


AN ABSTRACT OF THE THESIS OF Tom S. Potter for the Master of Science in Biology presented March 11, 1986.

Title: Effects of Different Habitats on Morphological Variation Within Natural Populations of Three Reported Species of Dictyota (Phaeophyta)

Approved:



Roy T. Tsuda, Chairman, Thesis Committee

Three species of tropical Phaeophyta in the genus Dictyota have been traditionally grouped taxonomically on the basis of morphology. However, the morphologies of these algae have been reported in the literature to be highly variable and on Guam they have been observed to vary considerably in different habitats. In this field study, the species D. friabilis, D. cervicornis, and D. bartayresii were recognized in Guam waters to be ecomorphs of a single species. The different growth morphologies and subsequent zonation of D. friabilis, D. cervicornis, and D. bartayresii were found to be influenced primarily by habitat, with water motion as the major environmental parameter differing in these habitats. In situ transplantation of individuals transformed one species (or growth form) into another.

Assessment of environmental parameters seemed to indicate that changes in water current were related to the generation of morphological variation between species and to

the transformation of one growth form into another. Since significant taxonomic differences were not found to exist between the Guam specimens of *D. friabilis*, *D. cervicornis*, and *D. bartayresii*, and since the latter has priority, the others have been placed in synonymy under it. In addition, some aspects of the seasonality of these algae have been examined.

EFFECTS OF DIFFERENT HABITATS ON MORPHOLOGICAL VARIATION
WITHIN NATURAL POPULATIONS OF THREE REPORTED SPECIES
OF DICTYOTA (PHAEOPHYTA)

BY
TOM S. POTTER

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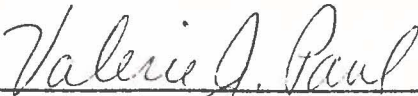
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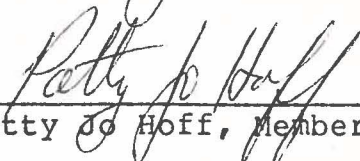
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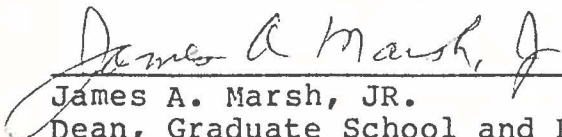


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INTRODUCTION

Many species of marine algae exhibit pronounced morphological variation which is often correlated with habitat (Knaggs, 1966; Druehl, 1967; Peterson, 1972; Steneck and Adey, 1976; Munda, 1976; Sideman and Mathieson, 1985) and is attributable to plastic modification of certain individuals or populations. Cause and effect relationships have demonstrated the strong influence that environmental factors have on inter- and intra-specific morphological variation within marine algal populations (reviewed by Norton et al., 1981).

Environmentally influenced inter- and intra-specific variation in branching morphology of sessile marine organisms has traditionally been troublesome for the taxonomist. Taxonomic discrimination on the basis of branching of many species of coral (Hoffmeister, 1925), crustose coralline algae (Adey, 1970), and fleshy marine algae (Eubank, 1946) has been a continuing source of debate. Several investigators (Druehl, 1967; Peterson, 1972; Steneck and Adey, 1976; Gerald and Mann, 1979) have demonstrated that intraspecific variation of branching morphology in marine algae is highly dependent upon the macro- and microenvironment of a given plant or individual thallus.

Tropical species of the genus Dictyota are extremely variable morphologically (personal observation). Taxonomic distinctions between species have been assigned according to

branch-related gross algal morphology (i.e., branch length and degree of twisting). Cellular arrangement, growth, and reproductive structures are similar within the genus. As a result, demarcation of individuals into species has historically been confusing (see Taylor, 1960).

Three such species of Dictyota inhabit the lagoon and reef flats of Guam in the western Pacific. The three species, Dictyota friabilis Setch., Dictyota bartayresii Lamx., and Dictyota cervicornis Kutz. are the predominant species of Dictyota on Guam, and often thrive on the same reef flat. They inhabit areas from the wave-washed margin through the deeper, less turbulent waters of the back reef (moat). The original descriptions of these algae, later accounts (Collins and Hervey, 1917; Howe, 1920; Taylor, 1960; Misra, 1966) and subsequent published descriptions of these three species on Guam (Tsuda, 1972) indicate that taxonomic distinctions have been based on gross growth morphology.

From reports cited above, the following composite descriptions were derived for each species. D. friabilis has narrow or wide prostrate thalli, 2-4 cm in length with iridescent green, short, rounded or tapered apices. Sporangia are scattered on the thallus. D. bartayresii thalli may be iridescent in color, with branches linear and broad at the base, narrowing gradually towards rounded or acute apices. The upper portions of thalli are repeatedly but often asymmmetrically dichotomously branched, and

slightly twisted. Sporangia are scattered over the thallus surface. Plants range in size from 3-10 cm in height. D. cervicornis has erect twisting thalli with branch patterns subdichotomous to asymmetrical tapering to acute tips. Plants are bushy to 17 cm tall, with sporangia scattered on the dorsal side of the thallus.

Each of these three species has at some time been taxonomically grouped with at least one other of the species just mentioned. Many investigators, among them Tsuda (1972) and Taylor (1960), have mentioned similarities existing between these species. In the field, intermediate thalli have been observed which possess branches characteristic of two different species. Intermediate thalli have been found possessing characteristics of both D. friabilis and D. bartayresii, and of both D. bartayresii and D. cervicornis (personal observation). Collins and Hervey (1917) observed thalli of D. bartayresii with apices characteristic of two different species. Furthermore, they state, "it is probable that all species of the genus are subject to much variation with age and environment, and much study of living plants is needed before we can get a clear idea of specific lines". Based on these findings and repeated textual references to the taxonomic difficulties encountered with these species, the present study was undertaken to determine whether or not the morphological variation between these three species is genetically based or simply an environmental modification.

MATERIALS AND METHODS

Study Sites

Three study sites were chosen (Fig. 1) based on the abundance and species composition of algae in the area. The first site was located at the northern end of Pago Bay reef flat, on the windward side of Guam. Pago Bay is a shallow reef flat formed by a fringing reef and ranges in depth from 0.3 m to 1.2 m at high tide in the area of study. The study site was located just south of the University of Guam Marine Laboratory and extended from the reef margin along a 140-m transect to the shallow back reef moat.

The second site, Luminao reef flat, a submerged reef which was also formed by a shallow fringing reef, is located on the leeward side of Guam, and is comparatively deep, ranging in depth from 0.5 m to 3 m at high tide. There is no shore at Luminao, instead the back reef moat butts against a man-made seawall in 1-2 m of water. The study site here was located across the road from Family Beach. A 3-m² plot just behind the reef margin and an identically sized plot on the seawall were established. Both plots were at either end of a 160-m transect which was perpendicular to shore. The water over the entire reef flat drains through the moat along the seawall.

The third site was located in Cocos Lagoon which is formed by a barrier reef at the southernmost tip of Guam. Experimental zones were located in 1-4 m of water on small

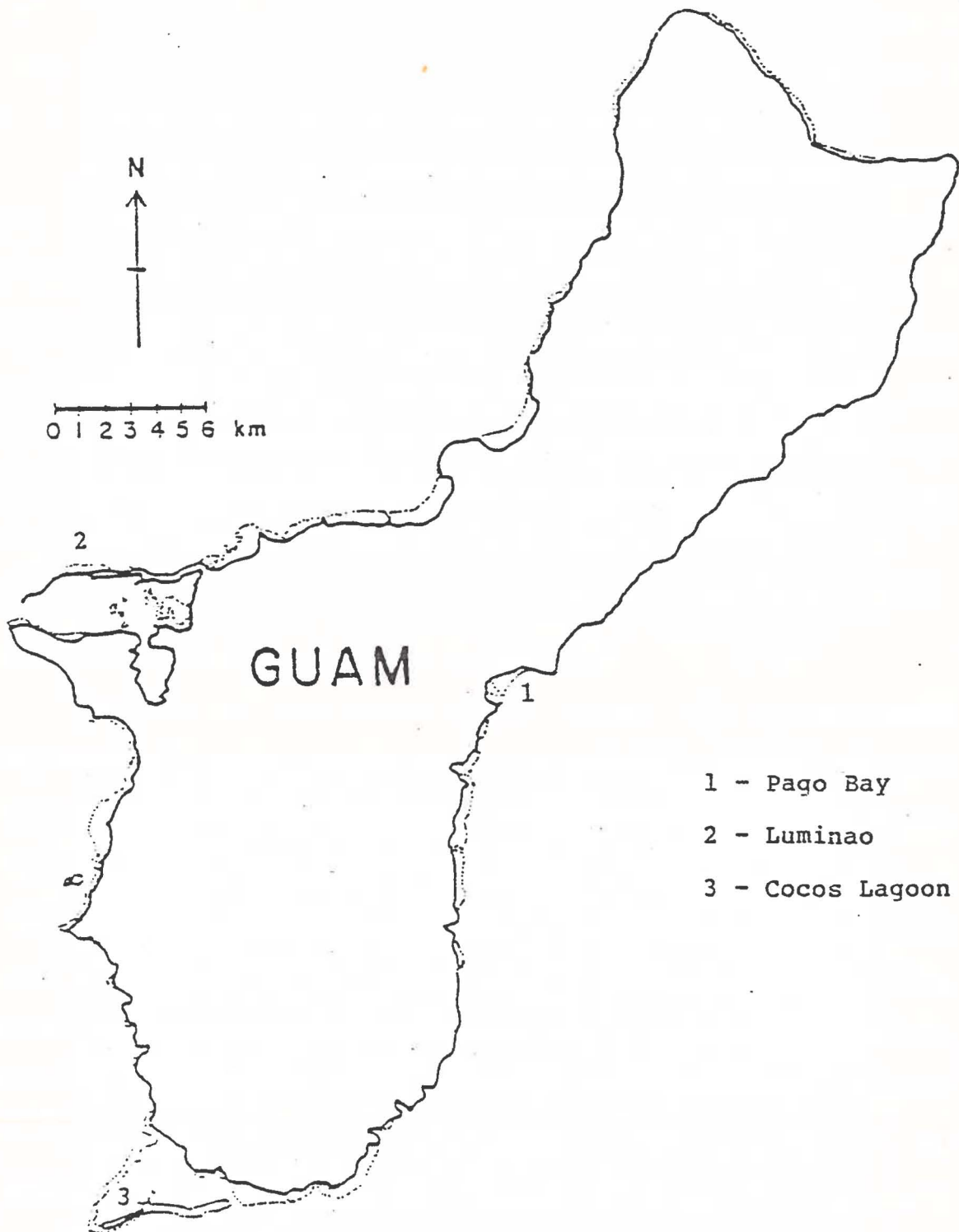


Fig. 1. Map of Guam showing sites for transplant studies and collection of Dictyota.

patch reefs in two of the many sand halos in the seagrass beds just off Cocos Island. One halo was located in about 1 m of water; the other at a depth of about 4 m.

Specimens of all three species of Dictyota used during the course of this study were collected at one of the three study sites. While more than one species often inhabited a given study site, each species appeared to be thriving particularly well at one site. D. bartayresii (Fig. 2) was collected at Pago Bay, D. friabilis (Fig. 3) was collected from both areas at Luminao, and D. cervicornis (Fig. 4) was collected from both areas at Cocos Lagoon.

Assessment of Environmental Parameters

At each of the three study sites, six environmental parameters were measured: salinity, water motion, temperature, light, grazing pressure by herbivorous fish and urchins, and substrate. Salinity was measured with a refractometer (Bio-Marine INC., Aquafauna), water motion with a rotating gurley hooked up to a sound source (Teledyne Pygmy Current Meter), temperature with a standard scientific mercury thermometer and light with an integrating quantum photometer (Li-cor, inc., M1 188B). Grazing pressure was assessed by observing all herbivores from a stationary visual position for a 10-min time interval. Substrate was also assessed visually. All water properties were measured at high and low tide. In addition, measurements of water motion were completed during incoming and outgoing

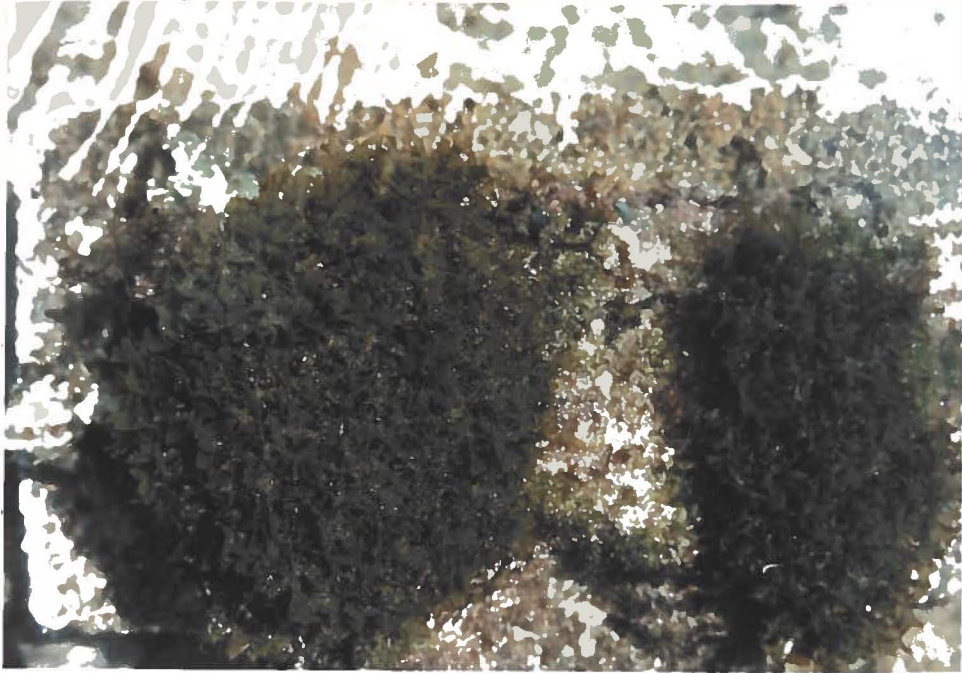


Fig. 2. Natural growth form of Dictyota bartayresii at Pago Bay.

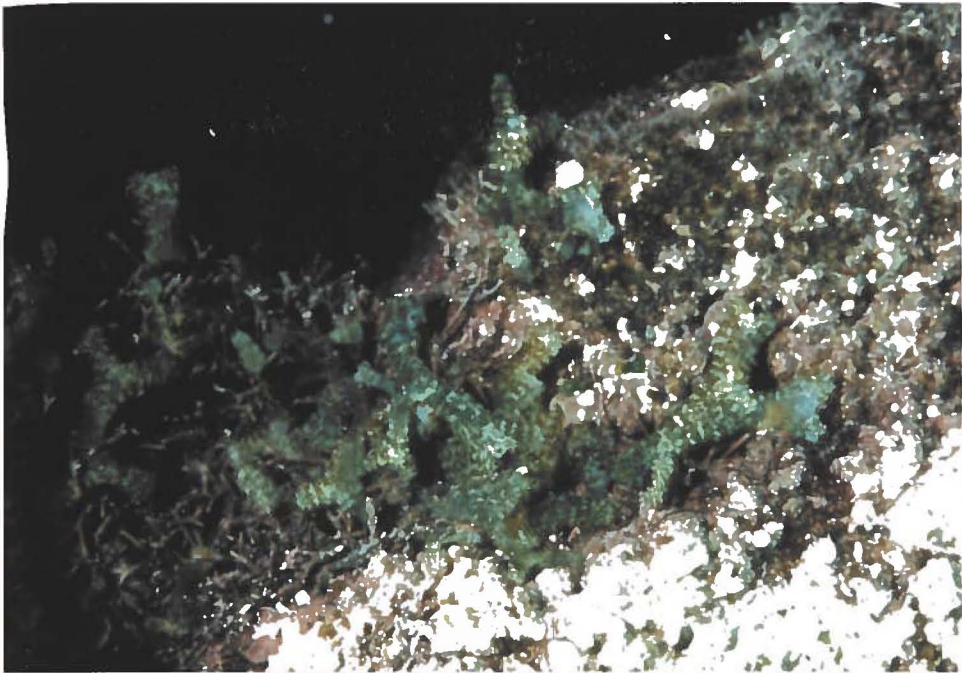


Fig. 3. Natural growth form of Dictyota friabilis at Luminao.

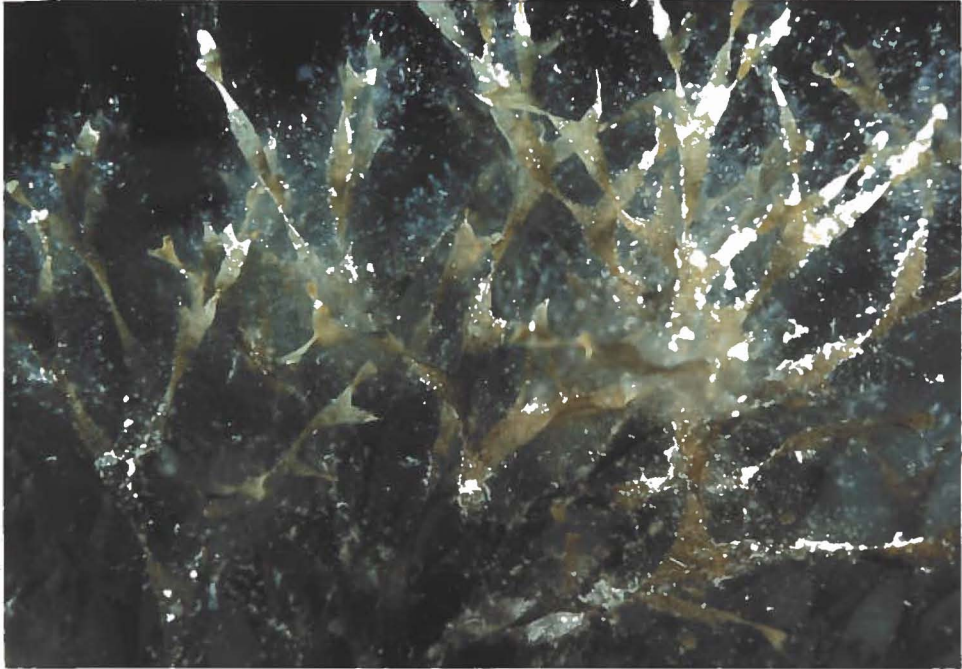


Fig. 4. Natural growth form of Dictyota cervicornis at Cocos Lagoon.

tides at Pago Bay and Luminao. Light measurements were completed during a day with unobstructed sun illumination.

Transplant Experiments

Plants characteristic of one growth form (single species colonies about 8 cm in diameter) were transplanted still intact to the original substrate. Juvenile plants were used whenever possible. These were easily obtained and recognized at areas of algal recolonization. It was thought that morphology may already have been determined in mature plants and that they may not grow as quickly as juvenile plants. The substrate and colony were broken into approximately three equal portions; one stayed at the experimental site of collection as a control and the remaining pieces were placed at the other two experimental sites. Transport from the site of origin to the transplant site was carried out by placing the transplant (attached to substrate) in a plastic tub filled with enough seawater to cover the entire plant. The plants were never in the tub for more than two hours. When this was completed, all three species were present in all three study sites. All transplants were done in replicate format so that there were four transplants of each species at all three sites.

Assessment of Transplant Progress

Transplants at all three sites were observed weekly or biweekly for any change in branch length, morphology, degree

of twisting, or spatial orientation. This was carried out until the morphology of the transplant was virtually indistinguishable from the naturally occurring Dictyota species (i.e., native phene) surrounding it. Transplant experiments were run for a period of 1-2 months or until algal transformations were observed. Before-and-after transplant branch lengths (to the nearest mm) were measured with a small plastic metric ruler. Before-and-after transplant growth forms were assessed visually and documented photographically, and were compared statistically with the McNemar test for significance of changes. Prior to transplantation, thalli were collected from each algal clump, measured, and preserved with 10% formalin in seawater. These preserved specimens were displayed adjacent to post-transplant specimens of the same species for the purpose of the before-and-after transplantation photographic comparisons.

RESULTS

Transplant Experiments

Some degree of morphological change was recorded for all the transplants, while no change except for natural growth of thalli was observed for any of the control specimens. In an area on Pago Bay inhabited by D. bartayresii where D. friabilis from Luminao and clipped D. cervicornis from Cocos Lagoon were transplanted, all four experimental specimens of both transplants were naturally transformed into thalli morphologically identical to D. bartayresii (Figs. 5-6). The characteristically prostrate, iridescent blue-green thalli of D. friabilis changed in color morphology and growth orientation. The color became yellow, branching became more prominent and the thalli were slightly twisted and much longer in length. The thalli grew up off the substrate in an erect fashion so that only one end of the thallus was in contact with the substrate. These transformations in D. friabilis resulted in a plant that was recognized as D. bartayresii.

In Cocos Lagoon where D. bartayresii and D. friabilis were transplanted into an area occupied by D. cervicornis, D. bartayresii thalli grew approximately 10 cm in vertical length and became twisted. As a result, these specimens were indistinguishable from the surrounding naturally occurring D. cervicornis (Fig. 7). The transplanted D. friabilis at Cocos Lagoon did not appear to change to any

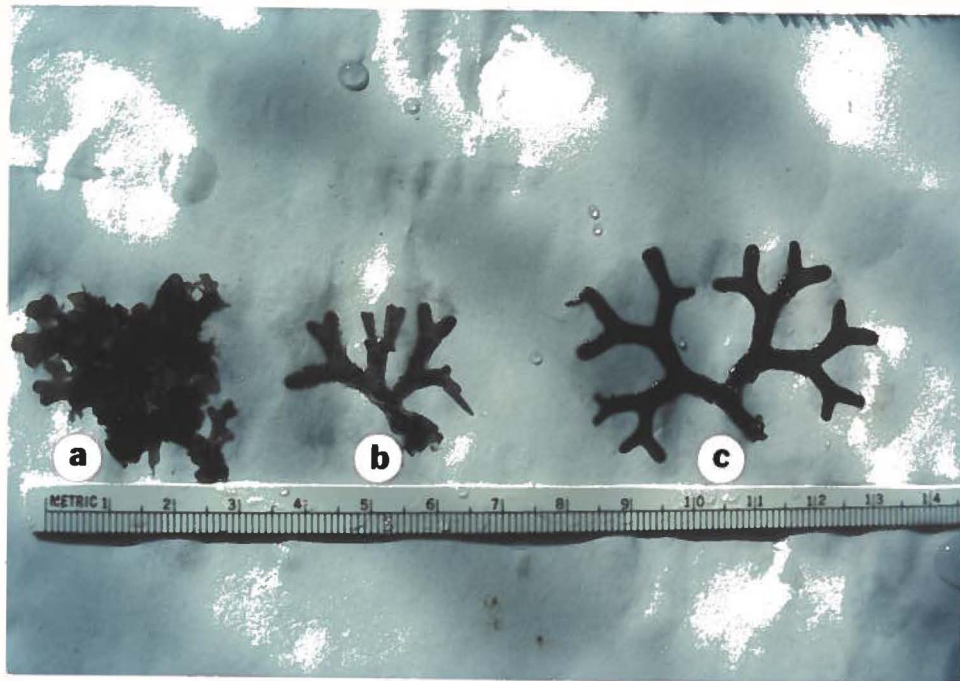


Fig. 5. Transformation of transplanted Dictyota friabilis thalli from Luminao into thalli recognized as Dictyota bartayresii. Pago Bay: a. D. friabilis thallus grouping, b. individual D. friabilis thallus, c. transformed thalli identified as D. bartayresii.

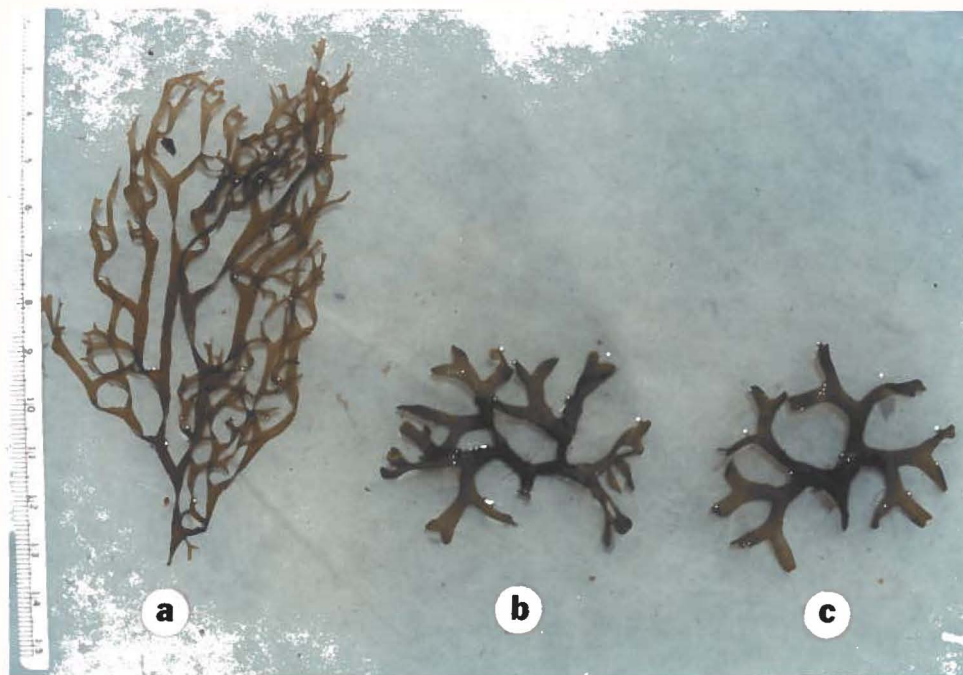


Fig. 6. Transformation of transplanted Dictyota cervicornis thalli from Cocos Lagoon into thalli recognized as Dictyota bartayresii. Pago Bay: a, untrimmed D. cervicornis, b. transformed trimmed thallus identified as D. bartayresii, c. D. bartayresii native to transplant site.

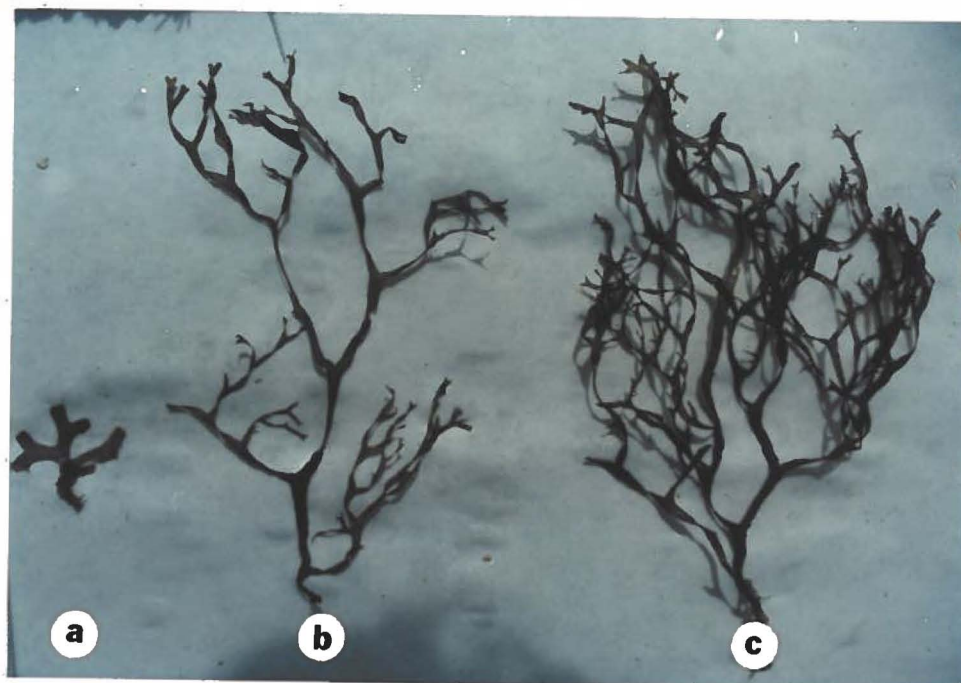


Fig. 7. Transformation of transplanted Dictyota bartayresii thalli from Pago Bay into thalli recognized as Dictyota cervicornis. Cocos Lagoon: a. juvenile D. bartayresii thallus, b. transformed thallus identified as D. cervicornis, c. D. cervicornis native to transplant site.

significant degree. This may have resulted from reduced nutrients or from plants that had already reached maturity before transplantation. At Luminao, in the zone thriving with D. friabilis where D. bartayresii and clipped D. cervicornis were transplanted, both species changed into thalli characteristic of D. friabilis (Figs. 8-9). In experimental specimens of both species, the blue-green pigmentation displayed by D. friabilis was exhibited.

In each case of transplantation, except D. friabilis at Cocos Lagoon, the degree of branch twisting and morphologic orientation to the substrate were similar for the post-experiment transplanted specimen and the surrounding native species. On Guam taxonomic distinctions between the three species under investigation were clearly made using a combination of these two characteristics. If the thallus was prostrate with no twists the specimen was recognized as D. friabilis. If the thallus was erect and had 0-2 twists then the species was identified as D. bartayresii, and if the thallus was erect and had more than two twists then it was recognized as D. cervicornis. Pre- and post-transplant comparisons were made using the McNemar test for significance of changes. In all cases except for the D. friabilis transplanted to Cocos Lagoon, the combination of these two taxonomic characteristics exhibited by pre-transplant species was significantly different ($p < .001$ in all cases) than that of the same post-transplant specimen of identical species (Tables 1-2).

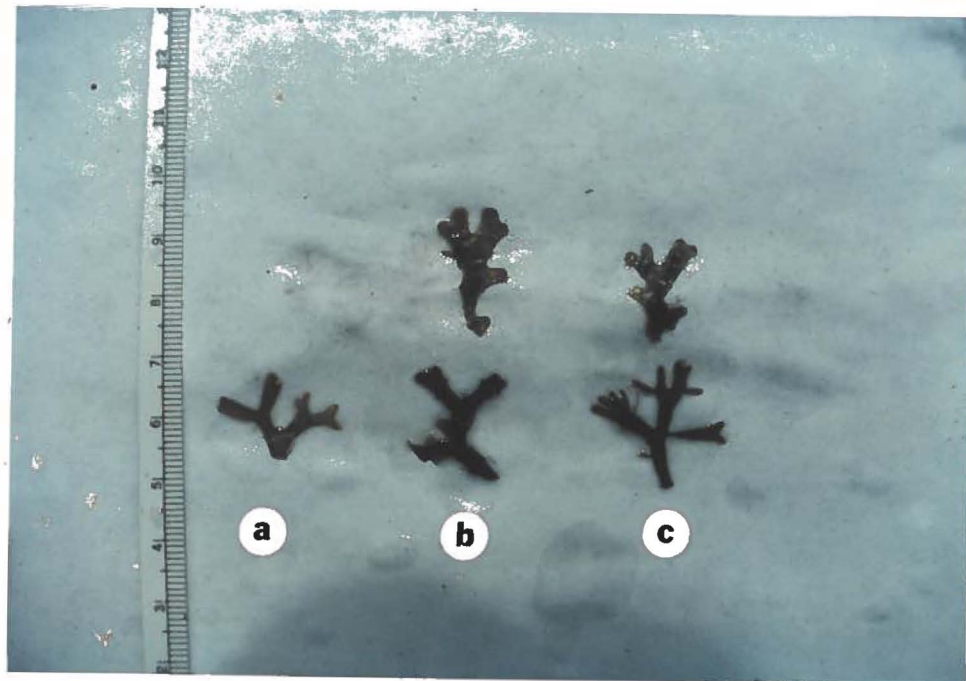


Fig. 8. Transformation of transplanted Dictyota bartayresii thalli from Pago Bay into thalli recognized as Dictyota friabilis. Luminao: a, juvenile D. bartayresii thallus, b. transformed thalli identified as D. friabilis, c. D. friabilis native to transplant site.



Fig. 9. Transformation of transplanted Dictyota cervicornis thalli from Cocos Lagoon into thalli recognized as Dictyota friabilis. Luminao: a. untrimmed D. cervicornis thallus, b. transformed trimmed thalli identified as D. friabilis, c. D. friabilis native to transplant site.

Table 1. Pre- and post-transplant twists per thallus of Dictyota bartayresii, Dictyota cervicornis, and Dictyota friabilis at native and transplant sites. All changes shown from the pre-transplant specimen to the post-transplant specimen were significant at $p < .001$ using the McNemar test of significance for changes. This table in combination with Table 2 records significant changes distinguishing one species from another.

Algal Species	Twists Per Thallus At Native Site N=100	Pre/Post-Transplant Twists Per Thallus N=30		
		Luminao	Cocos Lagoon	Pago Bay
D. <u>bartayresii</u>	0-2	0-2/0	0-2/>2	-----
D. <u>cervicornis</u>	>2	>2/0	-----	>2/0-2
D. <u>friabilis</u>	0	-----	-----	0/0-2

Table 2. Pre- and post-transplant thallus orientation to the substrate of Dictyota bartayresii, Dictyota cervicornis, and Dictyota friabilis at native and transplant sites. All changes shown from the pre-transplant specimen to the post-transplant specimen were significant at $p < .001$ using the McNemar test for significance of changes. This table in combination with Table 1 records significant changes distinguishing one species from another.

Algal Species	Thallus Orientation at Native Site N=100	Pre/Post-Transplant Thallus Orientation N=30		
		Luminao	Cocos Lagoon	Pago Bay
<u>D. bartayresii</u>	erect	erect/prostrate	erect/erect	-----
<u>D. cervicornis</u>	erect	erect/prostrate	-----	erect/erect
<u>D. friabilis</u>	prostrate	-----	-----	prostrate/erect

Assessment of Environmental Parameters

The salinity (31‰), temperature (28°C), grazing pressure (0 sitings), and substrate composition (coralline rubble), were identical at all three sites. In addition, these values were the same for the three zones at Pago Bay each occupied by one of the three Dictyota species. Light measurements varied between sites and within sites. The light values were so variable that no correlation could be made with a given relative light value and a particular site or species of algae. D. friabilis was found growing on top of rocks in direct sunlight, but 30 cm away it was found growing underneath a constantly shaded overhang. D. bartayresii was found growing in shallow clear water illuminated by direct sunlight, in murky water, under overhangs, and to depths of 15 m. D. cervicornis was found in shallow well-lit waters and in murky waters at a depth of 10.5 m. As a result, there was no trend for any one species to have consistently higher or lower values for the environmental parameter of light in comparison to the other species.

The only factor that appeared to be interrelated with a particular study site or a discrete algal zone was the degree of water motion present. Measurements in all three study sites, and in specific habitats of each of the three species of algae revealed that each species inhabited a unique area characteristic of a certain relative current strength. Unfortunately, for purposes of data presentation,

only relative values were obtained. At each revolution of the gurley a sound click was produced in the headphone. By counting the number of clicks made by the rotating gurley, a conversion can be completed which gives water speed in meters per second. In many of the areas where water current was measured, the gurley rotated so fast that distinct clicks could not be counted. Relative values though of high, medium, and low for water current were easily distinguished.

At Luminao, in the study site where D. friabilis was growing, the value for the degree of water motion was the highest in comparison to the other two sites. The Cocos Lagoon site, where D. cervicornis was dominant, had a water motion value much lower than that obtained at Luminao. At the Pago Bay site, inhabited by D. bartayresii, the value was intermediate between the values measured at the other two study sites. In addition, at Pago Bay, where all three species grow, the highest value obtained for current speed was in the zone inhabited by only D. friabilis, the lowest value was in the zone inhabited by D. cervicornis, and the intermediate values were measured in zones thriving only with D. bartayresii.

Additional Field Observations

The results of months of field study yielded interesting supplementary ecological observations pertaining to the three algal species under scrutiny. The principal

population of each species was found to inhabit its own characteristic zone.

Dictyota friabilis was found in areas of high wave energy, usually just behind the reef margin. At Luminao, it was found behind the margin and on the seawall. Both areas possessed strong water currents. This species grew completely prostrate on the substrate, with virtually all parts of the thalli in contact with the substrate. In Hawaii, this ecomorph was prevalent on the wave washed seawall of the Waikiki Natatorium (Tsuda, personal communication). The color is often iridescent bluish green, but can also be almost translucent white to yellow. Thalli shape and branching were variable morphologically.

Dictyota bartayresii was found in areas of medium wave or water energy usually inhabiting the outer reef flat through the back reef. Small compact clumps were often found bordering the shoreward boundary of the D. friabilis zone. The further from the source of wave energy a plant was (either by depth or distance), the less compact the thallus grouping became. Thalli also increased in length. At the Pago Bay study site, a gradation of plants was observed ranging in tightness of thallus groupings, size of mat, and length and degree of twisting of thallus. This growth morphology gradient paralleled the wave energy gradient to which the plants were exposed.

Dictyota cervicornis was present in areas removed from sources of wave energy and current either by distance or depth or both. It was found in back reef moats, and calm areas attached to rocky coralline substrate or wrapped around algal or coral branches. This ecomorph was also often found unattached in seagrass beds where it had gotten trapped after being naturally removed (by water motion) from its original substrate. It was also present suspended in the water column until it settled out or became entangled around an immobile object.

There was a definite seasonality in the abundance of all three species of algae at the Pago Bay site. The other two sites did not appear to show such pronounced seasonal variation. Development of each species began at different annual periods, as did their decline, but specimens of all three species were increasingly hard to find during the period of June through September. At Pago Bay, D. friabilis was present from January through May, D. bartayresii, from September through May or June, and D. cervicornis, from February through May or June.

DISCUSSION

The present study emphasizes that morphological variation among *D. bartayresii*, *D. cervicornis* and *D. friabilis* is habitat related and is not an accurate indication of genetic differences between species. Such habitat-linked variation in brown algae is very common, and the question often arises as to whether it is environmentally or genetically based (Sideman and Mathieson, 1985). Since transplants of various species and growth forms did not maintain their differences when grown together under common conditions, morphological distinctions appear to be environmentally based, and genetically unstable.

The presence of unaltered controls supports the suggestion that the morphological changes witnessed in the transplants were indeed due to environmental differences. There is considerable evidence for water motion affecting these differences. The lack of any relationship between the other five environmental parameters tested and the species distributions supports this hypothesis that zonation and growth morphology of these *Dictyota* species are controlled by water motion. Furthermore, distributional studies of *D. friabilis*, *D. bartayresii* and *D. cervicornis* indicate that the latter two are excluded from areas of surf action. Furthermore, *D. cervicornis* is found only in areas sheltered from strong to moderate water currents. There is an obvious relationship between thalli elongation (height increase),

consequent twisting, and diminishing water motion. Also, the thallus tends to grow up from the substrate in an erect manner under reduced current strengths.

The morphological continuum observed between forms of D. bartayresii contiguous with, and extending from, the D. friabilis zone through the D. cervicornis zone indicates that phenotypic plasticity in Dictyota may be important in determining morphological variability. This is further evidenced by the incredible similarity in thalli morphology of D. friabilis, D. bartayresii and D. cervicornis when viewed in juxtaposition (Fig. 10). In the field, individual D. friabilis thalli are difficult to visualize due to the compact grouping of thalli and due to their completely prostrate nature on the substrate. This observation resembles Setchell's original observation (1926) of this species in Tahiti.

"There occurred here and there, always in small quantity, a very puzzling Dictyota of which it was difficult to obtain good specimens. The decumbent habit, the frequent attachment by masses of rhizoids, and the friable texture all combined to yield only fragments to the collector."

When care is taken though, and single thalli are removed from the substrate they are very similar to, if not identical to, individual thalli of D. bartayresii.

The taxonomic distinctions between these two species have traditionally been the difference in color and in the

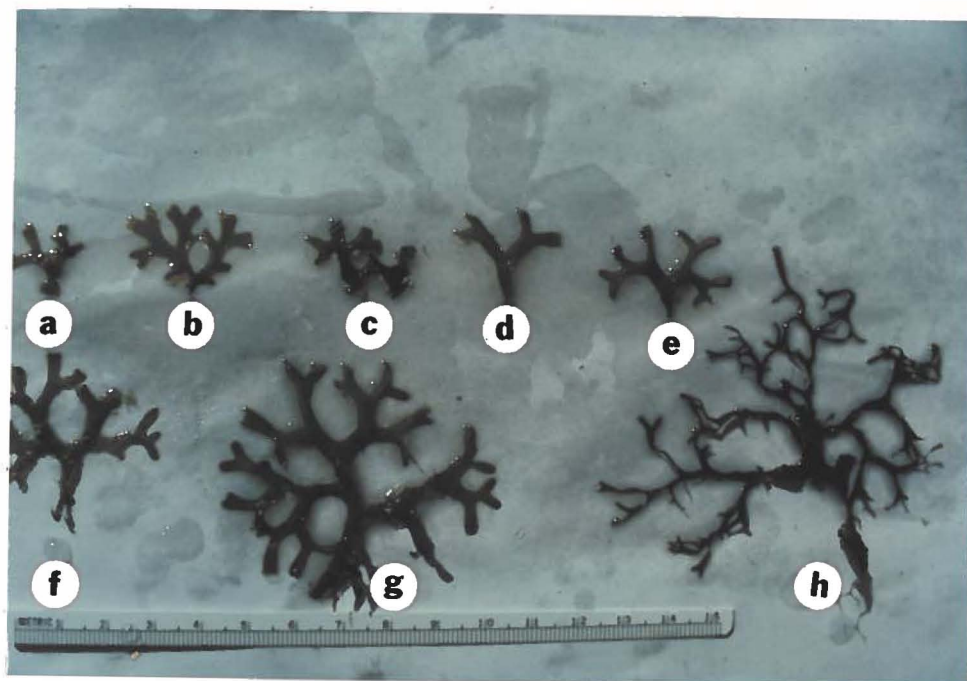


Fig. 10. Juxtaposition of thalli of Dictyota friabilis, Dictyota bartayresii, and Dictyota cervicornis. a and b are D. friabilis, c-g show a gradation of D. bartayresii thalli, and h is D. cervicornis.

morphological appearance of "entire plants." From this study, color differences appear to be habitat related and not necessarily species specific. Whole plants are composed of discrete thalli, and these have been shown to be almost identical for D. bartayresii and D. friabilis. In addition, if D. friabilis thalli are allowed to grow in areas of reduced water motion, they take on the grouping organization and color observed for D. bartayresii. Conversely, if D. bartayresii thalli are grown in areas of increased water motion they take on the appearance of D. friabilis.

As already presented in the results, similar relationships were determined between D. bartayresii and D. cervicornis, and D. friabilis and D. cervicornis. These affinities for variation in morphology of a single thallus moved between habitats adds further evidence to the morphological plasticity of the Dictyota species under investigation.

Seasonality of these three species was attributed to minus tides occurring at midday. Midday minus tides, whose lowest levels occurred between 0900 and 1500 hours, were absent from December through March. They began in April and peaked in June and July before declining in number (Fig. 11). Exposure to midday minus tides has also been suggested to explain the seasonality of several species of Phaeophyta on the Pago Bay reef flat of Guam (Tsuda, 1971, 1974, 1977). In addition, the periods of peak abundance for D. bartayresii and D. cervicornis on Guam (reported herein)

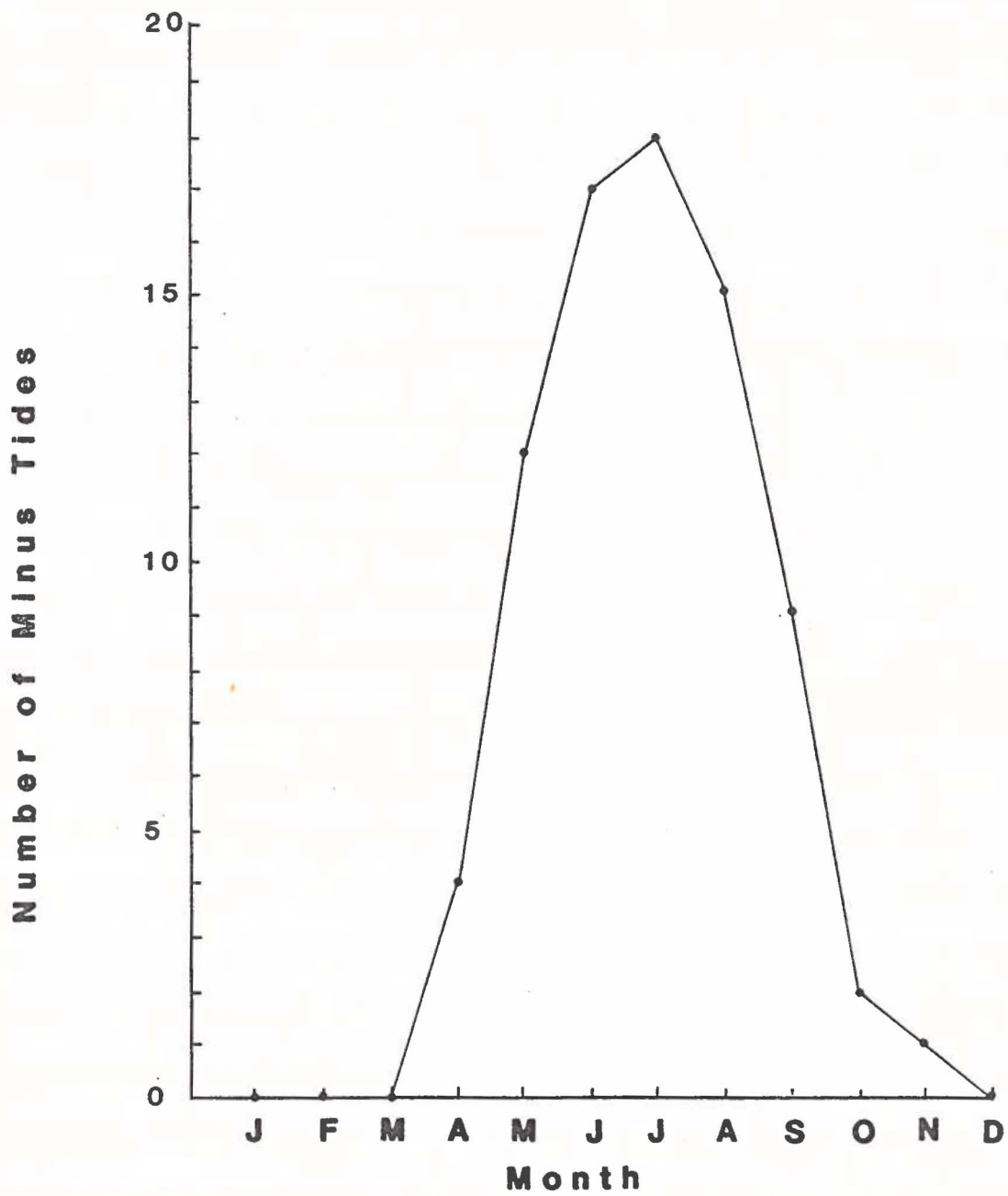


Fig. 11. Frequency of midday minus tides for Guam during each month of 1985.

corroborate those results reported by Tsuda (1974) for the same species on Guam.

The correlation between decreased abundance of all three species of Dictyota on Guam's Pago Bay reef flat and midday minus tides may be due to desiccation damage resulting from atmospheric exposure during periods of high light intensity. The possibility that low tide exposure influences seasonality is further evidenced by the fact that areas of most prolonged growth were reef flat depressions and deeper areas not exposed at low tide. In addition, the deeper Luminao reef flat which was not exposed at low tides did not show any pronounced seasonality with respect to the two species of Dictyota found there.

The seasonality of D. cervicornis on Pago Bay exhibited some rather peculiar patterns which were observed over an extended period. At Pago Bay, the seasonality of D. cervicornis seemed to be controlled by the aforementioned factors but also by the presence of D. bartayresii. It was observed that a D. bartayresii thallus grouping after reaching a certain age was no longer able to remain attached to the substrate. This led to the presence of this species drifting in the water column near the bottom, unattached to the substrate. This was the only species of Dictyota in the water column. Approximately one month after these column blooms of D. bartayresii, D. cervicornis was also observed in the water column. The peculiar phenomenon surrounding the presence of D. cervicornis in the water column was the

almost total absence of any thalli of this species growing attached to the substrate. This observation, in addition to the presence of gradations of D. bartayresii to D. cervicornis in the water column, lead to the hypothesis that the majority of the D. cervicornis in the water column originated from thalli resembling D. bartayresii.

CONCLUSIONS

Dictyota cervicornis, Dictyota bartayresii and Dictyota friabilis demonstrated a remarkable ability to change their growth form under varying degrees of water motion. Degree of water motion most probably determines the morphological features distinguishing the forms of these three species and thus determines their relative zonation and distribution. Such results raise the question about the validity of these three species. It appears that these three species as recognized on Guam are not genetically controlled, but are rather influenced by environmental factors. This suggests that the classification of these different growth forms as distinct species is erroneous, and that these algal forms would more properly be referred to as ecophenes of a single algal species. Since Dictyota bartayresii is the oldest named species of this group, this name must be used for these three major growth forms of Dictyota on Guam, and perhaps on other Pacific islands.

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