaction between winds and tides.In calm periods the tides produce northeast-southwest haloclines down the long axis of Card Sound, and circulation and exchange are inhanced by wind forced circulation as outlined above. During calm periods and under drier winter conditions salinities can reach relatively high values in the extreme southeast portion of the Sound. Salinities of up to 45 parts per thousand have been recorded in this area (Lee and Rooth, 1972). The denser, higher salinity water then sinks and moves to the west, and forms a layer which lies beneath the lower salinity water above. The important point here is that circulation appears to be very limited in the southeastern area of the Sound.The nutrient concentrations in the water of this area seem to be somewhat higher than in any other part of Card Sound (Segar, Gerchakov and Johnson, 1971), and may be related to the poorer circulation and stirring up of fine bottom sediments.

During windy winter periods the tidal jet that penetrates Card Sound may be severely restricted, reducing the tidal exchange between the ocean and the interior of Card Sound. During the summer, east winds

may enhance this exchange on the flood tide as water is forced further east (Lee and Rooth, 1972).

In summary, previous work has shown that circulation and exchange patterns are complex. In general, oceanic exchange is limited to a relatively small area in north-eastern Card Sound. Tidal exchange is also important between Card Sound and Biscayne Bay which occurs across Cutter Bank and in the passes between the Arsenicker Keys in north Card Sound. Strong tidal currents also flow over Card Bank and southward to Barnes Sound, indicating significant exchange between Card and Barnes Sounds. However, this exchange is even more limited than that which occurs in Card Sound (Lee and Rooth, 1972; Riege, 1974).

3.4 SEDIMENTS

The marine carbonate sediments of Biscayne Bay and Card Sound are believed to be the result of deposition during the past Wisconsin sea level rise. During the Sangammon interglacial period, water levels were 25 feet above present and Card Sound was a lagoon behind living coral reefs which today lie exposed as the Florida Keys (Hoffmeister, 1972). The water level began to fall during the Wisconsin Glacial period, and about 20,000 years ago the sea level reached its lowest point, some 300 feet below the present level. Geological evidence suggests that during this period, the bottom of what is

now Biscayne Bay and Card Sound was completely exposed. Water drainage created dendritic stream beds and solution holes in the bedrock. Both solution holes and dendritic stream beds were eventually filled with sediment from mangrove swamps which later inhabited the area (Figure 4). Zieman (1972) showed that the circular solution holes are filled with mangrove peat and are now inhabited with Thalassia. Sediment depth in the holes varies from 0.5 to 5 meters in thickness. A thin layer of marine carbonate mud overlies the thicker, slightly acid peat. The acidic nature of the peat may mean that enlargement of the original solution holes has occurred. Carbon dating of a single core from one of these circular Thalassia beds showed that the peat was 3,680 years old ± 120 years (Zieman, 1972). This corresponds well to the post-Wisconsin sea level rise curve of Scholl and Stuiver (1967) in south Florida. It appears that the mangroves were killed by the rising sea, and the Thalassia invaded the sediment left behind. As the rising sea entered the Bay Basin about 5,400 years ago, the marine carbonate sediments began forming as a result of deposition in the deeper troughs along the inside of the barrier islands. Later, beginning perhaps 3,000 years ago, deposition began in shallower mid-bay areas (Wanless, 1969). The present distribution of sediments in Card Sound have been described by Earley and Goodell (1968),

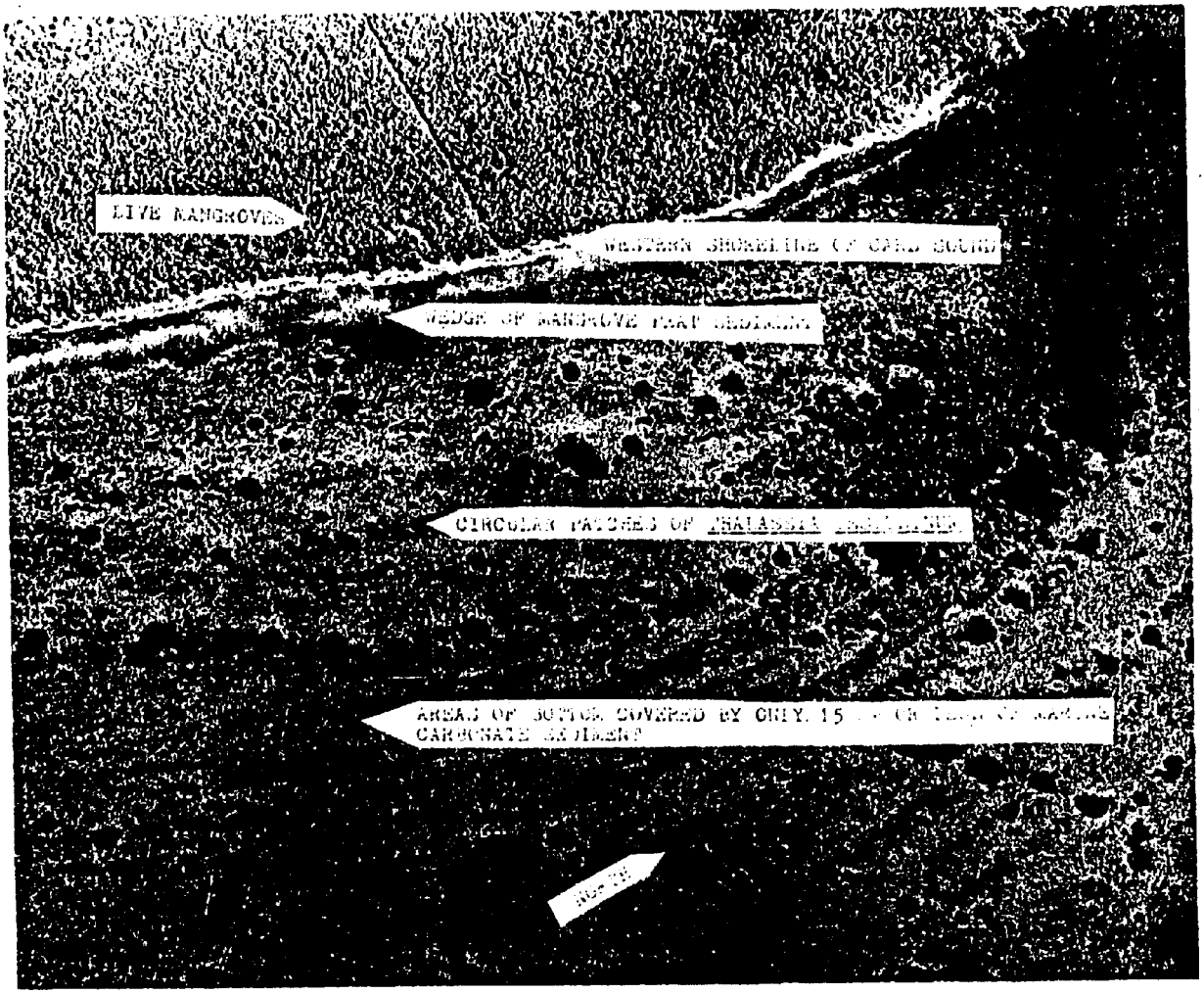


Figure 4. Aerial photograph of the northwest shoreline of Card Sound, Florida, showing the circular patches of Thalassia and mangrove peat sediment wedge along the shore. Mangrove peat sediment depth beneath the circular patches of Thalassia is from 0.5 to 5.0 meters (Zieman, 1972). Sediment depth in areas between the patches is less than 15 cm (Wanless, 1969).

Segar, et al. (1971) and Wanless (1969). The sediments of most of Card Sound are less than 15 cm in depth and lie directly on Miami Oolite bedrock (Figure 5). Sediment depth is greatest around the edges of the basin in the areas of mangrove peat, and in the tidal bars of sand and mud (Figure 5). The major sedimentary feature of the sound is the actual lack of deep deposits over a large portion of the bottom, and the restriction of deeper sediments to a smaller fringing area. The absence of deeper sediments in the central parts of the bay has been attributed to wave and current scouring of the bottom. The area of the least sediment coincides with the 3 - 3.5 meter depth contour of the bedrock (Wanless, 1969). Above this level wave action prevents sediment buildup as well as the establishment of Thalassia testudinum. Below this limit sediment is allowed to build, and Thalassia, which requires a critical amount of sediment to grow, also flourishes. Thalassia stablizes bottom sediments in several ways. It creates a "semi-motionless" layer of water just above and between the blades into which suspended particles of sediment fall and are then trapped between the Thalassia blades (Ginsburg, 1956). The root-rhizome system of Thalassia also binds the sediment and helps to prevent erosion by currents (Wanless, 1969). Other mechanisms include the trapping of fine suspended material by epiphytic algae and the retention of material produced by sediment

Figure 5. Sediment depth contours of Biscayne Bay and Card Sound, Florida. Contours given in cm. Sediment depth determined by hand probing at each location shown by dots (from Wanless, 1969).

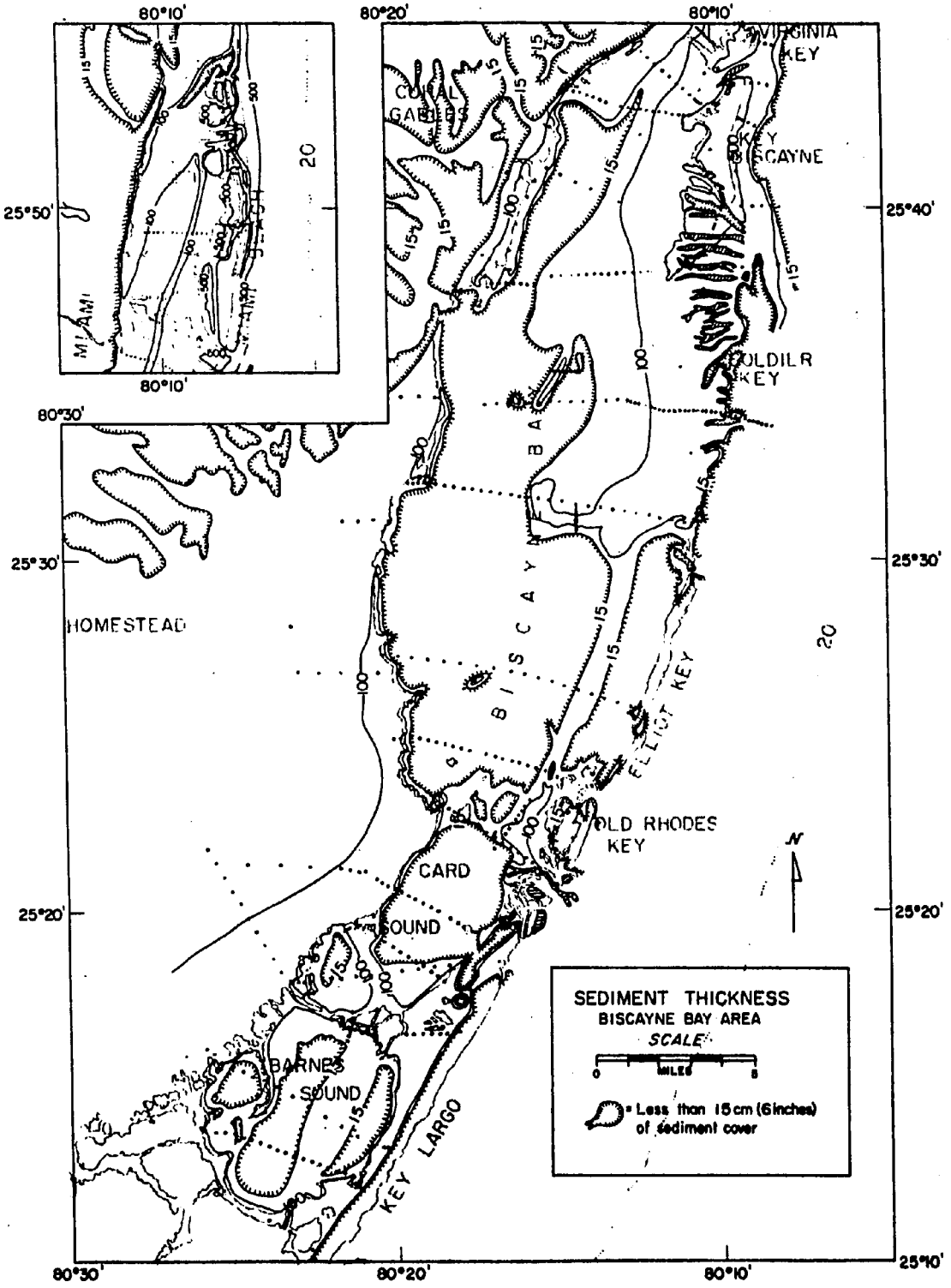

80°10'
80°20'
80°10'
25°50'
25°40'
80°30'
25°30'
25°20'
80°30'
80°20'
80°10'
25°10'
MIAMI
CORAL GABLES
VIRGINIA KEY
KEY BISCAYNE
SOLDIER KEY
BISCAYNE BAY
HOMESTEAD
ELLIOT KEY
OLD RHODES KEY
CARD SOUND
BARNES SOUND
KEY LARGO
N
SEDIMENT THICKNESS
BISCAYNE BAY AREA
SCALE
0
MILES
5
= Less than 15 cm (6 inches) of sediment cover

Figure 5

building algae and molluscs in the Thalassia bed.

Earley and Goodell believe that Card Sound represents a transitional zone between non-carbonate sediments to the north and carbonate sediments to the south, and that it is "a cul-de-sac in which the quartz sand brought by long shore drift from the north is trapped." A general trend exists in which quartz becomes increasingly uncommon in the sediments from north to south in the Sound. There is also a regular decrease in grain size and an accumulation of fine sediments in the lower Sound. In summary, the distribution of sediments in Card Sound is determined by the depositional history, bedrock topography, internal circulation, wind and wave action, and the sediment trapping ability of Thalassia.

3.5 MAJOR PLANT COMMUNITIES

The major plant communities in Card Sound include phytoplankton, benthic macro and microalgae, seagrasses, and epiphytic algae. Mangrove leaves also enter the system and are an important detrital food source (Heald, 1971; Odum, 1971). The relative rates of primary productivity of the aquatic plants have not yet been thoroughly worked out. Measurements of blade growth of Thalassia in Card Sound have been reported by Thorhaug (1974a). These studies indicate that T. testudinum produces from 0.2 to 5.6 g dry wt/m^2/day. Estimates of T. testudinum blade production by Buesa (1974) in Cuba

range from 1.6 to 18.1 g dry wt/m^2/ day. In Jamaica, Greenway (1974) showed that blade growth of T. testudinum ranged from 2.3 to 5.7 g dry wt/m^2/day. Jones (1968) estimated that T. testudinum primary productivity was about 700 gC/m^2/yr and estimated that the epiphytes produced another 200 gC/m^2/yr. The applicability of the oxygen electrode method which Jones used in these studies has been criticized because T. testudinum possesses a system of air spaces, or lacunae, in the leaves which may mask the actual photosynthetic and respiratory mediated oxygen exchange (Hartman and Brown, 1967).

Much work has been done on the distribution and production of T. testudinum in Card Sound by Thorhaug (1974a). T. testudinum blade growth was greatest in late summer and in organically rich sediments at station 1103. Blade abundance,however, was greatest in sandy sediment at station 0104. In general, blade abundance of T. testudinum was greatest around the rim of Card Sound in deeper sediments, while the majority of the central part of the sound supported a sparse population.

Work has also been done on the growth of the red macroalga Laurencia poitei in Card Sound. Based on growth measurements, Thorhaug and Garcia-Gomez (1972b) estimated a daily production of 0.069 g dry wt/m^2/day and an annual production of 9×10^5 kg dry wt/yr for all of Card Sound. Based on growth and biomass estimates

Josselyn (1975) calculated that L. poitei produced from 0.01 to 0.74 g dry wt/m^2/day in Card Sound and estimated a total annual production of 3 x 10^5 kg/yr for all of Card Sound. Growth was greatest in early spring and late fall.

The primary productivities of microalgae in the sediment and water column of Card Sound were briefly measured by Bunt, et al. (1971b). These workers reported that microalgae in the sediment produced from 500 to 600 g C/m^2/yr but cautioned that this estimate was based on extrapolation of the rate measured over a very short time period to a 10 hour day and that the numbers were "critically dependent" on the method used. Bunt, et al. (1971b) estimated that the phytoplankton in the water column produced 13 to 15 g C/m^2/yr, but again cautioned that these numbers were highly variable and only tenative. They attributed the large observed variation to the "complexity and inconstancy of the environment" of Card Sound such as the temporary but strong haloclines close to the surface, thermoclines next to the bottom, very rapid changes in the water clarity brought on by tides, weather and variation in the sediment type of the bottom.

The physical distribution of the different bottom types has been described by Roessler and Beardsley (1974) and is shown in graphic form in Figure 6 (Wilson, 1975). The map shows the large barren area

Figure 6. Major bottom types of Card Sound, Florida as estimated visually by a diver towed behind a boat. Data are originally from Roessler and Beardsley (1974), figure from Wilson (1975).

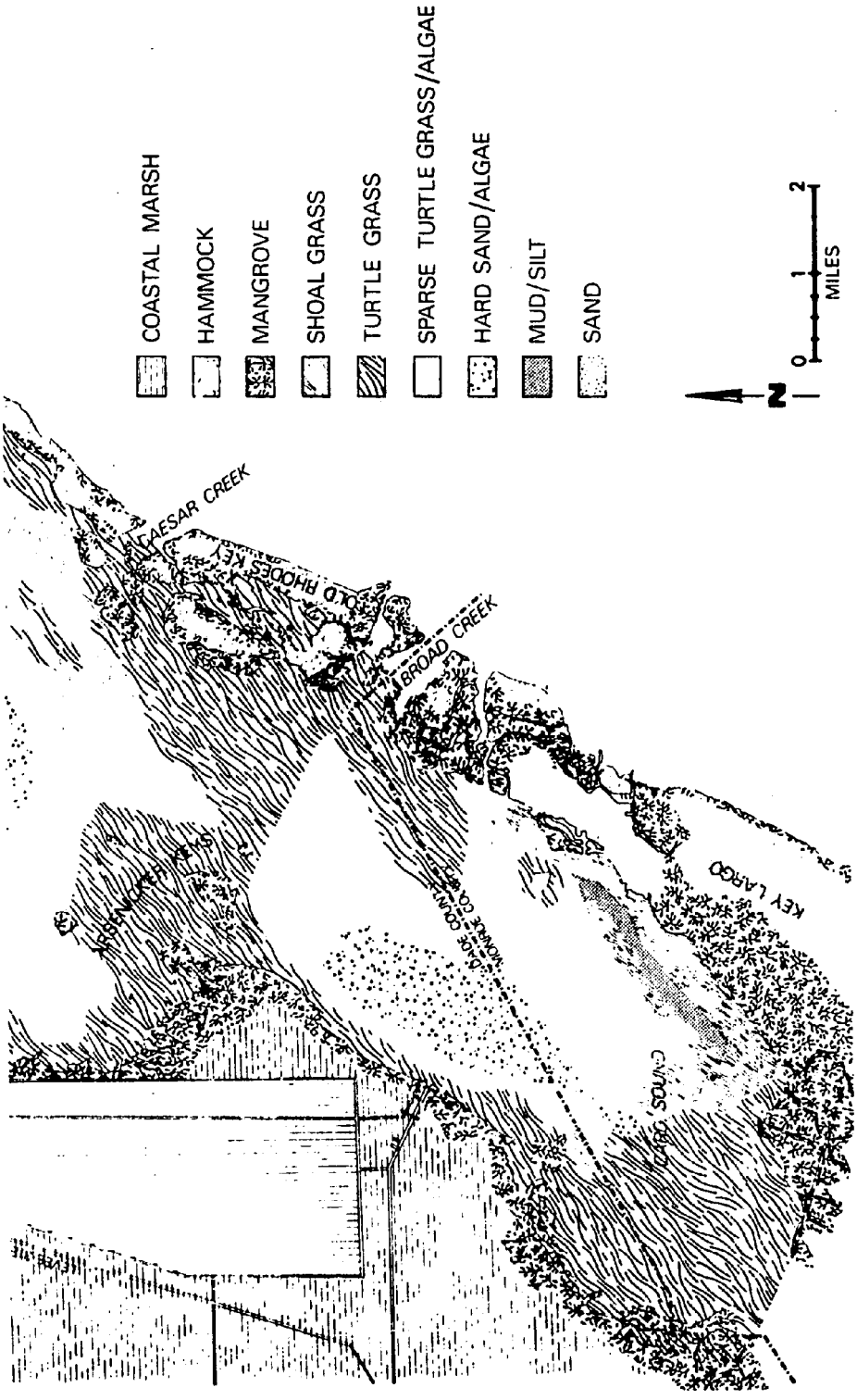

COASTAL MARSH
HAMMOCK
MANGROVE
SHOAL GRASS
TURTLE GRASS
SPARSE TURTLE GRASS/ALGAE
HARD SAND/ALGAE
MUD/SILT
SAND
0
1
2
MILES
N
CAESAR CREEK
OLD RHODES KEY
BROAD CREEK
KEY LARGO
CARD SOUND

Figure 6

which covers most of the central Card Sound basin, and shows that in general most of the benthic plants are concentrated around the edges of the basin.

3.6 NUTRIENTS

The concentrations of the major micronutrients in the water column of Card Sound have been reported by Segar, et al. (1971). Colorimetric methods were used to determine the concentrations of most of these nutrients at 62 stations in Card Sound over the period of one year. Table 1 presents the ranges of nutrient and metals in the water of Card Sound. The authors speculated that the summer rainy season may be responsible for an influx of nutrients washed out of the adjacent watershed. During the winter, nutrients in the sediment may be resuspended by storm turbulence.

Table 1. Summary of nutrient and total dissolved metal data for Card Sound, Florida (from Segar, Gerchakov and Johnson, 1971). All values are in microgram-atoms per liter of water (except metals).

	Range of Concentration in Water Column	
Nitrate	0.01 - 1.70	µg.at. NO_3·N/l
Nitrate	0.01 - 0.20	µg.at. NO_2·N/l
Ammonia[1]	0.20 - 9.78	µg.at. NH_3·N/l
Inorganic Phosphate	0.05 - 3.1	µg.at. NH_3·N/l
Total Dissolved Phosphate	0.19 - 1.1	µg.at. P/l
Silicate	*BDL - 7.0	µg.at.SiO_4·Si/l
Iron	16 - 127	parts per million
Copper	5 - 25	parts per million

[1] collected and determined by M. Josselyn

* Below Detection Limit

3.7 STATIONS USED IN PRESENT STUDY

Figure 7 is a map of Card Sound showing the grid of stations used. The grid was originally established by the University of Miami to study the effects of thermal effluents on the biota of Card Sound (Bader and Roessler, 1971), and 16 were permanently maintained with a system of buoys and blocks. In the present study, stations 0106, 0409, 0507, 0707, 0905 and 1007 were also marked with buoys. Table 2 is a summary of the major characteristics of the stations used in all parts of the present study. It is obvious that within Card Sound there is a great variety of environmental types.

Figure 7. Original systematic grid of stations in Card Sound, Florida, (after Bader and Roessler, 1971). Station 0409 was added to the original grid for use in the present study. Legend indicates stations designated for earlier thermal pollution studies in Card Sound, carried out by the University of Miami Rosenstiel School of Marine and Atmospheric Science.

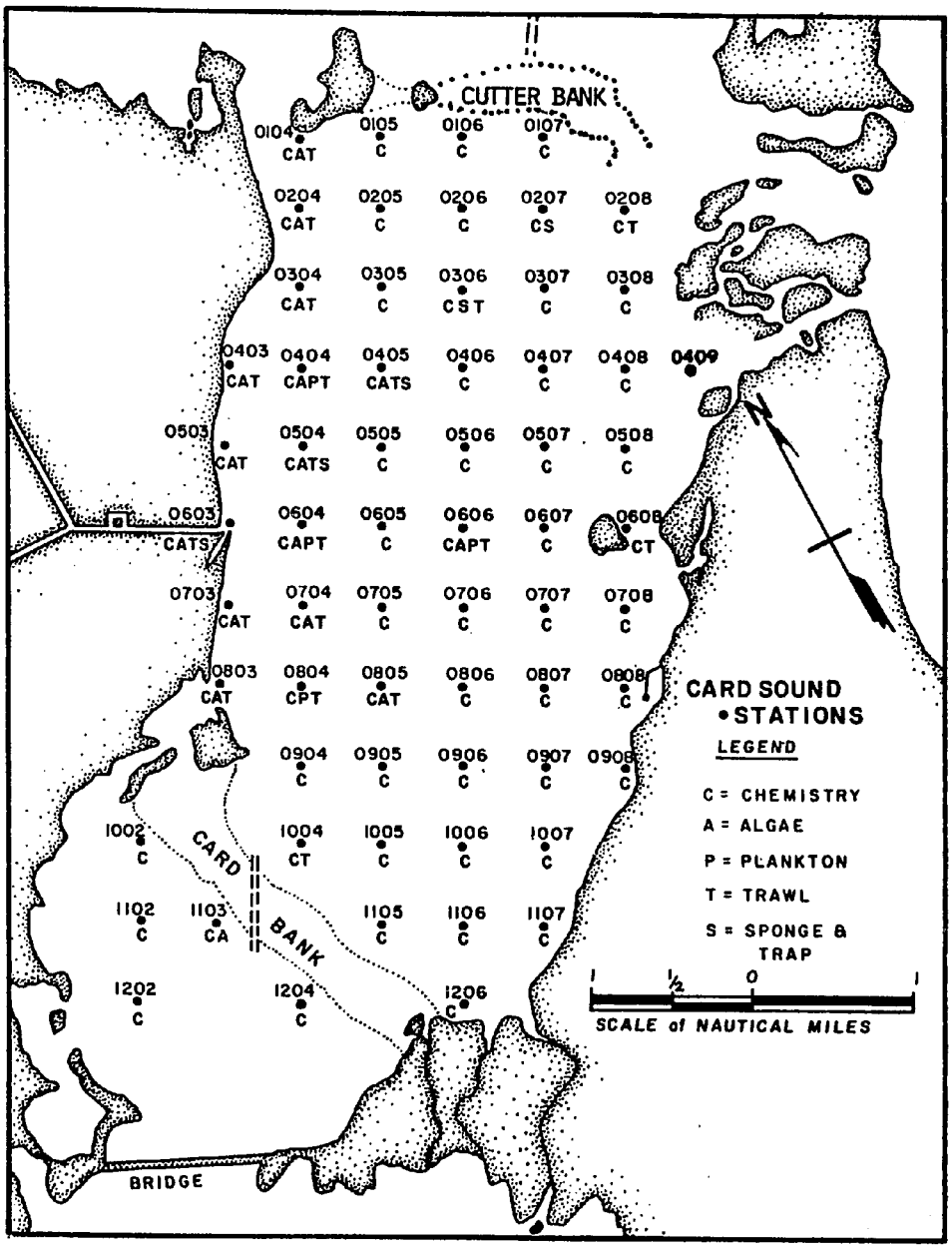

CUTTER BANK
0104 CAT
0105 C
0106 C
0107 C
0204 CAT
0205 C
0206 C
0207 CS
0208 CT
0304 CAT
0305 C
0306 CST
0307 C
0308 C
0403 CAT
0404 CAPT
0405 CATS
0406 C
0407 C
0408 C
0409
0503 CAT
0504 CATS
0505 C
0506 C
0507 C
0508 C
0603 CATS
0604 CAPT
0605 C
0606 CAPT
0607 C
0608 CT
0703 CAT
0704 CAT
0705 C
0706 C
0707 C
0708 C
0803 CAT
0804 CPT
0805 CAT
0806 C
0807 C
0808 C
0904 C
0905 C
0906 C
0907 C
0908 C
1002 C
1004 CT
1005 C
1006 C
1007 C
1102 C
1103 CA
1105 C
1106 C
1107 C
1202 C
1204 C
1206 C
CARD BANK
BRIDGE
CARD SOUND
•STATIONS
LEGEND
C = CHEMISTRY
A = ALGAE
P = PLANKTON
T = TRAWL
S = SPONGE & TRAP
1 ½ 0 1
SCALE of NAUTICAL MILES

Figure 7

Table 2. Description of stations in Card Sound used in the present study.

station	water depth* (m)	sediment type**	sediment thickness+ (cm)	relative current velocity	water clarity	Thalassia density++ (blades/m^2)	salinity (o/oo) max.+	salinity (o/oo) min.+	temperature ( ) max.+	temperature ( ) min.+
0104	0.95	sand	>100	moderate	good	5461	38.2	28.2	34.0	16.2
0106	1.60	sand	>100	high	good	-	38.2	29.4	31.0	17.0
0403	1.85	peat,sand	>100	low	good	1967	38.5	28.2	31.0	16.5
0405	3.10	sand	<15	low	good	1741	38.5	29.9	31.0	16.8
0409	1.20	1	>100	high	good	-	37.1	33.8	31.0	16.0
0507	3.20	sand	>100	low	poor	-	34.4	30.4	31.0	17.0
0604	3.30	sand	<15	low	good	825	-	-	-	-
0606	3.30	sand	<15	low	good	979	39.3	31.6	31.5	17.0
0707	3.60	silt,clay	>100	low	poor	-	39.3	30.4	31.0	17.0
0804	3.00	sand	<15	low	good	-	39.3	29.2	31.0	16.8
0805	3.30	sand	<15	low	poor	824	-	-	-	-
0905	3.90	1	>100	low	poor	-	40.1	30.4	31.0	17.5
1105	-	1	>100	low	poor	-	-	-	-	-
1107	1.55	sand,bedrock	<15	low	poor	-	40.9	30.5	31.0	17.5
1103	2.90	silt,clay	>100	low	poor	1639	33.2	29.9	31.0	17.0

* from Josselyn (1975)
** from Earley and Goodell (1968)
\+ from Wanless (1969)
++ from Thorhaug et al. (1974)
1 sand, silt and clay
\+ maximum and minimum for whole year measured at any one station and date

CHAPTER IV

METHODS

4.1 STANDING CROP MEASUREMENTS

Four separate surveys of standing crop were conducted during 1973 and 1974. The objective was to obtain an estimate of the spatial distribution of standing crop of calcareous algae within Card Sound (standing crop is here defined as that protion of the plant above the sediment). In the first survey, three 1-m^2 samples of the plants were harvested with a collapsable 1-m^2 quadrat at random locations along a 30 meter transect at 11 different stations (Figure 7). The locations along the 30 meter line were chosen from a table of random numbers and only the above ground parts of the plants harvested. After examining the results of this survey it was decided that a larger sample and a more random method would be statistically desirable. In the next survey on 12/7/73 six 1-m^2 samples were harvested using randomly chosen compass bearings and distances beginning at the center of a 10-m radius circle as the point from which to locate the squares. The center of the circle was located by placing it 15 meters in a randomly chosen bearing from the permanent buoy block at each station. The same field stations were used in this second survey. Following examination of the results of this survey it was decided to increase the sample size to twelve 1-m^2

samples in the third and fourth surveys on 3/13/74 and 7/1/74. Since this consumed much more time, only three samples were taken at stations 0409, 1007 and 0707 on 3/13/74. Twelve samples were taken at the remaining survey stations (shown in Figures 10 to 25). Following the analysis of the data from all of these first surveys it was recognized that the sample variances were too large and the samples taken too far apart in time to make seasonal comparisons possible. It was decided that seasonal variations could be determined by using another method and effort was put into using the standing crop data to determine the spatial patterns of the plants within the Sound. For this, the data gathered in surveys 2, 3 and 4 could be used. Nonparametric multiple comparison tests were used to determine differences in plant standing crop between stations.

It was also discovered that the method used in the second, third and fourth surveys might not have resulted in truly random sampling, but could have been biased towards the central point of the circle used as the starting point of the sampling. However, nearest neighbor measurements carried out on sample coordinates using graph paper (Clark and Evans, 1954) showed that the sampling procedures applied in the second, third and fourth surveys were not significantly different from random (at $p = 0.05$).

A 1-m^2 quadrat was used for harvesting the standing crop samples for several reasons. A larger quadrat (even a collaspable one) would be extremely difficult to handle underwater. Too small a quadrat suffers from increased edge effects. A 1-m^2 quadrat makes extrapolation of raw data to a 1-m^2 basis unnecessary, as would be the case if a 1/2 or 1/4-m^2 quadrat had been used. According to Greig-Smith (1964), the safest procedure is to use the smallest quadrat that is "desirable" or "practical." The ideal sampling procedure is to determine the plant distribution pattern first by grid analysis or other methods, and base the quadrat size on this, making the quadrat size smaller than the mean clump size. In actual practice the chosen quadrat size is the one that gives no more blank quadrats than quadrats with one individual (Greig-Smith, 1964). Furthermore, the size quadrat required will not be the same for different plant species and for different levels of contagion (Greig-Smith, 1964). In most studies a compromise of some sort must be reached therefore with respect to the size of the quadrat used. In the present study the use of the 1-m^2 quadrat represents this compromise since it was not possible to investigate all the above mentioned factors which affect the results of random sampling.

4.2 BELT TRANSECTS

To examine the relationship of the distribution of

the plants to the depth of the mangrove peat sediment wedge lying close to the shoreline of Card Sound (Figure 4) as well as to the peat lying in the numerous solution holes scattered all over the Sound (Figure 4), line transects were set up perpendicularly to the shoreline at 2 separate locations along the shore and across several peat filled circles farther out from shore (Figure 4). A stake was placed in the sediment (or a lead weight used where no sediment existed) and a 1/8-inch polypropylene line laid out and staked at the end of the transect. A 1-m^2 aluminum frame was used to count all the calcareous algae along the belt transect. The square was turned over continuously and every other square counted to provide greater statistical efficiency as well as to cut down on underwater time. The shoreline transects were 60 meters long and the peat bed transects 30 meters long. On the peat bed transects a 1/4-m^2 quadrat was used because of the high density of P. capitatus in the area. Line transects were counted out from shore at stations 0203 and 0303, and peat bed transects counted at stations 0304, 0504 and 0604.

4.3 SPATIAL AND TEMPORAL PATTERNS OF GROWTH AND YIELD

4.3.1 Definition of Terms

The production terminology used in the present study follows the recommendations of the International Seagrass Workshop, held in October, 1973 by the International

Decade of Ocean Exploration (McRoy and Helssfrich, in press). The workshop recommended the use of the terminology of Westlake (1963) in production studies by all future workers in seagrass related studies to provide for clarity and improved communication of information. The following definitions have therefore been adopted:

Standing crop: "The weight of plant material that can be sampled or harvested by normal methods, at any time from a given area..." (Westlake, 1963). This does not include portions of the plant that are beneath the sediment. If all the plant were harvested both above and below the sediment, including roots and rhizomes, the sample would be termed a biomass sample. In the present study only the standing crop was measured.

Crop: The total dry weight of plant material that has been removed from a certain area over a period of time. In the present study, replicate 1-m^2 samples were employed.

Yield: The crop expressed as harvested weight per unit time.

Ash-free dry weight: ash-free dry weight = (total dry weight) - (carbonate) - (ash left after decalcified plants ignited in muffle furnace at 550^{o}C for 1 hour) Carbonate was removed by soaking the plants in 25 percent glacial acetic acid for 1 hour. Twenty decalcified plants of each species were ashed, and from 30 to 60 plants of

each species were decalcified to determine percent carbonate.

Growth: In this study growth refers to the emergence of individual plants through 1 x 20-m strips of clear 1.25 cm mesh monofilament net staked on the bottom of Card Sound over a specified time period. The plants were allowed to grow through the net for 8 weeks and then the portion which was above the net was harvested. In the case of H. incrassata,growth was found to be in the form of individual "branches" sporadically emerging through the netting. Thus, growth of H. incrassata was uncorrected for losses due to death and sluffing off of plant material. These losses as well as growth that may have occurred under the net were estimated separately, and were considered when calculating the yield of H. incrassata.

4.3.2 Yield Estimates Based on Direct Harvest Method

Every 8 weeks for a year, all the P. capitatus, R. phoenix and U. flabellum which grew through net strips located at stations 0104, 0106, 0403, 0409, 0606 and 0805 were harvested with a 1-m^2 frame. One mesh strip was placed on the bottom at each station. The frame was placed at one end of the strip and all the plants were collected in succession by turning over the frame until 15 to 20 samples had been taken. All plant material was stored in Whirlpak plastic bags on ice and

returned to the laboratory where they were frozen until weighed. In the laboratory the plants from each square meter were sorted according to species and dried at 80°C to constant weight in preweighed aluminum foil tares. All plants were weighed immediately after removal from the oven to avoid absorption of atmospheric moisture.

After harvesting, each 1 x 20-m monofilament strip was cleaned with a brush and restaked in an adjacent position on the bottom. All strips were purposefully oriented in a north-south position at each station.

4.3.3 Yield Estimates Based on Life-Span and Standing Crop

An alternate method of estimating the yield of P. capitatus, R. phoenix and U. flabellum involved combining the estimates of life span and standing crop. This method estimated the yield in g dry weight/m^2/year by multiplying the mean g dry weight/m^2 by the mean number of plant generations/year according to the following formula:

$$\text{g dry wt}/m^2/\text{yr} = (\text{g dry wt}/m^2{}^*)(\text{crops/yr}^{**})$$

* mean standing crop of all four surveys
** based on life span observed in tagging study

Since H. incrassata produced plant material by sporadic bursts of growth this method was not applied to this plant.

Determinations of life spans were made by tagging plants inside two 1-m^2 frames placed on the bottom at each of five stations in Card Sound. The plants were

marked with a numbered plastic tag made from a DYMO labeling device. The condition of a total of over 800 plants was observed at five stations every two weeks for 15 months. Plant condition was recorded as "mature," "senescent," "completely senescent" or "juvenile." This classification is based on the terminology of Thorhaug (1974a). Any other noticeable features of the plants' condition was also recorded. If a fully grown plant was green and showed few signs of decay or extensive epibiontic overgrowth it was called "mature." If a plant was pale white or pale green and decaying away it was recorded as being "senescent." Often plants were found which were intermediate between mature and senescent. These plants were green, with parts decaying away and epiphytic algae growing on them, and were classified as senescent since they usually died shortly after reaching this state. By the time the plant turned completely white is was considered completely senescent. Thus, the "life span" was based on the point of which I called "complete senescence," not "senescent," since senescent plants might still be alive. It should be noted that "dead" in this case is a purely relative term since the rhizoidal system of the plant was probably alive and producing a new plant a short distance away.

4.3.4 Yield Estimates Based on Growth and Density of *Halimeda*

Growth measurements of individual *H. incrassata*

and H. monile plants were combined with the density data from the standing crop surveys to obtain an estimate of yield. Early efforts of measuring growth centered on tagging individual H. incrassata branches and measuring increases in the number and weight of plates, but these methods were abandoned because fish and urchins removed the tags. Consequently, the growth of individual H. incrassata and H. monile plants through the monofilament net was used as the basis for estimating yield. The production of the whole plant was calculated by combining estimates of growth above and below the mesh with adjustments for losses of dead plant material incurred during the growth period.

Visual estimates in the field showed that about 75 percent of the average H. incrassata plant was above the mesh at the end of an 8 week period. Therefore, approximately 25 percent of the growth that occurred in the whole plant was unaccounted for. However, visual observations also showed that only about 10 percent of the growing tips were beneath the mesh at the end of the harvest period, since most of the plant under the mesh was stalk material. As a compromise it was assumed that about 15 percent of the total amount of growth occurred beneath the mesh.

To estimate the amount of plant material lost during the growth period, 1.5 mm mesh nylon bags were tied over

38 H. incrassata plants at station 0106. These plants were harvested, returned to the laboratory, and the portion of the plant which grew through the bag was separated from the portion inside the bag. The material inside the bag was sorted into white plates representing dead material lost during the measuring period and live green material. Since growth was vigorous and comparable to the growth measured by the monofilament it was felt that the effect of the bags was minimal. The bag experiment showed that 24.6±9.7 percent of the total average individual plant weight was lost as dead plates over a period of 40 days (from 9/6/74 to 10/15/74).

Growth in g dry weight/plant/day was calculated by dividing the number of grams produced above the net by the number of days of growth and then multiplying this figure by 1.4 to account for the loss of dead plant material and the growth estimated to occur under the net. Estimates of yield in g dry weight/m^2/day were made by multiplying the density by the growth/plant for each station and date. The following formula summarizes this method:

$$\text{g dry wt/m}^2\text{/day} = (\text{g dry wt/day/plant}^*)(\text{plants/m}^{2**})(1.4^{***})$$

* mean for each harvest period

** mean for all four surveys for each station

*** correction factor to account for growth under net and losses of dead plant material

To determine the number of samples required to show a significant difference in growth between any two stations, Snedecors' (1967) formula for required sample size was used:

$$n = \frac{4s^2}{L^2}$$

in which n equals the required sample size to show a significant difference between two means of variance s^2 and L equals the smallest amount of difference desired to be detected between the two means. Usually L = 5 percent of the mean. The decision that had to be made in the present study was the magnitude of L that could be accepted in the growth measurements. It was soon discovered that a large amount of variation was present in the data and that to detect a 5 percent difference in the means of the growth at most stations would require a number of samples beyond the capabilities of the resources available. Fifty, the final sample size used, represented a compromise between time, available resources and the number recommended by the formula. Once the results were assembled a basic data description was performed on the data from each station. This included calculation of mean, median, variance, standard deviation, coefficient of variation and the Kolmogorov-Smirnov goodness of fit to a normal distribution (Sokal and Rohlf, 1969). A logarithmic ($\log_{10}$) transformation was

used since the data were not normal in many cases and the variances were heterogenous. The transformation was employed because the Student-Newman Keuls test assumes that the data are normally distributed and that the variances of the different samples to be compared are statistically equal. Following transformation the data were retested for normality and homogeneity of variances. The Student-Newman Keuls multiple comparison test (Sokal and Rohlf, 1969) was employed to determine specific differences in individual plant growth between stations and dates.

4.4 GRAZING EXPERIMENTS

To study the extent and nature of grazing on the algae several enclosure and exclosure experiments were performed using metal cages. In the first field experiment, 8 metal cages were placed in a row on the bottom at station 0106, where many urchins, (Lytechinus variegatus) had been observed. The cages were made from wire fencing material 1.25 cm in mesh and measured 10-m x 0.5-m x 0.5-m. In the field, the cages were positioned 1 meter apart in a row and all the calcareous macroalgae inside numbered with plastic tags. Three L. variegatus were placed inside each of 4 cages, and no urchins were placed in the other 4 cages. The cages were visited every two weeks for four months and the condition of the plants were recorded. Observations of unprotected plants were

also made in the regular tagging frames. The health of each plant was noted as mature, senescent or completely senescent. Any change in the general appearance of the plants was also recorded.

In a separate experiment to determine if "knobby" morphology observed in many plants was associated with grazing by L. variegatus, 20 "healthy" H. incrassata that did not have the "knobby" appearance were transplanted into a single cage at station 0106. Ten L. variegatus were placed inside the cage with the algae and allowed to feed over the next two weeks, after which the urchins were removed. The condition of the algae in the cages were recorded every two weeks for two months. Observations of the condition of the plants were also made in the permanent square at station 0106 in an attempt to correlate the increased numbers of L. variegatus with "knobbiness."

L. variegatus were also kept in the laboratory and fed P. capitatus and H. incrassata to see if they were capable of consuming the plant material and therefore substantiate the field observations that grazing did occur. They were kept for 2 weeks in a 10 gallon flow-through seawater tank in the laboratory and were fed calcareous algae daily.

4.5 SEDIMENTS

Some data on the sediment distribution is already

available for most of Card Sound (Earley and Goodell, 1968) but a more detailed particle analysis was desired specifically for the stations in the present study. The author collected a single core sample from each of the 16 stations and Mr. Michael Josselyn carried out a particle size analysis of each core.

4.6 ENVIRONMENTAL FACTORS

Temperatures were recorded with a thermometer at each of 16 stations every two weeks throughout the study period. Temperatures were recorded at each station encountered during the course of day in the field. This corresponded to between 9 A.M. and 4 P.M. on an average field day. Consequently, no effort was made to take the measurements during a particular tidal cycle or time of day. Temperatures were recorded on the bottom with a mercury thermometer accurate to within $0.1^{o}C$.

The same procedure applied to salinity samples, which were taken at each station every two weeks. Samples were taken at each station as they were encountered in the course of the day, and were taken in Nalgene plastic bottles, stored in a cooler and returned to the laboratory. Samples were thus taken throughout the day, and no effort was made to sample within the same cycle for any given sampling day. Salinity in parts per thousand (ppt) was determined by using an American Optical Company refractometer.

Solar radiation data was obtained from the records of Subtropical Testing Service in South Miami. Solar radiaiton was continuously measured with an Eppley pyrheliometer at this facility. For the purposes of this study the daily rates were used as a basis to calculate weekly mean values of solar radiation.

CHAPTER V

RESULTS

5.1 ENVIRONMENTAL FACTORS

Temperature minima and maxima as recorded in the field from August, 1972 to May, 1975 for all stations in Card Sound are given in Figure 8. Temperatures dropped from 29 to 30°C in August to 16 to 19.5°C in December, 1973. They then rose until the next summer peak was reached in July-August, 1974 (30 to 34°C). The highest temperature of 34°C was recorded only on one date at station 0104. Another winter low of 18.5 to 20.0°C was recorded in December, 1974. The seasonal cycle is obvious from the graph in Figure 8.

Salinity never dropped below 24 ppt (parts per thousand) during the study period (Figure 8). Lower salinities coincided with the peak of the rainy season in September-October, although the salinity was much lower in September-October, 1973 than in September-October, 1974 (Figure 8). Salinities generally rose during the winter months in the dry season and then began to drop by September.

Solar radiation data in Langleys per day were obtained from Sub-tropical Testing Service, Inc., of south Miami, Florida. Weekly averages of the mean daily values of solar radiation were calculated and are presented in Figure 8. Two annual peaks in solar

Figure 8. Top: water temperature maxima and minima (in ^{o}C) observed in Card Sound, Florida, from August, 1973 to May, 1975. Temperatures were measured on the bottom with a mercury thermometer at each station. Maximal and minimal temperatures are for all stations observed on each date. Middle: Mean salinity in parts per thousand recorded at each station in Card Sound, Florida from September, 1973 to May, 1975 (mean of 16 stations on each date). Bottom: mean weekly solar radiation in Langleys/day recorded at Subtropical Testing Service in south Miami, Florida. Measurements made with an Eppley pyrheliometer.

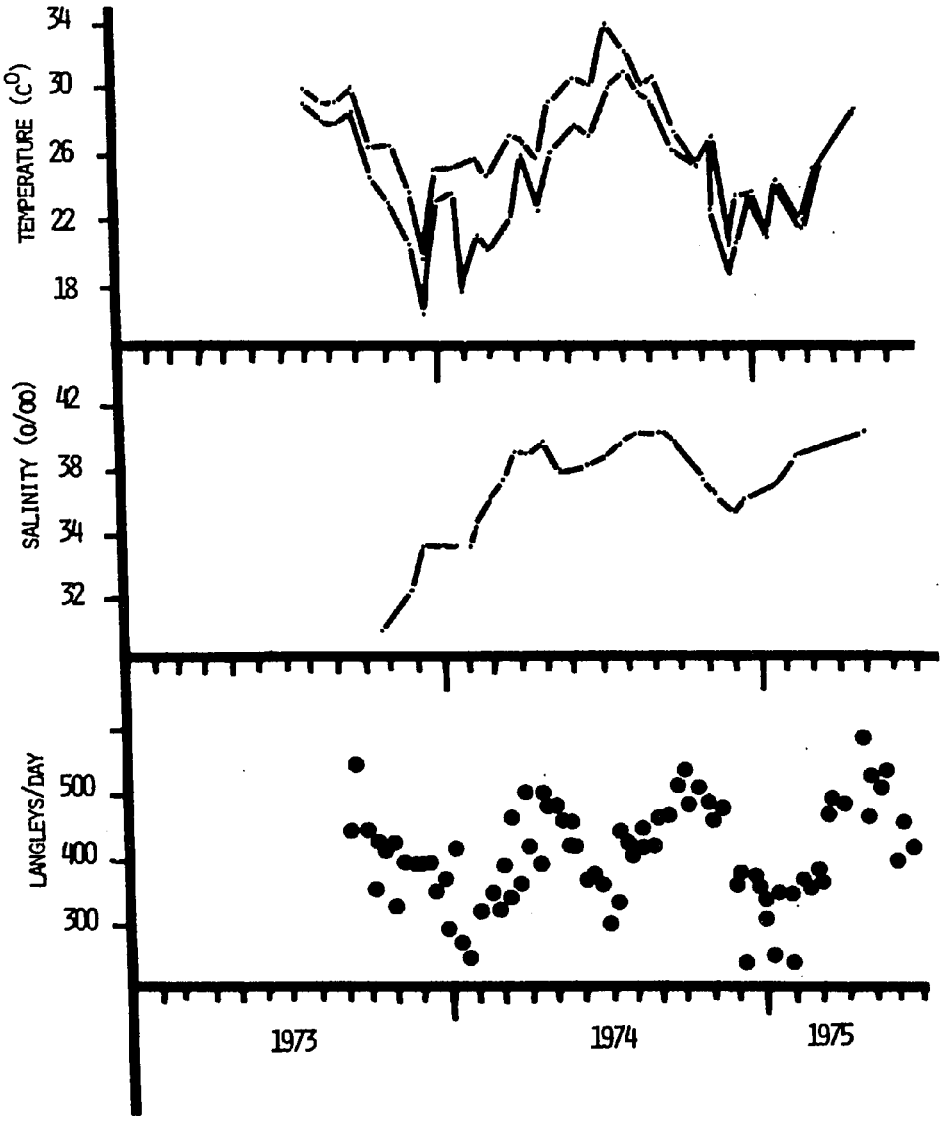

TEMPERATURE (C°)
34
30
26
22
18
SALINITY (0/00)
42
38
34
32
LANGLEYS/DAY
500
400
300
1973
1974
1975

Figure 8

Figure 9. Particle size analysis of Card Sound sediments. Vertical axis on graphs is the percentage composition of each particle size class out of 100%. The horizontal axis represents the particle size classes. Note the very fine particle size at station 1103 and the coarser sediments in mid-south areas. Samples collected by S. Bach and analyzed by M. Josselyn. Figure taken from Josselyn, 1975.

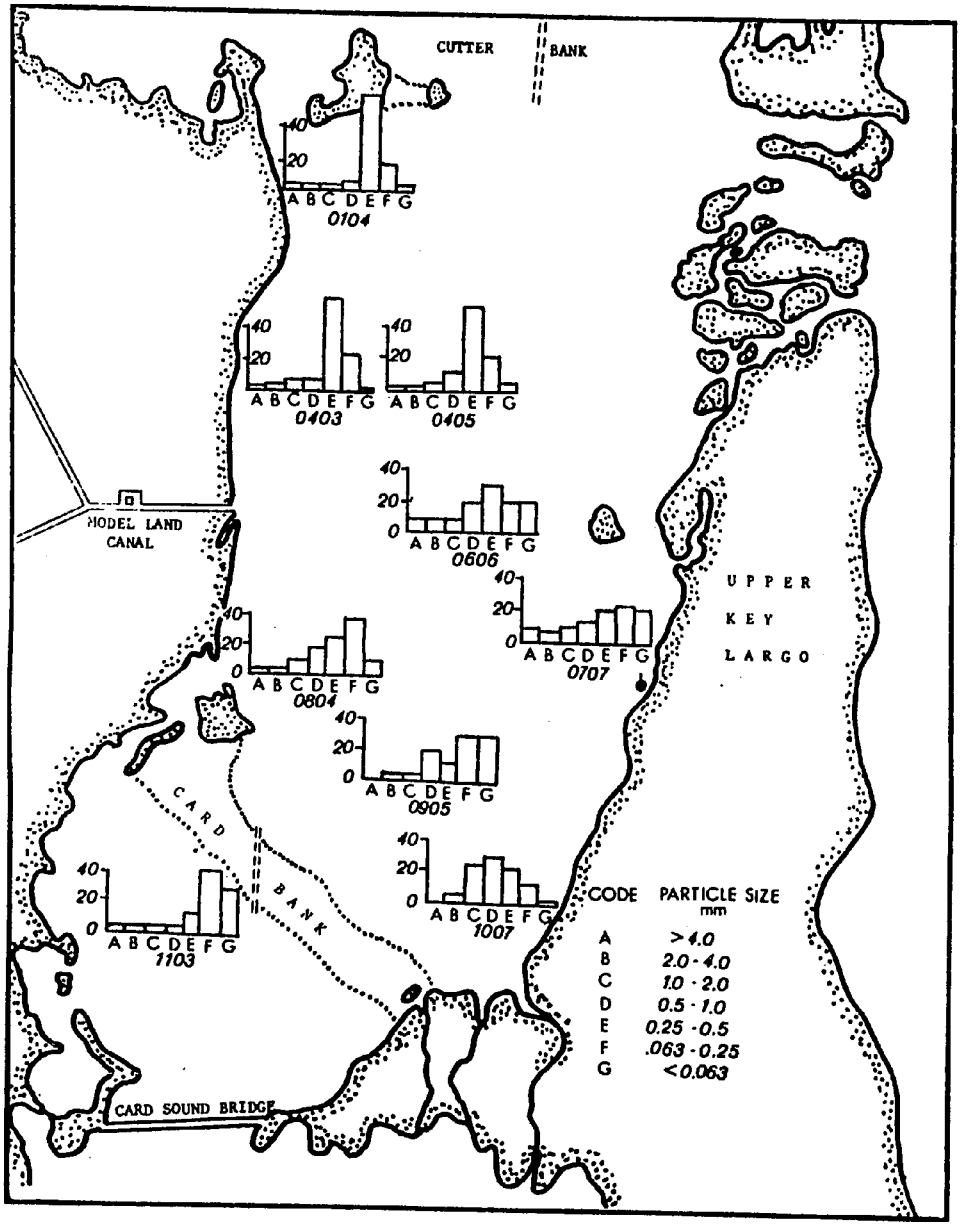

CUTTER
BANK
0104
0403
0405
0606
0707
0804
0905
1007
1103
MODEL LAND
CANAL
UPPER
KEY
LARGO
CARD
BANK
CARD SOUND BRIDGE
CODE PARTICLE SIZE
mm
A >4.0
B 2.0 - 4.0
C 1.0 - 2.0
D 0.5 - 1.0
E 0.25 - 0.5
F .063 - 0.25
G <0.063

Figure 9

radiation were evident, one in March-April, and one in September-October, 1974. Seasonal lows in solar radiation were recorded in December-January and in June-July. The low points in solar radiation corresponded to the increased cloudiness during the passage of normal winter cold fronts, and the buildup of clouds which occurs during the summer rainy season.

5.2 SEDIMENTS

The results of the sediment particle analysis are given in Figure 9. The most important trends are the gradual increase in fine particles in southern Card Sound and the coarser sediments in mid northern Card Sound.

5.3 STANDING CROP AND DENSITY MEASUREMENTS

5.3.1 Determinations of Ash-Free Dry Weight and Percentage Carbonate

Table 3 summarizes the results of the determinations of ash and carbonate content. To determine the percentage carbonate, preweighed specimens of each algal species were soaked in approximately 100 cc of 25 percent glacial acetic acid in individual beakers for 1 hour, and the dry weight loss determined by redrying and reweighing each specimen. Percentage calcium carbonate was calculated by dividing the dry weight loss by the original dry weight of each plant and then multiplying the resulting number by 100. Means and standard deviations

Table 3. Organic and calcium carbonate content of calcareous macroalgae from Card Sound, Florida. The percentage carbonate is based on loss of weight following treatment of plants with 25 percent acetic acid for 1 hour. Ash content is based on weight loss of decalcified plant material after ignition in a muffle furnace at 550°C for 2 hours. Total ash content = mean percent ash content of decalcified plants + mean percent $CaCO_3$ content.

Algal Species	number of replicates	mean % $CaCO_3$ content ± SD*		number of replicates	mean % ash content of decalcified plants ± SD		total % ash content*
Halimeda Incrassata	50	25.57	4.14	28	1.27	0.66	26.84
Penicillus capitatus	52	40.98	7.37	32	1.73	1.24	42.71
Rhipocephalus phoenix	31	52.95	13.27	20	3.78	1.78	56.73
Udotea flabellum	37	34.06	11.54	16	2.58	2.06	36.64
Halimeda monile	18	15.99	3.05	15	1.27	0.81	17.26

* % of dry weight

presented in Table 3 thus are based on differences between individual plants.

Ash content normally would be measured by determining the dry weight loss following ignition at 550°C (Westlake, 1963). However, carbonate loss occurs above 350°C and the percentage ash content of decalcified material had to be determined and then added to the percent carbonate to give the total ash content. In the present study, individual plants were first decalcified as described above, rinsed in fresh water and re-dried in an oven to constant weight at 105°C. These plants were weighed and then ignited in a muffle furnace at 550°C and the dry weight loss determined. The dried decalcified plants were left in the oven at 550°C for two hours. The material remaining following ignition represented the ash content of the decalcified plants. This percentage was added to the percent of calcium carbonate to give the estimated of total ash content as shown in Table 3.

5.3.2 Standing Crop of Halimeda Incrassata

A summary of the standing crop and density data for this species is provided in Figures 10 and 11. Large variation in the standing crop and density was observed in all four surveys, despite the fact that more samples were taken in the later surveys. The coefficients of variation recorded in all 4 surveys

Figure 10. Standing crop of Halimeda incrassata in Card Sound, Florida, on September, 1973 (left) and December, 1973 (right). Standing crops are given in a g dry wt/m^2 ± 1 SD for each station sampled. For September, 1973, n=3; for December, 1973, n=6 samples at each station.

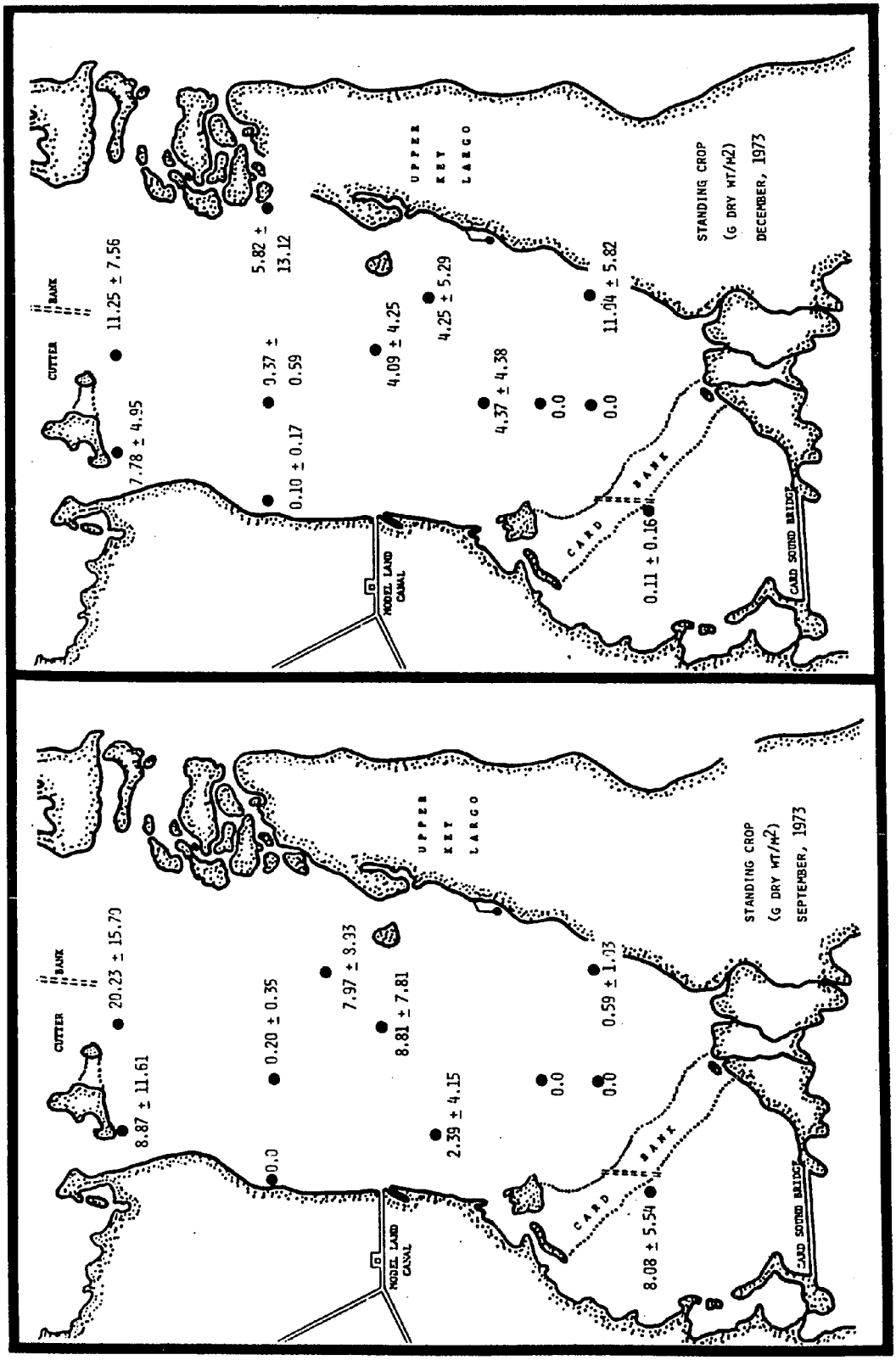

CUTTER BANK
20.23 ± 15.70
8.87 ± 11.61
0.20 ± 0.35
0.0
7.97 ± 8.33
8.81 ± 7.81
2.39 ± 4.15
0.0
0.0
0.59 ± 1.03
8.08 ± 5.54
CARD BANK
MODEL LAND CANAL
CARD SOUND BRIDGE
UPPER KEY LARGO
STANDING CROP
(G DRY WT/M2)
SEPTEMBER, 1973
CUTTER BANK
11.25 ± 7.56
7.78 ± 4.95
0.37 ± 0.59
0.10 ± 0.17
5.82 ± 13.12
4.09 ± 4.25
4.25 ± 5.29
4.37 ± 4.38
0.0
0.0
11.04 ± 5.82
0.11 ± 0.16
CARD BANK
MODEL LAND CANAL
CARD SOUND BRIDGE
UPPER KEY LARGO
STANDING CROP
(G DRY WT/M2)
DECEMBER, 1973

Figure 10

Figure 11. Standing crop of Halimeda incrassata in Card Sound, Florida, on March, 1974 and July, 1974. n=12 for all stations except 0409, 0707 and 1007 on March, 1974 (n=3 for these stations on March, 1974). n=12 for all stations on July, 1974. See Figure 10 for explanation of data.

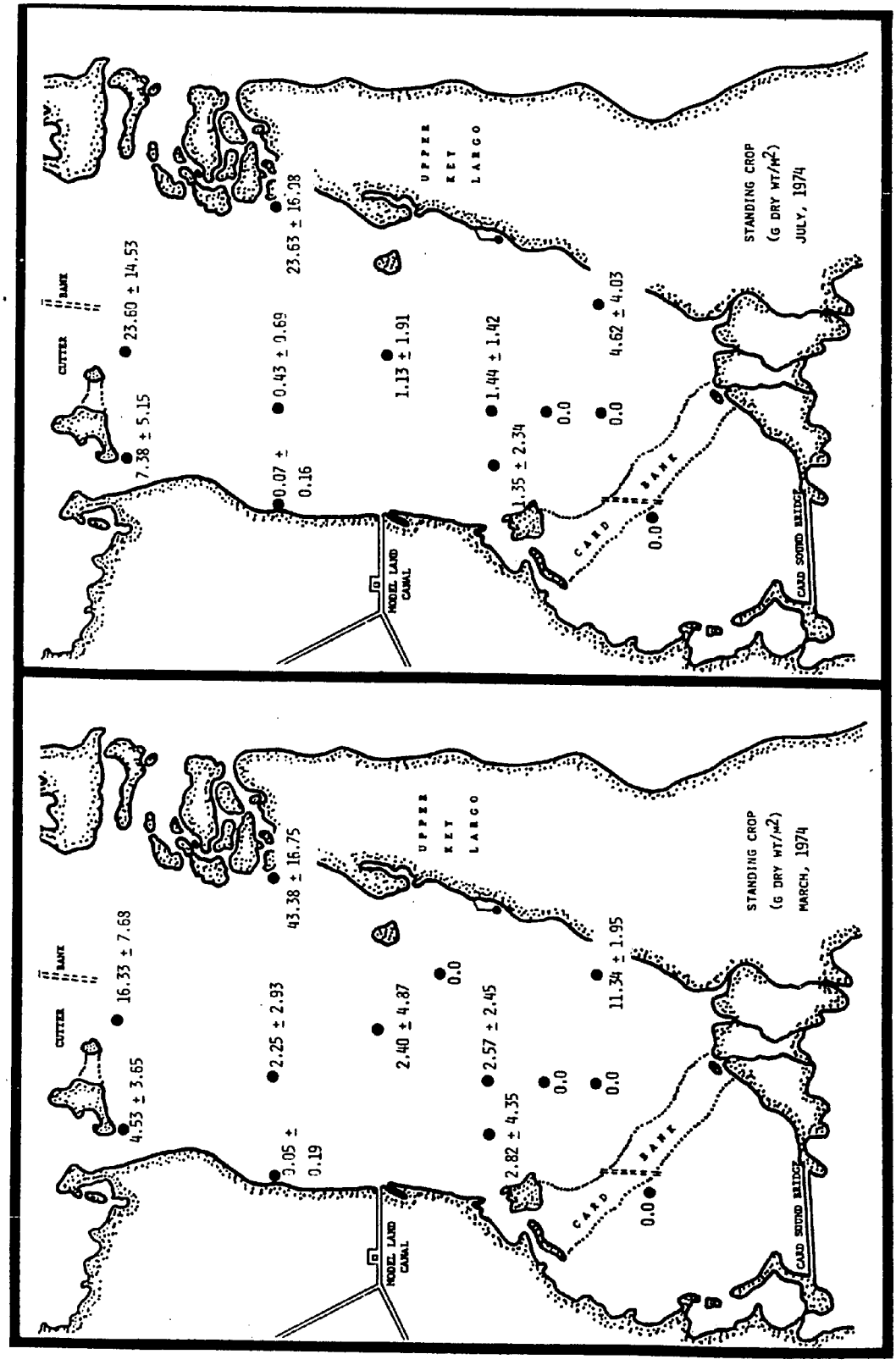

CUTTER
BANK
16.33 ± 7.68
4.53 ± 3.65
2.25 ± 2.93
3.05 ± 0.19
43.38 ± 16.75
2.40 ± 4.87
0.0
2.57 ± 2.45
2.82 ± 4.35
0.0
0.0
11.34 ± 1.95
UPPER KEY LARGO
MODEL LAND CANAL
CARD BANK
CARD SOUND BRIDGE
STANDING CROP (G DRY WT/M2) MARCH, 1974
CUTTER
BANK
23.60 ± 14.53
7.38 ± 5.15
0.07 ± 0.16
0.43 ± 0.69
23.63 ± 16.38
1.13 ± 1.91
1.44 ± 1.42
1.35 ± 2.34
0.0
0.0
4.62 ± 4.03
0.0
UPPER KEY LARGO
MODEL LAND CANAL
CARD BANK
CARD SOUND BRIDGE
STANDING CROP (G DRY WT/M2) JULY, 1974

Figure 11

ranged from 47.03 to 346.4 percent. Both values of this range were observed in the survey in March 1974 (n = 12). A nonparametric a posteriori multiple comparison procedure (Sokal and Rohlf, 1969) was applied to the data of July 1974 to test for differences in standing crop between different stations (Figure 12). The test indicated that the data can be grouped as follows with respect to the relative standing crop at each station:

0403, 0905, 1005, 1103	<	0104, 0405, 0606 0804, 0805, 1007	<	0106 0408

Overlapping occurred within the intermediate range group and the results were that standing crop at station 0405 was significantly greater than 0104 and 1007 when compared on a paired basis. These results agree with subjective field observations.

In conclusion, statistical analysis and field observations showed that the mean standing crop of H. incrassata at stations 0106 and 0408 was higher than all the rest of Card Sound. The mean standing crop varied from 5.82 to 43.38 g dry wt/m^2 at these two stations. Intermediate size populations were found at stations 0104, 0405, 0606, 0804 and 1007 and much lower standing crops were found at stations 0403, 0405, 0905 and 1005.

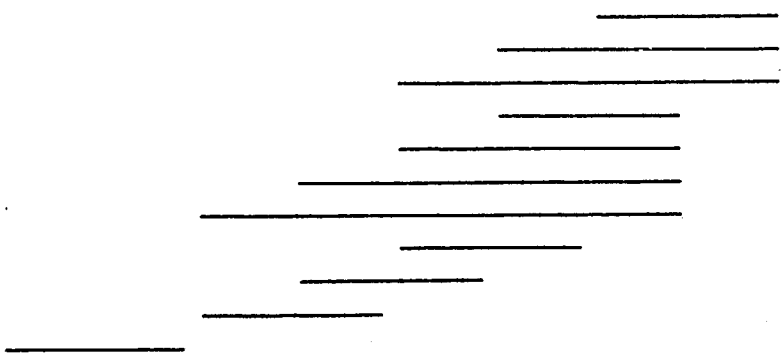
Figure 12. A posteriori nonparametric comparison test applied to Halimeda incrassata standing crop data from July, 1975 (after Sokal and Rohlf, 1969). Asterisked value in grid indicates significant difference ($p<0.05$) between two stations shown. (U_s critical = 125.7)

Summary of U_s Values

stations	0104	0106	0403	0405	0408	0606	0804	0805	1007
0104									
0106	134*								
0403	144*	144*							
0405	143*	144*	142*						
0408	126*	78	144*	143*					
0606	124	144*	144*	102*	140*				
0804	134*	144*	142*	103	138*	98			
0805	132*	144*	142*	115	139*	102	94		
1007	98	143*	144*	139*	131*	121	131*	144	

Grouping: Lines connect maximum nonsignificant ranges of means.

0408 0106 0104 1007 0805 0804 0606 0405 0403



5.3.3 Standing Crop of Halimeda Monile

A summary of the standing crop and density data for H. monile is provided in Figures 13 and 14. The standing crop of H. monile was much less than that of H. incrassata at every station.

From the nonparametric multiple comparison (Sokal and Rohlf, 1969) test applied to the data (Figure 15) the following conclusions can be drawn:

1. The mean standing crop of H. monile was significantly less ($p<0.05$) at stations 0104, 0403, 0405 and 0408 than at stations 1007, 0606, 0804, 0106 and 0805.

2. The mean standing crop was greater at stations 0106 and 0805 than at 1007.

3. Due to overlapping no further differences were discernable.

4. The anomalous "difference" between the standing crop at station 0409 and all other stations was caused by a single sample with a large standing crop at this station.

5.3.4 Standing Crop of Halimeda Opuntia

This species was the least abundant one recorded in the surveys, although visual observations showed that high standing crops existed in a few relatively small areas of bare rock and high tidal current velocity near Card Sound Bridge, East Arsenicker Key and in quiet water areas on rockey bottom at station 1007. H. opuntia

Figure 13. Standing crop of Halimeda monile in Card Sound, Florida, on September, 1973, and on December, 1973. See Figure 10 for rest of legend.

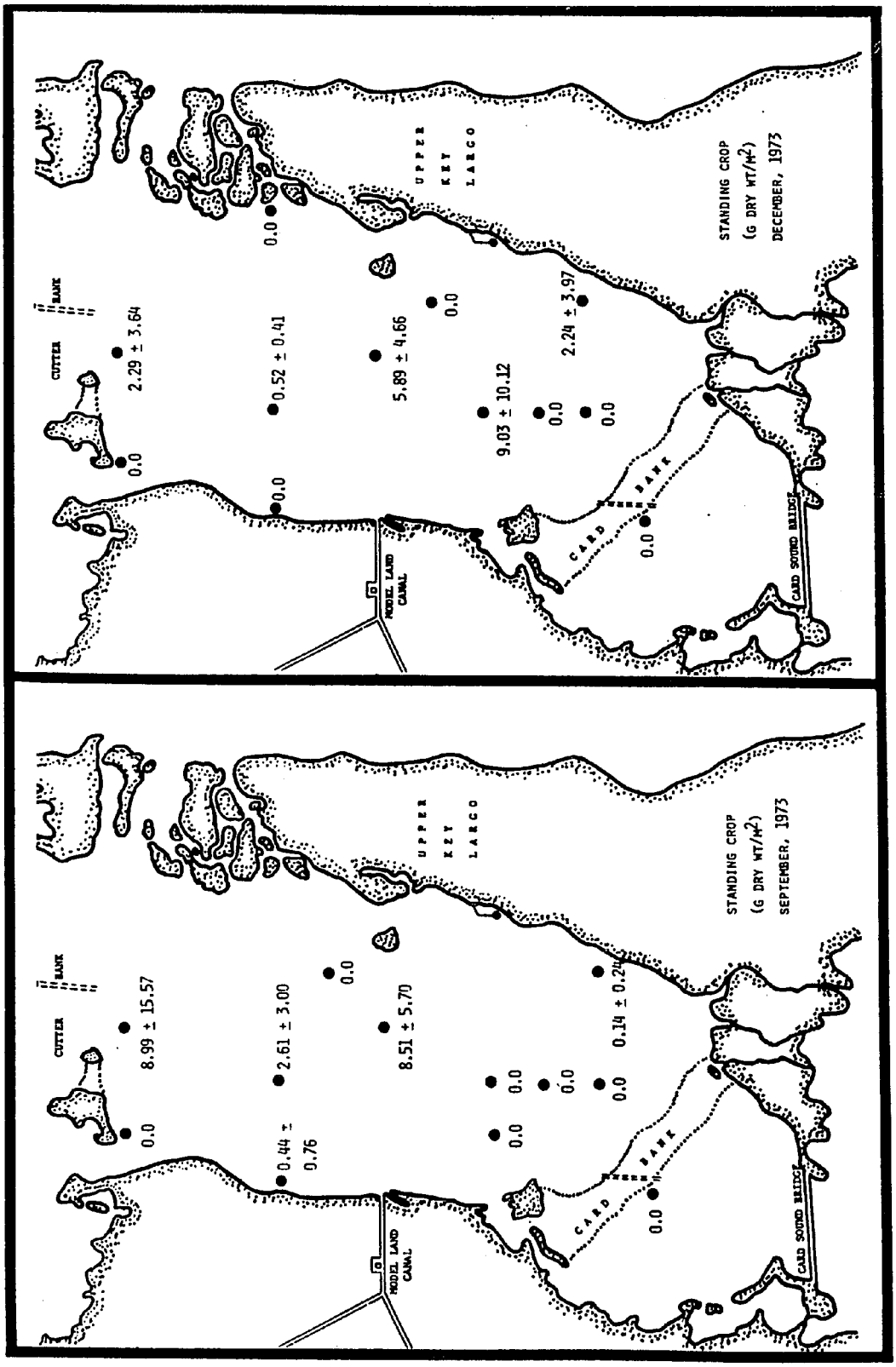

STANDING CROP
(G DRY WT/M²)
SEPTEMBER, 1973
STANDING CROP
(G DRY WT/M²)
DECEMBER, 1973
UPPER KEY LARGO
CARD BANK
CARD SOUND BRIDGE
MODEL LAND CANAL
CUTTER BANK
0.0
8.99 ± 15.57
0.44 ± 0.76
2.61 ± 3.00
8.51 ± 5.70
0.14 ± 0.24
2.29 ± 3.64
0.52 ± 0.41
5.89 ± 4.66
9.03 ± 10.12
2.24 ± 3.97

Figure 13

Figure 14. Standing crop of Halimeda monile in Card Sound, Florida, on March, 1974, and on July, 1974. See Figure 11 for rest of legend.

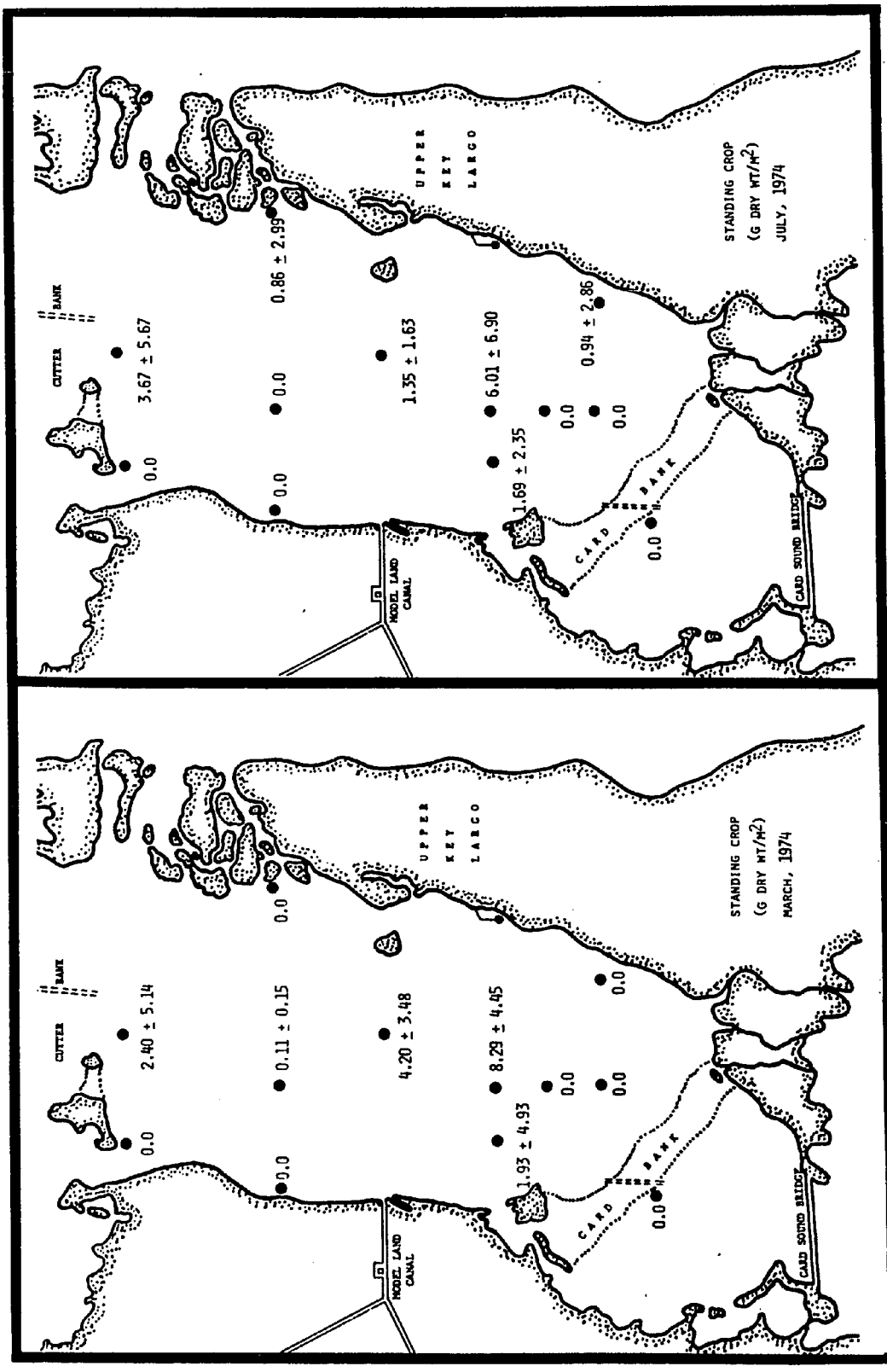

STANDING CROP
(G DRY WT/M²)
MARCH, 1974
STANDING CROP
(G DRY WT/M²)
JULY, 1974
UPPER KEY LARGO
CARD BANK
CARD SOUND BRIDGE
MODEL LAND CANAL
CUTTER BANK
0.0
2.40 ± 5.14
0.11 ± 0.15
4.20 ± 3.48
8.29 ± 4.45
1.93 ± 4.93
3.67 ± 5.67
0.86 ± 2.99
1.35 ± 1.63
6.01 ± 6.90
1.69 ± 2.35
0.94 ± 2.86

Figure 14

Figure 15: A posteriori nonparametric comparison test applied to Halimeda monile standing crop data from July, 1974 (after Sokal and Rohlf, 1969). Asterisked value in grid indicates significant difference ($p<0.05$) between two stations shown. (U_s critical = 125.7)

Summary of U_s Values

stations	0409	1007	0606	0804	0106	0805
0409						
1007	132*					
0606	132*	125				
0804	132*	124	80			
0106	134*	126*	96	80		
0805	134*	131*	133	115	106	

Grouping: Lines connect maximum nonsignificant ranges of means

0104 0403 0405 0409 1007 0606 0804 0106 0805

was consistently found growing attached to rocky or hard substrates, unlike H. monile and H. incrassata, which were found most commonly in areas of deeper sediment or in mid-sound areas of non-accumulation and <15 cm of sediment. A very low (<3 g dry wt/m^2) standing crop was recorded in the rocky area at station 0403 on the western shoreline of Card Sound. The results of the surveys are shown in Figures 16 and 17.

5.3.5 Standing Crop of Penicillus capitatus

The standing crop and density of P. capitatus was greatest at stations 0804, 0805 and 0606 (Figures 18 and 19). However, large temporal and spatial changes in the populations were observed. For example the standing crop of P. capitatus was 23.3 ± 4.5 g dry wt/m^2 at station 0606 in the survey in September, 1973 and 18.14 ± 25.76 g dry wt/m^2 in December, 1973. However, by March 1974 the standing crop had dropped to 4.89 ± 2.42 g dry wt/m^2 at station 0606 and plants had virtually disappeared from the area by July, 1974. The standing crop was only 0.05 ± 0.73 g dry wt/m^2 by July, 1974. The density of plants had fallen from 56.7/m^2 ± 4.0/m^2 on September, 1973 to only 1.8/m^2 ± 1.7/m^2 in July, 1974. Visual observations every two weeks throughout this time period confirmed this pattern. A nonparametric multiple comparison test carried out on the data (Figure 20) showed that there was significantly greater standing

Figure 16. Standing crop of Halimeda opuntia in Card Sound, Forida, in September, 1973 and December, 1973. See Figure 10 for rest of legend.

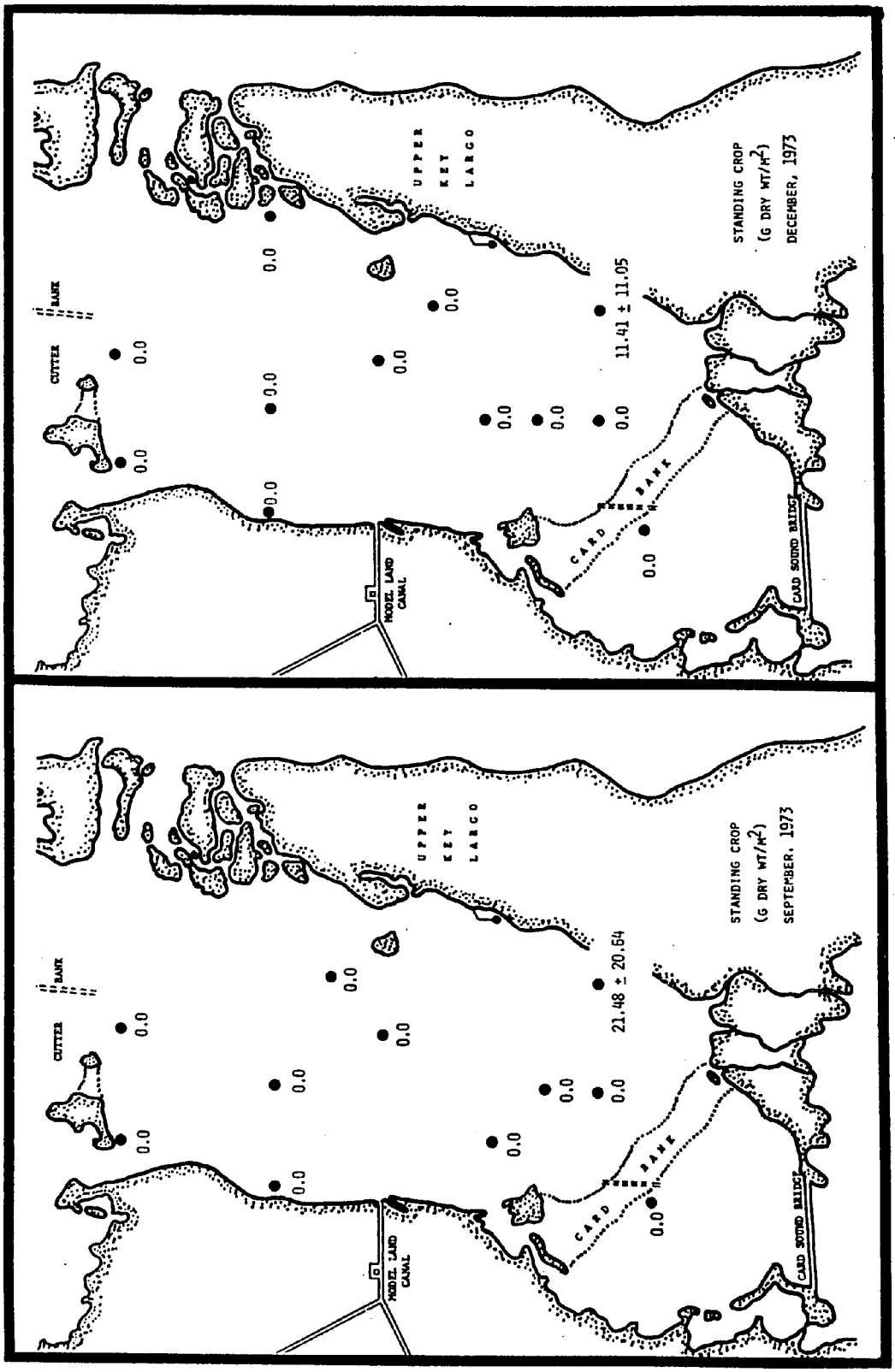

STANDING CROP
(G DRY WT/M²)
DECEMBER, 1973
STANDING CROP
(G DRY WT/M²)
SEPTEMBER, 1973
UPPER KEY LARGO
CARD BANK
CARD SOUND BRIDGE
MODEL LAND CANAL
CUTTER BANK
11.41 ± 11.05
21.48 ± 20.64
0.0

Figure 16

Figure 17. Standing crop of Halimeda opuntia in Card Sound, Florida, on March, 1974, and on July, 1974. See Figure 11 for rest of legend.

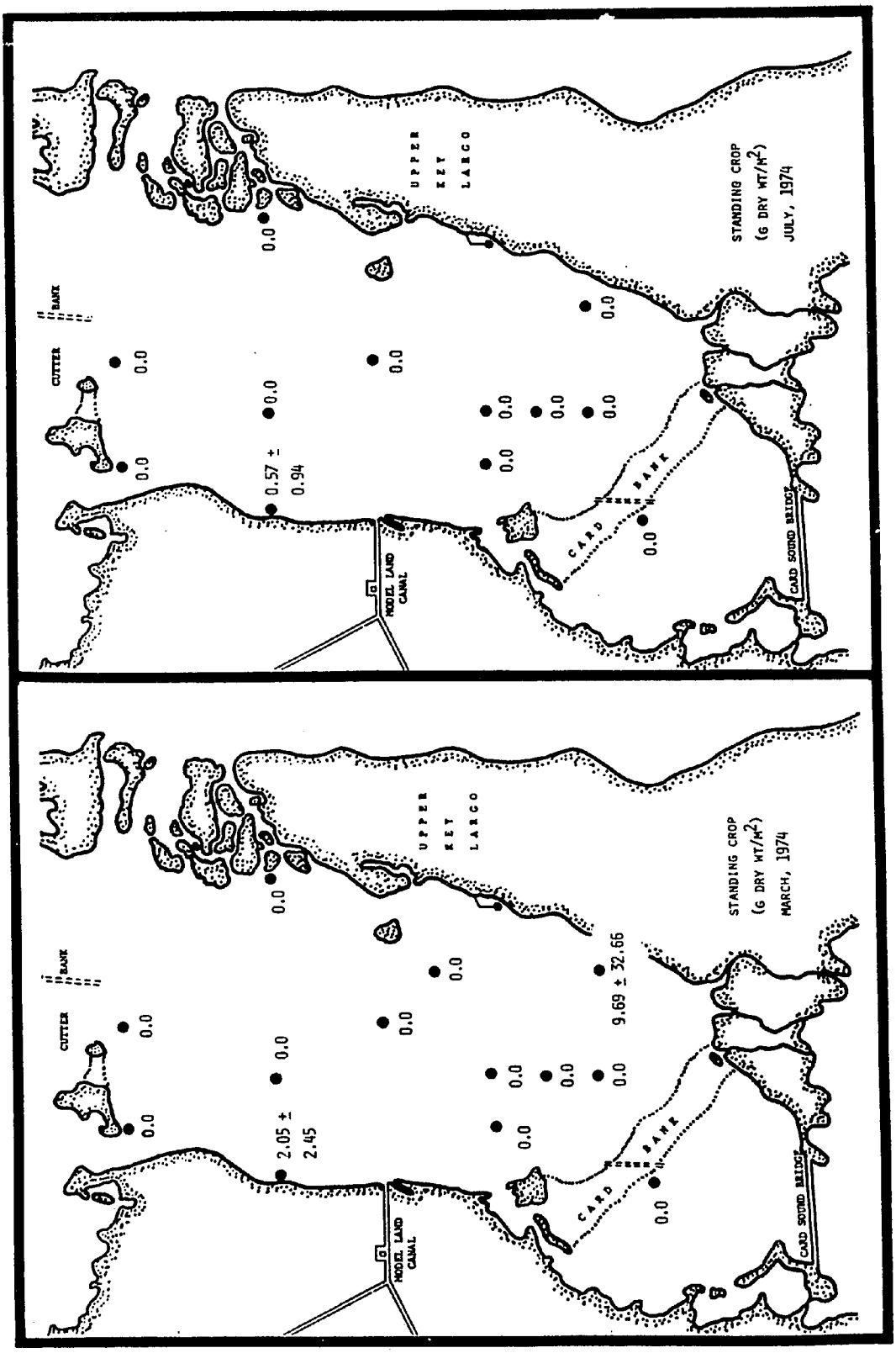

STANDING CROP
(G DRY WT/M²)
MARCH, 1974
STANDING CROP
(G DRY WT/M²)
JULY, 1974
UPPER
KEY
LARGO
CUTTER
BANK
CARD
BANK
MODEL LAND
CANAL
CARD SOUND BRIDGE
0.0
2.05 ± 2.45
9.69 ± 32.66
0.57 ± 0.94

Figure 17

Figure 18. Standing crop of Penicillus capitatus in Card Sound, Florida, on September, 1973, and on December, 1973. See Figure 10 for rest of legend.

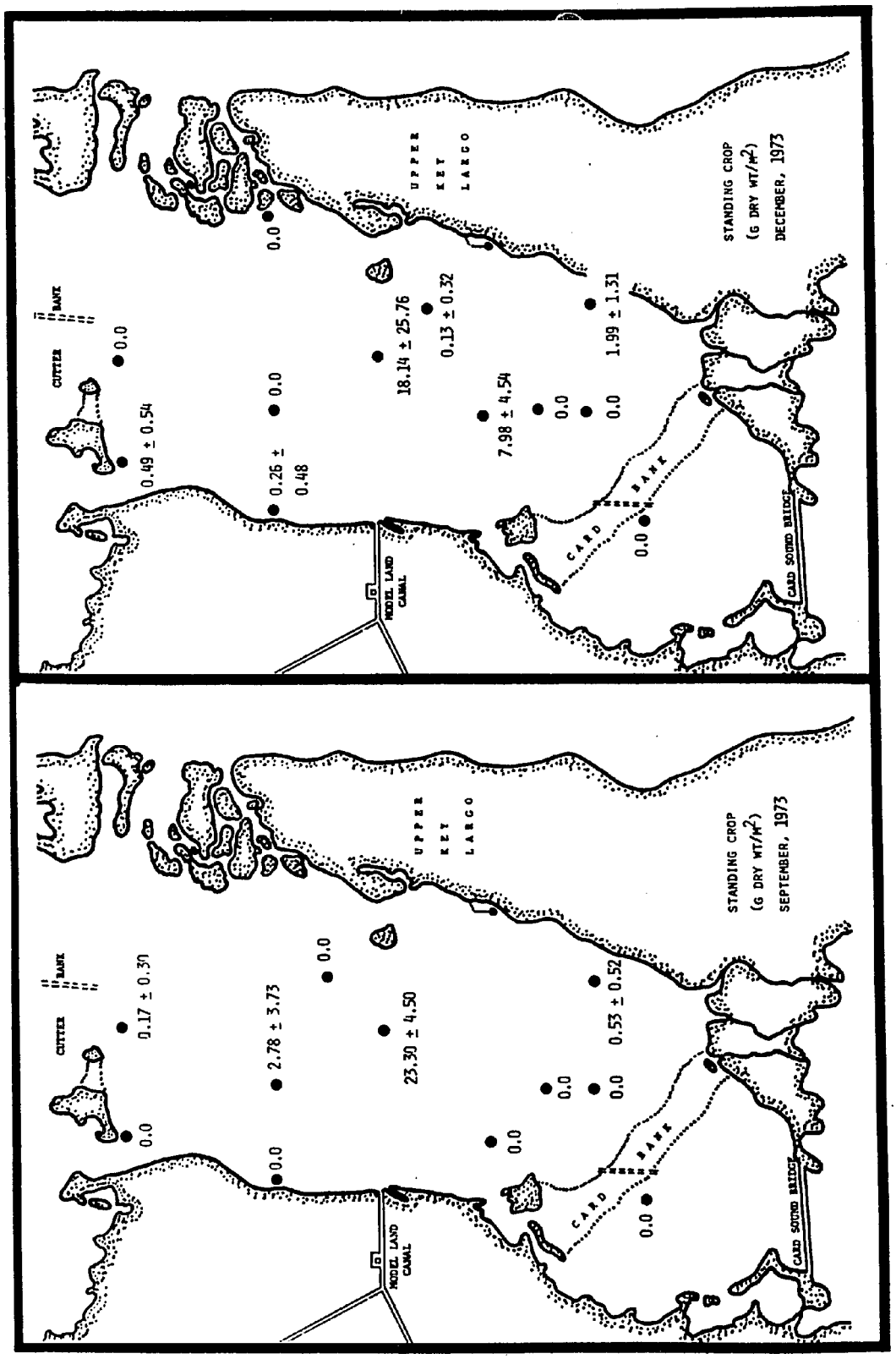

CUTTER BANK
0.0
0.49 ± 0.54
0.0
0.26 ± 0.48
0.0
18.14 ± 25.76
0.13 ± 0.32
7.98 ± 4.54
0.0
0.0
1.99 ± 1.31
UPPER KEY LARGO
MODEL LAND CANAL
CARD BANK
CARD SOUND BRIDGE
STANDING CROP (G DRY WT/M2) DECEMBER, 1973
CUTTER BANK
0.0
0.17 ± 0.30
0.0
2.78 ± 3.73
0.0
23.30 ± 4.50
0.0
0.0
0.0
0.53 ± 0.52
UPPER KEY LARGO
MODEL LAND CANAL
CARD BANK
CARD SOUND BRIDGE
STANDING CROP (G DRY WT/M2) SEPTEMBER, 1973

Figure 18

Figure 19. Standing crop of Penicillus capitatus in Card Sound on March, 1974, and on July, 1974. See Figure 11 for rest of legend.

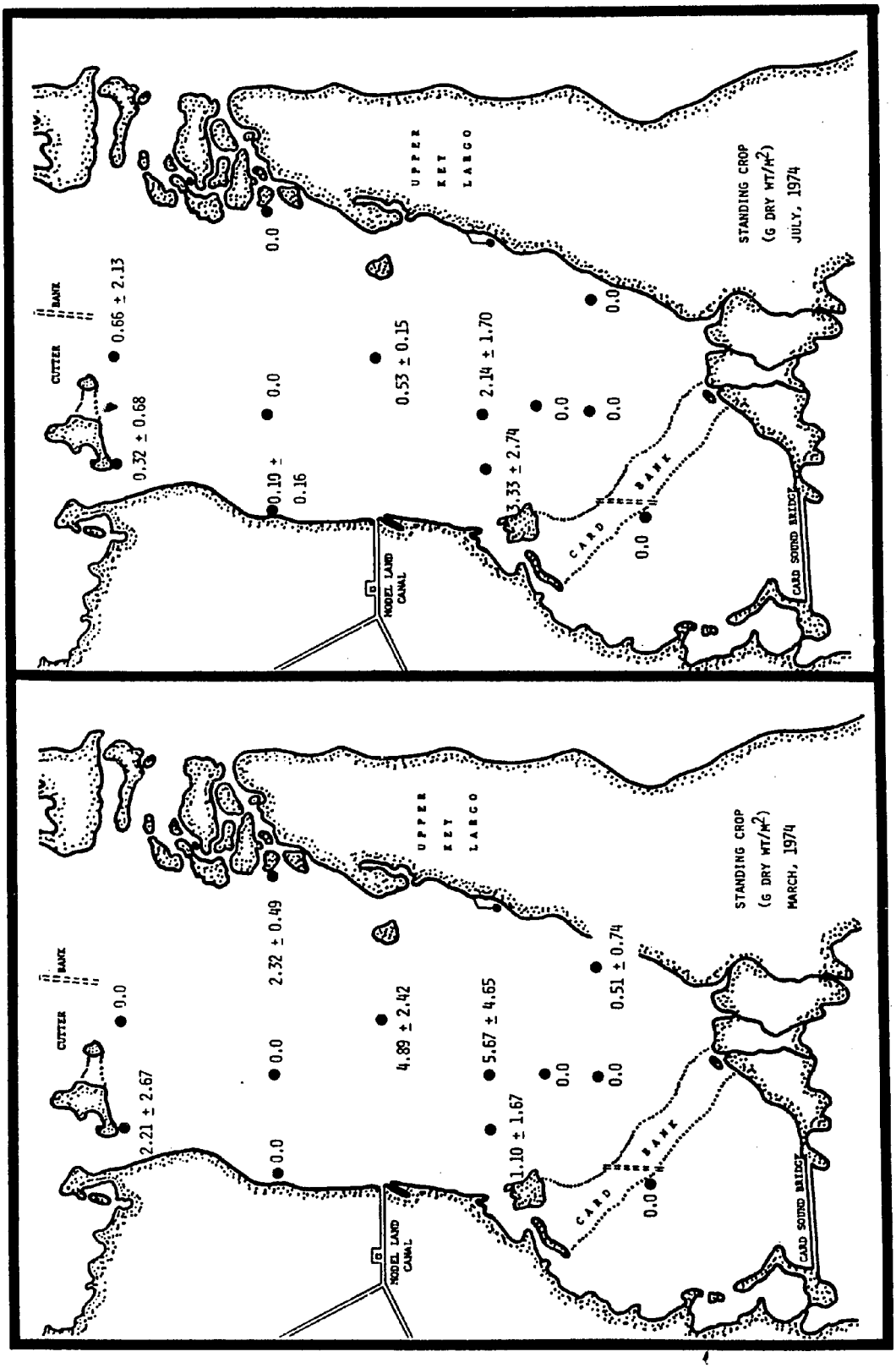

CUTTER BANK
0.0
2.21 ± 2.67
0.0
0.0
2.32 ± 0.49
4.89 ± 2.42
5.67 ± 4.65
1.10 ± 1.67
0.0
0.0
0.51 ± 0.74
0.0
NODEL LAND CANAL
CARD BANK
CARD SOUND BRIDGE
UPPER KEY LARGO
STANDING CROP (G DRY WT/M²) MARCH, 1974
CUTTER BANK
0.66 ± 2.13
0.32 ± 0.68
0.0
0.10 ± 0.16
0.0
0.53 ± 0.15
2.14 ± 1.70
3.33 ± 2.74
0.0
0.0
0.0
0.0
NODEL LAND CANAL
CARD BANK
CARD SOUND BRIDGE
UPPER KEY LARGO
STANDING CROP (G DRY WT/M²) JULY, 1974

Figure 19

Figure 20: A posteriori nonparametric comparison test applied to Penicillus capitatus standing crop data from July, 1974 (after Sokal and Rohlf, 1969). Asterisked value in grid indicates significant difference ($p<0.05$) between two stations shown. (U_s critical = 125.7)

Summary of U_s Values

stations	0104	0106	0403	0405	0408	0606	0804	0805
0104								
0106	108							
0403	109	114						
0405	108	110	88.5					
0408	109	110	88	123				
0606	124	120	127*	139*	136*			
0804	133*	129*	132*	140*	140*	126*		
0805	130*	130*	139*	143*	143*	123	73	

Grouping: Lines connect maximum nonsignificant ranges of means (no plants were recorded at station 1007).

0804 0805 0106 0606 0104 0403 0408 0405

crop at station 0804 than at all the other stations in July, 1974, supporting these observations.

Changes of an opposite nature were recorded at station 0604 where a large population of P. capitatus appeared in a circular path of Thalassia in 1974 where only a few months before very few plants had been observed. Although samples were not taken in the area in any of the surveys, 5 random 1-m^2 samples were taken in this Thalassia bed in January, 1975 to test for differences in the weight of individual plants in Thalassia beds versus those in the surrounding area. The mean standing crop and density of the P. capitatus inside the Thalassia bed was 12.69 ± 4.22 g dry wt/m^2 and the mean density was 36.8 ± 13.7 plants/m^2 (n=5).

From all the above observations it can be concluded that P. capitatus was capable of rapid changes in relative numbers both in space and time, and that it reached its greatest numbers in southern mid-sound areas. Very sparse populations were observed in extreme southern Card Sound, on either side of Card Bank (stations 1103, 0905, 1005), along the western shoreline and on Cutter Bank and the Angelfish-Broad Creek shoal areas (Figures 18 and 19).

5.3.6 Standing Crop of Rhipocephalus phoenix

This species was never as abundant as P. capitatus or H. incrassata. The highest standing crops recorded

were in September, 1973 at stations 0606 (4.35 ± 3.92 g dry wt/m^2) and 0405 (3.4 ± 3.58 g dry wt/m^2) as shown in Figures 21 and 22. The pattern of distribution of R. phoenix closely resembled that of P. capitatus. Neither was found in great abundance in dense Thalassia beds, but both species were more numerous at stations 0606 and 0805 in areas of lower density Thalassia and sediment depth of less than 15 cm. A nonparametric multiple comparison test (Sokal and Rohlf, 1969) showed that in July, 1974 the standing crop of R. phoenix was significantly lower at stations 0403 and 0104 than at all the other stations sampled (Figure 23). In the multiple comparison test overlapping occurred in the remaining stations, but the test showed that the standing crop was higher at 0606 than at 0106, 1007 and 0408 when compared on an individual basis. This coincides well with field observations which indicated very sparse populations at these three stations.

5.3.7 Standing Crop of Udotea flabellum

This species was most common in central and lower Card Sound (Figures 24 and 25). In general it followed the same pattern of spatial distribution as P. capitatus and R. phoenix. Standing crop was highly variable as was the case with all the other plants. Coefficients of variation ranged from a low of 39.9 percent in the September, 1974 survey to 346.4 percent in the July, 1974 survey.

Figure 21. Standing crop of Rhipocephalus phoenix in Card Sound, Florida, on September, 1973 and December, 1973. n=3 for all stations in September, and n=6 in December. See Figure 10 for rest of legend.

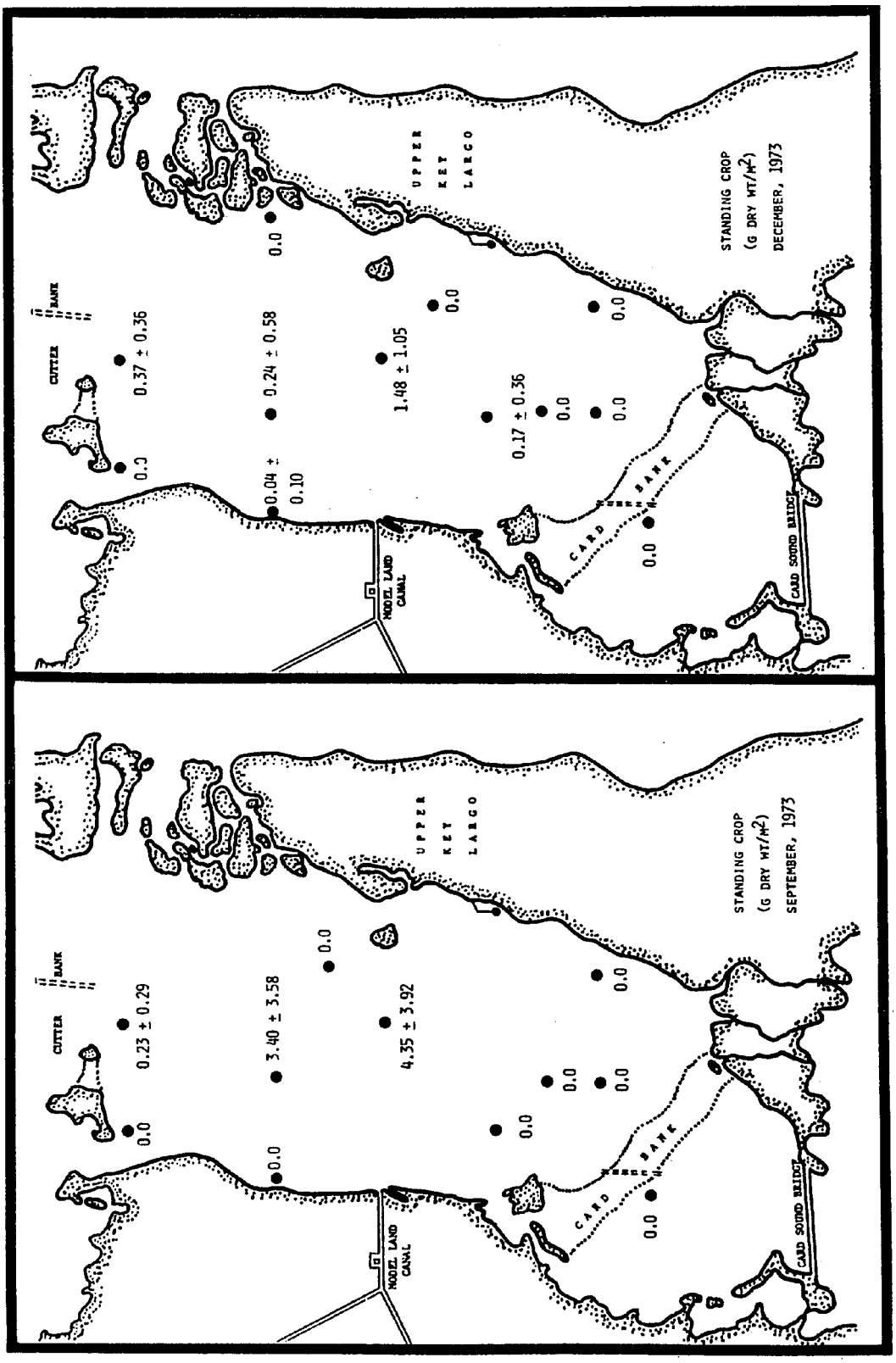

CUTTER BANK
0.0
0.23 ± 0.29
0.0
3.40 ± 3.58
0.0
4.35 ± 3.92
0.0
0.0
0.0
0.0
0.0
UPPER KEY LARGO
NDDZ. LAND CANAL
CARD BANK
CARD SOUND BRIDGE
STANDING CROP (G DRY WT/M2) SEPTEMBER, 1973
CUTTER BANK
0.0
0.37 ± 0.36
0.0
0.04 ± 0.10
0.24 ± 0.58
1.48 ± 1.05
0.0
0.17 ± 0.36
0.0
0.0
0.0
0.0
0.0
UPPER KEY LARGO
NDDZ. LAND CANAL
CARD BANK
CARD SOUND BRIDGE
STANDING CROP (G DRY WT/M2) DECEMBER, 1973

Figure 21

Figure 22. Standing crop of Rhipocephalus phoenix in Card Sound, Florida, on March, 1974, and July, 1974. n=12 for all stations except 0409, 0707 and 1007 in March, (n=3 at these three stations). n=12 at all stations in July, 1974. See Figure 10 for rest of legend.

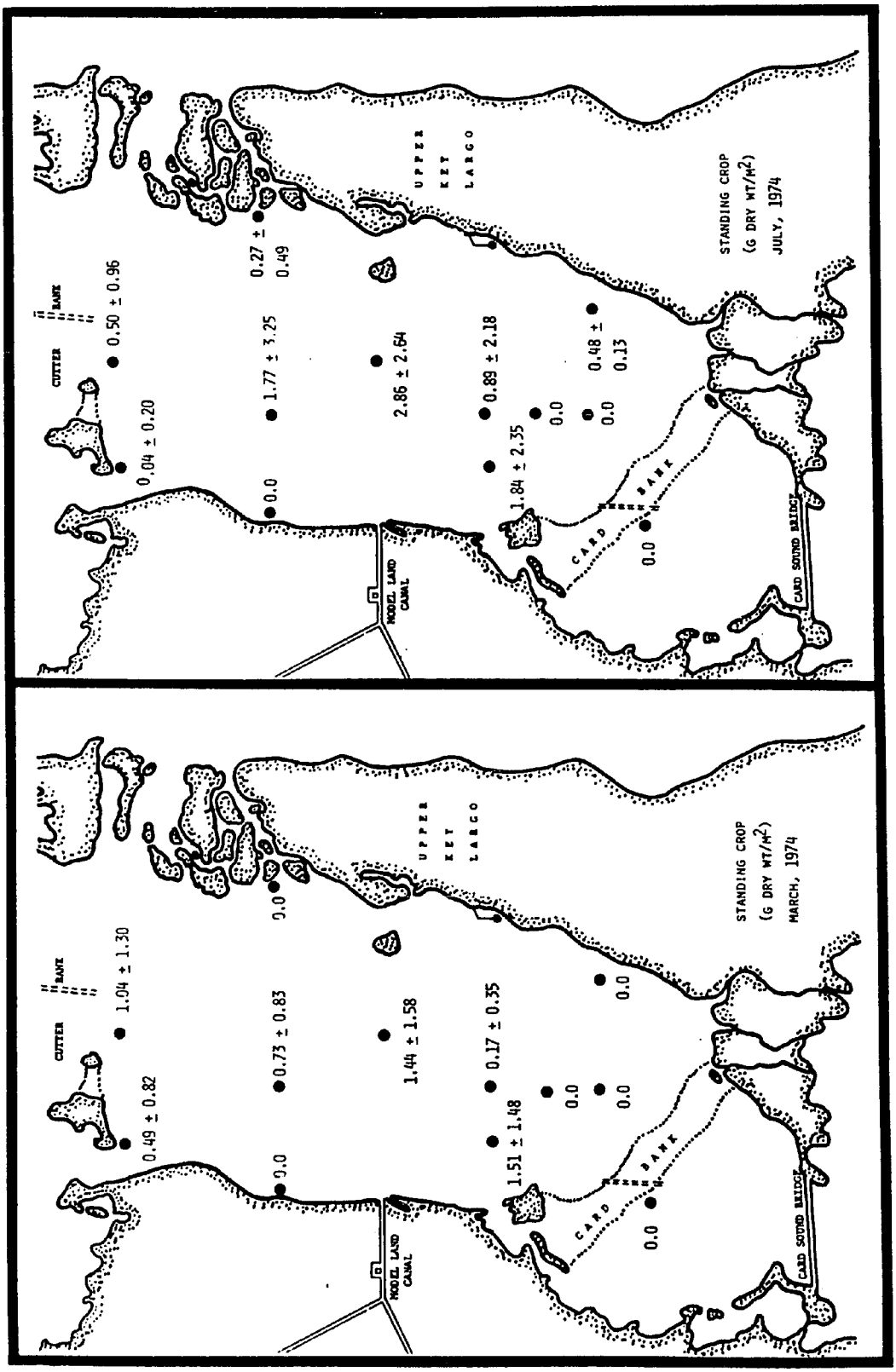

STANDING CROP
(G DRY WT/M²)
JULY, 1974
STANDING CROP
(G DRY WT/M²)
MARCH, 1974
UPPER KEY LARGO
CARD BANK
CARD SOUND BRIDGE
MODEL LAND CANAL
CUTTER BANK
0.50 ± 0.96
0.04 ± 0.20
0.27 ± 0.49
1.77 ± 3.25
2.86 ± 2.64
0.89 ± 2.18
1.84 ± 2.35
0.48 ± 0.13
1.04 ± 1.30
0.49 ± 0.82
0.73 ± 0.83
1.44 ± 1.58
0.17 ± 0.35
1.51 ± 1.48

Figure 22

Figure 23: A posteriori nonparametric comparison test applied to Rhipocephalus phoenix standing crop data from July, 1974 (after Sokal and Rohlf, 1969). Asterisked value in grid indicates significant difference ($p<0.05$) between two stations shown. (U_s critical = 125.7)

Summary of U_s Values

stations	0403	0104	0408	1007	0106	0805	0405	0804	0606
0403									
0104	144*								
0408	144*	135*							
1007	144*	133*	108						
0106	144*	136*	113	129*					
0805	144*	134*	114	128*	94				
0405	144*	136*	117	129*	102	124			
0804	144*	138*	123	132*	119	123	111		
0606	144*	143*	138*	142*	132*	125	111	99	

Grouping: Lines connect maximum nonsignificant ranges of means.

0403 0104 0408 1007 0106 0805 0405 0804 0606

Figure 24. Standing crop of Udotea flabellum in Card Sound, Florida, on September, 1973 and December, 1973. n=3 for all stations in September, and n=6 for all stations in December. See Figure 10 for rest of legend.

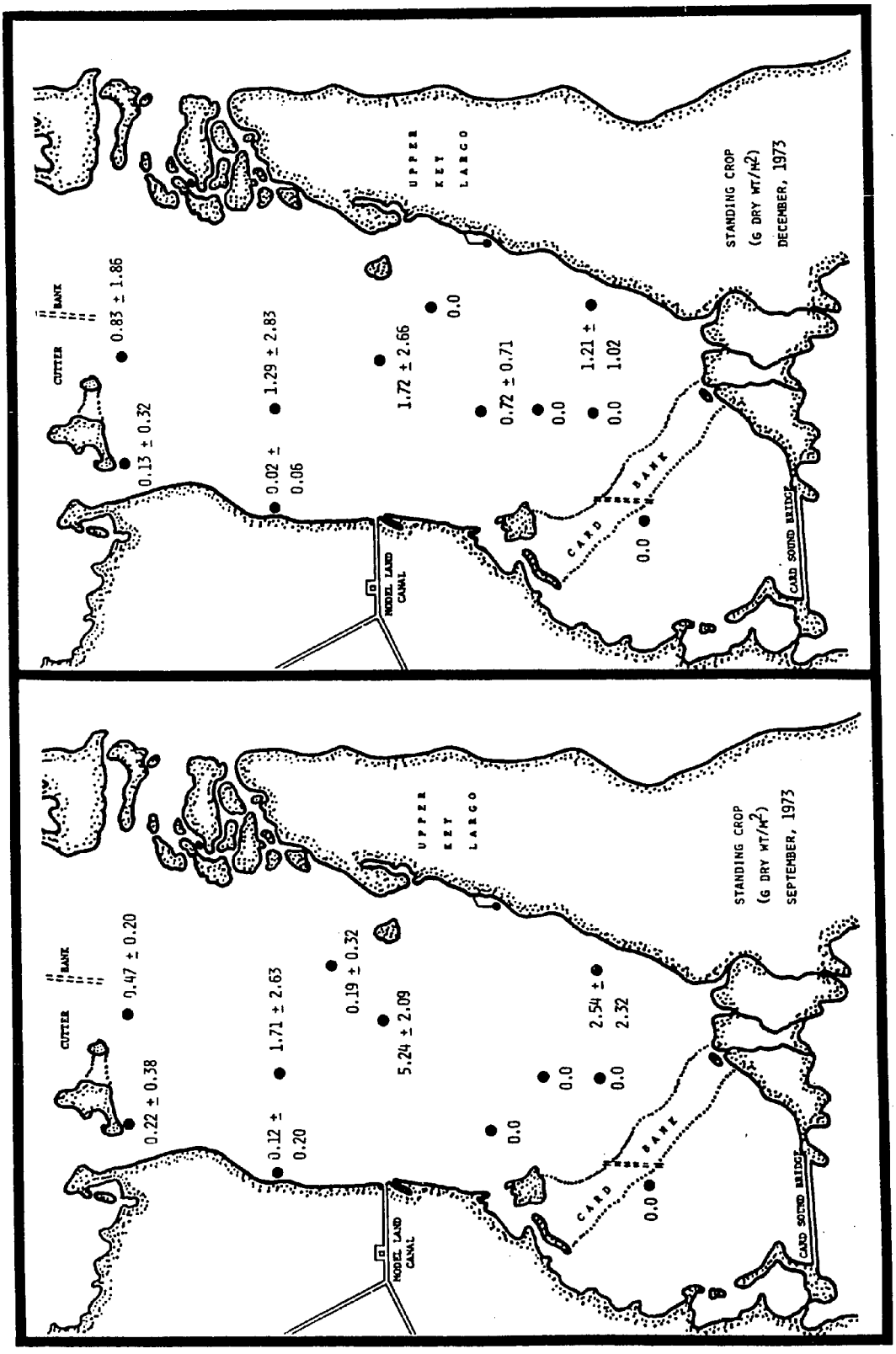

STANDING CROP
(G DRY WT/M2)
SEPTEMBER, 1973
STANDING CROP
(G DRY WT/M2)
DECEMBER, 1973
UPPER KEY LARGO
CUTTER BANK
CARD BANK
CARD SOUND BRIDGE
MODEL LAND CANAL
0.22 ± 0.38
0.47 ± 0.20
0.12 ± 0.20
1.71 ± 2.63
0.19 ± 0.32
5.24 ± 2.09
0.0
0.0
2.54 ± 2.32
0.0
0.0
0.13 ± 0.32
0.83 ± 1.86
0.02 ± 0.06
1.29 ± 2.83
1.72 ± 2.66
0.0
0.72 ± 0.71
0.0
1.21 ± 1.02
0.0
0.0

Figure 24

Figure 25. Standing crop of Udotea flabellum in Card Sound, Florida, on March, 1974 and July, 1974. n=12 for all stations except 0409, 0707 and 1007 on March, 1974 (n=3 for these stations). n=12 for all stations on July 1974. See Figure 10 for rest of legend.

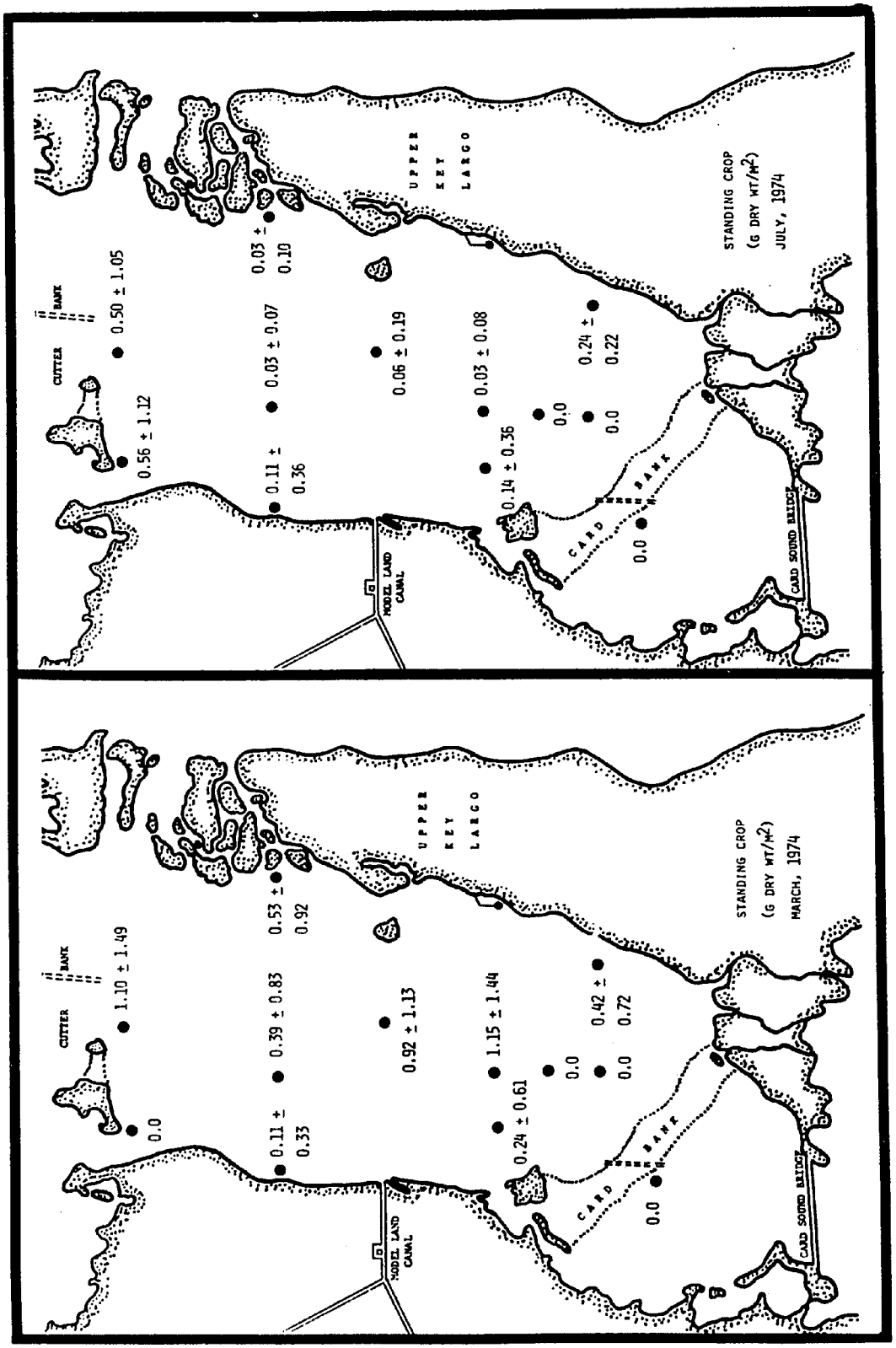

CUTTER BANK
1.10 ± 1.49
0.0
0.11 ±
0.33
0.39 ± 0.83
0.53 ±
0.92
0.92 ± 1.13
1.15 ± 1.44
0.24 ± 0.61
0.0
0.0
0.42 ±
0.0
0.72
0.0
CARD BANK
MODEL LAND CANAL
CARD SOUND BRIDGE
UPPER KEY LARGO
STANDING CROP (G DRY WT/M²) MARCH, 1974
CUTTER BANK
0.50 ± 1.05
0.56 ± 1.12
0.11 ±
0.36
0.03 ± 0.07
0.03 ±
0.10
0.06 ± 0.19
0.14 ± 0.36
0.03 ± 0.08
0.0
0.0
0.24 ±
0.22
0.0
CARD BANK
MODEL LAND CANAL
CARD SOUND BRIDGE
UPPER KEY LARGO
STANDING CROP (G DRY WT/M²) JULY, 1974

Figure 25

5.3.8 Comparison of Standing Crops

In order to provide a comparison among the different plants, mean standing crops for all stations and for all four surveys were calculated. The summary is given in Table 4. The mean standing crop of H. incrassata for all of Card Sound and for all four surveys was 5.51 g dry wt/m^2, which accounted for 49.6 percent of the total mean standing crop. The mean standing crops of H. monile and H. opuntia were about the same (1.50 and 1.43 g dry wt/m^2, respectively) and together accounted for 26.4 percent of the total standing crop in all the surveys. By itself, P. capitatus accounted for 15.2 percent (1.69 g dry wt/m^2) of the total mean standing crop. The standing crop of R. phoenix and U. flabellum were approximately the same (0.51 and 0.48 g/m^2, respectively) and these two algal species accounted for 8.9 percent of the total standing crop.

5.3.9 Variance: Mean Ratio

In almost every case the variance to mean ratio was much greater than 1, which would seem to indicate a contagiously distributed population. However, Greig-Smith (1964) suggests using caution in interpreting variance: mean ratio data since the number of samples taken and quadrat size both seriously effect the results. This is especially true when the mean is very low. Since most of the observed means were low and only 12 samples

Table 4. Comparison of mean standing crops of all six calcareous algae measured in Card Sound, Florida.

Plant	Mean standing crop*	Percent of Total Standing Crop
Halimeda incrassata	5.51	49.6
Halimeda monile	1.50	13.5
Halimeda opuntia	1.43	12.8
Penicillus capitatus	1.69	15.2
Rhipocephalus phoenix	0.51	4.6
Udotea flabellum	0.48	4.3
Total	11.12	100%

*Grand mean of all 14 stations sampled and all 4 surveys (September 1973, December 1973, March 1974 and July,1974) given in g dry wt/m^2; n = 48 stations).

were taken using one quadrat size, the results must be related to other observations and care taken in the interpretation of the plant pattern.

5.3.10 Belt Transects

Figures 26 and 27 show results of the counts made in the two belt transects at stations 0303 and 0403. The transects were placed perpendicular to the axis of the shoreline and across the peat wedge which overlay the Miami oolite bedrock. Figures 26 and 27 show how the peat wedge thinned out completely as the water depth increased to two meters at stations 0303 and 0403. The photograph of this part of Card Sound in Figure 4 shows the same sediment wedge lying along the shoreline. The transect counts show that the number of H. incrassata steadily decreased as the distance from shore increased and the depth of the peat sediment decreased. Relatively few plants were counted beyond the outer boundary of the peat wedge in the areas covered by less than 15 cm of marine carbonate sediment. Visual observations at stations 0503, 0603, 0703, 0803 and 1007 indicated that this same pattern existed at other areas where the sediment wedge was present and where it thinned out to almost bare bedrock.

The results of the belt transects counted across two circular Thalassia beds such as shown in the photograph in Figure 4 are presented in Figures 28 and 29.

Figure 26. Relationship of relative abundance of Halimeda incrassata to perpendicular distance from the northwestern shoreline of Card Sound, Florida. Line transects were laid our perpendicularly to the shoreline at station 0303. All the Halimeda incrassata in every other 1-m^2 quadrat placed along the entire length of the transect were counted. At every meter along the transects water depth and depth of the sediment were also measured.

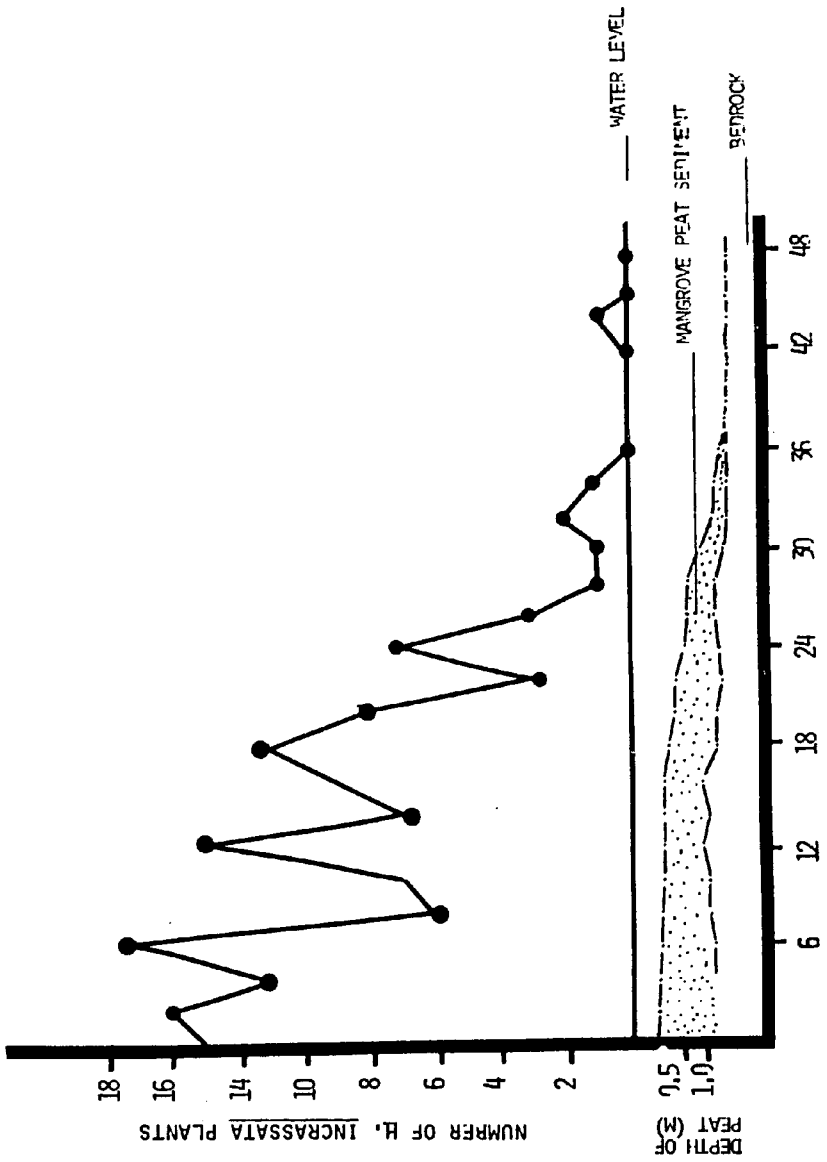

WATER LEVEL
MANGROVE PEAT SEDIMENT
BEDROCK
NUMBER OF B. INCRASSATA PLANTS
DEPTH OF PEAT (M)
DISTANCE (METERS)
18
16
14
10
8
6
4
2
0.5
1.0
6
12
18
24
30
36
42
48

Figure 26

Figure 27. Relationship of relative abundance of Halimeda incrassata to perpendicular distance from the northwestern shoreline of Card Sound, Florida, at station 0403.

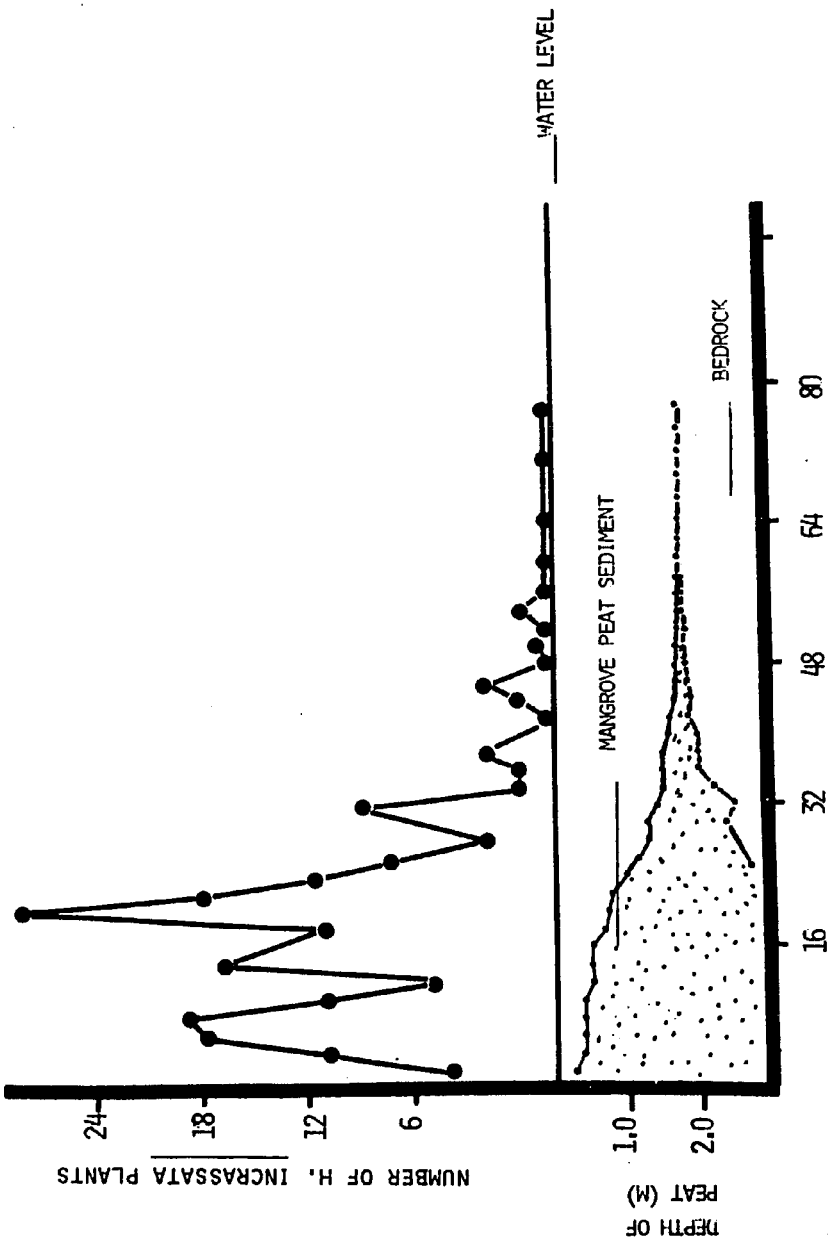

WATER LEVEL
MANGROVE PEAT SEDIMENT
BEDROCK
NUMBER OF H. INCRASSATA PLANTS
24
18
12
6
DEPTH OF PEAT (M)
1.0
2.0
16
32
48
64
80
DISTANCE (METERS)

Figure 27

Figure 28. The relationship of the number of Penicillus capitatus to the distance across a circular patch of Thalassia testudinum at station 0504. A transect line was laid out on the bottom across the bed of Thalassia and several meters beyond each edge. All the Penicillus capitatus in sequentially placed 1/4-m^2 quadrats were counted for the full length of the transect. The dotted vertical lines represent the edge of the Thalassia bed where sediment depth dropped rapidly from 0.5 to 5.0 inside the bed to less than 15 cm outside the bed.

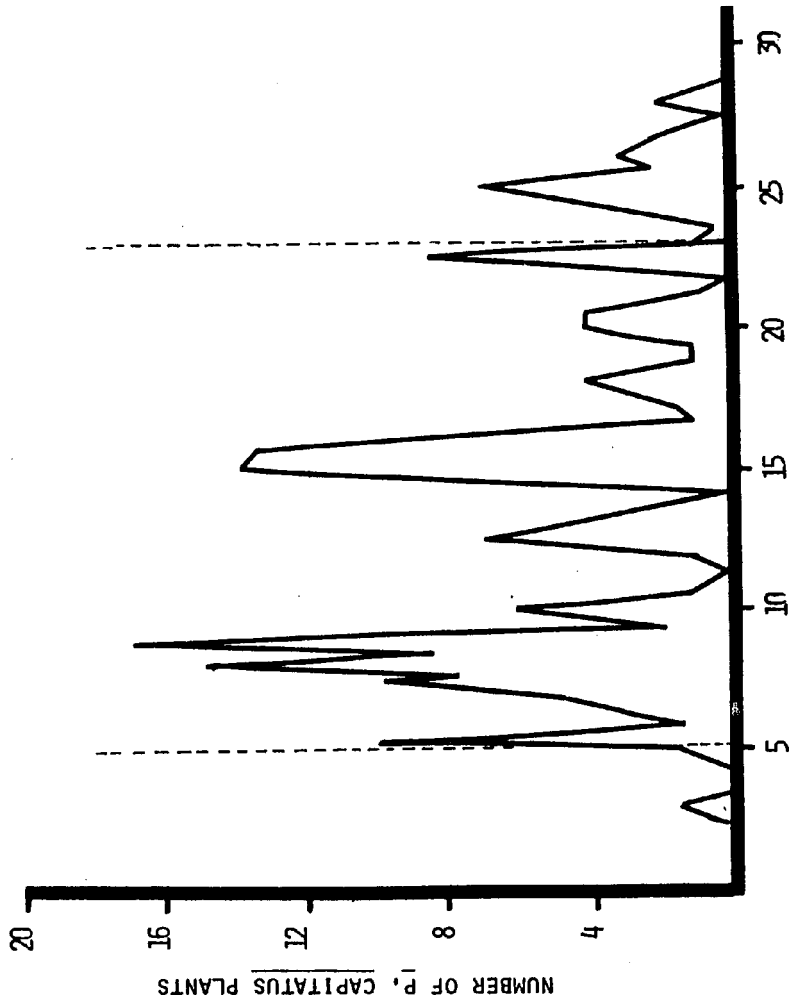

NUMBER OF P. CAPITATUS PLANTS
20
16
12
8
4
5
10
15
20
25
30
DISTANCE ACROSS THALASSIA BED (METERS)
(DOTTED VERTICAL LINES MARK THE EDGES OF THE BED)

Figure 28

Figure 29. The relationship between the number of Penicillus capitatus plants to the distance across a circular patch of Thalassia at station 0404.

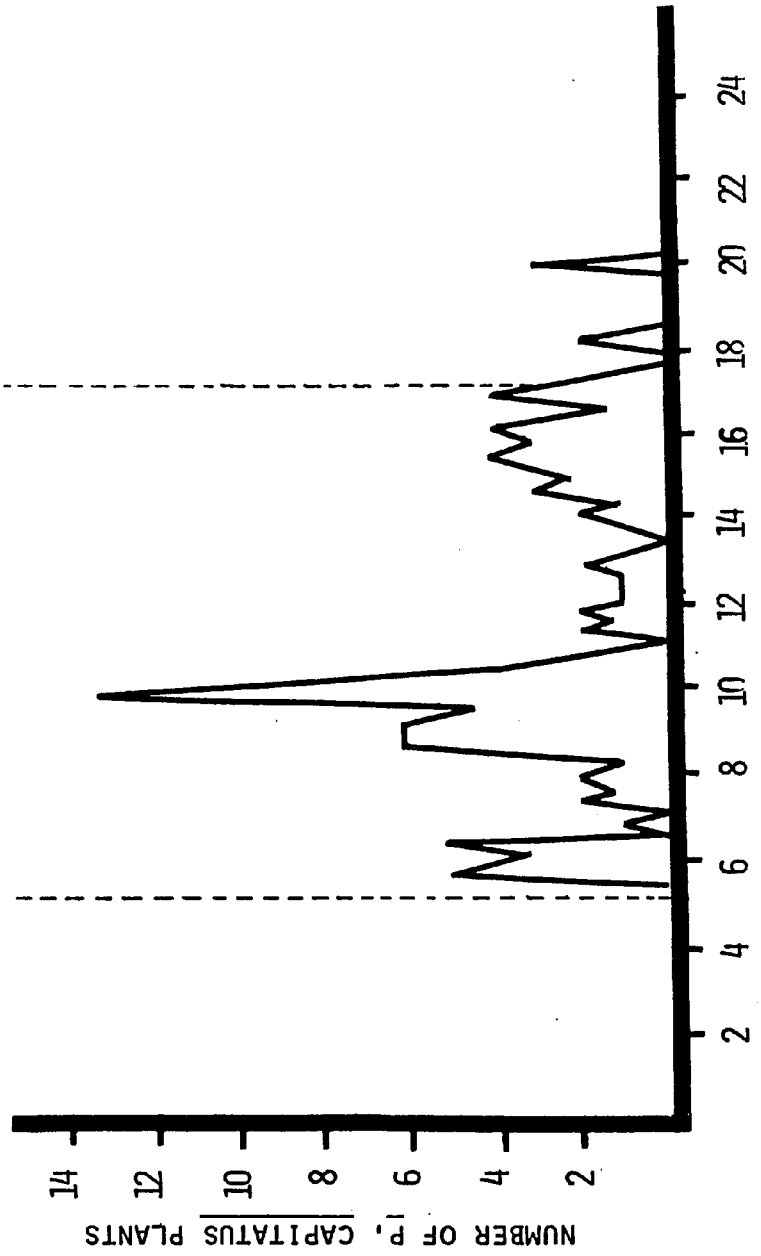

NUMBER OF P. CAPITATUS PLANTS
14
12
10
8
6
4
2
2
4
6
8
10
12
14
16
18
20
22
24
DISTANCE ACROSS THALASSIA BED (METERS)
(DOTTED VERTICAL LINES MARK THE EDGES OF THE BED)

Figure 29

P. capitatus was the only species counted. Transects were also counted across Thalassia beds at stations 0204 and 0304 but no calcareous algae were present at either of these stations. Where P. capitatus was present, it occurred in greater numbers inside the Thalassia beds than in the outlying area of shallow marine carbonate sediment overlying Miami oolite bedrock (Figures 28 and 29). No measurements of sediment depth inside the circular Thalassia beds were made, but sediment depth of beds in this same area have been described by Zieman (1972) and ranged from 0.5 to 5.0 meters as compared to less than 15 cm in the surrounding area. The sediment in the solution holes was composed primarily of mangrove peat covered with a thin layer of marine carbonate mud.

5.3.11 General Underwater Observations

Ability to grow on corals and sponges: Certain features of the distribution of these plants were noted on dives throughout the study. At station 0606, where the bottom is covered with a very thin (less than 15 cm) layer of sediment in most places, there were also coral and rock outcroppings which provided attachment for macroalgae. On one occasion at station 0606 at least 20 large P. capitatus were found growing on the top and sides of a coral outcropping. There were only a few small P. capitatus in the immediate area surrounding the coral, but the P. capitatus growing on the outcropping were among the biggest ever observed in Card Sound. The plants

on the coral lived for approximately 60 days based on direct observations every 14 days. The other calcareous macroalgae were also observed to grow epiphytically on large sponges. At station 0403 large loggerhead sponges, most of which were covered with a carpet of other macroalgae and smaller animals such as serpulid worms, were also observed to support populations of all four genera of calcareous algae.

Growth of calcareous algae in invertebrate mounds: P. capitatus and R. phoenix were also commonly seen growing on elevated mounds of the burrowing invertebrate Arenicola sp., especially at stations 0805 and 0106. This invertebrate produces a conical mound of sediment which protrudes several inches above the surrounding bottom. P. capitatus and R. phoenix were commonly observed growing in groups on these mounds. Often there would be several healthy adults, some juveniles, and some senescent plants on the mounds, while few plants would be found nearby.

Halimeda - Thalassia relationship: A relationship was observed between the roots of H. incrassata and the rhizome-root system of T. testudinum. Examination of the roots and rhizome of Thalassia showed that the Halimeda holdfast was thoroughly penetrated by both the rhizomes and the roots of Thalassia. It was most likely that the Halimeda holdfast had grown around the Thalassia,

since the Thalassia rhizomes are extremely long lived (Zieman, 1972). This relationship was observed wherever Thalassia and Halimeda incrassata grew together and it was a permanent feature of many Thalassia beds. No further investigation of this relationship was undertaken in this study. It seems likely that the Thalassia rhizome and root system is an excellent anchor for the Halimeda. It also seems possible to hypothesize that a parasitic or hemiparasitic relationship might exist, but this was not investigated.

Ability to regrow: It was very common to see light green H. incrassata plants regrowing from a pale, almost white, basal stalk. It was also common to see R.phoenix growing a new cap directly out of an older senescent cap. Several P. capitatus were also observed to grow new caps directly from the old ones, or filaments would even be seen to arise directly out of the stalk of the plant.

5.4 SPATIAL AND TEMPORAL PATTERNS OF PLANT YIELD

5.4.1 Direct Harvest Method

In this method, calcareous algae which grew up through the strip of monofilament at each station were harvested by systematically collecting all the plants in successive 1-m^2 frames. Tables 23 through 36 in the Appendix contain the results of the direct harvest measurements for all the algae. The raw data and mean

daily rates of yield for each harvest period are presented. Table 5 was constructed from the data in the Appendix tables and presents the mean daily yield estimate for each algal species for the entire period from March, 1974 to May, 1975. The mean daily yield for the study period was calculated by averaging the mean daily yields for each separate period. This figure was converted to ash-free dry weight and also to calcium carbonate based on the data in Table 3.

Halimeda incrassata: Mean organic yield of H. incrassata for the whole study period varied from 1.8 mg ash-free dry wt/m^2/day at station 0606 to 39.2 mg ash-free dry wt/m^2/day at station 0106 (Table 5). Yield was greatest at stations 0106 and 0409. Mean carbonate yield varied from 0.6 to 13.7 mg/m^2/day.

Halimeda monile: Growth of this species was only observed at 2 stations. The mean daily yield of this species based on the direct harvest method was 3.03 mg ash-free dry wt/m^2/day and 0.59 mg calcium carbonate/m^2/day at station 0606. The yield at station 0805 was 2.27 mg ash free dry wt/m^2/day and 0.44 mg calcium carbonate/m^2/day. These yields compare to the lower range of the yield of H. incrassata.

Penicillus capitatus: Mean yield varied from 0.08 mg ash-free dry weight/m^2/day at station 0106 to 17.59 mg ash-free dry weight/m^2/day at station 0606 (Table 5).

Table 5. Summary of the direct harvest method of yield estimation of four major species. Mean annual yield based on average of harvests made every 8 weeks for 1 year.

station	Halimeda incrassata		Penicillus capitatus		R. phoenix		Udotea flabellum	
	organic yield*	$CaCO_3$ yield+	organic yield*	$CaCO_3$ yield+	organic yield*	$CaCO_3$ yield+	organic yield*	$CaCO_3$ yield+
0104	21.13	7.38	2.06	1.47	0.50	0.61	0.13	0.08
0106	39.21	13.71	0.08	0.06	0.69	0.85	1.37	0.74
0403	12.62	4.48	0.34	0.26	0.05	0.05	0.13	0.08
0409	28.94	10.12	0.34	0.26	1.76	2.16	0.32	0.17
0606	1.80	0.63	17.59	12.59	8.38	10.25	1.21	0.65
0805	7.08	2.47	6.23	4.45	2.41	2.95	0.44	0.24
$\bar{x}$ =	18.46	6.47	4.44	3.18	2.30	2.81	0.60	0.33

*mean of all dates sampled in mg ash-free dry weight/m^2/day at each station
+mean of all dates sampled in mg calcium carbonate/m^2/day

Carbonate yield varied from 0.06 mg ash-free dry wt/m^2/day to 12.59 mg ash-free dry weight/m^2/day. Stations 0606 and 0805 produced the highest amount of plant material (Table 5).

Rhipocephalus phoenix: The lowest mean yield was at stations 0403, 0104, 0408 and 0106 (Table 5). The highest mean yields of 8.38 mg ash-free dry wt/m^2/day and 10.25 mg calcium carbonate/m^2/day were recorded at station 0606.

Udotea flabellum: This algal species averaged from 0.13 to 1.37 mg ash-free dry wt/m^2/day and from 0.08 to 0.74 mg calcium carbonate/m^2/day during the study period (Table 5). U. flabellum had the lowest yield of all species measured.

5.4.2 Tagging Study

Station 0104: All the 55 originally healthy plants in the 2 squares at this station were H. incrassata. In mid February, 1974,a large mat of Laurencia poitei moved into the area as a result of a combination of currents and wind action (Josselyn, 1975). The mat completely covered the tagging squares, and the plants began dying, presumably due to lack of light, since the dense mat averaged 0.2 to 0.5 m in thickness. Over 50 percent of the plants in the squares died back to seemingly dead stalks by the end of May, 1974 and most of the tags were lost as a result, even though they had

been stapled around the basal portion of each plant. Regrowth of the same plants from the seemingly dead portion as well as production of 15 new juvenile H. incrassata plants were observed in June and part of July, 1974. A storm caused more Laurencia poitei to accumulate in July, 1974, and the Laurencia remained in the area covering the square for the rest of 1974. All the plants in the squares again died back to the stalk and were observed to remain in this state until the square was lost in September of 1974 because of removal of a marking stake by an unknown cause.

Based on the above observations, H. incrassata at station 0104 had a life span of at least 216 days, but this is an underestimate because the plants were reduced to the basal stalk and were not observed for the remainder of the year as a result of being lost underneath the Laurencia mat.

Station 0106: The two tagging squares at station 0106 contained 48 "mature" H. incrassata in November of 1973 when the observations began. No other species of calcareous algae were observed in the squares. By January, 1974 the number of mature plants had dropped sharply to only 18. Almost all 18 plants appeared chewed on and had a "knobby" morphology, such as is shown in Figure 30. Many tags were lost during this time period but several remained and visual observations

Figure 30. "Knobby" Halimeda incrassata observed at station 0106 in December, 1974. Darker plates have grown back from the lighter stalk portion.



Figure 30

Figure 31. Heavily grazed specimen of Halimeda incrassata at station 0106 in December, 1974. Note torn edges of thallus and absence of branches of green (dark in black and white) plates. This is the "resistant stalk" form mentioned in the discussion from which new branches regrew.



Figure 31

Figure 32. Halimeda incrassata branches regrowing from a resistant stalk portion that had been previously grazed on by Lytechinus variegatus at station 0106 in December, 1974. The resistant stalk is the lighter colored portion in the photography while the new growth appears darker.



Figure 32

as well as exclosure experiments showed that the H. incrassata had been grazed on by L. variegatus, many of which had been recorded in the tagging square. A heavily grazed plant is shown in Figure 31. By March, 1974 there were 30 mature plants in the square but no new juvenile plants had yet appeared. This increase was caused by a regrowth of plants that had been grazed on by L. variegatus as shown in Figures 30, 31 and 32.

More grazing followed until only 17 mature plants remained in the two squares in April, 1974. Regrowth of knobby plants then occurred until a total of 30 plants was reached by May, 1974. In September of 1974 five new juvenile H. incrassata appeared in the squares, but the numbers of mature plants steadily decreased throughout the fall and winter. By January, 1975 there were no mature plants left in the tagging squares, primarily because of a large increase in the numbers of L. variegatus.

The life span of H. incrassata can therefore be as great as 12 months and is probably longer according to these observations, and juveniles grew into the tagging square at least once a year. Most H. incrassata plants observed completely regrew lost portions of the thallus at least 3 times a year.

Station 0409: Sixty mature H. incrassata were tagged at station 0409 in November, 1973. H. incrassata was the only alga observed in the square. By April, 1975

only 35 mature plants remained in the single square at this station. Field notes show that this was definitely due to a loss of branches since most of the original tags were still on the remaining stalks. Large numbers of the chicken liver sponge (Chondrilla nucula) were observed to completely cover H. incrassata and Thalassia at this station, and I believe that this was a major cause of the branch loss, especially since only a few Lytechinus were seen in the area all year and there were few "knobby" plants. Regrowth from the stalk portion occurred in the same tagged plants during most of May, June and July and 11 new juveniles were also added to the square during this same period.

The density of H. incrassata was so great here that the square was reduced to 0.5 m^2 in July of 1974. Two other periods of branch loss and regrowth were observed to occur from August, 1974 to May, 1975. A second group of 10 new juveniles was also observed to grow into the square in September, 1974.

The tagging data shows that individual H. incrassata plants commonly lived up to at least 16 months and that it was possible for up to 2 new generations per year to be introduced into the existing tagging squares at this station.

Station 0606 (Halimeda incrassata): Urchins destroyed all the calcareous algae in the tagging square at this

station within 8 months after starting the tagging. Because of the long life span of H. incrassata as compared to the other algae it was difficult to maintain tags on the plants for more than 1 month, since the tags were removed by L. variegatus. Regrowth of plants no. 5, 34, 57, 59, 61 and 81 from the familiar knobby structure was observed during the time plants occupied the square. Observations for 4 months following urchin grazing showed that no regrowth of calcareous algae into the square had occurred. Individual H. incrassata lived for at least 6 months in the square but urchin grazing stopped the measurements at this point.

Station 0606 (Penicillus capitatus): The mean life span of 48 P. capitatus measured from the time they emerged as juveniles to the time they became completely senescent adults was 87 ± 28 days (where 28 days = 1 standard deviation of the mean life span). Roughly three times this many P. capitatus were originally tagged in the 2 squares in order to obtain complete life spans of 48. This is because the life span must be measured using plants that emerge after the original tagging in order to start from time zero.

Station 0606 (Rhipocephalus phoenix and Udotea flabellum): These species were much less common in the area and consequently only a few complete life spans were recorded for each plant. Even though many more were

actually tagged, only a few juveniles were followed through a complete life span because of the low abundance. Five R. phoenix at station 0606 had a mean life span of 50 ± 25 days. Six U. flabellum had a mean life span of 87 ± 13 days.

Station 0805 (Halimeda incrassata): From 52 originally tagged plants in November, 1973, the number of "mature" H. incrassata steadily dropped in the counting squares at this station until less than 4 plants were present in May, 1974. The number of mature plants never rose above 4 for the remaining 10 months of the study. No new H. incrassata plants were produced in the entire 16 month period of observation. Regrowth of "knobby" plants number 8,70 and 348 was observed in the squares. Lytechinus was seen commonly in the area and in the tagging squares although not nearly in the large numbers as at stations 0606 and especially 0106. From the available data it appears that individual H. incrassata plants can live up to 6 months or more, but since urchin grazing destroyed the plants this is an underestimation, especially in view of the data from the other stations.

Station 0805 (Penicillus capitatus and Rhipocephalus phoenix): The mean life span (± 1 standard deviation of this mean) of 27 P. capitatus plants at station 0805 was 46 ± 12 days and the mean life span of 16 R. phoenix was 54 ± 20 days (also ± 1 standard deviation of this mean).

5.4.3 Life-Span Standing Crop Method of Yield Estimation

P. capitatus, R. phoenix and U. flabellum: To estimate the annual yield, the mean standing crop for all four surveys was multiplied by three different numbers of generations per year (Tables 6, 7 and 8). The number of generations (crops) per year was determined in the tagging study. For each algal species a grand mean of the life spans determined at all stations was calculated. In practice this meant averaging the life spans at stations 0805 and 0606 since these were the only stations at which these three species were measured. For example, averaging the estimated mean life spans of P. capitatus at stations 0805 and 0606 gave a grand mean of 5.4 crops per year which was used in Table 6 to calculate the yield of this alga. To estimate the range of algal yield the largest standard deviation observed in the life span was used. For example, the mean life span of P. capitatus at station 0606 was 87 ± 28 days, and 46 ± 12 days at station 0805. To estimate the range of yield for this species 115 days was therefore used as the largest life span and 34 days was used as the smallest life span, based on these figures.

The yield in g dry wt/m^2/yr for each station was then converted to organic matter yield in g ash-free dry wt/m^2/yr and g calcium carbonate/m^2/yr (Tables 6, 7 and 8). The conversion was based on the ash and carbonate contents given in Table 3.

Table 6. Life-span standing crop method of annual yield estimate for Penicillus capitatus in Card Sound, Florida.

station	mean standing crop (g dry wt/m^2)	yield (10.7 crops per year)		yield (5.4 crops per year)		yield (3.2 crops per year)	
		organic* matter	$CaCO_3$**	organic* matter	$CaCO_3$**	organic* matter	$CaCO_3$**
0104	0.76	4.6	3.3	2.3	1.7	1.4	1.0
0106	0.21	1.3	0.9	0.6	0.5	0.4	0.3
0403	0.03	0.2	0.1	0.1	0.1	0.1	0.1
0405	0.70	4.3	3.1	2.2	1.6	1.3	0.9
0409	1.16	7.1	5.1	3.6	2.6	2.1	1.5
0507	0.00	0.0	0.0	0.0	0.0	0.0	0.0
0606	11.73	71.8	51.4	36.3	25.9	21.5	15.4
0707	0.13	0.8	0.6	0.4	0.3	0.2	0.2
0804	1.48	9.1	6.5	0.5	0.3	2.7	1.9
0805	5.26	32.3	23.1	16.3	11.6	9.6	6.9
0905	0.00	0.0	0.0	0.0	0.0	0.0	0.0
1005	0.00	0.0	0.0	0.0	0.0	0.0	0.0
1007	0.76	4.6	3.3	2.4	1.7	1.4	1.0
1103	0.00	0.0	0.0	0.0	0.0	0.0	0.0
		$\bar{x}$ = 9.7	7.0	4.6	3.3	2.9	2.1

* yield of organic matter given in g ash-free dry wt/m^2/year; based on 57.29% organic content

** yield of calcium carbonate in g calcium carbonate/m^2/year; based on 40.98% carbonate content

Table 7. Life-span standing crop method of annual yield estimate for Rhipocephalus phoenix in Card Sound, Florida.

station	mean standing crop (g dry wt/m^2)	yield (14.6 crops per year)		yield (7.3 crops per year)		yield (3.2 crops per year)	
		organic* matter	$CaCO_3$**	organic* matter	$CaCO_3$**	organic* matter	$CaCO_3$**
0104	0.13	0.8	1.0	0.4	0.5	0.2	0.2
0106	0.54	3.4	4.2	1.7	2.1	0.7	0.9
0403	0.01	0.1	0.1	-	-	-	-
0405	1.54	9.7	11.9	4.8	5.9	2.1	2.6
0409	0.07	0.4	0.5	0.2	0.3	0.1	0.1
0507	0.00	0.0	0.0	0.0	0.0	0.0	0.0
0606	2.53	16.0	19.5	8.0	9.8	3.5	4.3
0707	0.00	0.0	0.0	0.0	0.0	0.0	0.0
0804	1.12	7.1	8.7	3.5	4.2	1.6	1.9
0805	0.73	4.6	5.6	2.3	2.8	1.0	1.2
0905	0.00	0.0	0.0	0.0	0.0	0.0	0.0
1005	0.00	0.0	0.0	0.0	0.0	0.0	0.0
1007	0.12	0.8	1.0	0.4	0.5	0.2	0.2
1103	0.00	0.0	0.0	0.0	0.0	0.0	0.0
		$\bar{x}$ = 3.1	3.8	1.8	2.0	0.7	0.9

* yield of organic matter in g ash-free dry wt/m^2/day; based on 43.27% organic content

** yield of calcium carbonate in g calcium carbonate/m^2/year; based on 52.95% calcium carbonate content

Table 8. Life-span standing crop of annual yield estimate for Udotea flabellum in Card Sound, Florida.

station	mean standing crop (g dry wt/m^2)	yield (4.9 crops/year)		yield (3.7 crops/year)	
		organic* matter	$CaCO_3$**	organic* matter	$CaCO_3$**
0104	0.23	0.7	0.4	0.6	0.3
0106	0.73	2.3	1.2	1.7	0.9
0403	0.09	0.3	0.1	0.2	0.1
0405	0.86	2.7	1.4	2.0	1.1
0409	0.19	0.6	0.3	0.4	0.3
0507	0.19	0.6	0.3	0.4	0.3
0606	2.00	6.2	3.3	4.7	2.5
0707	0.00	0.0	0.0	0.0	0.0
0804	0.13	0.4	0.2	0.3	0.2
0805	0.63	2.0	1.1	1.5	0.8
0905	0.00	0.0	0.0	0.0	0.0
1005	0.00	0.0	0.0	0.0	0.0
1007	1.10	3.4	1.8	2.6	1.4
1103	0.00	0.0	0.0	0.0	0.0
		$\bar{x}$ = 1.4	0.7	1.0	0.6

* yield in g ash-free dry wt/m^2/year; based on 63.36% organic content

** yield in g calcium carbonate/m^2/year; based on 34.06% calcium carbonate content

The mean estimated organic yield of P. capitatus for all of Card Sound was 9.7, 4.6 and 2.9 g ash-free dry wt/m^2/yr and was based on 10.7, 5.4 and 3.2 generations (Table 6). Mean annual P. capitatus carbonate production was estimated to be 7.0, 3.3 and 2.1 g calcium carbonate/m^2/yr.

The estimated mean annual yield of organic matter by R. phoenix for all stations was 3.1, 1.8 and 0.7 g ash-free dry wt/m^2/yr based on 14.6, 7.3 and 3.2 generations per year. A mean of 3.8, 2.0 and 0.9 g calcium carbonate/m^2/yr for all stations were estimated to be produced by R. phoenix (Table 7).

U. flabellum was estimated to produce 1.4 and 1.0 g ash-free dry weight/m^2/year based on 4.9 and 3.7 generations/year (Table 8). Carbonate production for U. flabellum was estimated to be 0.7 and 0.6 g calcium carbonate/m^2/year. Only two generation times were used to calculate U. flabellum yield because the standard deviation of the mean life span was only 13 days.

5.4.4 GROWTH-DENSITY METHOD OF ESTIMATING YIELD

Adjusted mean growth was calculated by first dividing the actual observed mean growth of individual Halimeda plants above the mesh by the growth period in days and then multiplying this figure by 1.4 to account for growth under the net and losses due to sluffing off of dying plant material during the harvest period as described in the methods section.

A large amount of growth variation was observed between different H. incrassata plants. For example, plants in the same weight class produced considerably different amounts of material in the same time period and at the same station (Figure 33). This variation is indicated by the relatively poor fit of the expected least squares regression line of weight and growth in Figure 33 (poor fit is indicated by the low value of the observed coefficient of determination).

Relationships were also observed between the growth of H. incrassata plants and the temperature and salinities which were recorded during the growth periods. Figures 34 and 35 are plots of H. incrassata growth against the mean temperatures and salinities recorded during each harvest period. Growth seemed to be optimal between 28°C and 29°C but dropped rapidly off above 30°C. Also, growth appeared to be optimal at around 38 and 39 parts per thousand salinity.

The Kolmogorov-Smirnov test for goodness of fit to a normal curve (Sokal and Rohlf, 1969) indicated that the growth data was not normally distributed. Considerable heterogeneity of variances was also indicated by the observed proportionality between the variance and the mean of the growth data (Tables 9 to 16). Since the SNK test assumes that the data are normally distributed and that the variances of the different sets of data are homogeneous (statistically equal) the data were

Figure 33. The relationship between individual plant weight (x-axis) and growth per plant (y-axis) of Halimeda incrassata. 1.5 mm nylon mesh bags were tied around 38 plants at station 0106 on September 9, 1974. On October 15, 1974 the plants were removed and returned to the laboratory and the plant material that had grown through the mesh and total plant weight were measured. The graph shows the relationship between the amount of plant material that had grown through the mesh to the total weight of each plant. The data was fitted to the least squares regression line shown, but resulted in a relatively poor fit, since r^2, the coefficient of determination, was only 0.58.

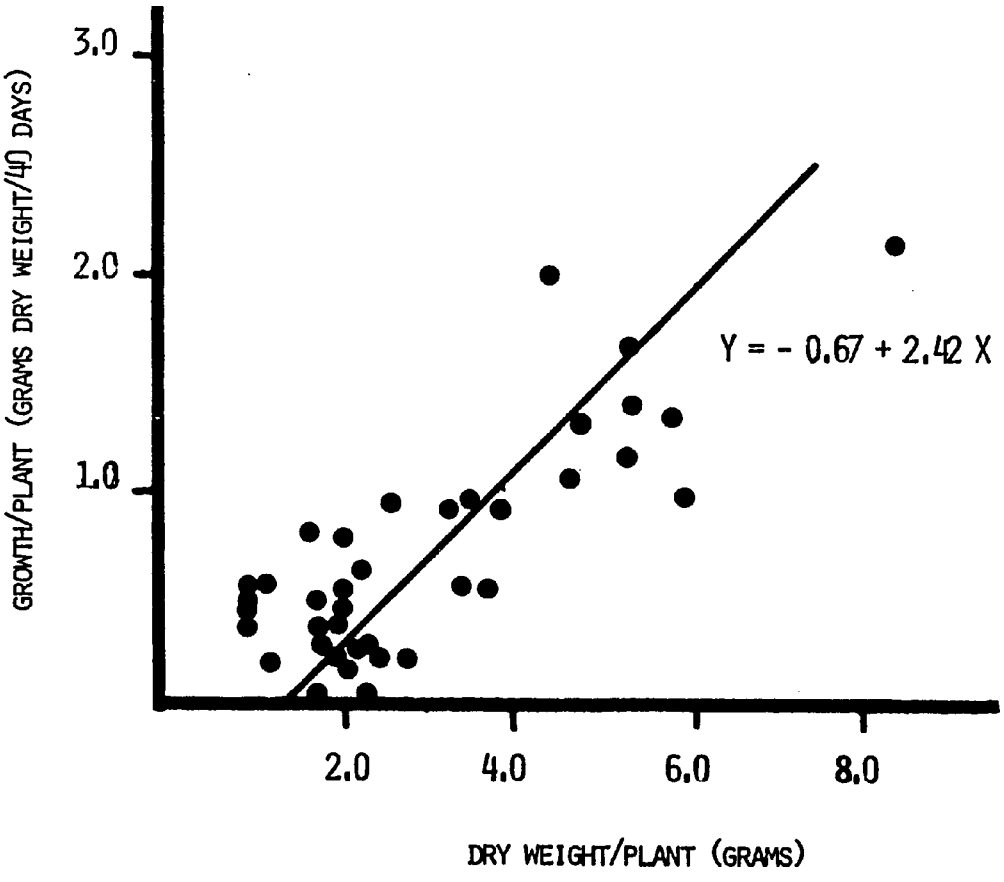

3.0
2.0
1.0
GROWTH/PLANT (GRAMS DRY WEIGHT/40 DAYS)
Y = - 0.67 + 2.42 X
2.0
4.0
6.0
8.0
DRY WEIGHT/PLANT (GRAMS)

Figure 33

Figure 34. The relationship of growth of Halimeda incrassata to the temperatures at which growth was measured in the field. Each point represents the mean growth of individual Halimeda incrassata plants as measured by the monofilament mesh method discussed in the text. The mean growth and temperature for all six stations for each harvesting period was used to calculate each point. Each temperature equals the mean for each harvest period.

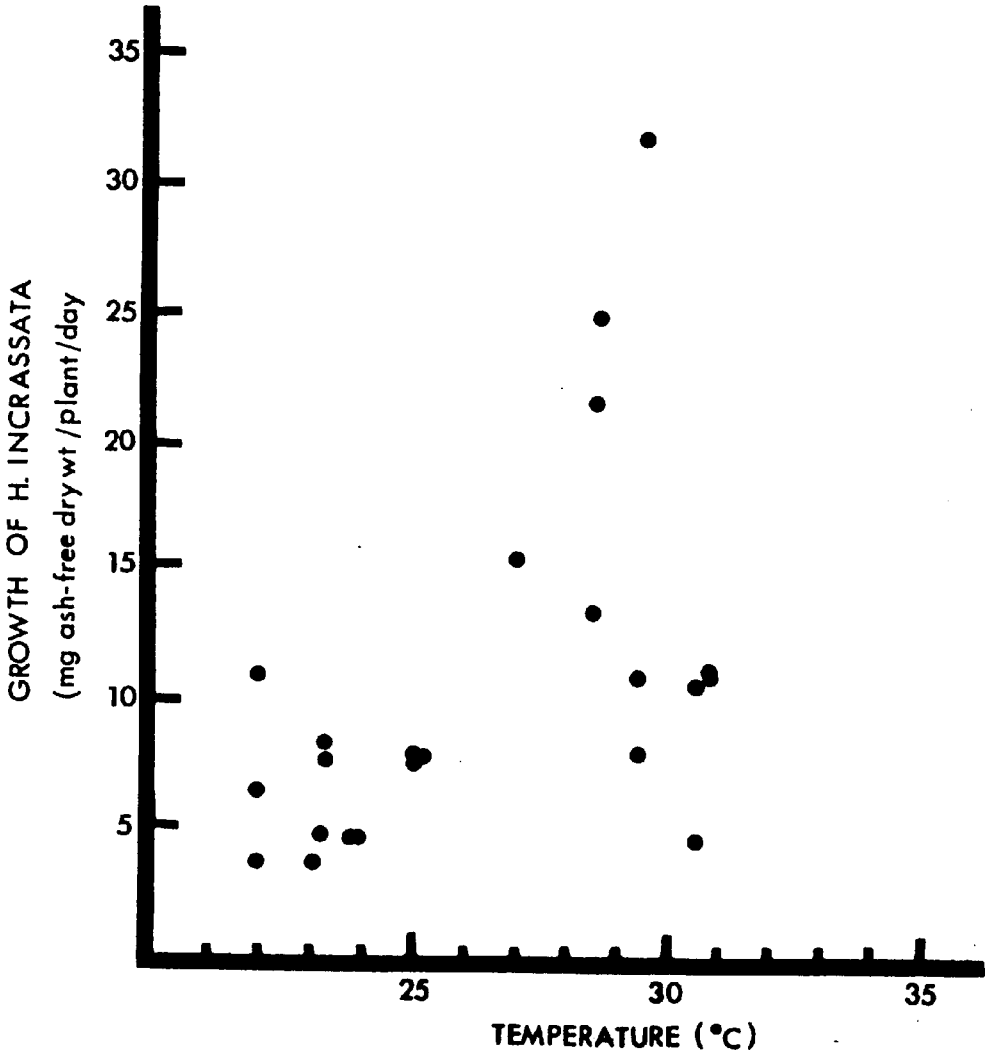

GROWTH OF H. INCRASSATA
(mg ash-free dry wt /plant/day
35
30
25
20
15
10
5
25
30
35
TEMPERATURE (°C)

Figure 34

Figure 35. The relationship of growth of Halimeda incrassata to the salinity at which growth was measured in the field. Each point represents the mean growth of Halimeda incrassata plants as measured by the monofilament mesh method discussed in the text. The mean growth and salinity for all six stations for each harvest period was used to calculate each point. Each salinity equals the mean for each harvest period.

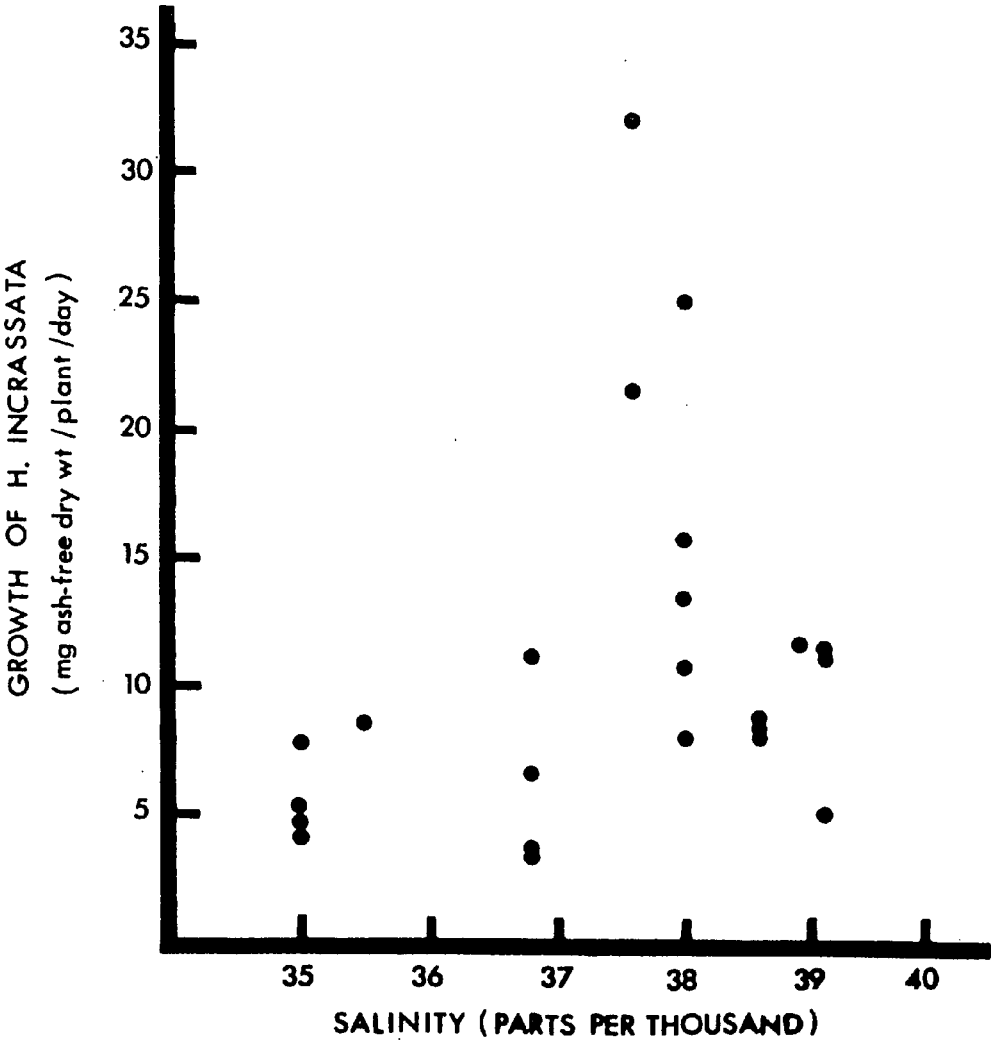

GROWTH OF H. INCRASSATA
(mg ash-free dry wt /plant /day)
35
30
25
20
15
10
5
35
36
37
38
39
40
SALINITY (PARTS PER THOUSAND)

Figure 35

transformed to common logarithims and retested. The transformation normalized the data and eliminated most of the differences among the variances.

A preliminary single classification analysis of variance showed that in almost every case significant ($p<.005$, two tail test) differences existed in growth between stations and dates. The Student-Newman Keuls multiple comparison test (SNK test) was applied to the data sets which showed significant differences in the preliminary ANOVA. The results are shown in Tables 9 through 16.

Mean growth of H. incrassata plants harvested at station 0104 in February, 1975 and December, 1974 was significantly ($p<.05$) lower than growth during May, August and October, 1974. The lower growth corresponded to a period when solar radiation and temperature were at their seasonal lows. Growth ranged from 3.92 ± 3.57 mg dry wt/plant/day in February, 1975 to 11.91 ± 9.66 mg dry wt/plant/day in October, 1974 (Table 9).

At station 0106 (Table 10) growth/plant was highest from June to July, 1974 (31.99 ± 25.06 mg dry wt/plant/day) and lowest (8.05 ± 5.31 mg dry wt/plant/day) from February to May, 1975. From February to May, 1975 intense grazing by the urchin L. variegatus on H. incrassata was observed at this station.

Table 9. Results of the Student-Newman-Keuls multiple comparison test for differences in growth of Halimeda incrassata between different harvest periods.

Station 0104

sample number	number of replicates	adjusted mean growth/plant ± SD*	harvest period (month/day/year) from	to
3	50	3.92 ± 3.57	12/4/74	2/16/75
4	36	4.72 ± 4.57	10/8/74	12/4/74
2	61	8.36 ± 8.11	2/16/75	5/5/75
1	36	10.86 ± 9.83	7/8/74	8/20/74
5	46	11.91 ± 9.66	8/20/74	10/5/74

* mean growth in mg dry weight/plant/day as measured by the monofilament method

maximum nonsignificant ranges of means:

sample numbers	subset
2-5	1
3-4	2

conclusions: Means bounded by samples 2-5 are not significantly different. Means bounded by samples 3-4 are not significantly different. Subsets 1 and 2 are significantly different from one another ($p = 0.05$).

Table 10. Results of the Student-Newman-Keuls multiple comparison test for differences in growth of Halimeda incrassata between different harvest periods.

Station 0106

sample number	number of replicates	adjusted mean growth/plant ± SD*	harvest period (month/day/year) from	to
4	14	8.05 ± 5.31	2/16/74	5/5/75
3	33	8.53 ± 6.06	10/8/74	12/4/74
1	21	12.50 ± 11.51	7/9/74	9/6/74
6	60	15.86 ± 13.03	4/17/74	6/19/74
2	46	21.43 ± 21.48	9/6/74	10/8/74
5	29	31.99 ± 25.06	6/19/74	7/9/74

* mean growth in mg dry weight/plant/day as measured by the monofilament method

maximum nonsignificant ranges of means:

sample numbers	subset
4-1	1
6-2	2

conslusions: Means bounded by samples 4-1 are different ($p = 0.05$) from means bounded by samples 602. Sample number 5 is significantly different from subsets 1 and 2.

Due to the large variation in the data no other logical results could be extracted from the SNK test at station 0106.

The results of the SNK test for individual plant growth at station 0403 for different times of the year are given in Table 11. Growth in the period September 4 to October 19, 1974 was significantly greater (13.73 ± 17.11mg dry wt/plant/day) than during the rest of the year. Growth was lower in winter and also during the period from July 9 to September 4, 1974. Lower growth in winter is an expected result because of the lower temperature and light but lower growth in the period from July 9 to September 4, 1974 is not readily explainable.

At station 0409 growth was greatest (25.02 ± 17.12 mg dry wt/plant/day) during September and October, 1974 and was significantly lower during the winter months (Table 12). The lower growth during the period February 15 to May 5, 1975 coincided with an observed period of branch loss by Halimeda incrassata. In contrast, the higher growth in the period September 4 to October 8, 1974 coincided with a period of rapid regrowth from the stalk portion which was visibly observed in the tagging square.

Since growth of Halimeda incrassata occurred during only 1 harvest period at station 0606 and since no significant differences in growth were found in the preliminary ANOVA for station 0805, growth data at these two stations were not analyzed.

Table 11. Results of the Student-Newman-Keuls multiple comparison test for differences in growth of Halimeda incrassata between different harvest periods.

Station 0403

sample number	number of replicates	adjusted mean growth/plant ± SD*	harvest period (month/day/year) from	to
2	24	3.77 ± 3.11	12/3/74	3/7/75
1	54	4.59 ± 2.52	7/9/74	9/4/74
3	11	4.97 ± 2.52	10/9/74	12/3/74
4	55	13.73 ± 12.11	9/4/74	10/9/74

* mean growth in mg dry weight/plant/day as measured by the monofilament method

maximum nonsignificant ranges of means:

sample number	subset
2-3	1

conclusion: Means included in the subset bounded by samples 2 and 3 are not significantly different from each other. Sample 4 is significantly different ($p = 0.05$) from the means in subset 1.

Table 12. Results of the Student-Newman-Keuls multiple comparison test for differences in growth of Halimeda incrassata between different harvest periods.

Station 0409

sample number	number of replicates	adjusted mean growth/plant ± SD*	harvest period (month/day/year) from	to
4	37	6.65 ± 7.85	12/4/74	2/15/75
2	38	7.76 ± 2.58	10/8/74	12/4/74
3	26	7.98 ± 8.44	2/14/75	5/5/75
1	50	25.02 ± 17.12	9/4/74	10/8/74

* mean growth in mg dry weight/plant/day as measured by the monofilament method

maximum nonsignificant ranges of means:

sample number	subset
4-3	1

conclusion: means included in the subset bounded by sample means 4 and 3 are not significantly different. Mean of sample 1 is different from means in subset 1.

The SNK procedure was also applied to the data to test for differences in the growth of H. incrassata between different stations. A preliminary ANOVA showed that in all but one harvesting period significant differences ($p<0.025$) existed in H. incrassata growth between stations. The SNK test showed that for the period August-September, 1974, growth was significantly lower ($p<0.05$) at station 0403 (4.59 ± 4.39 mg dry wt/plant/day) than at stations 0104, 0106 and 0805 (Table 13.). Station 0409 was not included since it was not added to the study until 1 month later. Growth during September to October, 1974 was significantly greater at station 0106 (21.43 ± 21.48 mg dry wt/plant/day) and station 0409 (25.02 ± 17.12 mg dry wt/plant/day) than it was at stations 0104, 0403 and 0805 (mean growth of these three stations was 10.86 mg dry wt/plant/day; see Table 14). In October, November and December 1974, H.incrassata growth was less at station 0104 than at all the other stations measured, and no significant differences in growth were detectable between the remaining stations (Table 15). Growth of H. incrassata was significantly greater at station 0805 (11.10 ± 7.00mg dry wt/plant/day) than at stations 0403 and 0104 during the months of December, 1974 through February,1975 (Table 16). No differences were found between stations 0104, 0106 and 0409 from February to May, 1975 but since stations 0606

Table 13. Results of the Student-Newman-Keuls multiple comparison test for differences in growth of H. incrassata between different stations.

Growth Period: August-September 1974

sample number	number of replicates	adjusted mean growth/plant ± SD*	station
3	54	4.59 ± 4.39	0403
4	32	11.20 ± 15.50	0805
2	21	11.75 ± 7.83	0106
1	35	11.91 ± 9.66	0104

*mean growth in mg dry weight/plant/day as measured by the monofilament method

maximum nonsignificant ranges of means:

sample numbers	subset
4-1	1

conclusion: Means bounded by samples 4-1 are not significantly different (p=0.05). The mean of sample 3 is different from the means in subset 1.

Table 14. Results of the Student-Newman-Keuls multiple comparison test for differences in growth of H. incrassata between different stations.

Growth Period: September-October 1974

sample number	number of replicates	adjusted mean growth/plant ± SD*	station
5	15	7.99 ± 6.40	0805
1	46	10.86 ± 9.83	0104
3	55	13.73 ± 12.11	0403
2	46	21.43 ± 21.48	0106
4	50	25.02 ± 17.12	0409

*mean growth in mg dry weight/plant/day as measured by the monofilament method

maximum nonsignificant ranges of means:

sample numbers	subset
5-3	1
2-4	2

conclusions: The means of samples in subsets 1 and 2 are significantly different (p=0.05).

Table 15. Results of the Student-Newman-Keuls multiple comparison test for differences in growth of H. incrassata between different stations.

Growth Period: October-December 1974

sample number	number of replicates	adjusted mean growth/plant ± SD*	station
1	36	4.72 ± 4.57	0104
5	6	4.89 ± 4.17	0805
3	11	4.97 ± 2.52	0403
4	38	7.76 ± 2.58	0409
2	33	8.53 ± 6.06	0106

*mean growth in mg dry weight/plant/day as measured by the monofilament method

maximum nonsignificant ranges of means:

sample numbers	subset
5-2	1
1-3	2

conclusions: The means of samples in subset 1 are not significantly different (p=0.05) from each other. Means 4 and 2 are different from mean 1.

Table 16. Results of the Student-Newman-Keuls multiple comparison test for differences in growth of H. incrassata between different stations.

Growth Period: December, 1974 to February, 1975

sample number	number of replicates	adjusted mean growth/plant ± SD*	station
5	24	3.77 ± 3.11	0403
4	50	3.92 ± 3.57	0104
2	9	3.96 ± 3.57	0606
3	37	4.75 ± 5.61	0408
1	9	11.10 ± 7.00	0805

*mean growth in mg dry weight/plant/day as measured by the monofilament method

maximum nonsignificant ranges of means:

sample numbers	subset
5-3	1
2-1	2

conclusions: The means of samples in subset 1 are significantly different (p=0.05) from the mean of sample 1.

and 0805 were lost during this time period and since only one plant grew at station 0403 the test was limited to stations 0104, 0106 and 0408.

A summary of the yield estimates for H. incrassata and H. monile is given in Tables 17 and 18. Adjusted mean growth in mg dry wt/plant/day for each growth period was multiplied by the mean plant densities for all the surveys to give mg dry wt/m^2/day. For H. incrassata this figure was multiplied by 0.7316 to convert the dry weight estimate to mg ash-free dry wt/m^2/day, and by 0.2557 to convert the dry weight estimate to mg calcium carbonate/m^2/day.(For H. monile 82.74 percent organic content and 15.99 percent carbonate content were used).

For all stations and dates, organic matter yield of H. incrassata was estimated to range from 0.8 to 488.7 mg ash-free dry wt/m^2/day. Calcium carbonate yield varied from 0.3 to 170.8 mg calcium carbonate yield varied from 0.3 to 170.8 mg calcium carbonate/m^2/day. The mean organic and carbonate yields of H. incrassata were as shown in Table 17. The mean organic and carbonate yield of H. monile was comparable to the lower range of that of H. incrassata (Table 18).

Table 17. Estimate of Halimeda incrassata yield based on density and growth of individual plants.

station	harvest period (month/day/yr) from	to	mean adjusted growth* per plant	mean plant density**	mean organic matter yield+	mean $CaCO_3$ yield++
0104	7/8/74	8/20/74	11.13	6.4	52.1	18.2
	8/20/74	10/5/74	10.86	6.4	50.9	17.8
	10/5/74	12/4/74	4.72	6.4	30.2	7.7
	12/4/74	2/16/74	3.92	6.4	18.4	6.4
	2/16/75	5/5/75	8.36	6.4	39.1	13.7
0106	4/17/74	6/19/74	15.86	11.9	138.1	48.3
	6/19/74	7/9/74	31.99	11.9	278.6	97.3
	7/9/74	9/6/74	11.75	11.9	102.3	35.8
	9/6/74	10/8/74	21.43	11.9	186.6	65.2
	10/8/74	12/4/74	8.53	11.9	74.3	26.0
	12/4/74	2/16/75	0.00	11.9	0.0	0.0
	2/16/75	5/5/75	8.05	11.9	70.1	24.5
0403	7/9/74	9/4/74	4.59	0.3	1.0	0.4
	9/4/74	10/9/74	13.73	0.3	3.0	1.1
	10/9/74	12/3/74	4.97	0.3	1.1	0.4

* mean mg dry wt/plant/day
** mean number of plants/m^2 of all surveys made at each station.
\+ mg ash free dry wt/m^2/day; based on 73.16% organic content
++ mg calcium carbonate/m^2/day; based on 25.57% calcium carbonate content

Table 17 (continued): Estimate of Halimeda incrassata yield based on density and growth of individual plants.

station	harvest period (month/day/yr) from	to	mean adjusted growth*	mean plant density**	mean organic matter yield+	mean $CaCO_3$ yield++
0403 (cont)	12/3/74	3/7/75	3.77	0.3	0.8	0.3
0408	9/4/74	10/8/74	25.07	26.7	488.7	170.8
	10/8/74	12/4/74	7.76	26.7	151.6	53.0
	12/4/74	2/14/75	6.65	26.7	130.0	45.4
	2/15/75	5/5/75	7.98	26.7	155.9	54.4
0606	12/5/74	2/15/75	3.96	2.6	7.5	2.6
0805	7/9/74	8/19/74	11.20	2.6	21.3	7.4
	8/19/74	10/9/74	7.99	2.6	15.2	5.3
	10/9/74	12/5/74	4.89	2.6	9.3	3.3
	12/5/74	2/15/75	11.10	21.1	7.4	7.4

* mean mg dry wt/plant/day
** mean number of plants/m^2 of all surveys made at each station
\+ mg ash free dry wt/m^2/day; based on 73.16% organic content
++ mg calcium carbonate/m^2/day; based on 25.57% calcium carbonate content

Table 18. Estimate of Halimeda monile yield based on density and growth of individual plants.

station	harvest period (month/day/yr) from	to	mean adjusted growth*	mean plant density**	mean organic yield+	mean $CaCO_3$ yield++
0104	no growth recorded for any harvest periods					
0106	no growth recorded for any harvest periods					
0403	no growth recorded for any harvest periods					
0409	no growth recorded for any harvest periods					
0606	6/20/74	8/20/74	6.57	7.2	39.1	7.6
	8/20/74	12/5/74	2.90	7.2	17.3	3.3
0805	8/20/74	10/9/74	15.34	7.7	97.7	18.9
	10/9/74	12/5/74	8.04	7.7	51.2	9.9

* mean mg dry wt/plant/day

** mean number of plants/m^2/ of all surveys made at each station

\+ mg ash free dry wt/m^2/day; based on 82.74% organic content

++ mg calcium carbonate/m^2/day; based on 15.99% carbonate content

5.4.5 Estimates of Annual Yield

To estimate the annual yield using the direct harvest method, the mean amounts of plant material which grew through the mesh during each harvest period in g/m^2 were added up to give the total for the year at each station (Table 19). The mean of the resulting figure for all six stations represents the average yield for each plant and for all stations measured in Card Sound in g ash-free dry $wt/m^2/yr$ (Table 19).

The range was based on the differences in yield among stations for each algal species. The total estimated yield for all 5 species of algae shown in Table 19 was 8.6 g ash-free dry $wt/m^2/yr$ and ranged from 0.5 to 23.6 g ash-free dry $wt/m^2/yr$. Carbonate yield amounted to 4.2 $g/m^2/yr$, and ranged from 0.2 to 12.7 g ash-free dry $wt/m^2/yr$. H. incrassata accounted for 69 percent of the total organic yield, and 50 percent of the carbonate yield (Table 19). P. capitatus accounted for 16 percent of the total organic yield and 24 percent of the total carbonate yield. Thus, these two species alone accounted for over three-fourths of the total amount of organic and carbonate material produced.

To estimate the annual yield using the life span-standing crop method, the means and ranges of annual yield estimates given in Tables 6, 7 and 8 were used. The results are summarized in Table 20. P. capitatus

Table 19: Estimates of annual yield of calcareous macroalgae in Card Sound, Florida. Estimates based on the direct harvest method as described in text. Means are average total annual yields for each station measured. Ranges are for all stations measured.

algal species	annual organic matter yield (g ash-free dry wt/m^2/yr)		annual calcium carbonate yield (g/m^2/yr)	
	mean	range	mean	range
Halimeda incrassata	5.9	0.5-13.9	2.1	0.2-4.9
Halimeda monile	0.4	0.0- 1.2	0.1	0.0-0.3
Penicillus capitatus	1.4	0.0- 5.3	1.0	0.0-3.8
Rhipocephalus phoenix	0.7	0.0 - 2.9	0.9	0.0-3.5
Udotea flabellum	0.2	0.0 - 0.3	0.1	0.0-0.2
column totals:	8.6	0.5-23.6	4.2	0.2-12.7

Table 20: Summary of estimates of annual yield based on the life-span standing crop method. Data summarized from Tables 6, 7 and 8.

algal species	annual organic yield (g ash-free dry wt/m^2/yr)		annual carbonate yield (g/m^2/yr)	
	mean*	range+	mean*	range+
Penicillus capitatus	4.6	0.0 - 71.8	3.3	0.0 - 51.4
Rhipocephalus phoenix	1.8	0.0 - 16.0	2.0	0.0 - 19.5
Udotea flabellum	1.2	0.0 - 6.2	0.7	0.0 - 3.3

* mean of all stations in Tables 6, 7 and 8.

+ range of all stations in Tables 6, 7 and 8.

was estimated to produce 4.6 g ash-free dry wt/m^2/yr, and the range of yield was from 0.0 to 71.8 g ash-free dry wt/m^2/yr. Carbonate yield averaged 3.3 g/m^2/yr and ranged from 0.0 to 51.4 g/m^2/yr. Organic matter yield of R. phoenix averaged 1.8 g ash-free dry wt/m^2/yr and ranged from 0.0 to 16.0 g/m^2/yr. Carbonate yield of R. phoenix averaged 2.0 g/m^2/yr and ranged from 0.00 to 19.5 g/m^2/yr. U. flabellum was estimated to produce 1.2 g ash-free dry wt/m^2/yr and to range from 0.0 to 6.2 g/m^2/yr. Carbonate yield for this species varied from 0.0 to 3.3 g/m^2/yr and averaged 0.7 g/m^2/yr.

The yield estimates based on the life-span standing crop method and the direct harvest method thus compare favorably with each other except that the ranges of the estimates based on the life-span standing crop method were larger than the ranges of the direct harvest method. All ranges were close to within one order of magnitude of one another, however.

An attempt was also made to calculate yearly rates of yield for H. incrassata and H. monile by extrapolation of daily rates to the whole year to provide a comparison of the density-growth method to the direct harvest method. Daily rates given for each harvest period were multiplied by 365 days and a grand mean calculated for all stations and dates given in Tables 17 and 18. However, extrapolation of daily rates to the entire year is a risky

process which usually results in an overestimation of the actual rates of plant production and should be avoided (Westlake, 1963). In the present study the attempt of extrapolating the daily rates of yield based on the life-span standing crop method resulted in yields much higher than those observed in the direct harvest method, indicating that this extrapolation should not be made. However, it was felt that a comparison of daily rates estimated by the density-growth and direct harvest methods was needed to help substantiate the annual yield estimates for H. incrassata and H. monile. Table 21 is a summary of the comparison of the daily rates of yield estimates by both methods for these two algal species. The means are fairly close to one another and the ranges are close to within one order of magnitude of one another, the density-growth estimate being the higher of the two. It is likely therefore that the annual rates as determined by the direct harvest method are reasonable estimates.

5.4.6 Estimates of Total Yield for all of Card Sound

An estimate of the total amount of organic matter and calcium carbonate produced in Card Sound per year can be made by multiplying the mean yield estimates in Table 19 by the area of Card Sound ($5.76 \times 10^7 m^2$ as estimated by Dean, 1971). The estimated organic matter yield thus equals 5.0×10^5 kg ash free dry weight/yr, and the carbonate yield amounts to 2.4×10^5 kg/yr.

Table 21: Comparison of direct harvest and density-growth methods of yield estimates for Halimeda incrassata and Halimeda monile. Comparison of daily rates of yield.

algal species	organic yield (mg ash free dry wt/m^2/day)		carbonate yield (mg/m^2/day)		method
	mean	range	mean	range	
Halimeda incrassata	18.5	0.0 - 39.2	6.5	0.0 - 13.7	1
Halimeda incrassata	56.5	0.0 -488.7	19.8	0.0 -170.8	2
Halimeda monile	1.3	0.0 - 4.2	0.2	0.0 - 0.8	1
Halimeda monile	5.6	0.0 - 97.7	2.3	0.0 - 18.9	2

1 direct harvest method; taken from Table 5 and from Appendix.

2 density growth method; means and ranges taken from Tables 17 and 18.

5.5 THE EFFECT OF GRAZING ON CALCAREOUS ALGAE IN CARD SOUND

The results of the exclosure experiments are shown graphically in Figure 36. In the 4 control cages with no Lytechinus variegatus the number of healthy Halimeda incrassata decreased steadily with time due to the effect of caging, but the decrease was not nearly so rapid as that in the cages with urchins. Figure 36 shows that in the cages with urchins there was a relative increase in the number of "knobby" plants 35 to 40 days after starting the experiment, while the control cages showed no such increase. Tagged plants outside the cages in the tagging squares were observed to alternate between "mature" with lots of branches, and "knobby", with no branches or merely stubby branches. Many Lytechinus were in the area at the time. The plants in the cages ,including H. incrassata, T. testudinum and L.poitei ,were steadily consumed or died due to the caging effect. The bottom of the cages with urchins was grazed almost bare, leaving only stubs of Thalassia and H. incrassata sticking up through the sediment surface.

When 20 mature (not knobby) H. incrassata were placed in a cage with 10 Lytechinus, and the urchins allowed to feed for 2 weeks, several plants were completely consumed and the others were reduced to stumps. Following

Figure 36. Results of the enclosure experiment at station 0106. Time zero is equal to March 10, 1974. Eight 0.5 m x 1.0 m wire mesh cages (1.25 cm diameter mesh) were placed in a row in 1 meter intervals on the bottom at station 0106. Three Lytechinus variegatus were placed in the first four cages, and no urchins were placed in the other four cages. All the healthy Halimeda incrassata plants in cages were tagged with a numbered plastic strip and their state of health recorded over a period of 3 1/2 months. Top: number of healthy Halimeda incrassata in the four cages with Lytechinus versus time. Middle: number of healthy Halimeda incrassata in four control cages versus time. Bottom: number of "knobby" looking plants versus time in cages with urchins.

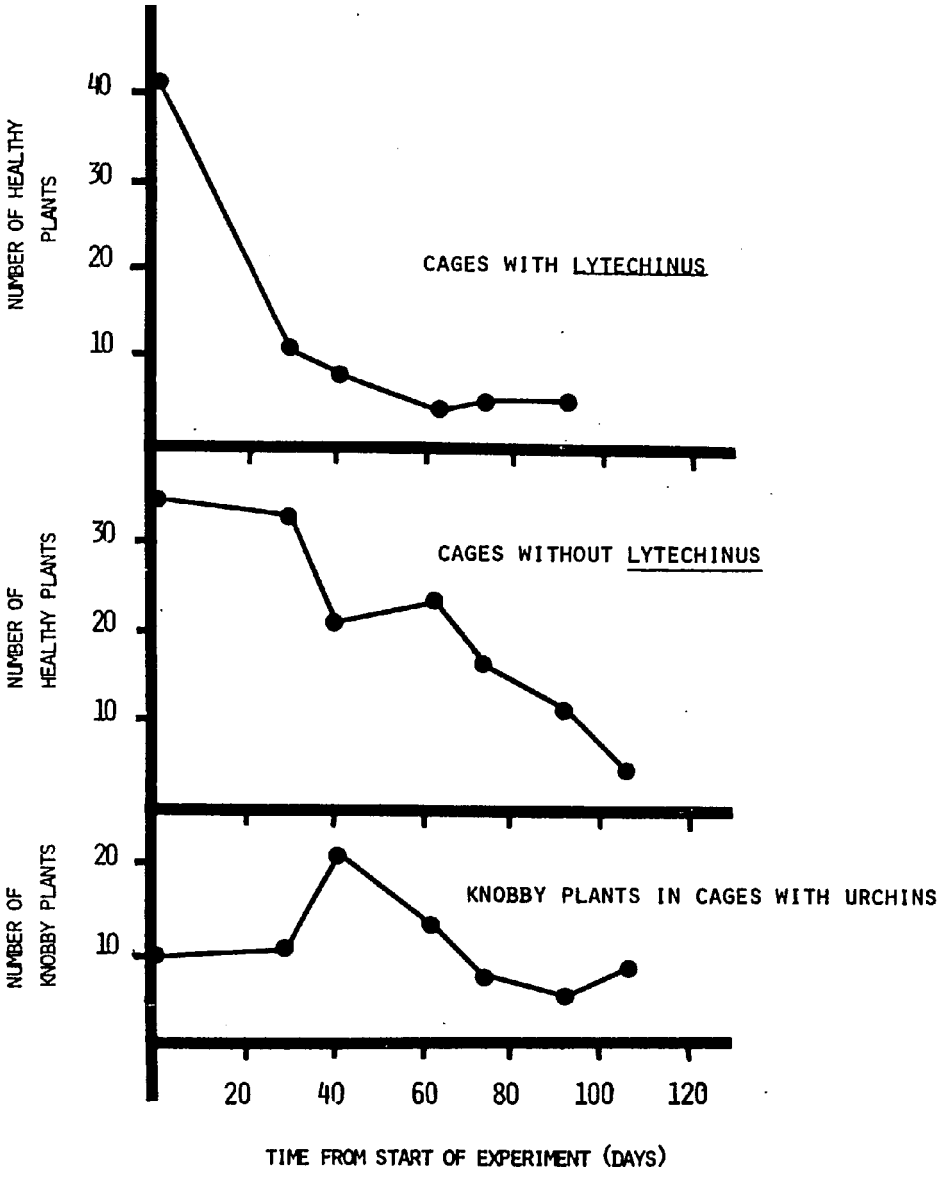

NUMBER OF HEALTHY PLANTS
40
30
20
10
CAGES WITH LYTECHINUS
NUMBER OF HEALTHY PLANTS
30
20
10
CAGES WITHOUT LYTECHINUS
NUMBER OF KNOBBY PLANTS
20
10
KNOBBY PLANTS IN CAGES WITH URCHINS
20
40
60
80
100
120
TIME FROM START OF EXPERIMENT (DAYS)

Figure 36

the removal of the urchins these stumps regrew into the "knobby" looking plants. Eventually these "knobby" plants regrew several branches and became "mature" healthy plants after one month.

Other observations were made of the grazing activities of Lytechinus in Card Sound. Very dense populations were noted in areas of shallow (<2 meters) water and higher tidal current velocity such as Cutter Bank and Card Bank, where virtual denudation of the bottom vegetation was observed in January and February, 1974. Many juvenile Lytechinus were also observed during this time period at both of these locations, and the urchins were found clumped together in groups of up to 8 animals. Usually these animal clumps had large amounts of the red macroalga Laurencea poitei attached to them as well as shells of molluscs and other debris. When urchins were overturned H. incrassata and blades were observed in their mouths.

In the laboratory experiments several L. variegatus were kept in 2.5 gallon aquariums and fed H. incrassata and P. capitatus for several days. The urchins would almost always consume the plant material and green fecal pellets were constantly produced, showing that the plant material had passed completely through the body of the urchin. Several H. incrassata plants that had been partially chewed down to stumps in the laboratory were

planted in an outside flowing seawater tank and allowed to grow for several weeks. The knobby structure usually was the first to develop and then more plates and branches were added until a complete H. incrassata plant had grown back. Usually, however, the resulting morphology resembled H. monile in that the individual plates were more cylindrical than triangular and flat as in H. incrassata. Previous experiments showed that this was a response of the plants to the culture conditions rather than a result of grazing activity.

CHAPTER VI

DISCUSSION

The objectives of this study were to examine the spatial distribution and seasonal growth and yield of the major calcareous siphonales in Card Sound, to explore some of the major factors which limit their production and to show how this particular group of calcareous macroalgae is an important functional component of the Card Sound Thalassia community. The discussion which follows developes each of these three basic objectives in detail.

6.1 SPATIAL DISTRIBUTION OF STANDING CROP

6.1.1 Patterns of Contagion and Sampling Error

An effort was made in the present study to show whether or not the plants were contagiously distributed primarily because this knowledge would aid in assessing the magnitude of error expected in the standing crop estimates. If contagion exists, large variation would be expected in the estimates of density and standing crop even though these estimates are based on random sampling techniques (Cole, 1946). Usually an underestimation of the actual density or standing crop would be expected to occur, because in a contagiously distributed population more sample units will contain zero or only a few organisms (Cole, 1946).

In the present study, visual observations provided excellent examples of contagious distribution, such as in the case of P. capitatus which grew selectively on sponges, invertebrate mounds and coral outcroppings. Distinct patches of various sizes were also commonly observed in Card Sound, other areas of Florida and the Bahamas. Other workers have also recorded observing patches of these plants (Goreau, 1963; Thorhaug, 1965; Mathieson and Dawes, 1975).

Contagion on a somewhat larger scale was also shown to exist by the transect counts across the peat circles and across the sediment wedge along the western shoreline of Card Sound. Calcareous algae, primarily P. capitatus, were found in greater numbers inside the peat circles and H. incrassata was found in greater densities in the sediment wedge, showing this larger level of contagion.

Another indication that the plants were contagiously distributed was the fact that the variance:mean ratio of the density data for each station sampled was in most cases much greater than 1.0. While this measure must be regarded with caution, especially when the sample size is low, in view of all the visual evidence and the transect data above, it appears that the variance: mean ratio did indicate contagion.

There are several possible causes of contagion, two

of which were observed to be most important in the present study (Cole, 1946; Whittaker, 1972):

1. Heterogeniety of the sampling area: This was obvious as shown in the examples of plants growing selectively on coral outcrops, sponges, invertebrate mounds and in peat wedges and circles. Small open areas in between more dense Thalassia were also observed to support clumps of calcareous algae. On the larger scale, the circular patches of Thalassia were examples of heterogeniety also.

2. Reproduction from parent plant: Adult P. capitatus were dug up and were commonly found to produce juvenile and adult P. capitatus directly out of the parent holdfast and also by rhizoids at a short distance from the parent. This was observed in the field and in the laboratory in the case of R. phoenix, U. flabellum and H. incrassata also. I believe it is a major factor in producing small (1-2 meters diameter) patches of plants in the field. Thorhaug (1965), and Mathieson and Dawes (1975) also reported that these same algae reproduce by vegetative propagation in the above manner.

In conclusion, there is good evidence that the calcareous algae of Card Sound were contagiously distributed on several levels. It is expected therefore that a large amount of variation would be introduced into the measurements of standing crop even though random samples

were taken (Cole, 1946). Since randomly distributed organisms are more the exception than the rule in nature this situation is a common one facing most biologists interested in sampling density and biomass in the field, and should be considered as a major cause of observed variation.

6.1.2 Sampling of Standing Crop and Density

According to Greig-Smith (1964), "the sampling procedure must always be related to the importance of the information being sought to the problem under investigation and to the degree of precision necessary." In the present study, greater accuracy was sacrificed in the form of a smaller number of standing crop samples at each station in return for sampling over a broad area. However, general patterns of standing crop and density over the entire area of Card Sound were still discernable because the actual differences in standing crop were very large. The large variation which was observed was an inherent quality of the plant population itself and increasing the sample size to theoretically required levels would not have eliminated this variation. For this reason, no further surveys of standing crop were done after July, 1974. Instead, the data already collected was examined and analyzed closely in conjunction with subjective field observations to try and determine the broader patterns of calcareous algal distribution in Card Sound.

The single most obvious spatial pattern which emerged was that the distribution of H. incrassata was almost exactly opposite that of P. capitatus, R. phoenix and U. flabellum as a group. Very dense populations of H. incrassata were observed at stations 0409 and 0106. The standing crops at these two stations were shown to be statistically greater than that observed at all other stations. Visual observations on the shallow flats both on the ocean side and on the Card Sound side of Key Largo revealed that very dense populations of H. incrassata were present in the shallow water (<1-m) on the tidal bars. Up to 70 plants per square meter were recorded at station 0409. This density of plants was never observed anywhere else in the study area. The smallest densities and standing crops were found in the areas of very shallow marine carbonate sediment which overlay Miami oolite bedrock in western Card Sound. Very sparse H. incrassata populations were also found in the areas of extremely fine mud on either side of Card Bank. Wave action on the bottom probably limited extensive development of H. incrassata in the shallow sediment areas while poor light penetration and difficulty of attachment in extremely fine mud limited development on either side of Card Bank. Intermediate plant density was found along the western shoreline of Card Sound in the sediment wedge and in mid-southern Card Sound where sediments were slightly deeper, such as at station 0805.

The pattern discussed above was also observed in the case of H. monile, because this alga was limited entirely to hard substrates. However, abundance of H. opuntia was definitely greatest in the rocky high current areas just east of Long Arsenicker Key and also in the area near the Card Sound Bridge. Very large thick mats of H. opuntia were found in these two areas.

One of the main questions that arises from all of these observations is why the spatial pattern of H. incrassata was different from the other algae observed. On the basis of comparing data from several areas of the world Ginsburg, et al., (1963) predicted that Halimeda should be found in greater abundance in areas of intermediate current speed. The observations in the present study would confirm this idea. Conover (1968) also showed a relationship between seagrass and macro-algal biomass and current speed. However, why were dense populations of P. capitatus, R. phoenix and U. flabellum found in very low current areas? In the case of H. incrassata several observations made during the present study may provide some explanation for this phenomenon. The basal rhizoids of H. incrassata penetrated more deeply into the Thalassia root-rhizome system than did any of the other algae observed. Also, it grew so that the holdfast was intricatly entwined with the root and rhizome system of the Thalassia. This would provide a

much better attachment for H. incrassata than for the other calcareous algae which did not penetrate the sediment as far. H. incrassata also possessed a much longer life span of from several months to well over a year, as well as the ability to loose its branches and form a resistant "stalk" in times of stress. Resistant H. incrassata stalks were commonly observed to form following extensive stress of any kind exerted on the H. incrassata such as grazing, heavy overgrowth of Chondrilla nucula or smothering by mats of Laurencia. When the stress was removed, regrowth of new H. incrassata branches usually followed. A major point to make here is that many biological pressures were observed to be exerted on H. incrassata throughout the study period. Any adaptation which would enable the plant to survive in response to these stresses would help to insure the success of H. incrassata over another macroalga in the same Thalassia bed. H. incrassata therefore seems particularly well adapted in this respect, and it is not surprising that P. capitatus, R. phoenix and U.flabellum are not able to survive in large numbers and over long periods of time in Thalassia beds where H. incrassata already had fully established itself.

The distribution of P. capitatus, R. phoenix and U. flabellum observed in the present study agrees with the interpretation by Wanless (1969), Humm (1973) and

Thorhaug (1974), in that greater numbers of these algae were found in central sound areas of non-accumulation with coarse sediment less than 15 cm in depth and sparse Thalassia. As the sediment became very deep (greater than 100 cm) and fine south of station 0805 the numbers of all the calcareous macroalgae dropped to virtually zero. Very low standing crops were also found in the extremely fine sediments at station 1103 just south of Card Bank. The combination of poor visibility and inability to become attached probably were the main factors limiting the development of the calcareous algae in these areas. In the large mid-sound areas however, P. capitatus, R. phoenix and U. flabellum truly exploit an "open niche" that few other macroplants can occupy. Caulerpa mexicana and C. cupressoides and H. incrassata were also found in this area but in low densities as compared to the areas of high tidal velocity, deeper sediment and dense Thalassia.

6.2 TEMPORAL DISTRIBUTION OF GROWTH AND YIELD

The basic temporal pattern exhibited by these plants was produced by their modes of growth and longevity. H. incrassata was different from P. capitatus, R. phoenix and U. flabellum because of its very long life span (from 6 to greater than 16 months) and because of its sporadic mode of branch growth. In contrast, the life spans of P. capitatus, R. phoenix and U. flabellum were much

shorter (about 30 to 90 days) and they grew by maturation of a single cap and stalk.

These basic temporal patterns were integrated with and altered by the larger temporal changes which occurred in Card Sound over the course of the year. For example, growth of H. incrassata was lowest in mid-winter during the seasonal lows of temperature and solar radiation and during the seasonal high points of urchin grazing and epibiontic growths. The greatest growth of H. incrassata occurred in late summer and early fall during the seasonal maxima of temperature and solar radiation and at the time of minimal urchin grazing and minimal epibiont growth. It is clear that in addition to the physical stress of winter the plants also simultaneously faced the seasonal maxima of biological pressures. The observed response of H. incrassata of loosing its branches and surviving the period of stress as a stalk is a good example of successful adaptation of an organism to its environment. While no such mechanism was observed to occur in the case of P. capitatus, R. phoenix and U. flabellum, the possibility exists that they could also survive such stress periods in the form of a buried mass of basal rhizoids.

The pronounced seasonality observed in the present study was also expected partly because of the shallow water situation and because the study area is situated

to the north of the central part of the geographic range of all the algal species studied (Diaz-Piferrer, 1963). Because the water in Card Sound is so shallow and exchange with the ocean is limited, it is more rapidly influenced by air temperature changes than waters on the ocean side of Key Largo. During midwinter the water in Card Sound becomes much colder than the water on the coral reefs (i.e., Turtle Reef) just a few miles to the east. Therefore, in winter Card Sound actually resembles a more northerly geographic area with larger seasonal changes in temperature than waters of the Atlantic in the same latitude. Because other studies have shown that the largest variation in seasonal occurrence of Florida marine macroalgae was at the location associated with the widest annual temperature difference (Mathieson and Dawes, 1975), and since the larger number of tropical and perennial algae in deep water (30 to 60 m) has been related to the more stable temperature and salinity as well as the greater water clarity at these depth (Dawes and Van Breedweld, 1969) these results are not surprising. Shallow waters with large variations in hydrographic conditions such as Card Sound would be expected to show a large amount of temporal variation in benthic plant growth and abundance over and above variation introduced by biological factors as discussed above.

6.3 GROWTH AND YIELD OF HALIMEDA INCRASSATA

Growth of H. incrassata was highly variable. This was expected since many other workers have also reported large variation in macroalgal growth (Parke, 1947; Goreau, 1963; Colinvaux, et al., 1965; North, 1967; Mann, 1973). The two most important factors causing growth variation were probably size differences between plants and natural differences in growth rates between plants of the same size. Larger plants would logically seem to produce proportionately more plant material and therefore an attempt was made to relate the amount of H. incrassata produced per plant to the weight of individual plants (Figure 31). One interesting result was the relatively poor fit of the data to the predicted least squares regression line. The coefficient of determination, r^2, would be 1 for a perfect fit and 0 for no fit at all. The observed value of $r^2 = 0.58$ indicated a relatively poor fit but indicated a relationship did exist between plant size and growth. Several factors can account for the observed results. The most important of these is the fact that growth of H. incrassata was observed to be extremely sporadic. Some H. incrassata would grow through the monofilament vigorously, and others would grow very little or not at all in the same harvest period. This fact is shown graphically in Figure 31. A 2.0 to 3.0 gram H. incrassata

plant (dry weight) produced from 0.02 to 1.00grams (dry weight) of plant material in the same 40 day period. Since these data were obtained by a separate method (mesh bag method), and since observations at all the other stations measured showed that it was common for H. incrassata not to grow through the mesh at all, it would seem reasonable to conclude that this was a natural mode of growth. Long term laboratory studies by other workers confirm these observations. For example,Goreau (1963) reported that plants of Halimeda in the laboratory often grew actively for several days and then would enter a "quiescent stage" in which little or no growth occurred.Colinvaux,et al. (1965) reported that some Halimeda monile plants would grow new segments for 1-2 weeks and then growth would stop for 1-2 months. Also, growth of H. monile plants in different aquaria occurred at the same time. Perhaps most importantly, heavy epiphytic growth was reported to be common in the field and in the laboratory and plants in the laboratory were observed to respond by loosing their branches and surviving as a more heavily calcified stalk portion from which regrowth of new branches eventually occurred. While virtually nothing is known concerning the factors controlling this type of growth, it nevertheless seems to be characteristic of these plants, and would account for a very large portion of the variation in growth between plants observed in the present study. Another possible source of variation in growth between

Halimeda plants would be differences in growth between plants of different age classes. In the classic growth situation (Westlake, 1966) growth of young plants first enters a lag and then a logarithmic phase of growth and growth in older plants is much slower as senescence is approached. Therefore, variation would be introduced by the differences in growth among the different age classes. The other possible source of variation was introduced by the net lying at different distances off the bottom. This was caused primarily by natural irregularities in the bottom topography, and little could be done to eliminate this factor.

No attempt was made to measure nutrient availability and its possible effects on H. incrassata growth. An increase in nutrient supply would be expected to result in an increase of H. incrassata growth. Other studies (Mathieson and Dawes, 1975; Josselyn, 1975) have shown that the "winter-spring" period is the usual time of maximal nutrient availability in south Florida waters, and it would therefore appear that other factors caused the decreased growth of Halimeda in mid-winter. During winter, winds are much higher than the rest of the year due to the regular passage of cold fronts through south Florida. Increased turbidity, lower temperatures and decreased solar radiation combined with the effects of urchin grazing and epibiontic growths probably account for the much lower growth of Halimeda during this time of year.

Spatially, the growth of H. incrassata was greater at stations 0106 and 0408, in Thalassia beds with deep sediment and high current velocities. The SNK test showed that this was true at least during the period of maximal seasonal growth in late summer and early fall. During other times of the year growth was reduced at the higher current stations by urchin grazing or Chondrilla overgrowth. When significant H. incrassata growth did occur, however, it was much greater in the areas of high tidal velocity. Many other studies have shown that increased metabolism, growth and biomass are related to increases in current speed and wave energy. Feldmann (1937) and Funk (1927, 1954) stressed the fact that growth of benthic plants living on rocky coasts is maximal in areas of higher turbulence and wave energy which presumably create higher O_2 and CO_2 content of the water. Odum (1956) pointed out the higher relative primary productivities of streams as compared to standing bodies of water. Odum and Hoskin (1957) related increased plant metabolism to increased stream flow. Conover (1968) demonstrated that an increase in current is related to increases in the gross and net production rates of eelgrass (Zostera marina) as well as the biomass of several marine seagrasses and macroalgae. Whitford and Schumacher (1961) demonstrated an increase in uptake of P^{32} by Oedogonium with an increase in current velocity.

All the data indicate that plants are exposed to dissolved nutrients and other substances in natural waters in direct proportion to the current speed. Since both active and passive entry of dissolved nutrients into the cell ultimately depend on the availability of the nutrient material, an increase in current speed would therefore be expected to make more nutrients available to the plant and an increase in primary production should usually result (Conover, 1968).

An important point to be made about the above relationship is that in certain situations such as in the case of H. incrassata, an increase in current is one way of supplying an increase in the "auxillary energy flow" which the plant would otherwise have to supply itself for mineral recycling, internal physiological maintenence, and other physiological requirements (Odum, 1967). With nutrients being constantly swept over the surface of the plant,energy is left to meet all of the plants' physiological requirements, including the requirement of growth. This is another important reason why growth would be expected to be greater in areas of higher current.

In summary, growth, and consequently production, should logically be greater in higher current areas up to the point where plants are dislodged or physically damaged by the current (Conover, 1968).

6.4 RESERVATIONS CONCERNING THE YIELD ESTIMATES

The yield estimates made in this study are given with several important reservations. They are given for Card Sound specifically and any extrapolations made to other areas must take into consideration known variation of several factors. For example, Marszalek (personal communication) found that the carbonate content of H. incrassata near Rodriguez Key,Florida, accounted for 90% of the dry weight of the plant while in the present study it was only 24.6%. Even within Card Sound the carbonate content was shown to vary as much as ± 40% of the mean as was the case of R. phoenix. Carbonate content variation was observed between plants of different ages and between different parts of the same plant. Carbonate content is also known to change with depth, and the change is dependent on the species, some plants, such as P. capitatus, R. phoenix and U. flabellum calcifying less at greater depth, and others such as H. discoidea calcifying more at greater depths (Goreau, 1963). Variation in plant composition is an important point to consider therefore when making carbonate or organic matter production estimates.

Yield was both much higher and much lower in different parts of the sound. Over most of the sound, calcareous algae averaged 8.6 g carbonate and 23.2 g ash-free dry wt/m^2/year. Yield of H. incrassata was observed

to be much higher (up to 488 mg ash free dry wt/m^2/day) in certain areas which were proportionately a very small part of Card Sound. The point I wish to make here is that higher local rates of yield should not be extrapolated to larger areas. Similarly, extrapolations of short term measurements could lead to extreme errors in the estimation of annual rates.

6.5 INTERACTIONS OF GRAZING ANIMALS AND CALCAREOUS MACROALGAE

The results of this study confirm the recent statement that "profound alteration of attached marine flora by herbivorous organisms are becoming more widely documented" (Forster, 1959). The virtual elimination of exposed plant material on Card Bank and Cutter Bank in Card Sound by Lytechinus variegatus during the winter of 1974-75 was a striking example of this phenomena. Since other cases of mass feeding by this urchin have been reported in which large bare areas and even paths were produced in Florida Thalasssia beds (Camp, Cobb and Van Breedveld, 1972), it appears that Thalassia communities are periodically exposed to this kind of pressure. The present study has shown that by being able to regenerate new growth from a basal stalk, H. incrassata is well adapted to withstand heavy grazing pressure by urchins and other biological stresses in the tropical marine environment. This represents an adaptation which

probably has evolved over millions of years. Furthermore, because grazing on these benthic plants is so intense it would also seem highly probable that the coevolution of the herbivore-plant relationship, which has been shown to be so important in the terrestrial environment (Ehrlich and Raven, 1974), has also been an important factor in the evolutionary development and structure of the Thalassia community, even though two of the major Thalassia grazers, sea turtles and manatees, have recently been greatly reduced in numbers by mans' activities (Margalef, 1962).

The large populations of Lytechinus observed in the present study also raised other questions. Urchin devastation of California kelp beds has been related to a chain of events involving organic pollution and the disappearance of the major urchin predator, the sea otter (North and Pearse, 1970). Human predation on the lobster, Homarus americanus has been suggested as a possible contributing factor to large increases in urchins in kelp beds on the east coast of the United States which resulted in large bare areas of the bottom (Mann and Breen, 1972). It is thus interesting to consider the possibility that the large numbers of Lytechinus recently observed in Florida waters are in some way related to possible human effects on a particular urchin predator.

6.6 THE IMPORTANCE OF CALCAREOUS MACROALGAE IN THE *THALASSIA* COMMUNITY

The spatial distribution of the calcareous macroalgae examined in the present study differs from that of the dominant benthic plant in Card Sound, *Thalassia testudinum*. The standing crop of *P. capitatus*, *R. phoenix* and *U. flabellum* was greatest in mid-sound areas where sediment depth was less than 15 cm and *Thalassia* was very sparse. *H. incrassata* also was common in these areas, but reached its greatest standing crops in the shoal areas of higher current speed, deeper sediment and dense *Thalassia*. The important point is that as macroplants these particular calcareous algae have the almost unique ability (*Caulerpa* also grows in the same areas) to occupy areas of shallow, loose sediment. This is good evidence to support the hypothesis that they may be important as an early stage in the successional events leading to the *Thalassia* community, especially when the results of other workers are examined in relation to this idea. For example, Margalef (1962) has suggested this same possibility based on observations in Puerto Rico where *Halimeda* and *Penicillus* (no species given) preceeded the development of the *Thalassia* community. Margalef has suggested that the *Thalassia* community could be reached by starting from several different substrates including soft mud, sand, *Porites*, coral rubble and solid rock. The calcareous macroalgae, he suggests, act as intermediate stages in

the succession by building up the sediment and by providing a place for attachment for Halodule, the seagrass that is usually the next stage in the successional sequence. The whole process may occur in a manner that is analogous to the way that Cymodocea nodosa prepares the substrate for the growth of Posidonia oceanica in the Mediterranean. C. nodosa starts the sequence by establishing itself in organically enriched depressions in sandy areas of the bottom and spreading outward from these locations with its horizontal rhizome system. Unattached P. oceanica plants become trapped by the network of C. nodosa rhizomes and eventually develop into a Posidonia bed (Molinier and Picard, 1952). Studies in south Florida by Thorhaug (1974) also support the view that a similar process occurs which involves calcareous macroalgae. Here, in a Thalassia community previously completely denuded by the thermal effluent of a fossil fuel power plant, the calcareous macroalgae H. incrassata, P. capitatus, R. phoenix and U. flabellum were the first macroplants to colonize the area following the closing of the effluent canal. Halodule wrightii then invaded by vegetative propagation of its rhizome system. This sequence is exactly as would be predicted by the theory of Margalef (1962) and discussed by den Hartog (1971). In view of the above discussion it would seem highly probable that an important function of these algae involves their

role as an early successional stage in the development of the Thalassia community.

When the spatial and temporal distribution of the calcareous macroalgae of Card Sound is examined and compared to the results of other studies, a different set of conclusions is reached concerning the functional role of this group of algae in the Thalassia community. The evidence presented in this study shows that the organic yield of the calcareous macroalgae is low over most of Card Sound in comparison to other primary producers. A summary of these relationships is provided in Table 22. In the case of the phytoplankton and benthic microalgal estimates the reservation is made that these were based on a very few highly variable observations which the authors give with extreme caution (Bunt, et al., 1971). Examination of Table 22 shows that organic production by calcareous algae in Card Sound is almost an order of magnitude lower than the dry weight production of Thalassia, mangroves and perhaps benthic microalgae of Biscayne Bay and Card Sound. Production of calcareous macroalgae compares more favorably with the lower rates given for the red alga Laurencia poitei and phytoplankton in the water column, assuming the phytoplankton rates somewhat approximate the real annual rates for these waters.

Table 22. Comparison of production by different primary producers in Card Sound, Florida.

plant	method of estimation	estimated annual production	source
Calcareous Siphonales (macroalgae)	growth (direct harvest method)	0.5 - 23.6 g ash-free dry wt/ m^2/year	present study
Thalassia testudinum	blade growth-stapling	65 - 1410 g dry/wt/m^2/year	Thorhaug (1974)
Mangroves	leaf-litter fall (Biscayne Bay)	300 g dry wt/ m^2/year*	Teas (1974)
Rhizophora mangle	leaf-litter fall (North River, Everglades)	300 - 400 g dry wt/m^2/year	Heald (1971)
Laurencia poitei	growth in frames	8.1 - 17.3 g dry wt/m^2/year	Josselyn (1975); Thorhaug and Garcia-Gomez(1972)
Benthic microalgae	Carbon-14 uptake	510 - 635 g C/m^2/year	Bunt, et al. (1971)
Phytoplankton	Carbon-14 uptake	13 - 15 g C/m^2/year	Bunt, et al. (1971)

The above estimates indicate that the contribution of organic matter by calcareous macroalgae to the detritus and grazing food chains of Card Sound is small and at best only important in certain areas of Card Sound where yield was estimated to be closer to that of the lower part of the range of Thalassia. Also, the possible contribution of the calcareous macroalgae to the detritus food chain via dissolved organic matter production is not known at the present time.

However, the rates of carbonate production calculated for these algae in the present study show that large amounts of sediment are being added to the Thalassia community of Card Sound each year. The basis for this conclusion lies in the similarity of previously estimated rates of carbonate production for these plants and the rates calculated in the present study. For example, Stockman, et al. (1967) estimated that production of 3.3 g calcium carbonate/m^2/yr by P. capitatus was sufficient to account for 1/3 of all the lime mud in Florida Bay, and that production of 25 g calcium carbonate/m^2/yr was enough to account for most of the lime mud in the Florida Reef tract. Similarly, Neumann and Land (in press) calculated that the most conservative estimates of production of carbonate by these same algae in the Bight of Abaco, Bahamas indicated an overproduction of 50 percent more lime mud than is present in the basin today.

Neumann and Land also observed that large amounts of carbonate material were lost from the shallow basin of the Bight of Abaco to deeper surrounding waters by tidal and storm activity. Since the rates of carbonate production given in these two studies are similar in Card Sound, it can be concluded that large amounts of sediment are being added to this system and that is is also likely that losses of sediment occur from Card Sound into deeper surrounding waters. Furthermore, when the large spatial and temporal variation of standing crop and yield is considered it is apparent that certain smaller areas are producing a proportionately large amount of carbonate, especially during late summer. These areas probably act as highly localized sources of carbonate mud. Furthermore, production and replacement of carbonate mud by calcareous macroalgae serves the important function of helping to maintain an adequate supply of sediment on which the successful survival of the Thalassia community has been shown to depend (McRoy and Helssfrich, in press). Mud production also aids in the building up and expansion of Thalassia beds (Bernatowicz, 1952) which may have important implications concerning the long range patterns of the development of Thalassia over larger areas.

What other possible roles may be served by the calcareous macroalgae in Card Sound based on the observations made in the present study? The fact that they are

virtually the only macroplants over large, flat open areas of Card Sound would indicate that they are important as shelter and habitat for small animals such as amphipods, foraminifera and micromolluscs which are important in the food web and perhaps also in the early successional events of the developing Thalassia community. By binding the sediment with their basal mass of rhizoids these algae also create a microhabitat in the sediment for many of the burrowing animals. Other research has also shown that this role in habitat formation is very important (Thorhaug, 1965; Dahl, 1973) and that there is even selectivity involved in the choice of calcareous macroalgae as a substrate in which to live (Warmke and Almodovar, 1963).

Another important aspect which involves a potential role of these plants in the Thalassia community is related to the fact that many calcareous algal species have been shown to produce antibiotic substances (Oleson, et al., 1964; Almodovar, 1964). However, little is presently known about the possible controlling functions these substances may play in the Thalassia community. Certain of these substances have been shown to control the seasonal and geographic distribution of epibiontic microorganisms on Sargassum (Siebruth, 1968) and a larger group of similar acting substances have been shown to control the eventual development of larger epibiontic

organisms on this same alga (Ryland, 1974). There are real implications that such compounds are very important in the ecology of benthic marine plant communities, but few studies have been done in this area.

CHAPTER VII

CONCLUSIONS AND SUMMARY

1. Organic matter yield by all five algae measured as determined by the direct harvest method was estimated to average 8.6 g ash-free dry wt/m^2/yr and to range from 0.5 to 23.6 g ash-free dry wt/m^2/yr. Calcium carbonate yield for all five species measured as determined by the direct harvest method was estimated to average 4.2 g/m^2/yr and range from 0.2 to 12.7 g/m^2/yr. H. incrassata accounted for 69 percent of the total organic yield. P. capitatus accounted for 16 percent of the organic yield and 24 percent of the carbonate yield. While the alternate methods used to determine the accuracy of the above yields gave more variable estimates of the range, the mean estimated yields were close to each other.

2. Large variation was encountered in the standing crop, growth and carbonate data. Large variation was observed both between different areas within Card Sound and within a given area which resulted in the large variation of the yield estimates. This is an important result in itself, since variation must be dealt with in sampling design and in determining the goals of any field study. In the present study general patterns of yield were recognizable. Yield by calcareous algae was high (up to 488 mg ash-free dry wt/m^2/day) in proportionately smaller areas of higher tidal velocities and deeper

sediment and during late summer in Card Sound, but the average yield for all of the Sound by these macroalgae was almost an order of magnitude lower than production by Thalassia, red mangrove and perhaps benthic microalgae in the same area. Two of the primary causes of this were the very small amount of auxillary current energy available for maintainance of large populations because of the restricted circulation and exchange patterns and the limitation of plant development over most of the sound by inadequate sediment conditions.

3. An important result of this study was the recognition of the dynamic mode of the growth of H. incrassata in which growth of new plates occurs sporadically several times per year. This pattern of growth is completely different from that of Penicillus, Rhipocephalus and Udotea, and must be considered if accurate production estimates are to be made.

4. H. incrassata was found in very great numbers (up to 70 plants/m^2) in areas of high tidal current velocity, deeper sediment and dense Thalassia. Higher numbers were also recorded in a mangrove peat sediment wedge along the western shoreline of Card Sound, although only in comparison to bare rocky areas farther to the east. H. monile was not plentiful over most of Card Sound but in general followed the distribution pattern of H. incrassata. H. opuntia was limited to rocky

substrates, but dense populations were found where a combination of high current and rocky substrate were present together.

Maximum development of P. capitatus, R. phoenix and U. flabellum in Card Sound occurred in central and southern areas of nonaccumulation (3-4 cm < sediment depth < 15 cm) and low Thalassia density. The ability of the algae to inhabit these areas of sparse sediment supports the previously made hypothesis (Humm, 1973) that they are thus able to compete with Thalassia for space. The observations also confirm the observations of Wanless (1969), Thorhaug (1974) and Ginsburg, et al. (1963) with respect to the expected distributions of calcareous macroalgae in relation to sediment and current conditions. Also, very poor development of all species of calcareous algae was observed on either side of Card Bank where very deep accumulation of extremely fine loose sediment occurred. Here, development was primarily limited by a combination of failure to stay attached to the loose bottom and extreme turbidity.

5. Seasonal changes were observed in the growth and yield of H.incrassata. Seasonal lows in growth and yield corresponded to the midwinter lows in daily irradiance and temperature, and perhaps the winter-spring maximum in nutrient availability. Grazing by the urchin Lythechinus variegatus severely reduced growth in Halimeda from

December to February of the winter of 1974-75 at station 0106. Large mats of Laurencia poitei blown and swept into northwest Card Sound during winter and summer storms severely reduced the standing crop of H. incrassata at station 0104. The chicken liver sponge, Chondrilla nucula, was commonly observed to grow over entire plants of H. incrassata and H. monile during mid-winter at stations 0106 and 0409, which resulted in a reduction of growth. Obviously, biological factors such as these are very important in controlling the temporal and spatial distribution of these algae. The response of H. incrassata to these various stresses was to lose its branches and survive as a resistant stalk portion from which new plant material was produced following removal of the stress. This is clearly a very successful adaptation which enables this plant to survive these periods.

6. Calcareous macroalgae are important as a functional component of the Thalassia community of Card Sound in the following ways:

A. They are important as a habitat for small food chain animals in large open areas in which there is little shelter and few other macroplants.

B. Supporting evidence has been given which indicates that calcareous macroalgae are important as an early stage of succession of the Thalassia community which involves both the building up of the substrate and also

providing a foothold for the development of intermediate successional stage seagrasses such as Halodule wrightii.

C. Their contribution to the detritus and grazing food chains is important only in a small area of Card Sound, but calcareous macroalgae are very important producers of calcium carbonate sediment. This function contributes to the maintainence of the physical structure of the Thalassia community and aids in the expansion of Thalassia beds, and consequently is of great importance.

APPENDIX

Table 23. Results of direct harvest method of yield estimate for Halimeda incrassata.

station	growth period (mo/day/yr) from	to	days of growth	Number of replicates	mean yield ± SD uncorrected for time*	Mean yield ± SD corrected for time**	adjusted mean yield ± SD+
0104	3/6/74	5/21/74	79	17	1.27 ± 1.47	16.08 ± 18.61	22.50 ± 26.05
	5/21/74	8/20/74	43	17	1.68 ± 1.38	39.07 ± 32.09	54.70 ± 44.93
	8/20/74	10/5/74	46	17	1.45 ± 1.98	31.52 ± 43.04	44.13 ± 60.26
	10/20/74	12/11/74	57	17	0.44 ± 0.44	7.01 ± 7.01	9.80 ± 10.81
	12/11/74	2/16/75	81	17	0.61 ± 0.59	7.53 ± 7.28	10.54 ± 10.19
	2/16/75	5/5/75	78	17	1.76 ± 1.6.	22.56 ± 20.64	31.58 ± 28.90
0106	2/13/74	4/17/74	63	18	6.59 ± 4.63	104.60 ± 73.49	146.40 ± 102.89
	4/17/74	6/19/74	63	18	2.86 ± 3.20	45.40 ± 50.79	63.56 ± 71.11
	6/19/74	7/9/74	20	18	0.63 ± 2.26	31.50 ± 113.0	44.10 ± 158.20
	7/9/74	9/5/74	59	18	0.62 ± 0.99	10.51 ± 16.78	14.71 ± 23.49
	9/5/74	10/8/74	32	18	1.92 ± 2.12	60.00 ± 66.25	84.00 ± 92.75
	10/8/74	12/4/74	57	18	0.64 ± 0.79	11.23 ± 13.89	15.72 ± 19.45
	12/4/74	2/16/75	74	18	0.00	0.00	0.00
	2/16/75	5/5/75	78	18	0.35 ± 0.57	4.49 ± 7.40	6.29 ± 10.36

* g dry weight/m^2 produced during stated harvest period

** g dry weight/m^2 divided by days of growth = mg dry weight/m^2/day

\+ mean mg dry weight/m^2/day corrected for losses due to sluffing off and growth under net = yield corrected for time multiplied by 1.4

Table 24. Results of direct harvest method of yield estimate for Halimeda incrassata.

station	growth period (mo/day/yr) from	to	days of growth	number of replicates	mean yield ± SD uncorrected for time*	mean yield ± SD corrected for time**	adjusted mean yield ± SD+
0403	5/1/74	7/9/74	68	14	0.69 ± 0.86	10.15 ± 12.65	14.21 ± 17.71
	7/9/74	9/4/74	57	14	0.69 ± 0.64	12.19 ± 11.23	16.94 ± 15.72
	9/4/74	10/9/74	31	14	1.36 ± 1.15	43.87 ± 37.09	61.42 ± 51.93
	10/9/74	12/3/74	55	14	2.73 ± 5.09	2.73 ± 5.09	3.81 ± 7.13
	12/3/74	3/7/75	94	14	0.43 ± 0.42	4.57 ± 4.57	6.39 ± 6.40
	3/7/75	5/5/75	59	14	0.03 ± 0.10	0.50 ± 1.70	0.7 ± 2.4
0409	9/4/74	10/8/74	30	14	2.47 ± 2.26	82.23 ± 75.30	115.12 ± 105.42
	10/8/74	12/4/74	57	14	0.86 ± 1.03	15.08 ± 18.07	21.11 ± 25.30
	12/4/74	2/15/75	73	14	0.37 ± 0.49	5.07 ± 6.71	7.10 ± 9.40
	2/15/75	5/15/75	77	14	0.82 ± 1.14	10.65 ± 14.81	14.91 ± 20.73

* g dry weight/m^2 produced during stated harvest period

** g dry weight/m^2 divided by days of growth = mg dry weight/m^2/day

\+ mean mg dry weight/m^2/day corrected for losses due to sluffing off and growth under net = yield corrected for time multiplied by 1.4

Table 25. Results of the direct harvest method of yield estimate for Halimeda incrassata.

station	growth period (mo/day/yr) from	to	days of growth	number of replicates	mean yield ± SD uncorrected for time*	mean yield ± SD corrected for time**	adjusted mean yield ± SD+
0606	1/23/74	3/15/74	41	6	0.13 ± 0.35	3.17 ± 8.54	4.44 ± 11.96
	3/5/74	4/17/74					
	4/17/74	6/20/74	64	14	0.11 ± 0.28	1.72 ± 4.38	2.41 ± 6.13
	6/20/74	8/20/74	61	14	0.06 ± 0.14	0.98 ± 2.30	1.37 ± 3.22
	8/20/74	12/5/74	107	16	0.06 ± 0.24	0.56 ± 2.24	0.78 ± 3.14
	12/5/74	2/15/75	72	11	0.17 ± 0.25	2.36 ± 3.47	3.30 ± 4.86
	2/15/75	5/5/75	station lost in storm				
0805	1/23/74	5/1/74	98	15	0.78 ± 0.67	7.96 ± 6.84	11.14 ± 9.58
	5/1/74	7/9/74	69	15	0.31 ± 0.55	4.49 ± 7.97	6.29 ± 11.16
	7/9/74	8/19/74	41	15	0.70 ± 1.43	17.07 ± 34.07	23.89 ± 48.83
	8/19/74	10/9/74	51	15	0.29 ± 0.42	5.69 ± 8.24	7.97 ± 11.54
	10/9/74	12/5/74	57	15	0.09 ± 0.20	1.58 ± 3.51	2.21 ± 4.91
	12/5/74	2/15/75	74	15	0.35 ± 0.47	4.73 ± 6.35	6.62 ± 8.89
	2/5/75	5/5/75	station lost in storm				

* g dry weight/m^2 produced during stated harvest period

** g dry weight/m^2 divided by days of growth = mg dry weight/m^2/day

\+ mean mg dry weight/m^2/day corrected for losses due to sluffing off and growth under net = yield corrected for time multiplied by 1.4

Table 26. Results of the direct harvest method of yield estimate for Halimeda monile.

station	growth period (mo/day/yr) from	to	days of growth	number of replicates	mean yield ± SD uncorrected for time*	mean yield ± SD corrected for time**	adjusted mean yield ± SD+
0104	no growth recorded throughout the study						
0106	no growth recorded throughout the study						
0403	no growth recorded throughout the study						
0409	no growth recorded throughout the study						
0606	1/23/74	3/5/74	41	6	0.26 ± 0.46	6.34 ± 11.22	8.88 ± 15.71
	3/5/74	4/17/74	43	12	0.00	0.00	0.00
	4/17/74	6/20/74	64	16	0.15 ± 0.20	2.34 ± 3.13	3.30 ± 4.40
	6/20/74	8/20/74	61	14	0.50 ± 0.97	8.20 ± 15.90	11.48 ± 22.26
	8/20/74	12/5/74	107	16	0.15 ± 0.33	1.40 ± 3.08	1.96 ± 4.31
	12/5/74	2/15/75	72	11	0.00	0.00	0.00
	2/15/75	5/15/75	72	station lost in storm			

Note: estimate of adjusted yield for H. monile was based on the same correction factor (1.4) as that used for Halimeda incrassata.

* g dry weight/m^2 produced during stated harvest period

** g dry weight/m^2 divided by days of growth = mg dry weight/m^2/day

\+ mean mg dry weight/m^2/day corrected for losses due to sluffing off and growth under net = yield corrected dor time multiplied by 1.4

Table 27. Results of the direct harvest method of yield estimate for Halimeda monile.

station	growth period (mo/day/yr) from	to	days of growth	number of replicates	mean yield ± SD uncorrected for time*	mean yield ± SD corrected for time**	adjusted mean yield ± SD+
0805	1/23/74	5/1/74	98	15	0.06 ± 0.22	0.6 ± 2.2	0.8 ± 3.1
	5/1/74	7/9/74		15	0.00	0.00	0.00
	7/9/74	8/19/74		15	0.00	0.00	0.00
	8/19/74	10/9/74	51	15	0.71 ± 1.67	13.92 ± 32.75	19.49 ± 45.85
	10/9/74	12/5/74	57	15	0.11 ± 0.23	1.93 ± 4.04	2.70 ± 5.65
	12/5/74	5/5/75		15	station lost in storm		

* g dry weight/m^2 produced during stated harvest period

** g dry weight/m^2 divided by days of growth = mg dry weight/m^2/day

\+ mean mg dry weight/m^2/day corrected for losses due to sluffing off and growth under net = yield corrected for time multiplied by 1.4

Table 28. Results of the direct harvest method of yield estimate for Penicillus capitatus.

station	growth period (mo/day/yr) from	to	days of growth	number of replicates	mean yield ± SD uncorrected for time*	mean yield ± SD corrected for time**
0104	3/6/74	5/21/74	79	17	0.18 ± 0.52	2.28 ± 6.58
	5/21/74	8/20/74	43	17	0.27 ± 0.66	6.28 ± 15.35
	8/20/74	10/5/74	46	17	0.07 ± 0.21	1.5 ± 4.6
	10/5/74	12/11/74	57	17	0.19 ± 0.36	3.33 ± 6.32
	12/11/74	2/16/75	81	17	0.02 ± 0.09	0.3 ± 1.2
	2/16/74	5/5/75	78	17	0.61 ± 1.04	7.82 ± 13.33
0106	2/13/74	4/17/74	63	14	0.07 ± 0.22	1.1 ± 3.5
	4/17/74	6/19/74	63	14	0.00	0.00
	6/19/74	7/9/74	20	14	0.00	0.00
	7/9/74	9/5/74	59	14	0.00	0.00
	9/5/74	10/8/74	32	14	0.00	0.00
	10/8/74	12/4/74	57	14	0.00	0.00
	12/4/74	2/16/75	74	14	0.00	0.00
	2/16/75	5/5/75	78	14	0.00	0.00
0403	all 0.					

* g dry weight/m^2 produced during stated harvest period

** g dry weight/m^2 divided by days of growth = mg dry weight/m^2/day

Table 29. Results of the direct harvest method of yield estimate for Penicillus capitatus.

station	growth period (mo/day/yr) from	to	days of growth	number of replicates	mean yield ± SD uncorrected for time*	mean yield ± SD corrected for time**
0409	9/4/74	10/8/74	30	14	0.04 ± 0.15	1.3 ± 5.0
	10/8/74	12/4/74	57	14	0.02 ± 0.07	0.4 ± 1.2
	12/4/74	2/14/75	73	14	0.00	0.00
	2/15/75	5/5/75	77	14	0.00	0.00
0606	1/23/74	3/5/74	41	6	3.72 ± 2.52	91.22 ± 61.46
	3/5/74	4/17/74	43	8	1.48 ± 0.13	34.41 ± 3.02
	4/17/74	6/20/74	64	14	1.33 ± 1.11	20.78 ± 17.34
	6/20/74	8/20/74	61	14	1.49 ± 1.46	24.42 ± 23.93
	8/20/74	12/5/74	107	16	0.93 ± 1.05	8.69 ± 9.81
	12/5/74	2/15/75	72	11	0.34 ± 0.59	4.72 ± 8.19
	2/15/75	5/5/75	station lost in storm			

* g dry weight/m^2 produced during stated harvest period

** g dry weight/m^2 divided by days of growth = mg dry weight/m^2/day

Table 30. Results of the direct harvest method of yield estimate for Penicillus capitatus.

station	growth period (mo/day/yr) from	to	days of growth	number of replicates	mean yield ± SD uncorrected for time*	mean yield ±SD corrected for time**
0805	1/23/74	5/1/75	98	15	0.56 ± 0.75	5.71 ± 7.65
	5/1/74	7/9/74	69	15	0.21 ± 0.58	3.04 ± 8.41
	7/9/74	8/15/74	41	15	1.23 ± 1.52	30.00 ± 37.07
	8/15/74	10/9/74	51	15	0.70 ± 0.99	13.73 ± 19.41
	10/9/74	12/5/74	57	15	0.12 ± 0.21	2.11 ± 3.68
	12/5/74	2/15/75	74	15	0.79 ± 1.03	10.68 ± 13.92
	2/15/75	5/5/75	77	station lost in storm		

* g dry weight/m^2 produced during stated harvest period

** g dry weight/m^2 divided by days of growth = mg dry weight/m^2/day

Table 31. Results of the direct harvest method of yield estimate for Rhipocephalus phoenix.

station	growth period (mo/day/yr) from	to	days of growth	number of replicates	mean yield ± SD uncorrected for time*	mean yield ±SD corrected for time**
0104	5/21/74	8/20/74	43	17	0.02 ± 0.06	0.5 ± 1.4
	8/20/74	10/5/74	46	17	0.09 ± 0.27	2.0 ± 5.9
	10/5/74	12/11/74	57	17	0.07 ± 0.18	1.2 ± 3.2
	12/11/74	2/16/75	81	17	0.03 ± 0.14	0.4 ± 1.7
	2/16/75	5/5/75	78	17	0.13 ± 0.26	1.67 ± 3.33
0106	2/13/74	4/17/74	63	18	0.00	0.00
	4/17/74	6/19/74	63	18	0.00	0.00
	6/19/74	7/9/74	20	18	0.00	0.00
	7/9/74	9/5/74	59	18	0.00	0.00
	9/5/74	10/8/74	32	18	0.13 ± 0.25	4.06 ± 7.80
	10/8/74	12/4/74	57	18	0.12 ± 0.31	2.11 ± 5.44
	12/4/74	2/16/74	74	18	0.00	0.00
	2/16/74	5/5/75	78	18	0.39 ± 0.61	5.00 ± 7.82

* g dry weight/m^2 produced during stated harvest period

** g dry weight/m^2 divided by days of growth = mg dry weight/m^2/day

Table 32. Results of the direct harvest method of yield estimate for Rhipocephalus phoenix.

station	growth period (mo/day/yr) from	to	days of growth	number of replicates	mean yield ± SD uncorrected for time*	mean yield ±SD corrected for time**
0403	5/1/74	7/9/74	68	14	0.00	0.00
	7/9/74	9/4/74	57	14	0.02 ± 0.09	0.4 ± 1.6
	9/4/74	10/9/74	31	14	0.00	0.00
	10/9/74	12/3/74	55	14	0.00	0.00
	12/3/74	3/7/75	94	14	0.00	0.00
	3/7/75	5/5/75	59	14	0.01 ± 0.05	0.2 ± 0.9
0409	9/4/74	10/8/74	30	14	0.11 ± 0.31	3.67 ± 10.33
	10/8/74	12/4/74	57	14	0.29 ± 0.57	5.09 ± 10.00
	12/4/74	2/15/75	73	14	0.55 ± 0.49	7.53 ± 6.71
	2/15/75	5/5/75	77	14	0.00	0.00
0606	1/23/74	3/5/74	41	7	0.87 ± 0.61	21.22 ± 14.88
	3/5/74	4/17/74	43	12	1.42 ± 1.35	33.02 ± 31.39
	4/17/74	6/20/74	64	16	1.19 ± 1.02	18.59 ± 15.94
	6/20/74	8/20/74	61	14	0.97 ± 0.91	15.90 ± 14.90
	8/20/74	12/5/74	107	16	0.44 ± 0.57	4.11 ± 5.32
	12/5/74	2/15/75	72	11	1.68 ± 1.31	23.30 ± 18.19

* g dry weight/m^2 produced during stated harvest period

** mg dry wieght/m^2 divided by days of growth = mg dry weight/m^2/day

Table 33. Results of the direct harvest method of yield estimate for Rhipocephalus phoenix.

station	growth period (mo/day/yr) from	to	days of growth	number of replicates	mean yield ± SD uncorrected for time*	mean yield ± SD corrected for time**
0606 (cont)	2/15/75	5/5/75	station lost in storm			
0805	1/23/74	5/1/74	98	15	0.51 ± 0.97	5.20 ± 9.89
	5/1/74	7/9/74	69	15	0.43 ± 1.13	6.23 ± 16.38
	7/9/74	8/19/74	41	15	0.39 ± 0.63	9.51 ± 15.36
	8/19/74	10/9/74	51	15	0.10 ± 0.19	1.96 ± 3.72
	10/9/74	12/5/74	57	15	0.03 ± 0.07	5.3 ± 1.2
	12/5/74	2/15/75	74	15	0.38 ± 0.68	5.14 ± 9.19
	2/15/75	5/5/75	station lost in storm			

* g dry weight/m^2 produced during stated harvest period

** g dry weight/m^2 divided by days of growth = mg dry weight/m^2/day

Table 34. Results of direct harvest method of yield estimate for Udotea flabellum.

station	growth period (mo/day/yr) from	to	days of growth	number of replicates	mean yield ± SD uncorrected for time*	mean yield ± SD corrected for time**
0104	3/6/74	5/21/74	29	17	0.00	0.00
	5/21/74	8/20/74	43	17	0.00	0.00
	8/20/74	10/5/74	46	17	0.00	0.00
	10/5/74	12/11/74	57	17	0.07 ± 0.03	1.2 ± 0.5
	12/11/74	2/16/75	81	17	0.00	0.00
	2/16/75	5/5/75	78	17	0.00	0.00
0106	2/13/74	4/17/74	63	18	0.20 ± 0.32	3.17 ± 5.08
	4/17/74	6/19/74	63	18	0.06 ± 0.25	9.5 ± 3.9
	6/19/74	7/9/74	20	18	0.00	0.00
	7/9/74	9/5/74	59	18	0.00	0.00
	9/5/74	10/8/74	32	18	0.09 ± 0.25	2.8 ± 7.8
	10/8/74	12/4/74	57	18	0.08 ± 0.24	1.4 ± 4.2
	12/4/74	2/16/75	74	18	0.00	0.00
	2/16/75	5/5/75	78	18	0.02 ± 0.14	0.4 ± 1.8
0403	5/1/74	7/9/74	68	14	0.00	0.00
	7/9/74	8/4/74	57	14	0.00	0.00
	8/4/74	10/7/74	31	14	0.00	0.00

* g dry weight/m^2 produced during stated harvest period

** g dry weight/m^2 divided by days of growth = mg dry weight/m^2/day

Table 35. Results of the direct harvest method of yield estimate for Udotea flabellum.

station	growth period (mo/day/yr) from	to	days of growth	number of replicates	mean yield ± SD uncorrected for time*	mean yield ± SD corrected for time**
0403 (cont)	10/7/74	12/3/74	55	14	0.01 ± 0.	0.2 ± 0.6
	12/3/74	3/7/75	94	14	0.00	0.00
	3/7/75	5/5/75	59	14	0.07 ± 0.18	0.2 ± 3.1
0408	9/4/74	10/8/74	30	14	0.00	0.00
	10/8/74	12/4/74	57	14	0.12 ± 0.05	2.1 ± 0.9
	12/4/74	2/15/75	73	14	0.00	0.00
	2/15/75	5/15/75	77	14	0.00	0.00
0606	1/3/74	3/5/74	41	6	0.43 ± 1.06	10.48 ± 25.86
	3/5/74	4/17/74	43	11	0.00	0.00
	4/17/74	6/20/74	64	16	0.00	0.00
	6/20/74	8/20/74	61	14	0.00	0.00
	8/20/74	12/5/74	102	16	0.00	0.00
	12/5/74	2/15/74	72	11	0.08 ± 0.21	1.1 ± 2.9
	2/15/75	5/5/75	station lost during storm			
0805	1/23/74	5/1/74	98	15	0.00	0.00
	5/1/74	7/9/75	69	15	0.00	0.00

* g dry weight/m^2 produced during stated harvest period

** g dry weight/m^2 divided by days of growth = mg dry weight/m^2/day

Table 36. Results of the direct harvest method of yield estimate for Udotea flabellum.

station	growth period (mo/day/yr) from	to	days of growth	number of replicates	mean yield ± SD uncorrected for time*	yield of ± SD corrected for time**
0805 (cont)	7/9/74	8/19/74	41	15	0.17 ± 0.07	4.1 ± 1.7
	8/19/74	10/9/74	51	15	0.00	0.00
	10/9/74	12/5/74	57	15	0.00	0.00
	12/5/74	2/15/75	74	15	0.00	0.00
	2/15/75	5/5/75	station lost in storm			

* g dry weight/m^2 produced during stated harvest period

** g dry weight/m^2 divided by days of growth = mg dry weight/m^2/day

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