

ATOLL RESEARCH BULLETIN

No. 289

THE DISTRIBUTION, ABUNDANCE AND PRIMARY PRODUCTIVITY
OF SUBMERGED MACROPHYTES IN A BELIZE BARRIER-REEF
MANGROVE SYSTEM

BY

MARK M. LITTLER, PHILLIP R. TAYLOR,
DIANE S. LITTLER, ROBERT H. SIMS
AND JAMES N. NORRIS

ISSUED BY
THE SMITHSONIAN INSTITUTION
WASHINGTON D. C., U.S.A.
MAY 1985

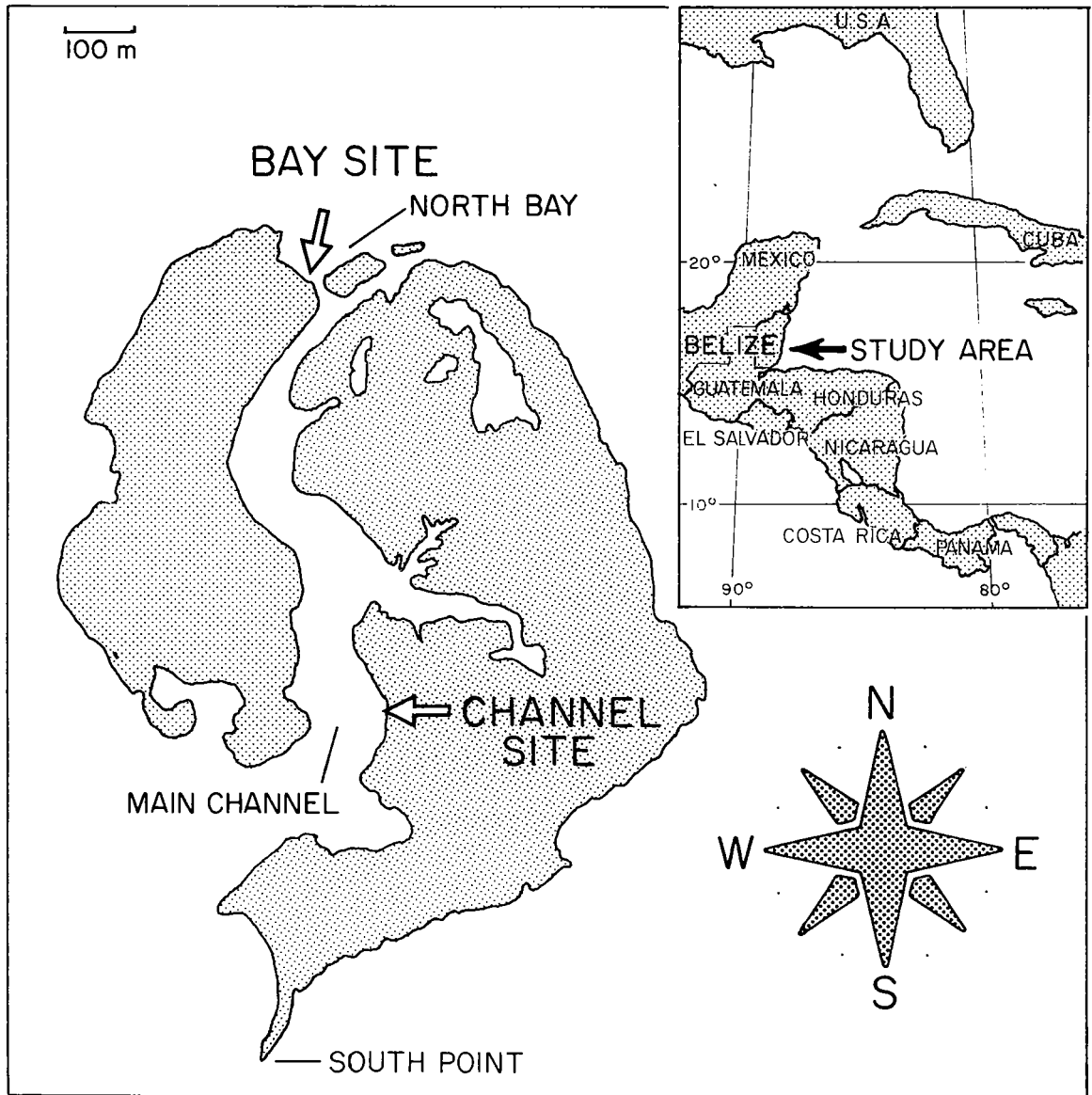


Figure 1. Location of Twin Cays study sites on the Belize barrier reef.

THE DISTRIBUTION, ABUNDANCE AND PRIMARY PRODUCTIVITY
OF SUBMERGED MACROPHYTES IN A BELIZE BARRIER-REEF
MANGROVE SYSTEM

By

MARK M. LITTLER*, PHILLIP R. TAYLOR,**

DIANE S. LITTLER*, ROBERT H. SIMS*

AND JAMES N. NORRIS*

ABSTRACT

The comparison of wave-exposed (bay) to sheltered (channel) macrophyte assemblages in a Belize mangrove system revealed higher standing stocks of productive filamentous algae in the latter, correlated with relatively low levels of physical disturbance from sea urchin herbivory and wave turbulence. The sheltered channel site, while containing fewer total species and lower species richness, exceeded the bay site in total cover and species evenness. The Shannon-Weaver index of diversity was nearly equal at both sites. Five species comprised 96% of the cover at the bay site, led by the jointed calcareous alga Halimeda opuntia f. triloba (37%) and Thalassia testudinum (26%); whereas, H. opuntia f. triloba (40%), Amphiroa fragilissima (22%) and T. testudinum (16%) provided the majority of the total community productivity. At the channel site, six taxa contributed 96% of the cover, dominated by a mat-forming, gelatinous, filamentous species of naviculoid diatom (29%) and Caulerpa verticillata (28%). Major primary producers at the channel site were the three cover dominants, the gelatinous diatom (24% of the total community carbon fixed), C. verticillata (22%) and H. opuntia f. triloba (20%). The total daylight community primary productivities at the two sites (bay = 17.2, channel = 13.4 grams carbon fixed per meter squared of substratum per day ranked among the higher rates recorded for dense seagrass beds and were considerably higher than those reported for most calcareous reef flat habitats. This high apparent photosynthetic potential may be related to reduced levels of herbivory and a greater availability of recycled nutrients near mangrove islands.

* Department of Botany, National Museum of Natural History,
Smithsonian Institution, Washington, D.C. 20560

** Present address: Biological Oceanography Program, National
Science Foundation, Washington, D.C. 20550

INTRODUCTION

The fringing-reef margins of tropical atolls and coastal zones represent shallow subtidal to intertidal calcareous frameworks with diverse epibiota that have received intensive study in recent years. Diverse algal standing stocks have been described for Curacao, Dutch West Indies (e.g. Van Den Hoek et al. 1975) and Saint Croix, U.S. Virgin Islands (Connor and Adey 1977) in the Caribbean. Pacific reefs, such as Enewetak Atoll, U.S. Trust Territory (Odum and Odum 1955); Waikiki reef, Hawaii (Doty 1971; Littler 1973a); Guam, U.S. Trust Territory (Tsuda 1971); American Samoa (Dahl 1972); Kaneohe Bay, Hawaii (Smith 1973); and Heron Island, Australia (Hatcher 1982; Hatcher and Larkum 1983), have been the subjects of comparable studies.

While mangrove communities coincide with the worldwide distributions of calcareous biotic reefs and dominate many of the world's tropical and subtropical coastal zones, relatively little work has been done on the standing stocks of benthic macrophytes on the flats that border mangrove islands. On mangrove islands, like coral islands, organisms comprise the major structural elements, but unlike most biotic reef communities, mangrove islands are intertidal, endure wider fluctuations in temperature and salinity and tend to contain silty submerged substrata. Because of their interesting characteristics and a paucity of background information, we initiated a quantitative survey of mangrove macrophyte distributions, abundances and productivities as a necessary basis for the design of further, more specialized experimental studies (e.g. Taylor, Littler and Littler, submitted).

A classification of marine plant functional-form groups [see Littler, Littler and Taylor (1983) for definitions] has been used to interpret (1) productivity patterns over broad geographic areas (Littler and Arnold 1982), (2) evolutionary changes with respect to fluctuations in herbivory through geological time (Steneck and Watling 1982), (3) holistic views of tropical barrier-reef seaweed ecology (Littler, Littler and Taylor 1983), (4) biogeographical responses of algae to herbivory (Gaines and Lubchenco 1982) and (5) the effects of disturbance on subtropical (Littler and Littler 1984) and temperate (Murray and Littler 1984) macrophyte communities. The functional-group approach is an effective mechanism for assessing complex community patterns without having to tediously deal with the demography of each of the component species. Consequently, we felt it would be instructive to analyze the Twin Cays macrophyte populations from this framework.

METHODS AND MATERIALS

Study Areas

Twin Cays is a mangrove system (16° 50' N, 80° 06' W) representative of similar pristine offshore islands within the lagoonal portion of the Belize barrier system. The island (Fig. 1; see also Rützler and Macintyre 1982) is divided by a main channel that grades toward each opening into shallow beds of Thalassia testudinum Banks ex König.

After extensive reconnaissance of the Twin Cays shoreline, the precise location of the upper end of each study transect was determined (by consensus of several experienced marine ecologists) along biologically representative portions of two major benthic habitat types. The channel study site, located on the east side of the main channel, is protected from wave action, with only moderate tidal currents controlling water exchange. The area studied is a typical subtidal mud bank extending 5.5 m outward to a dropoff from intertidal Rhizophora mangle Linnaeus into the meandering 0.5 to 4.0 m deep main channel dominated by Thalassia and Caulerpales. In contrast, the less-sheltered bay site on the northern margin of the island (Fig. 1) typifies habitats where waves and currents are greater, frequently resulting in the mud banks being partially eroded to form vertical walls or undercut ledges. The mud bank studied is 6.5 m wide and terminates abruptly where an undercut bank extends down to a 3.0 m deep silt substratum with sparsely scattered plants of the algal genus Caulerpa [C. mexicana (Sonder) Kützling and C. sertularioides (Gmelin) Howe].

Transects

Data were obtained on 11-12 April 1980 by photographing numbered quadrats perpendicular to the substratum with a 35 mm Nikonos camera equipped with an electronic flash unit and using Kodachrome 64 transparency film. Each quadrat contained a plastic label affixed to the upper left corner that was marked with a wax pencil to identify permanently each of the photosamples.

In the laboratory, the developed transparencies were projected onto a sheet (21 x 28 cm) of white bristol paper. The paper contained a grid pattern of dots at 2.0 cm intervals on the side of the transmitted light; this has been shown (Littler and Murray, 1975) to be an appropriate density (i.e. 1.0 per cm²) for consistently reproducible estimates of cover. The number of dots superimposed on each species was then scored twice (i.e. replicated after movement of the grid) with the percentage cover values expressed as the number of "hits" for each species divided by the total number of dots contained in the quadrats. Reproducibility was high and seldom varied more than ± 5% for a given species. Species that were not abundant enough to be scored by the replicated grid of point intercepts were assigned a cover value of 0.1%. In cases of multi-layered communities, more than one photograph per quadrat was taken to quantify each stratum after upper strata had successively been moved aside, often yielding total biotic coverages of greater than 100%.

The method as applied here does not allow for the quantification of microalgae (small epiflora or inflora) when they occur in low abundances. We realize that these may be metabolically very active, but their analysis requires special techniques and expertise, which comprise separate problems in themselves. For this reason, our measurements were restricted to macrophytes that could be discerned in the field with the unaided eye. However, we did quantify microflora (e.g. mats of a filamentous diatom) when it occurred in high abundances. Twenty three contiguous quadrats along a 6.65 m transect were taken at the bay site while 31 quadrats along a 7.25 m line were sampled at the channel site.

Community Productivity

Net apparent photosynthesis of the most abundant macrophytes found at the study sites was determined in a shallow current channel at ambient water temperatures (27 C) on 24 April 1980. Four replicate incubations per taxon were conducted between 0900 and 1430 hrs under a photon flux of 900 to 1900 micro Einsteins/m²/sec of photosynthetically active radiation (45,000 to 95,000 lux). This was the natural light in situ and within the range of light saturation values documented for other shallow macroalgal species (King and Schramm 1976; Arnold and Murray 1980; LaPointe et al. 1983). Net productivity was measured to 0.1 parts per million of dissolved oxygen by means of YSI Model 57 oxygen analyzer and calculated as milligrams carbon fixed per unit of thallus area per hour assuming a photosynthetic quotient of 1.00. To enable comparisons with other tropical marine ecosystems, daily daylight rates were approximated by multiplying the mean hourly rates by the number of daylight hours above the saturation intensity. All specimens used were from shallow locations in full sunlight. The methods concerning the selection of material, handling, incubation and oxygen analysis were within the limits recommended by Littler (1979) and Littler and Arnold (1980).

Analyses of Data

Data obtained by photogrammetric sampling enable quantification of the distributions and abundances of standing stocks in relation to transect distance and depth. All quadrat data were summed and averaged to yield mean cover values and used to interpret differences in macrophyte populations and communities between sites. The two-dimensional (i.e. planar area intercepting the light) species cover per square meter of substratum in conjunction with individual productivities per square meter of planar thallus area were multiplied to estimate the contribution of each abundant macrophyte to overall community production.

Diversity measurements have been widely employed by those responsible for assessing the effects of disturbances on biotic communities. Species diversity is often measured by indices (see Poole 1974 or Pielou 1975 for references and definitions) that include components of both species richness and equitability (the evenness with which the individuals are apportioned among species). The problem with any single index is that both the richness and equitability components of diversity are confounded. Many diversity indices also

contain the underlying assumption that the ecological importance of a given species is proportional to its abundance. We avoided these problems by using the commonly-applied Shannon and Weaver H' index (incorporating both richness and evenness) along with separate indices for richness (counts of taxa, Simpson's Index, Margalef's D') and evenness [equitability (E'), Pielou's J']. These were calculated for the cover data using natural logarithms of macrophyte cover and used as supplementary information to provide between-site comparisons of community structure.

To characterize natural species assemblages within each site grouping in an unbiased manner, the cover data for all quadrats were subjected to hierarchical cluster analyses (flexible sorting; Smith 1976) using the Bray and Curtis (1957) percentage distance statistic. This produced dendrograms of transect assemblages that were then interpreted according to their dominant biota and environmental affinities and used to map the prevalent zonal patterns for the two sites.

RESULTS

The channel site exceeded the bay site in all measured parameters (cover, productivity and diversity; Table 1) except species richness. Parameters for which the channel site was higher were as follows: total cover (1.5 times), total benthic community primary productivity (1.3X), Pielou's evenness index (J' , 1.2X) and equitability (E' , 1.5X). Conversely, Margalef's richness index (D') was 1.8 times higher at the bay site, while Simpson's index was 1.2 times greater. Shannon-Weaver diversity values (H') for the two sites were nearly equal, since the higher richness at the bay site balanced the greater evenness at the channel area.

Five species comprised 96% of the cover at the bay site (Table 2), led by Halimeda opuntia f. triloba (Decaisne) Barton (37%) and Thalassia testudinum Banks and König (26%); whereas, H. opuntia f. triloba (40%), Amphiroa fragilissima (Linnaeus) Lamouroux (22%) and T. testudinum (16%) provided the majority of the total community productivity. At the channel site (Table 3), six taxa contributed 96% of the cover, dominated by a filamentous, gelatinous diatom species (29%) and Caulerpa verticillata J. Agardh (28%). Major primary producers at the channel site were the three cover dominants, the gelatinous diatom (24% of the total community carbon fixed), C. verticillata (22%) and H. opuntia f. triloba (20%).

The cluster plots (Figs. 2 and 3) reveal distinctly different zonal patterns between the two sites. The bay site is characterized by (1) the Caulerpa/Halimeda assemblage forming a band nearest the mangrove roots which intergrades into (2) a zone dominated by the Halimeda/Dictyota assemblage. This last cluster group, in conjunction with (3) an assemblage characterized by the corallines Amphiroa and Neogoniolithon, forms a third zone, while the fourth most-seaward zone is delineated by the dominance of (4) a Thalassia/Halimeda assemblage. The channel site also contained four zonal assemblages as follows, proceeding from the edge of the mangrove

island toward the main channel: (1) a gelatinous diatom-dominated group overlying C. verticillata in very silty substrata nearest the mangrove roots, with Halimeda also present more channelward, (2) a Spyridia/Halimeda assemblage, followed by (3) a zone dominated by the Halimeda spp. cluster and, lastly, (4) a Thalassia assemblage that continues on across the Twin Cays main channel (Fig. 1).

In terms of production rates per square meter of thallus planar area (Fig. 4), the corallines Neogoniolithon strictum (Foslie) Setchell and Mason (0.38 g carbon/m²/h) Amphiroa fragilissima (0.29) and Amphiroa rigida Lamouroux var. antillana Børgesen (0.29) were highest, followed by the calcareous green alga Penicillus pyriformis A. & E.S. Gepp (0.19). In terms of production per unit of substratum, the channel site was nearly 1.3 times more productive on the average than the bay site, led by the gelatinous diatom (4.1 g carbon/m² of substratum/day). In contrast, the siphonaceous green alga, Halimeda opuntia f. triloba was by far the greatest contributor to community productivity (5.4 g C/m²/d) at the bay site.

DISCUSSION

Although the seagrass Thalassia testudinum was a conspicuous component of the floras at both sites, algae collectively were the predominant organisms (cf. Tables 2 and 3), providing 73.8% of the plant cover and 83.6% of the productivity at the bay site and 89.9% and 92.4% of the total plant cover and productivity at the channel site, respectively. The filamentous-group dominated production at the channel site; whereas, the soft-bottom siphonaceous algal forms provided the majority of production at the bay site. The overall community contribution of the seagrass was more than double in terms of both cover (26.2% vs. 10.1%) and productivity (16.4% vs 7.6%) at the bay site.

McRoy and Lloyd (1981) have contrasted marine macrophytes into two fundamentally different groups: (1) the macroalgae and (2) the seagrasses. The former group, according to these authors, is characterized as analogous to filter feeding animals (in their extraction of nutrients) while secured to two-dimensional hard substrata by means of a holdfast. The latter extract nutrients from both the water column and soft sedimentary, three-dimensional substrata by means of vascular root-rhizome systems that also serve to anchor them. This dichotomy ignores the many siphonaceous algal forms that we have shown (Tables 2 and 3) to be prevalent in association with Twin Cays mangrove islands. These algae, mainly of the order Caulerpales, also have root-like and rhizomatous systems for attachment in soft substrata and, because cross walls are minimal, can utilize cytoplasmic streaming to translocate nutrients taken up from both the sedimentary and aquatic milieu.

In terms of the predominant marine plant functional groups (Table 4), the Jointed-Calcareous-Group dominated the bay site with 48.6% of the total cover, followed by the Thick Leathery-Group (26.0%), Sheet-Group (12.6%), Filamentous-Group (11.7%), Crustose-Group (1.2%) and Coarsely-Branched-Group (0.1%). The Jointed-Calcareous-Group also

contributed a disproportionately large amount to the total marine macrophytic productivity (63.1%), the order of importance to production of the remaining groups was the same as for cover (Thick-Leathery, 16.1%; Sheet, 9.7%; Filamentous, 7.5%; Crustose, 3.4%; Coarsely-Branched, 0.1%). Members of the Sheet-Group and the Crustose-Group were largely absent from the channel site. For the channel site, the Filamentous-Group contributed the majority of total community cover (64.9%) as well as productivity (58.6%), whereas the Jointed-Calcareous-Group ranked second (20.8% of total cover and 29.8% of total productivity) and the Thick-Leathery-Group was third (10.2% of cover and 7.6% of productivity, respectively). Coarsely-Branched- and Crustose-Groups were minor components at both sites.

The two macrophyte communities are essentially quite similar (Tables 2 & 3), with the majority of differences (e.g. cover, productivity, evenness and richness; Table 1) due to the epiphytic overstory contributed by the Filamentous-Group at the sheltered channel site. This extensive mat-like canopy of a very delicate, filamentous/gelatinous diatom and weakly anchored Caulerpa verticillata may be very susceptible to wave damage at the more northerly, exposed bay site. We observed mats of the diatom being torn loose by the action of a boat wake on one occasion. The poor biomechanical resistance of filamentous algae has been documented for both temperate habitats (Littler and Littler 1980) and biotic reefs (Littler, Littler and Taylor 1983).

Mangrove island mud banks, such as those studied here, tend to be depauperate in regard to the photosynthetic corals, the Sheet-Group of macrophytes, non-calcified frondose forms (i.e. Coarsely-Branched- and Thick-Leathery-Group) and the Crustose-Group. In contrast, on hard-surfaced carbonate reefs (Littler and Littler 1984), corals, non-articulated coralline algae (Crustose-Group) and/or various small microscopic forms (Filamentous-Group) usually comprise the major cover. Larger non-calcareous frondose macrophytes (Sheet-, Coarsely-branched-, Thick-leathery-Groups) occur abundantly on reef flats (Doty 1971; Wanders 1976; Connor and Adey 1977), unstructured sand plains (Earle 1972; Dahl 1973; Hay 1981a) or deep-water sites (Littler et al. 1985) where herbivory is very low.

The inconspicuousness of non-calcified algae on many shallow reef-front systems is thought (Randall 1961; Wanders 1977; Borowitzka 1981) to result primarily from intensive grazing by the numerous herbivores and omnivores inhabiting these spatially heterogeneous systems. Where spatial heterogeneity (i.e. protective cover for fishes and sea urchins) is minimal on tropical reefs, herbivore activity is relatively low (Connor and Adey 1977; Brock 1979; Hay et al. 1983) and reasonably large standing stocks of macrophytes often develop (Doty 1971; Tsuda 1971; Connor and Adey 1977; Wanders 1976). On Twin Cays, the shallow bordering mud flats are extremely low in spatial heterogeneity, with the macrophytes themselves comprising most of the three-dimensional structure. Barracuda (Sphyraenidae), mangrove snapper (Lutjanidae), jacks (Carangidae) and other fishes are abundant predators near the channels and hanging roots of mangrove islands (personal observations), and this undoubtedly contributes to the reduced levels of herbivorous fishes.

Sea urchins can be locally abundant within the mangrove root habitat and often produce a grazing halo (cf. Ogden et al. 1973) that tends to be dominated by grazer-resistant (Paul and Fenical 1983) species of Halimeda (Figs. 4 & 5) adjacent to and between the Rhizophora mangle. Thalassia testudinum with other interspersed seagrasses and Caulerpales become abundant beyond the feeding ranges of urchins unless an eroded bank prevents such a transition. Sea urchins were numerous among the mangrove roots at the bay site and moved onto the algal/seagrass flats at night. Total sea urchin density in the vicinity of the bay site was $4.4 \cdot m^{-2}$, comprised mostly of Echinometra viridis Agassiz, E. lacunter (L.) and Lytechinus variegatus (Lamarck), with Diadema antillarum Philippi, Eucidaris tribuloides (Lamarck) and Tripneustes ventricosa (Lamarck) also present. During approximately 20 person-hours of searching, no urchins were encountered in the vicinity of the channel site. Other research (Taylor, Littler and Littler, submitted) indicates that such differences in herbivory may, in conjunction with the physical action of waves mentioned above, account for the reduction of delicate filamentous forms and epiphytes and the predominance of herbivore-resistant macrophytes at the bay site.

Such resistant plant populations often contribute (Rogers and Salesky 1981) a major portion of the total primary productivity of some reefs. However, most evidence (e.g. Wanders and Wanders-Faber 1974, Bunt 1975, Marsh 1976, Dahl 1976 Larkum 1981, Rogers and Salesky 1981) indicates that it is the fast-growing and opportunistic filamentous algae of sparse mats that result in the very high primary production rates per unit area of most biotic reefs. Conversely, tightly-compacted mats of algae (turfs), such as those of the channel site, usually show reduced productivity levels (Littler and Arnold 1980, Hay 1981b, Taylor and Hay 1984) due to overlapping diffusion gradients and self shading.

The total community primary productivity at the channel site was 28% higher than at the bay site (17.2 vs. 13.4 g C fixed $\cdot m^{-2}$ of substratum $\cdot d^{-1}$). This difference was largely due to the contributions of the filamentous/gelatinous diatom (4.1 g C fixed $\cdot m^{-2} \cdot d^{-1}$) and Spyridia filamentosa (2.2), epiphytes that were not abundant at the bay site.

The macrophytic daylight community productivities at both sites were quite high relative to reef systems and compare favorably with the upper rates reported from dense seagrass meadows (Table 5). Reported daily primary productivities of seagrass communities span the upper range from 5.8 to 18.7 g carbon/ m^2/d . Rates reported for reef systems range upwards to 7.2 g C/ m^2/d . We conclude that mud reef-flats adjacent to the mangrove islands of the Belize barrier reef system produce at rates comparable to dense seagrass beds and are considerably more productive than typical carbonate reef-flat habitats. This high photosynthetic capacity may be related to reductions in herbivory, enabling larger standing stocks to develop, and the recycling of nutrients from decompositional processes, which would be expected to augment the primary productivity of these otherwise nutrient-impooverished waters.

ACKNOWLEDGEMENTS

We appreciate the support made available as part of the Smithsonian Institution's Western Atlantic Mangrove Project, ably directed by K. Rützler. Additional sponsorship was provided by S. Dillon Ripley through the Secretary's Fluid Research Fund. This paper is Contribution No. 153 of the Smithsonian Institution's Reef and Mangrove Study, partly funded by the Exxon Corporation.

REFERENCES

- Arnold, K. E. and S. N. Murray. 1980. Relationships between irradiance and photosynthesis for marine benthic green algae (Chlorophyta) of differing morphologies. *J. Exp. Mar. Biol. Ecol.* 43: 183-192.
- Bakus, G. J. 1967. The feeding habits of fishes and primary production at Eniwetok, Marshall Islands. *Micronesica* 3: 135-149.
- Borowitzka, M. A. 1981. Algae and grazing in coral reef ecosystems. *Endeavour*, 5: 99-106.
- Brawley, S. H. and W. H. Adey. 1977. Territorial behavior of threespot damselfish (Eupomacentrus planifrons) increases reef algal biomass and productivity. *Envir. Biol. Fish.* 2: 45-51.
- Bray, J. R. and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27: 325-349.
- Brock, R. E. 1979. An experimental study on the effects of grazing by parrotfishes and role of refuges in benthic community structure. *Mar. Biol.* 51: 381-388.
- Buesa, R. J. 1972. Production primaria de las praderas de Thalassia testudinum de la plataforma noroccidental de Cuba. *INP, Cuba Cent. Inv. Pesqueras. Reva. Bal. Trab. CIP*, 3: 101-143.
- Bunt, J. S. 1975. Primary productivity of marine ecosystems. In: H. Lieth and R. H. Whittaker (Eds.), *Primary Productivity of the Biosphere*. Ecological Studies, Springer-Verlag, Berlin 14: 169-183.
- Connor, J. L. and W. H. Adey. 1977. The benthic algal composition, standing crop, and productivity of a Caribbean algal ridge. *Atoll. Res. Bull.* 211: 1-15.
- Dahl, A. L. 1972. Ecology and community structure of some tropical reef algae in Samoa. Pages 36-39, in K. Nisizawa (Ed.), *Proceedings of the Seventh International Seaweed Symposium*. University of Tokyo Press, Tokyo, Japan.

- Dahl, A. L. 1973. Surface area in ecological analysis: quantification of benthic coral-reef algae. *Mar. Biol.*, 23: 239-249.
- Dahl, A. L. 1976. Generation of photosynthetic surface area by coral reef algae. *Micronesica* 12: 43-47.
- Doty, M. S. 1971. Physical factors in the production of tropical benthic marine algae. Pages 99-121 in J. D. Costlow, Jr., (Ed.) *Fertility of the Sea*. Gordon and Breach, New York.
- Earle, S. A. 1972. The influence of herbivores on the marine plants of Great Lameshur Bay, with an annotated list of plants. Pages 17-44 in B. B. Collette and S. A. Earle (Eds.), *Results of the Tektite Program: Ecology of Coral Reef Fishes*, Science Bulletin 14, Los Angeles County Natural History Museum, Los Angeles, California.
- Gaines, S. D. and J. Lubchenco. 1982. A unified approach to marine plant-herbivore interactions. II. Biogeography. *Ann. Rev. Ecol. Syst.* 13: 111-138.
- Gessner, F. and L. Hammer. 1960. Die primarproduktion in Mediterranean Caulerpa-Cymodocea Wiesen. *Bot. Mar.* 2: 157-163.
- Hatcher, B. G. 1982. The interaction between grazing organisms and the epilithic algal community of a coral reef: a quantitative assessment. Pages 515-524 in E. D. Gomez et al. (Eds.), *Proceedings, Fourth International Coral Reef Symposium*, Marine Science Center, Quezon City, Philippines
- Hatcher, B. G. and A. W. D. Larkum. 1983. An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. *J. Exp. Mar. Biol. Ecol.* 69: 61-84.
- Hay, M. E. 1981a. Herbivory, algal distribution, and the maintenance of between-habitat diversity on a tropical fringing reef. *Am. Nat.* 118: 520-540.
- Hay, M. E. 1981b. The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. *Ecology* 62: 739-750.
- Hay, M. E., T. Colburn and D. Downing. 1983. Spatial and temporal patterns in herbivory on a Caribbean fringing reef: the effects on plant distribution. *Oecologia* (Berlin) 58: 299-308.
- Johnston, C. S. 1969. The ecological distribution and primary production of macrophytic marine algae in the eastern canaries. *Int. Revue ges. Hydrobiol.* 54: 473-490.
- King, R. J. and W. Schramm. 1976. Photosynthetic rates of benthic marine algae in relation to light intensity and seasonal variations. *Mar. Biol.* 37: 215-222.

- LaPointe, B. E., K. R. Tenore and C. J. Dawes. 1983. Interactions between light intensity and temperature on the physiological ecology of Gracilaria tikvahiae (Gigartinales, Rhodophyta). I. Growth, photosynthesis, and respiration. *Mar. Biol.*
- Larkum, A. W. D. 1981. Marine primary productivity. Pages 370-385 in M. N. Clayton and R. J. King (Eds.), *Marine Botany, an Australasian Perspective*. Longman Cheshire, Melbourne.
- Littler, M. M. 1973a: The population and community structure of Hawaiian fringing-reef crustose Corallinaceae (Rhodophyta, Cryptonemiales). *J. Exp. Mar. Biol. Ecol.* 11: 103-120.
- Littler, M. M. 1973b. The productivity of Hawaiian fringing-reef crustose Corallinaceae and an experimental evaluation of production methodology. *Limnol. Oceanogr.* 18: 946-952.
- Littler, M. M. 1979. The effects of bottle volume, thallus weight, oxygen saturation levels, and water movement on apparent photosynthetic rates in marine algae. *Aquat. Bot.* 7: 21-34.
- Littler, M. M. and K. E. Arnold. 1980. Sources of variability in macroalgal primary productivity: sampling and interpretative problems. *Aquat. Bot.* 8: 141-156.
- Littler, M. M. and K. E. Arnold. 1982. Primary productivity of marine macroalgal functional-form groups from southwestern North America. *J. Phycol.* 18: 307-311.
- Littler, M. M. and D. S. Littler. 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. *Am. Nat.* 116: 25-44.
- Littler, M. M. and D. L. Littler. 1984. Biogenesis of tropical reefs: the contribution of algae. In: F. E. Round and D. J. Chapman (Eds.), *Progress in Phycological Research*, 3: (in press).
- Littler, M. M., D. S. Littler, S. M. Blair and J. N. Norris. 1985. Deepest known plant life discovered on an uncharted seamount. *Science* 227: 57-59.
- Littler, M. M., D. S. Littler and P. R. Taylor. 1983. Evolutionary strategies in a tropical barrier reef system: functional-form groups of marine macroalgae. *J. Phycol.* 19: 229-237.
- Littler, M.M. and S.N. Murray. 1975. Impact of sewage on the distribution, abundance and community structure of rocky intertidal macro-organisms. *Mar. Biol.* 30: 277-291.
- Marsh, J. A., Jr. 1976. Energetic role of algae in reef ecosystems. *Micronesica* 12: 13-21.

- McRoy, C. P. and D. S. Lloyd. 1981. Comparative function and stability of macrophyte-based ecosystems. Pages 473-489 in A. R. Longhurst (Ed.), Analysis of marine ecosystems. Academic Press, New York.
- Murray, S. N. and M. M. Littler. 1984. Analysis of seaweed communities in a disturbed rocky intertidal environment near Whites Point, Los Angeles, Calif. U.S.A. In: Proceedings, Eleventh International Seaweed Symposium, Qingdao, China. Hydrobiologia, (in press).
- Odum, H. T. 1963. Productivity measurements in Texas Turtle grass and the effects of dredging an intracoastal channel. Publ. Inst. Mar. Sci. Texas 9: 45-58.
- Odum, H. T. and C. M. Hoskin. 1958. Comparative studies of the metabolism of marine waters. Publ. Inst. Mar. Sci. Univ. Texas 5: 16-46.
- Odum, H. T. and E. P. Odum. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecol. Monogr. 25: 291-320.
- Ogden, J. C., R. A. Brown and N. Selesky. 1973. Grazing by the echinoid Diadema antillarum Philippi: formation of halos around West Indian patch reefs. Science 182: 715-717.
- Paul, V. J. and W. Fenical. 1983. Isolation of halimedatrial: chemical defense adaptation in the calcareous reef-building alga Halimeda. Science 221: 747-749.
- Pielou, E. 1975. Ecological diversity. John Wiley and Sons, New York, New York.
- Poole, R. W. 1974. An introduction to quantitative ecology. McGraw-Hill, New York, New York.
- Qasim, S. Z. and P. M. A. Bhattathiri. 1971. Primary production of a seagrass bed on Kavaratti Atoll (Laccadives). Hydrobiologia 38: 29-38.
- Randall, J. E. 1961. Overgrazing of algae by herbivorous marine fishes. Ecology 42: 812.
- Rützler, R. and I. G. MacIntyre (Eds.) 1982. The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, I. Structure and Communities. Smithson. Contrib. Mar. Sci., No. 12. Smithsonian Institution Press, Washington, D.C.
- Rogers, G. S. and N. H. Salesky. 1981. Productivity of Acropora palmata (Lamarck), macroscopic algae, and algal turf from Tague Bay Reef, St. Croix, U.S. Virgin Islands. J. Exp. Mar. Biol. Ecol. 49: 179-187.

- Smith, R. W. 1976. Numerical Analysis of Ecological Survey Data. Ph.D. dissertation, University of Southern California, Los Angeles.
- Smith, S. V. 1973. Carbon dioxide dynamics: a record of organic carbon production, respiration, and calcification in the Eniwetok reef flat community. *Limnol. Oceanogr.* 18: 106-120.
- Sournia, A. 1976. Oxygen metabolism of a fringing reef in French Polynesia. *Helgoländer wiss. Meeresunters.* 28: 401-410.
- Steneck, R. S. and L. Watling. 1982. Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. *Mar. Biol.* 68: 299-319.
- Taylor, P. R. and M. E. Hay (in press). The functional morphology of intertidal seaweeds: the adaptive significance of aggregate vs. solitary forms. *Mar. Ecol. Prog. Ser.*
- Taylor, P. R., M. M. Littler and D. S. Littler (in review). Coexistence and non-coexistence escapes of herbivory as structuring forces in mangrove island macroalgal communities. *Ecology*.
- Tsuda, R. T. 1971. Morphological, zonal, and seasonal studies of two species of Sargassum on the reefs of Guam. Pages 40-44 in K. Nisizawa (Ed.), *Proceedings, Seventh International Seaweed Symposium*. Wiley & Sons, New York.
- Van Den Hoek, C., A. M. Cortel-Breeman and J. B. W. Wanders. 1975. Algal zonation in the fringing coral reef of Curacao, Netherlands Antilles, in relation to zonation of corals and gorgonians. *Aquat. Bot.* 1: 269-308.
- Wanders, J. B. W. 1976. The role of benthic algae in the shallow reef of Curacao (Netherlands Antilles). I: primary production in the coral reef. *Aquat. Bot.* 2: 235-270.
- Wanders, J. B. W. 1977. The role of benthic algae in the shallow reef of Curacao (Netherlands Antilles) III: the significance of grazing. *Aquat. Bot.*, 3: 357-390.
- Wanders, J. B. W. and A. Wanders-Faber. 1974. Primary productivity of the S.W. coast shallow reef and the N.E. coast brown algae of Curacao. *Br. Phycol. J.* 9: 223-224.

Table 1. Indices of richness, evenness and diversity, based on macrophytic species numbers and cover, for the bay and channel sites.

Indices	Bay	Channel
H' index	2.32	2.39
J' evenness	0.85	1.00
E' equitability	0.64	0.99
D' richness	2.52	1.44
Number of species	14	11
Simpsons index	0.11	0.09
Total cover	97.8	151.8
Total productivity (g carbon/m ² /d)	13.4	17.2

Table 2. The major contributors of community cover and primary productivity (g carbon/m²/d) at the bay site.

Taxa	Cover (%)	Productivity (m ² of substratum)
<u>Halimeda opuntia</u> f. <u>triloba</u> (Decaisne) Barton	36.1	5.4
<u>Thalassia testudinum</u> Banks & K�nig	25.6	2.2
<u>Dictyota dichotoma</u> (Hudson) Lamouroux	12.4	1.3
<u>Caulerpa verticillata</u> J. Agardh	11.2	1.0
<u>Amphiroa fragilissima</u> (Linnaeus) Lamouroux	10.0	2.9
<u>Neogoniolithon strictum</u> (Foslie) Setchell & Mason	1.2	0.5
<u>Halimeda monile</u> (Ellis & Solander) Lamouroux	0.4	0.07
<u>Dasya rigidula</u> (K�ttz.) Ardiss.	0.4	--
<u>Amphiroa rigida</u> Lamouroux var. <u>antillana</u> B�rgensen	0.3	0.09
<u>Valonia ventricosa</u> J. Agardh	0.07	--
<u>Wrangelia</u> sp.	0.04	--
<u>Hypnea</u> sp.	0.02	--
<u>Penicillus capitatus</u> Lamarck	0.02	0.01
<u>Dictyosphaeria cavernosa</u> (Forssk.) B�rgesen	0.02	0.01
Totals	97.8	13.4

Table 3. The major contributors of community cover and primary productivity (g carbon/m²/d) at the channel site.

Taxa	Cover (%)	Productivity (m ² of substratum)
Gelatinous diatom	43.6	4.1
<u>Caulerpa verticillata</u> J. Agardh	41.9	3.8
<u>Halimeda opuntia</u> f. <u>triloba</u> (Decaisne) Barton	22.6	3.4
<u>Thalassia testudinum</u> Banks & K�nig	15.4	1.3
<u>Spyridia filamentosa</u> (Wulfen) Harvey	13.2	2.2
<u>Halimeda monile</u> (Ellis & Solander) Lamouroux	9.0	1.5
<u>Penicillus capitatus</u> Lamarck	2.8	0.3
<u>Dictyosphaeria cavernosa</u> (Forssk.) B�rgesen	2.7	0.3
<u>Caulerpa mexicana</u> (Sound.) J. Agardh	0.5	0.04
<u>Amphiroa fragilissima</u> (Linnaeus) Lamouroux	0.08	0.2
<u>Penicillus pyriformis</u> A. & E.S. Gepp	0.08	0.02
Totals	151.8	17.2

Table 4. Functional-group categories and major component taxa.

Functional Groups	Characteristics	Taxa
Filamentous-Group	Thin, uniseriate, multiseriate or lightly corticated	Gelatinous diatom, <u>Caulerpa verticillata</u> , <u>Dasya rigidula</u> , <u>Spyridia filamentosa</u> , <u>Wrangelia</u> sp.
Sheet-Group	Uncorticated, foliose	<u>Dictyota dichotoma</u>
Coarsely-Branched-Group	Corticated	<u>Caulerpa mexicana</u> , <u>Dictyosphaeria cavernosa</u> , <u>Hypnea</u> sp., <u>Penicillus capitatus</u> , <u>Penicillus pyriformis</u> , <u>Valonia ventricosa</u> ,
Thick-Leathery-Group	Differentiated, heavily corticated, thick walled	<u>Thalassia testudinum</u>
Jointed-Calcareous-Group	Calcified genicula, uncalcified intergenicula	<u>Amphiroa fragilissima</u> , <u>Halimeda monile</u> , <u>Halimeda opuntia</u> f. <u>triloba</u>
Crustose-Group	calcified or uncalcified parallel cell rows, encrusting	<u>Neogoniolithon strictum</u>

Table 5. Comparative upper production rates of macrophyte communities in tropical marine shallow water ecosystems.

Community type	Productivity g carbon/m ² d	Location	Study
Mangrove banks			
channel	17.2	Belize	This study
bay	13.4	Belize	This study
Seagrass Meadows			
<u>Cymodocea nodosa</u> K.D.E. K�nig dominant	18.7	Mediterranean	Gessner & Hammer, 1960
<u>Syringodium isoetifolis</u> Archers and Graeb dominant	5.8	Laccadives	Qasim & Bhattathiri, 1971
<u>Thalassia testudinum</u> dominant	12.5	Cuba	Buesa, 1972
<u>Thalassia testudinum</u> dominant	16.0	Florida	Odum, 1963
<u>Thalassia testudinum</u> dominant	9.0	Texas	Odum & Hoskin, 1958
Carbonate Reefs			
Shallow fore and back reefs, algal turf dominated	5-7	St. Croix Virgin Is.	Brawley & Adey, 1977
Fringing reef, <u>Neogoniolithon frutescens</u> dominated	3.8	French Polynesia	Sournia, 1976
Intertidal, blue green algae dominated	0.65-2.15	Enewetak	Bakus, 1976
Macroalgal dominated	1.5 -3.0	Canary Is.	Johnston, 1965
Photosynthetic corals and algal turfs	1.6-7.2	Enewetak	Smith, 1973

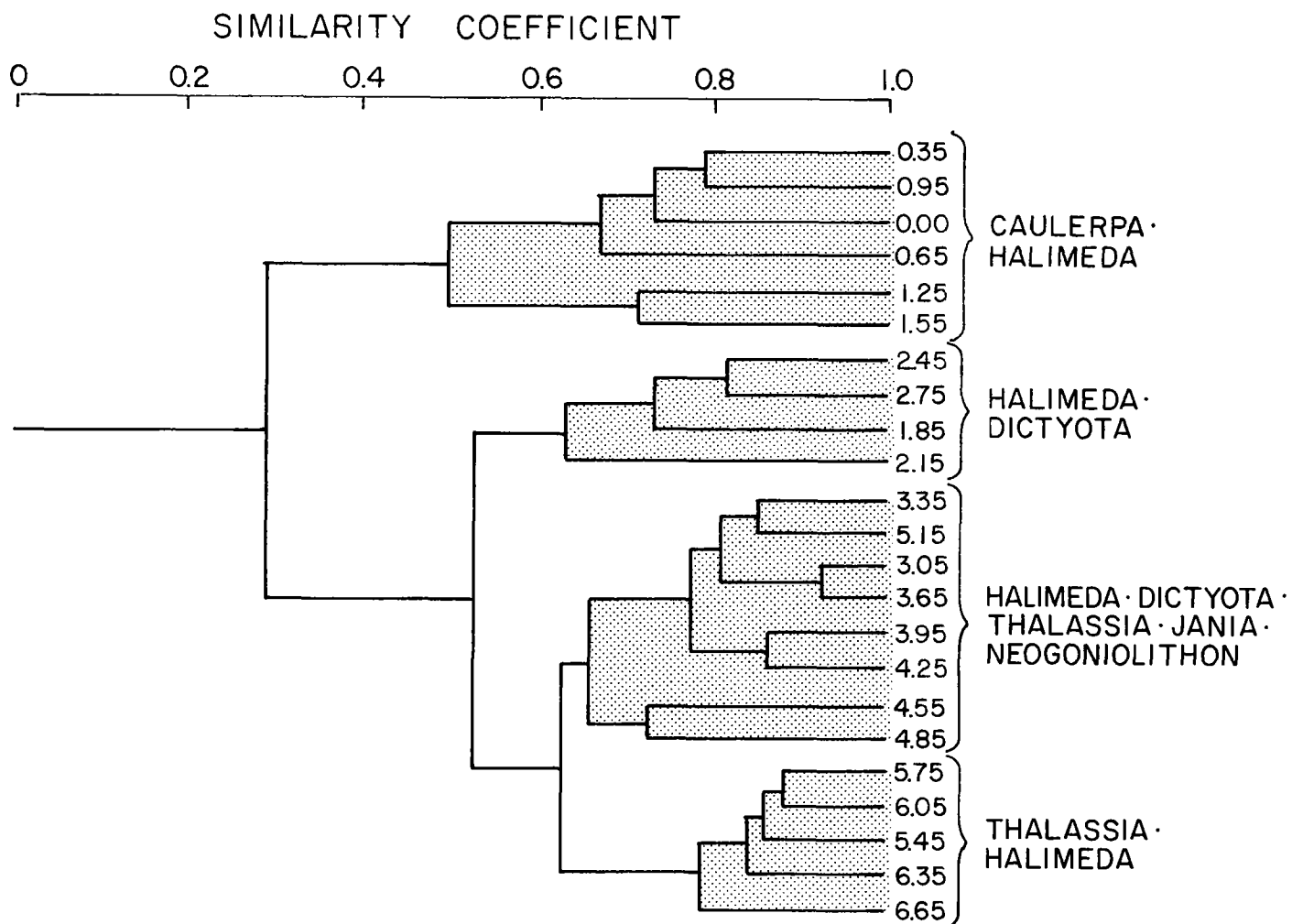


Figure 2. Cluster analysis based on percentage cover data for the bay site quadrats (labelled by distance along transect in meters) expressed as a dendrogram. Dominant cover organisms in each cluster group are given on the right.

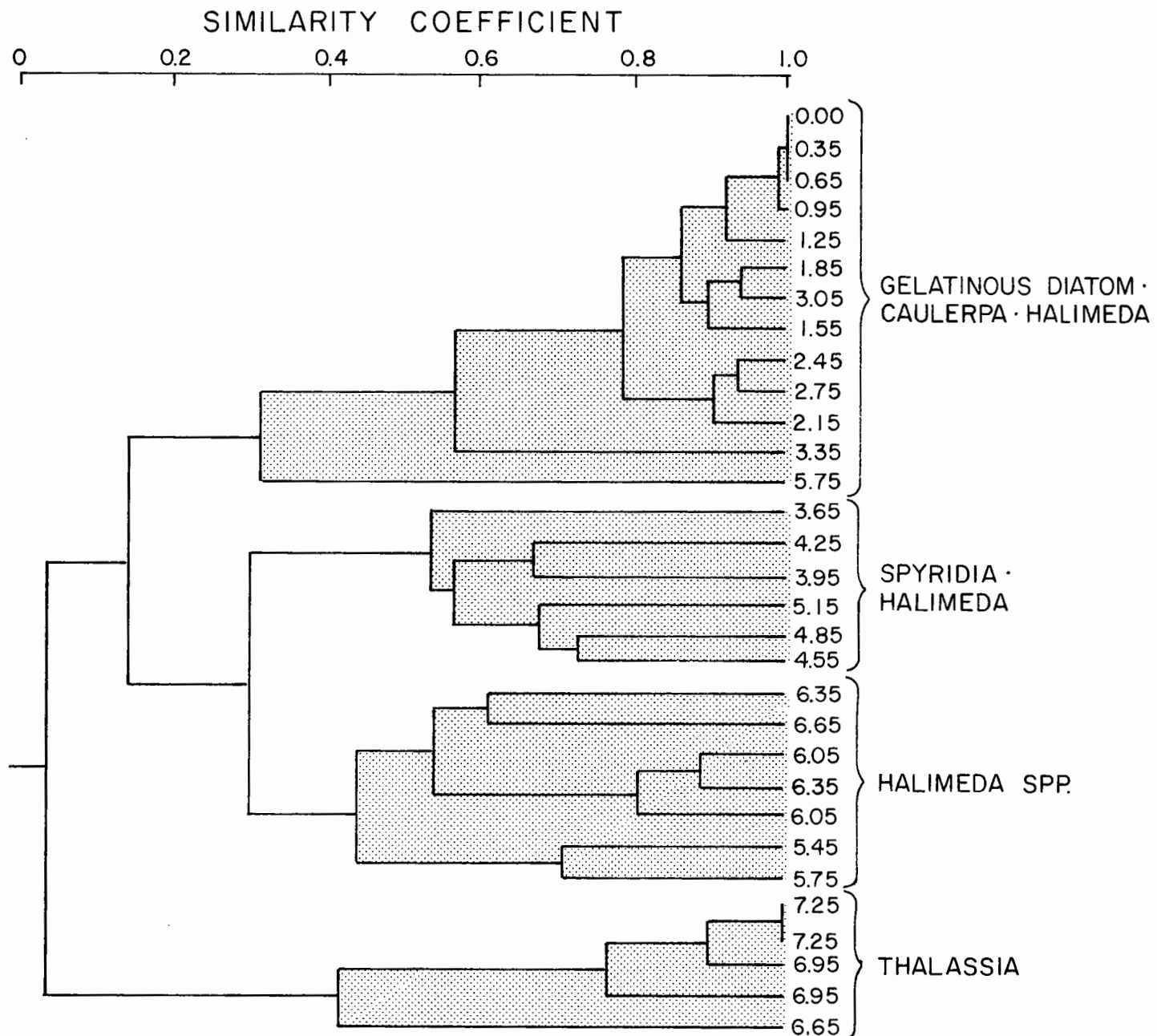


Figure 3. Cluster analysis based on percentage cover data for the channel site quadrats (labelled by distance along transect in meters) expressed as a dendrogram. Dominant

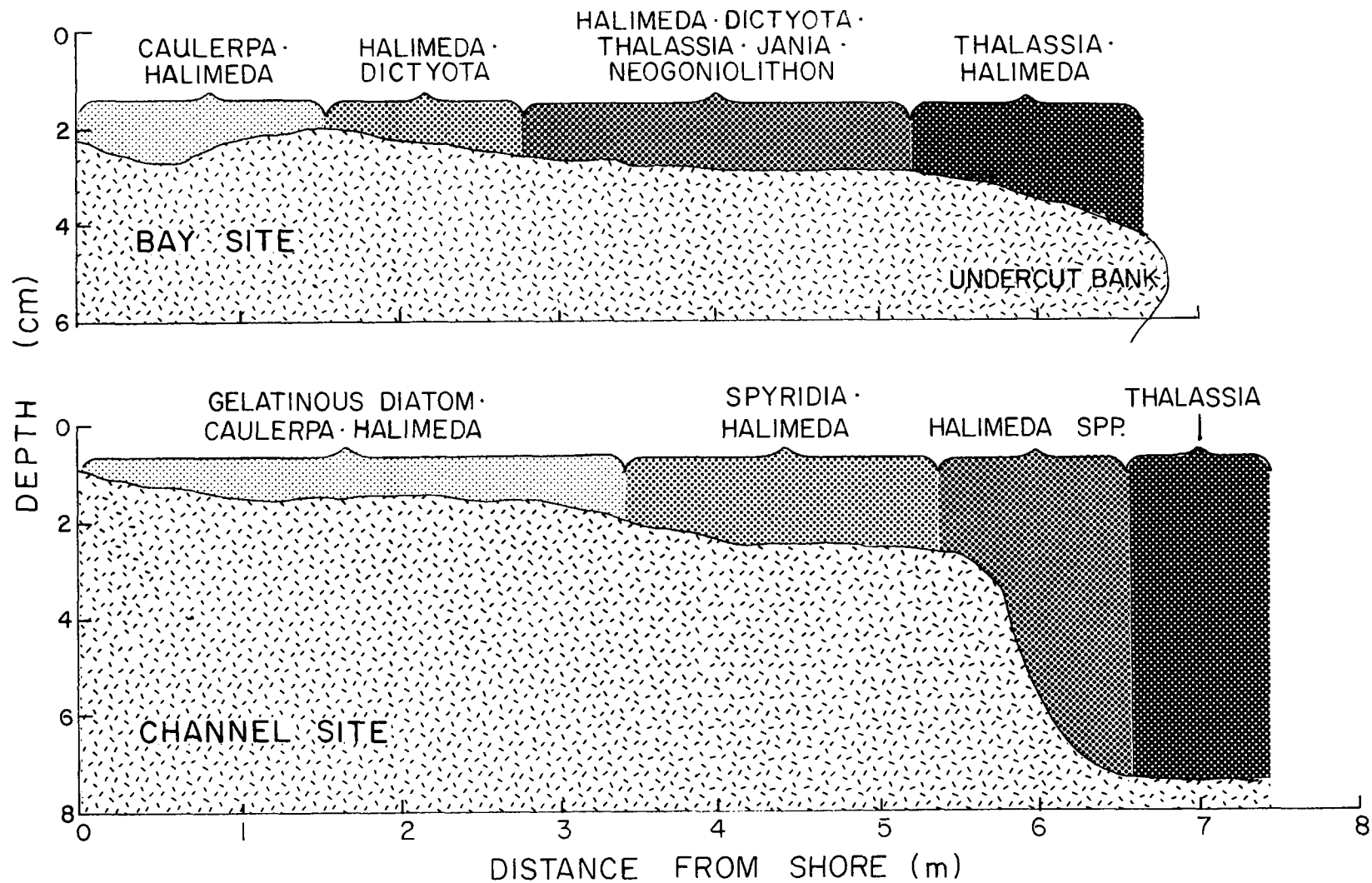


Figure 4. Diagrammatic locations of dominant cluster groups (determined from Figs. 2 & 3) in relation to depth profile and distance along the shoreline at the bay site (upper plot) and channel site (lower plot).

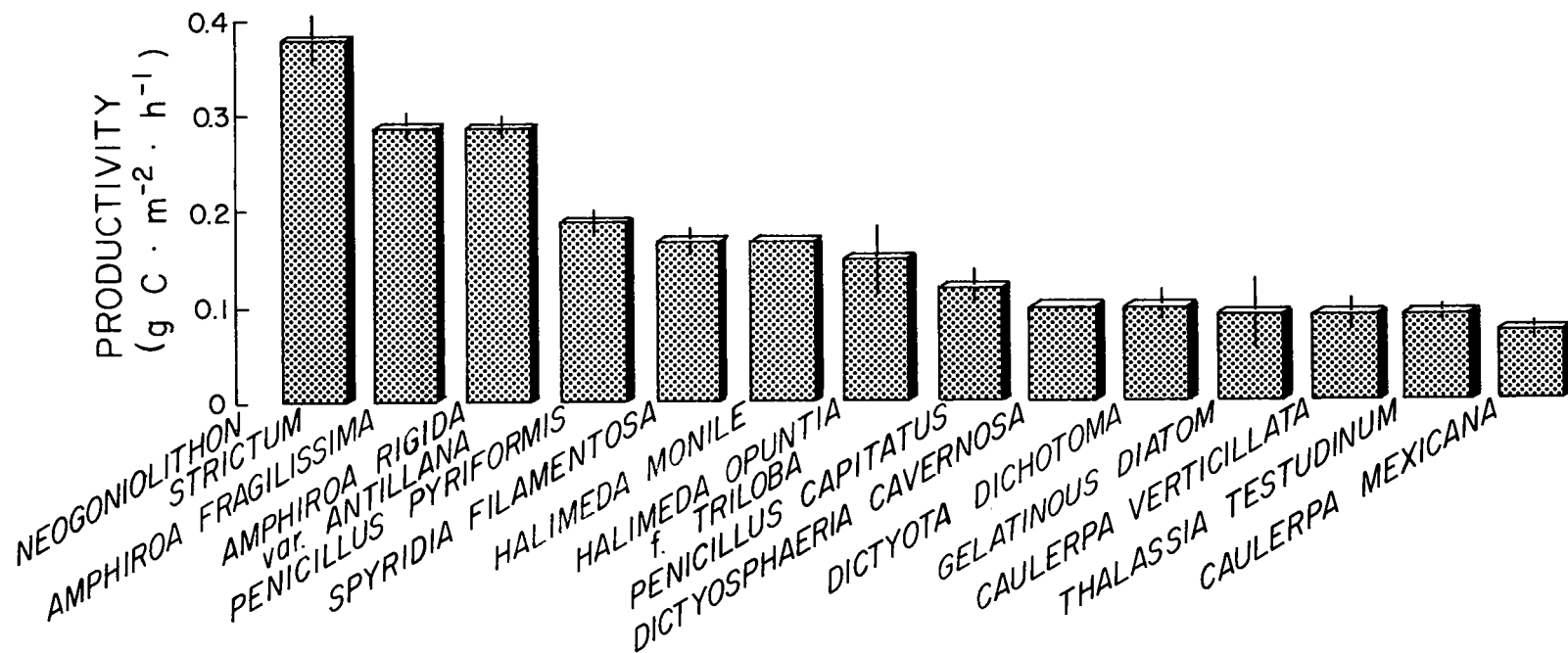


Figure 5. Net apparent primary productivities (m^{-2} substratum) of dominant macrophytes from Twin Cays on 24 April 1980. $\pm 95\%$ confidence limits given by vertical lines.