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BASELINE STUDIES OF HERBIVORY AND EUTROPHICATION ON DOMINANT REEF COMMUNITIES OF LOOE KEY NATIONAL MARINE SANCTUARY

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NOTICE

REPORT TO
NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
U.S. DEPARTMENT OF COMMERCE

NOAA TECHNICAL MEMORANDA SERIES NOS/MEMD

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U.S. DEPARTMENT OF COMMERCE
NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
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ABSTRACT

Presently, only limited knowledge is available regarding the dominant algal assemblages at Looe Key National Marine Sanctuary and the effects of herbivory and nutrient limitation in controlling the structure of these communities. The goals of this research are to: (1) provide a preliminary inventory and general distributional assessment of dominant algal communities, (2) initiate pilot studies of the effects of nutrient enrichment and grazing on structure of the reef communities and (3) contrast findings with other reef habitats for which comparable data are available. This research accomplishes these goals, increases our understanding of ecological processes that influence dominant reef communities and provides data of use in management decisions directed towards preserving Looe Key National Marine Sanctuary in a natural state.

INTRODUCTION

Current Status of Knowledge

Tropical reefs represent some of the most luxuriant natural ecosystems known (Westlake 1963; Lewis 1977) and stand out as productive "gardens" in many of the world's nutrient-poor warm oceanic systems. Sessile photosynthetic organisms predominate and consist of (1) symbiotic zooxanthellae within hermatypic corals, (2) microfilamentous algae (e.g., Polysiphonia, Herposiphonia, Centroceras, Ceramium and blue-green algae), (3) coralline algae and (4) macroscopic frondose algae (e.g., Laurencia, Sargassum, Dictyota, Caulerpa). In certain soft bottom habitats, seagrasses contribute significantly (McRoy and McMillan 1977) and provide attachment sites for epiphytic seaweeds. On reefs not dominated by corals, non-articulated coralline algae and various small filaments usually comprise the majority of cover. The larger frondose algae can occur abundantly on shallow reef flats (Doty 1971;Wanders 1976; Connor and Adey 1977), unstructured sand plains (Earle 1972; Dahl 1973; Hay 1981a) or deepwater sites (Littler et al. 1985) where herbivory is very low. Frondose algae are generally restricted from reef slopes by high rates of grazing (Littler and Doty 1975; Wanders 1976; Hay 1981a; Hay et al. 1983; Hatcher and Larkum 1983). The inconspicuousness of filamentous algae on shallow reef-front (fore reef) systems also is thought (Randall 1961; Wanders 1977; Borowitzka 1981) to primarily result from intensive grazing by the numerous herbivores and omnivores inhabiting these spatially heterogeneous systems. Where cover for herbivorous fishes from their predators (i.e., spatial heterogeneity) is minimal on tropical reefs, grazing activity is reduced (Brock 1979; Hay et al. 1983) and reasonably large standing stocks of macrophytes (Sargassum, Turbinaria, Acanthophora) often develop (Doty 1971; Connor and Adey 1977; Wanders 1976). Such macroalgal populations may contribute (Rogers and Salesky 1981) a major portion of the total primary productivity of some reefs. However, most evidence (e.g., Marsh 1976; Dahl 1976) indicates that it is the fast-growing and opportunistic sheet-like and filamentous algae of sparse mats that result in the very high primary production rates per unit area of biotic reefs.

Because coral reefs are highly productive yet occur in nutrient-poor surface waters of the tropical oceans, they represent somewhat of an ecological anomaly. To sustain such high levels of productivity, a great flux of nutrients (primarily nitrogen and phosphorus) is required, yet concentrations of these nutrients in waters surrounding reef systems are often very low or even undetectable the majority of the time. Consequently, previous studies of nutrient dynamics on coral reef systems have been largely concerned with nutrient cycling within the reef system. For example, Pomeroy and Kuenzler (1969) have shown the coral-zooxanthellae symbiosis is very efficient in conserving inorganic nitrogen and phosphorus. More recently, Meyer et al. (1983) have shown the importance of schooling fish to nutrient flux of reef corals. However, such studies have engendered the view that reefs are largely independent of their oligotrophic environment; as a corollary to this, marine ecologists often regard coral

reefs as black boxes and study them from inside the box while ignoring the influence of the surrounding ocean.

The inevitable flow of nutrients to and from reef systems suggests that allochthonous sources of nutrients are required for coral reef systems and recently Andrews and Gentian (1982) have hypothesized an importance of the upwelled nutrients to the major coral reef systems of the world. To date, the importance of upwelled nutrients has not been demonstrated for a coral reef system. Looe Key National Marine Sanctuary (Fig. 1) offers an ideal study site in this regard because frequent upwellings have been well documented along the continental shelf break in the southeastern United States (Atkinson et al. 1984). More studies are needed to distinguish between offshore (oceanic) versus nearshore (outwelling) nutrient supply processes to predict the influence of man's increasing activities on the nutritional state of Looe Key National Marine Sanctuary.

The specific objectives of the study were as follows:

1. Inventory dominant algae.

2. Identify and characterize major algal assemblages.

3. Conduct preliminary nutrient limitation studies.

4. Undertake initial studies of herbivory.

Project Significance

Baseline inventories represent necessary first stages in the development of a management plan for any biological system. Nutrient studies are relevant because Looe Key lies downstream from the municipal-sewage effluent plume released from Southeast Channel at Key West. The significance of this outfall to the ecology of the Looe Key Sanctuary is related to the potential for increased eutrophication, as a result of the expanding human population and corresponding development in the lower Florida Keys. In addition we have noted, as did Zieman (NOAA Report, in draft), a disproportionate abundance of herbivorous fishes (i.e., exceptionally large parrotfishes, numerous surgeonfishes and rudderfishes) associated with the Back-Reef and Fore-Reef habitats. If, as we hypothesize, nutrient levels and herbivore pressure are major forcing functions in the Looe Key system, then information that will enable managers to predict the impact of alterations on these parameters is of paramount significance. This project begins to examine the complex relationships of nutrients and grazing and sets the stage for subsequent experiments that will provide needed predictive insights.

METHODS

Study Area

Looe Key (24°N, 81°24'W) was established as a National Marine Sanctuary in 1981 and is located 12.9 km southwest of Big Pine Key, Monroe County, Florida. Within the 18.2-km^2 Sanctuary lies an inner "core" area (Fig. 1) of about 1.7 km^2 that includes rich seagrass, coral and macroalgal dominated assemblages. Some of these communities have recently received inventory-orientated study (Zieman, unpublished NOAA report; Bohnsack and Lidz, unpublished NOAA report); however, the macroalgal systems were virtually unknown prior to the present investigation.

Inventory and Mapping

The initial inventory included collection of voucher specimens of all major benthic species of algae during 19-21 June 1984. Specimens were preserved in buffered formalin seawater, labelled, mounted where appropriate, identified and deposited with the U.S. National Herbarium, Smithsonian Institution. The general distributional patterns of major macroalgal community types was completed on 20–21 June 1984. This work was based upon aerial photography (conducted by D. Littler from a NOAA helicopter on 29 October 1984), at a scale that permits the recognition of major zonal assemblages, in conjunction with ground truth data obtained by towing divers at slow speeds over Back-Reef (lagoon), Reef-Flat, Reef-Crest

and Spur-and-Groove habitats. Because corals and seagrasses had been inventoried and mapped during excellent previous studies by J.L. Wheaton and W.C. Jaap (NOAA Report, Chap. 6, in draft) and J.C. Zieman (NOAA Report, in draft), respectively, we concentrated our efforts on the complex, but virtually unknown, macroalgal communities in relation to the major controlling factors of herbivory and nutrient dynamics. The latter factor proved to be especially interesting and, as a consequence, we devoted much personal effort to conducting nutrient experiments that went considerably beyond the scope of our original proposal.

In addition, the opportunity arose through other funding to study a structurally and biologically similar reef in the Belizian Barrier Reef system. This reef, Curlew Cay, is quite comparable to Looe Key in terms of similarity of structure and size, with well developed Spur-and-Groove, Reef-Crest, Reef-Flat and Back-Reef habitats. Curlew Cay lies in the most pristine and oligotrophic (Type I, Jerlov, 1970) of oceanic waters, having nutrient levels approaching the lower limits of analytical detectability. By conducting nutrient/productivity studies parallel to those done under this contract, we were able to place our Looe Key findings in a uniquely appropriate perspective.

Relatively detailed estimates (Appendix A) of algal (and some sessile animals) abundances for three of the NOAA study spurs were recorded (20-22 June 1984) by an experienced ecologist (M. Littler). This was done by SCUBA along repetitive series of calibrated, 50 m long, line transects placed approximately midway on each spur (Figs. 1 and 2). Recorded measurements with an underwater housed tape-recorder (Fig. 3D) were made in situ. These estimates were used to produce interpretive profile diagrams based on measurements at a relatively fine scale (Appendix A). The field notes and profile diagrams, in conjunction with the coarse mapping and aerial photography, identify the major algal assemblages and will be instrumental in determining future higher-resolution sampling locations (strata) and regimes (including permanently marked transects) within the major community types. Visual observations of seasonal changes throughout the following year were made at haphazard intervals by B. Lapointe.

Herbivory

The suspended-line bioassay method of Littler et al. (1983) was used in the preliminary grazing experiments. Clumps of 16 macrophyte species (~ 10 cm^2) representative of the spectrum of frondose algal forms were placed between twists of a 3-stranded, 2-mm thick, white nylon line at 0.5 m intervals in a mechanically-randomized pattern that was consistently followed among replicate lines. The lines were placed in all four of the major habitat types on 19 and 21 June 1984 and used to compare herbivore pressures between the predominant reef ecosystems.

The results yield comparative herbivore information among habitats as well as provide insights into the differential resistances of the various morphological forms of seaweeds to herbivory. For all habitats on both days, four separate lines were used, each containing three clumps per species. The lines were photographed then placed ca. 0.3 m above the bottom in the water column (each end tied to a coral head) for a 3-h daylight period. Surgeonfishes and parrotfishes were not wary of the lines and began feeding as soon as the divers moved away. Fish typically moved from clump to clump taking small bites, becoming more persistent as they located a particularly palatable clump. After 3 h, the lines were returned to the boat, rephotographed and subsequently quantified in the relative comfort of the laboratory by the point intercept method (Littler et al. 1983). In this technique, the percent thallus area (2-dimensional) lost to grazing for each specimen was calculated from the color slides (Kodachrome 64) by projecting the transparencies onto a grid of dots (at stratified randomized intervals) that were directly related to surface area. The determination of biomass losses would have been relatively stressful to the algae as well as costly, since weights could not have been recorded rapidly on a small field boat. The differences between means were examined by the Duncan's Multiple Range Test (Steele and Torrie 1960) following ANOVA.

Productivity

Net apparent photosynthesis of 20 of the most abundant macrophytes found at the Looe Key study site also was determined on a seawall next to a boat channel on nearby Big Pine Key, at ambient seawater temperatures (27°C) and nutrient conditions, on 23 October 1984. For all photosynthesis measurements, six replicate incubations per taxon were conducted between 0900 and 1430 hrs under a photon flux of 900 to 1900 micro Einsteins/m^2/sec of photosynthetically active radiation (45,000 to 95,000 lux). This was the natural light level in situ both at Looe Key and Curlew Cay 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. 1984). Net productivity was measured to 0.01 parts per million of dissolved oxygen by means of an Orbisphere Model 2610 oxygen analyzer. 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). Net photosynthesis was calculated as mg C/g ash-free dry wt (or g dry wt)/h.

Nutrient Enrichment-Growth Studies

The individual and combined effects of NO_3^- and PO_4^{3-} enrichment on growth rate (i.e., biomass accumulation) of dominant macroalgae at Looe Key were studied as a test for nutrient limitation by using nutrient diffusers, cage cultures and a factorial design enrichment strategy. This method has been used previously in waters adjacent to Looe Key National Marine Sanctuary where it proved to be invaluable as an experimental bioassay to determine the relative importance of nitrogen and phosphorus limitation to macroalgal growth (Lapointe and Miller, 1985; Lapointe, 1985). The macroalgae studied were the three brown algae (Phaeophyta), Dictyota divaricata, Sargassum hystrix, and Sargassum ptereopleuron, and the two red algae (Rhodophyta), Meristiella (Eucheuma) gelidium and Gracilaria tikvahiae. With the exception of G. tikvahiae, which was obtained from the culture collection of the Harbor Branch Foundation on Summerland Key, the macroalgae were collected in the Back Reef area of Looe Key or in closely adjacent areas. Because of intense fish grazing in the Reef-Crest and Spur-and-Groove habitats that led to uncontrolled losses of algal portions that projected through the mesh-work of our caged populations, these experiments were restricted to the Back-Reef area where herbivory was found to be quite low (see RESULTS, Herbivory Studies). These experiments were performed both in early (25 June - 1 July 1984) and late (6-12 September 1984) summer.

The factorial experimental design consisted of four enrichment treatments that were located in different areas (spatially separated by about 50 m) to prevent cross-contamination of the treatments by the diffused nutrients. Accordingly, the four different areas (treatments) received various types of enrichment, which consisted of either NO_3^-, PO_4^{3-}, NO_3^- + PO_4^{3-} or a control (no enrichment). Two cages were used per treatment so that a total of eight enclosures were required per species. Vexar cages (2.0-cm mesh, 25 x 45 x 75 cm in size, surface area = about 0.6 m^2) were used to contain the macroalgae and were tethered to a PVC frame that was secured to the sand bottom in 4 m water depth in the Back-Reef area. Nutrient diffusers were placed beneath the cages and consisted of drilled PVC pipes (3.8 cm x 1.2 m) that were filled weekly with granular forms of the desired nutrients. Nitrogen was applied as NO_3^-, rather than as NH_4^+, because of the hypothesized importance of upwelled NO_3^- to nitrogen flux at Looe Key. Sodium nitrate was used as the source of NO_3^- and monosodium phosphate was used as the source of PO_4^{3-}. Replicate seawater samples were taken from each area to insure significant enrichment by the desired nutrient and to quantify background dissolved nutrient concentrations at the control site (see RESULTS, Nutrient Enrichment-Growth Studies). A comparison of dissolved nutrients at the control site and a site at the opposite end of the Back Reef was also performed to insure that cross-contamination was insignificant.

Experimental protocol consisted of inoculating preweighed populations of

macroalgae (ca. 150 g wet wt each) into the cages and monitoring these populations for 7-10 d to determine the growth response to the nutrient treatment. Changes in wet weight over time were used to calculate growth rates (u) as doublings/day according to the equation:

$$u = \frac{\log_n B_o - B(3.32)}{t}$$

where B_o is the initial biomass and B is the final biomass at time (t). The factor 3.32 is used to convert growth from $\log_{10}$ to $\log_2$ (i.e., to obtain doublings/day). At the end of the growth periods, samples of macroalgae were taken for tissue analysis for carbon, nitrogen and phosphorus to insure that the nutrient enrichments were effective (see RESULTS, Nutrient Enrichment-Growth Studies). Growth results were tested using two-way ANOVA.

Nutrient Enrichment-Productivity Experiments

Measurements of midday net photosynthesis under full natural sunlight were also performed to determine the effects of the above nutrient enrichments on photosynthetic performances. Techniques followed those described above and elsewhere by Littler (1980) and Lapointe et al. (1984), and only an overview is provided here. Sargassum pteropleuron, Dictyota divaricata and Meristiella (Eucheuma) gelidium were pulsed for 10 h with 200 uM NH_4^+, NO_3^- and 20 uM PO_4^-, in the same factorial experimental design we used in the above growth studies, and then flushed with clean seawater 4 h prior to incubation on 24 October 1984. Identical nutrient concentrations were used in the parallel studies with Dictyota divaricata and Acanthophora spicifera at Curlew Cay, Belize during 4 and 7 April 1985, respectively.

Tissue Analysis

Macroalgal samples were taken from the nutrient enrichment-growth studies as well as from random collections in the Back-Reef area (i.e., dominant macroalgae) for analysis of tissue carbon, nitrogen and phosphorus. Acanthophora spicifera and Dictyota divaricata were also analyzed from the Back Reef of Curlew Cay. Samples were rinsed briefly for 1-2 sec in deionized water and dried to constant weight (ca. 48 h at 60°C). After powdering with a mortar and pestle, carbon and nitrogen were determined using a Perkin-Elmer 240 Elemental Analyzer and phosphorus was measured using a persulfate digestion technique modified from the phosphorus analysis of Menzel and Corwin (1962).

Seawater Nutrient Analysis

Seawater samples for determination of dissolved inorganic nutrients (NO_3^-, NH_4^+, $PO_4^=$) were taken at the sites used for the experimental growth studies in the Back-Reef area as well at surface (lm) and bottom (9.0m) sites at the western study site (Fig. 1) in the Spur-and-Groove area. Seawater was also sampled for nutrients from the Curlew Cay Back Reef. Samples were collected in triplicate in acid-washed Nalgene bottles, filtered (0.45um) and quickly frozen. Subsequently, the samples were analyzed on a Technicon II Autoanalyzer according to the methods of Zimmerman et al. (1977).

RESULTS

Floristic Overview and Major Plant Cover

Because the plant life at Looe Key proved to be quite diverse (especially in the Back-Reef habitat), a significant portion of this initial effort has been devoted to taxonomic endeavors. Consequently, we first will present our floristic analysis based on the preliminary collections of 19-21 June 1984, given in Table 1.

A diverse tropical algal flora is present among the hermatypic corals, gorgonians and non-articulated coralline algae forming the Looe Key reef. Based on only this one limited effort, a total of 90 taxa were collected (Table 1) representing 28 plant families, including several apparently undescribed species (i.e., new to science). Although, nearly all of the algal taxa occur in mosaic patches anywhere suitable habitat is found, we were able to discern several major

Table 1*.
Checklist of benthic marine algae from Looe Key, Florida, deposited in the U.S. National Herbarium (Identifications of voucher specimens largely by S. Fredericq).

CHLOROPHYTA

Acetabulariaceae
- Acetabularia crenulata Lamouroux

Anadyomenaceae
- Anadyomene stellata (Wulfen) C. Agardh

Bryopsidaceae
- Bryopsis pennata Lamouroux
- Bryopsis sp.

Caulerpaceae
- Caulerpa cupressoides (Vahl) C. Agardh
- Caulerpa mexicana(Sonder) Kutzing
- Caulerpa sertularioides(Gmelin) Howe
- Caulerpa racemosa (Forsskal) J. Agardh

Cladophoraceae
- Cladophora fulginosa Kutzing

Dasycladaceae
- Dasycladus vermicularis (Scopoli) Krasser
- Neomeris annulata Dickie

Siphonocladaceae
- Cladophoropsis macromeres Taylor

Udoteaceae
- Halimeda goreauii Taylor
- Halimeda incrassata (Ellis) Lamouroux
- Halimeda opuntia (Linnaeus) Lamouroux
- Penicillus capitatus Lamarck
- Penicillus dumetosus(Lamouroux) Blainville
- Penicillus lamourouxii Decaisne
- Rhipocephalus phoenix (Ellis & Solander) Kutzing
- Udotea conglutinata (Ellis & Solander) Lamouroux
- Udotea flabellum (Ellis & Solander) Howe
- Udotea sublittoralis Taylor

Ulvaceae
- Enteromorpha flexuosa (Wulfen ex Roth) J. Agardh
- Enteromorpha sp.

Valoniaceae
- Dictyosphaeria cavernosa (Forsskal) Borgesen
- Valonia sp.

CYANOPHYTA

Various filamentous taxa (e.g., Lyngbya sp.)

PHAEOPHYTA

Chordariaceae
- Cladosiphon occidentalis Kylin

Dictyotaceae
- Dictyota bartayresii Lamouroux
- Dictyota divaricata Lamouroux
- Dictyota linearis (C. Agardh) Greville
- Dictyota mertensii (Martius) Kutzing
- Dictyota spp.
- Padina jamaicensis (Collins) Papenfuss
- Stypopodium zonale (Lamouroux) Papenfuss

Sargassaceae
- Sargassum hystrix J. Agardh
- Sargassum polyceratium Montagne
- Sargassum pteropleuron Grunow
- Sargassum sp.

RHODOPHYTA

Acrochaetiaceae
- Acrochaetium spp.

Ceramiaceae
- Centroceras clavulatum (C. Agardh) Montagne
- Ceramium subtile J. Agardh
- Ceramium flaccidum (Kutzing) Ardissone
- Ceramium fastigiatum f. flaccida H.E. Peterson
- Crouania attenuata (Bonnemaison) J. Agardh
- Griffithsia globulifera (Harvey) J. Agardh
- Griffithsia sp.
- Spermothamnion sp.
- Spyridia filamentosa (Wulfen) Harvey ex Hooker
- Wrangelia argus Montagne
- Wrangelia penicillata C. Agardh

Chaetangiaceae
- Galaxaura oblongata (Ellis & Solander) Lamouroux

Champiaceae
- Champia parvula (C. Agardh) Harvey
- Champia sp. (surface projections = new sp.??)

Coelothrix irregularis (Harvey) Borgesen

Corallinaceae
- Amphiroa fragilissima (Linnaeus) Lamouroux
- Amphiroa rigida var. antillana Borgesen
- Fosliella sp.
- Hydrolithon boergesenii (Foslie) Foslie
- Jania capillaceae Harvey
- Jania rubens (Linnaeus) Lamouroux
- Lithophyllum congestum (Foslie) Foslie
- Melobesia sp.
- Neogoniolithon strictum (Foslie) Setchell & Mason
- Porolithon pachydermum (Weber-van Bosse & Foslie) Foslie

Delesseriaceae
- Hypoglossum tenuifolium var. carolinianum Williams
- Nitophyllum sp.

Geldidaceae
- Gelidiella acerosa (Forsskal) Feldmann & Hamel
- Gelidium sp.

Goniotrichaceae
- Goniotrichum alsidii (Zanardini) Howe

Helminthocladiaceae
- Liagora farinosa Lamouroux
- Liagora pinnata Harvey
- Liagora valida Harvey
- Liagora spp.
- Liagora (undescribed species?)

Hypneaceae
- Hypnea cervicornis J. Agardh

Rhodomelaceae
- Acanthophora spicifera (Vahl) Borgesen
- Chondria polyrhiza Collins & Hervey
- Chondria collinsiana Howe
- Chondria sp.
- Digenia simplex(Wulfen) C. Agardh
- Herposiphonia tenella (C. Agardh) Ambronn
- Laurencia caraibica Silva
- Laurencia intricata Lamouroux
- Laurencia poitei (Lamouroux) Howe
- Laurencia spp.
- Polysiphonia sp.

Solieriaceae
- Agardhiella subulata (Ag.) Wynne & Taylor
- Eucheuma isiforme (C. Agardh) J. Agardh
- Meristiella (=Eucheuma) gelidium Cheney (unpublished)

Squamariaceae
- Peyssonnelia sp.

Wurdemanniaceae
- Wurdemannia miniata (Lamouroux) Feldmann & Hamel

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* Contributed by Suzanne Fredericq, Department of Botany, University of North Carolina, Chapel Hill, North Carolina.

community types (Figs. 2 and 4) that included Fore-Reef (i.e., Intermediate Fore-Reef, Spur-and-Groove, Reef Crest), Reef-Flat, and two types of Back-Reef macrophytic assemblages.

Most conspicuous in areas of heavy grazing (Intermediate Fore Reef, Spur and Groove, Reef Crest, Reef Flat, see Figs. 2 and 4) are the long-lived non-articulated coralline algae [Porolithon pachydermum (Fig. 3A), Lithophyllum congestum, Hydrolithon boergesenii], which form pink to purple coatings on virtually all solid reef rock surfaces. Nearly unialgal stands of the purple-red Wrangelia argus (Fig. 3B) are quite common. Filamentous genera of red algae such as Ceramium, Centroceras, Herposiphonia and Polysiphonia form broad expanses of delicate turfs, and the sheet-forming browns Dictyota bartayresii and D. divaricata (Fig. 5D) are present in patches. Reddish-orange Peyssonnelia sp. crusts are very conspicuous among the corallines and turfs. Sparsely distributed (Fig. 4) but conspicuous because of their size and upright stature, are Stypopodium zonale, Halimeda opuntia(Fig. 5B), H. incrassata, H. goreauii and Laurencia poitei. These host a multitude of epiphytes including Griffithsia, Ceramium, Polysiphonia, Melobesia, Fosliella and other encrusting algae. Less obvious, but far more abundant, are the turf-forming plants (usually less than 3-cm tall) consisting of complex intermingled assemblages of perennial species; the major components are Dictyota divaricata, Digenia simplex and Wrangelia argus. These turf formers often grow upon a relatively smooth understory pavement of crustose coralline algae. A dwarf form of

Digenia simplex, less than 0.5 cm tall above a rhizomatous expanding base, is predominant and is known to be indicative of intense grazing pressure (S.M. Lewis & J.N. Norris, personal communication).

In addition to these, a number of large fleshy forms implicated to contain chemical defense compounds against herbivory (e.g., Stypopodium zonale, Liagora spp. (Fig. 6D), Dictyota mertensii are abundant in the landward portion of the Reef-Flat macrophyte community. Free lying fragments of Neogoniolithon strictum (Fig. 5C) are also sparsely scattered in this region, and Padina jamaicensis occurs in isolated patches (Fig. 5E).

The Back-Reef habitat (Fig. 6) represents a special case in regard to the above patterns, being dominated by (1) seagrass meadows interspersed with (2) cobble basins containing an exceptionally rich and abundant assemblage of large frondose macroalgae. Herbivorous fishes are uncommon to rare in this environment, probably due to the lack of concealing cover and the presence of large predatory fishes such as barracuda (Sphyraenidae) and tarpon (Elopidae). The result is that rubble-rock pockets among the seagrass beds [Thalassia testudinum and Syringodium filiforme, with patches of siphonalean algae such as Udotea flabellum (Fig. 6C) and Rhipocephalus phoenix (Fig. 5A)] develop spectacular standing crops of the frondose algae Meristiella (Eucheuma) gelidium, Acanthophora spicifera (Fig. 6B), Laurencia poitei, Agardhiella subulata, Dictyota linearis, D. mertensii, Liagora valida, L. farinosa, L. pinnata, Chondria sp., Sargassum polyceratium (Fig. 6A) Sargassum pteropleuron, Penicillus capitatus and P. dumetosus.

This system (Fig. 7) of abundant algal biomass was observed to fluctuate dramatically, perennating from a low winter standing stock to a large summer biomass associated with a prolonged period of upwelling (Lapointe, personal observation) as well as increasing light and water temperatures. Apparently, this rich and varied macroalgal-dominated community has not been recognized by previous workers.

Herbivory Studies

The data for percent thallus loss to fish grazing (Fig. 8) clearly shows a dramatic reduction in herbivory associated with the Back-Reef habitat. All removal of algal material was due to herbivorous fishes, as evidenced by (1) the characteristic grazing scars in concert with (2) extensive observations of the suspended thalli on the lines by divers. Our methodology measured the relative vulnerability of each species to being consumed by natural populations of herbivorous fishes. We did not differentiate among fish species or determine individual preferences. Of the three Fore-Reef and Reef-Flat habitats, where an average of 63% or more of all algal thalli were consumed, losses to grazing were greatest on the Intermediate Fore-Reef. However, the magnitude of this difference (Fig. 8) was slight ($P>0.05$, Duncan's MRT) in contrast to differences between these three habitats and the Back Reef ($P>0.05$). On the average, consumption rates for the spectrum of 16 algae used were 14 times greater on the shallow Reef Flat, 12 times higher on the Fore-Reef Spur and Groove and 15 times higher on the Intermediate Fore-Reef than on the Back Reef. This agrees with our observations of herbivorous fish abundances and those recorded by Bohnsack (1982) and Bohnsack et al. (NOAA Report, Chap. 7, in draft) in the Looe Key environs. The most palatable algae included four of the more delicate species of the siphonaceous genus Caulerpa (Fig. 8) and the sea lettuce Ulva lactuca. The most resistant macrophyte across all habitats, the red alga Meristiella (Eucheuma) gelidium, was largely avoided except on the Reef Flat where it lost 87.5% of its area to fishes. Laurencia poitei also showed exceptionally high resistance to predation along with Dictyota divaricata and Caulerpa ashmeadii.

Productivity Studies

Figure 9 shows a clear separation between the extremely low production rates of crusts and calcified species and those of all other groups under ambient nutrient conditions. As was expected, the more delicate forms of macroalgae tended to show the highest productivities per unit of ash-free

dry weight (organic wt). Net apparent photosynthetic production ranged from a high of 21 mg C fixed/g ash-free dry wt/h for Dictyota divaricata turf from the Spur-and-Groove habitat to a low of 0.4 mg C/g AFDW/h for Peyssonnelia sp. from the same habitat. When photosynthetic rates are considered from the basis of two-dimensional (projected) surface area (Fig. 10), the same Dictyota divaricata turf showed lowest productivity (0.16 g C/m^2 of thallus/h), due to its high surface area to biomass ratio. Laurencia poitei ranked highest in terms of area-based productivity with 0.65 g C fixed/m^2 of thallus/h.

Nutrient Enrichment-Growth Studies

For all species tested, growth rates of NO_3^- and PO_4^{3-} enriched test macroalgae did not differ significantly ($P<0.05$) from that of the controls during either early (Fig. 11) or late (Fig. 12) summer. Growth rates ranged from low values for Meristiella (Eucheuma) gelidium (0.01-0.03 doublings/day) to high values for Dictyota divaricata (0.05-0.09 doublings/day; Figs. 11 and 12).

Nutrient Enrichment-Photosynthesis Studies

In general agreement with results of the above growth-enrichment studies, photosynthetic rates of the NO_3^- and PO_4^{3-} enriched macroalgae did not differ significantly from those of the controls in the Looe Key studies (Fig. 13). Photosynthetic rates ranged from 1.5 to 1.7 mg C/g dry wt/h for Meristiella gelidium, 2.5 to 4.3 mg C for Sargassum pteropleuron and 4.5 to 7.9 mg C for Dictyota divaricata (Fig. 13).

In contrast to the Looe Key studies, photosynthetic rates of NH_4^+ and PO_4^{3-} enriched macroalgae showed significant enhancement compared to controls in the Curlew Cay, Belize studies (Fig. 14). Photosynthetic rates of Dictyota divaricata and Acanthophora spicifera increased about threefold in response to nutrient enrichment; PO_4^{3-}, rather than NH_4^+, appeared most important in stimulating photosynthesis (Fig. 14).

Tissue Analysis

Tissue levels of nitrogen and phosphorus were significantly increased by diffuser enrichment during the experimental growth studies at Looe Key . Levels of nitrogen were raised by 50-100 % in both Meristiella gelidium and Dictyota divaricata; although no increase occurred in Sargassum pteropleuron (Table 2). Levels of phosphorus increased even more dramatically, some 400-800 %, in Meristiella gelidium and Dictyota divaricata and ca. 300 % in Sargassum pteropleuron. Because of these elevated levels of nitrogen and phosphorus and an unchanged carbon content, molar C:N and C:P ratios decreased, especially in Meristiella and Dictyota (Table 2). However, ambient levels of nitrogen and, in particular, phosphorus appeared relatively high in macroalgae collected in the various Looe Key habitats (Table 3) compared to the same species from nearshore. For example, the red algae Chondria sp. and Laurencia poitei each had phosphorus contents of ca. 0.15 % of dry weight, almost five-fold greater than the same algae collected nearshore in the relatively eutrophic Pine Channel (Table 4). The nitrogen content of Chondria and Laurencia from Looe Key were ca. 2.0 % (C:N = 10.0), also elevated in comparison to the same algae in Pine Channel (Table 4).

Seawater Nutrient Analysis

Elevated concentrations of NO_3^- and PO_4^{3-} in seawater at the experimental sites in the Back Reef area of Looe Key (as compared to the control site) also demonstrate significant enrichment by the nutrient diffusers (Table 5). Concentrations of NO_3^- reached up to 100 uM, and PO_4^{3-} reached up to 55.0 uM at the enriched sites (Table 5). Ambient concentrations of NO_3^- and PO_4^{3-} in the control areas ranged between 0.5 and 1.0 uM and 0.10 to 0.20 uM, respectively. Similar levels were observed in surface waters (1 m) in the Spur-and-Groove zone; whereas significantly elevated concentrations, ca. 2.5 uM NO_3^- and 0.38 uM $PO_4^{=}$, were observed in deeper water (9 m) at the base of the western study site -- indicating stratified nutrient conditions (Table 5).

Table 2.

Levels of carbon (C), nitrogen (N), phosphorus (P) and their molar ratios in macroalgae exposed to different nutrient treatments in Looe Key Marine Sanctuary (5 July 1984). Values represent means ± one standard deviation.

Species	Date	Treatment	%C	%N	%P	C:N	C:P	N:P
Meristiella gelidium		C	19.80 ±0.20	0.53 ±0.07	0.53 <±0.01	32	145	4.5
(n=4)		N	20.00 ±2.00	0.91 ±0.04	0.06 <±0.01	19	130	6.8
		P	23.50 ±1.4	0.62 ±0.01	0.40 ±0.01	33	23	0.7
		NP	20.30 ±1.30	0.89 ±0.02	0.40 ±0.03	20	20	1.0
Dictyota divaricata		C	27.23 ±0.46	0.63 ±0.01	0.09 <±0.01	37	114	3.0
(n=4)		N	27.80 ±0.27	0.87 ±0.08	0.01 <±0.01	27	114	4.1
		P	26.50 ±0.77	0.69 ±0.04	0.34 ±0.02	33	31	1.0
		ND	27.66 ±0.28	0.88 ±0.04	0.38 ±0.04	27	28	1.0
Sargassum pteropleuron		C	25.49 ±0.79	0.80 ±0.06	0.17 ±0.01	28	59	2.1
(n=4)		N	25.25 ±0.49	0.85 ±0.11	0.16 ±0.02	28	61	2.3
		P	25.89 ±1.11	0.69 ±0.03	0.40 ±0.03	33	25	0.8
		NP	25.60 ±0.71	0.79 <±0.01	0.50 ±0.07	28	20	0.7

Table 3.

Levels of carbon (C), nitrogen (N), phosphorus (P) and their molar ratios in dominant macroalgae of Looe Key National Marine Sanctuary (June 1984). Values represent means ± standard deviation.

Species	Habitat	%C	%N	%P	C:N	C:P	N:P
Padina jamaicensis	Back Reef	22.01 ±0.98	1.02 ±0.07	0.10 ±0.01	21.6	220	10.2
Chondria sp.	Back Reef	20.28	1.95	0.14	10.4	145	13.9
Dictyota divaricata	Back Reef	23.91 ±1.32	1.64 ±0.22	0.18 ±0.01	14.6	133	9.1
Stypopodium zonale	Reef Crest	35.30 ±1.00	1.53 ±0.09	0.12 ±0.03	23.1	294	12.8
Meristiella gelidium	Back Reef	22.10 ±2.96	0.78 ±0.02	0.08 ±0.00	28.3	276	9.8
Liagora sp.	Reef Crest	15.73 ±0.14	0.61 ±0.00	0.06 ±0.00	25.8	262	10.2
Laurencia poitei	Back Reef	21.00 ±0.30	2.05 ±0.10	0.15 ±0.00	10.2	140	13.6
Dictyota divaricata	West Study Spur	21.74 ±1.07	1.40 ±0.16	0.10 ±0.01	13.3	85	6.3
Dictyota divaricata	Intermediate Fore Reef	27.10 ±1.84	1.59 ±0.05	0.10 ±0.01	14.6	106	7.1

Table 4.

Levels of carbon (C), nitrogen (N), phosphorus (P) and their molar ratios in three red algae collected in South Pine Channel, Middle Torch Key. Values are given as means ± one standard deviation (N=2).

Species	Date	%C	%N	%P	C:N	C:P	N:P
Chondria sp.	26 May 1983	23.57 ±3.89	1.24 ±0.22	0.030 <±0.01	16.3	306	18.6
	30 Sept 1983	21.72 ±0.50	1.84 ±0.01	0.06 ±0.01	7.4	141	13.8
	25 May 1984	19.30 ±0.40	1.47 ±0.04	0.04 ±0.01	11.3	188	16.5
Laurencia poitei	26 May 1983	21.58 ±0.20	1.10 ±0.07	0.03 <±0.01	16.9	280	16.5
	30 Sept 1983	20.94 ±1.02	1.36 ±0.05	0.04 ±0.01	13.2	204	15.3
	25 May 1983	15.78 ±0.59	0.75 ±0.01	0.03 <±0.01	18.0	205	11.3
Gracilaria tikvahiae	10 June 1983	26.50 ±1.50	2.65 ±0.05	0.040 ±0.002	8.6	258	29.8

Table 5.

Nutrient concentrations of ambient water during growth-enrichment studies at Looe Key National Marine Sanctuary. Values are means ± one standard deviation (N=3).

Date	Treatment	NO_3^-	NH_4^-	PO_4^{-3}	N:P
28 June 1984	Control	0.99 ±0.09	0.17 ±0.08	0.22 ±0.08	5.27
	NO_3^-	76.30 ±8.20	0.25 ±0.50	0.17 ±0.07	—
	PO_4^{-3}	0.85 ±0.10	0.20 ±0.07	26.70 ±16.40	—
	$NO_3^-+PO_4^{-3}$	102.40 ±20.20	0.70 ±0.13	38.50 ±0.12	—
West Study Spur	(bottom)	2.44 ±0.43	0.20 ±0.05	0.38 ±0.12	6.95
	(surface)	1.09 ±1.00	0.08 ±0.04	0.17 ±0.06	6.88
9 Sept 1984	Control	0.51 ±0.33	0.18 ±0.02	0.10 <±0.01	6.90
	NO_3^-	95.50 ±26.80	0.28 ±0.09	0.11 ±0.06	—
	PO_4^{-3}	1.42 ±0.60	0.25 ±0.09	32.50 ±10.50	—
	$NO_3^-+PO_4^{-3}$	25.50 ±8.70	0.19 ±0.04	53.10 ±4.10	—
West Study Spur	(bottom)	1.24	V.D.	0.19 ±0.03	6.53
	(surface)	1.02 ±0.32	0.10 ±0.08	0.16 ±0.03	7.00

DISCUSSION

The maximal limits to algal biomass on reef systems such as Looe Key are generally set by nutrient levels (Hatcher and Larkum, 1983); whereas, the actual standing crops present are determined by the more proximate controlling factor of herbivory (Littler and Littler, 1984). The perennial long-lived forms of diminutive frondose algae and crustose corallines that dominate the Spur-and-Groove, Intermediate-Fore-Reef and Reef-Flat habitats (Fig. 4, Appendix A) are uniformly indicative of high grazing pressure. The herbivory bioassays (Fig. 8) demonstrate highly consistent and significant grazing pressure throughout all of the above habitats, which very likely maintains the taxonomic similarity of these three systems at Looe Key. Although the various algal populations occur in a very patchy manner on a microhabitat scale (Fig. 4), the between habitat floristic differences throughout the Fore Reef, with the exception of the Reef Crest (Fig. 2), are minimal. The inconspicuousness of large non-calcified algae on most 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 restricted 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). For example, larger non-calcareous frondose macrophytes (Sheet-like, Coarsely-branched and Rubbery-Forms) occur abundantly on extremely shallow reef benches (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). Similarly, the Looe Key Back Reef is qualitatively and quantitatively quite rich in plant life, being dominated by structurally weak but fast-growing macroalgae and seagrasses. On the extensive cobble-rubble pockets (Fig. 7), near the Back-Reef seagrass beds, a remarkable, fleshy, frondose, macroalgal flora develops (Fig. 2). Also abundant are siphonaceous forms of macroalgae, such as Udotea, Penicillus, Rhipocephalus, Caulerpa and Halimeda, adapted for soft-bottom-dwelling. On Looe Key, the Back-Reef habitat contains little spatial heterogeneity, with the macrophytes themselves comprising most of the three-dimensional structure. Barracuda

(Sphyraenidae) and other large carnivorous fishes are abundant predators and this undoubtedly contributes to the reduced levels of herbivores. The filamentous and fleshy forms of algae that come to dominate such habitats (e.g., Fig. 5B) are thought (Littler and Littler 1980) to be poorly resistant to herbivory but superior competitors due to their internal allocation of resources primarily to photosynthetic structure. This results in higher surface area to volume ratios and more rapid growth, which leads to better light gathering and nutrient sequestering capabilities, relative to the more structurally resistant algal forms (e.g., Figs. 3A, 5B, 5C) characteristic of environments with high herbivory.

In addition to the Fore-Reef, Reef-Flat and Back-Reef algal systems, we discerned an additional algal community localized in the upper Reef Crest (Fig. 2) of the Spur-and-Groove habitat. This extremely shallow high-energy portion of the reef is dominated by the crustose algal-ridge former Porolithon pachydermum along with the branched non-articulated coralline Lithophyllum congestum, which also appears abundantly and uniquely here (in patches). The crustose red alga Peyssonnelia sp. is present throughout the crest habitat, whereas frondose algae, including microalgal turfs, are greatly reduced.

On certain portions of the Reef Flat (bordering the Back Reef) that are spatially removed from heterogeneous structure which could harbor fish populations, occasional conspicuous patches of macroalgae such as upright forms of Dictyota mertensii, Stypopodium zonale, Laurencia poitei and various species of Liagora, most of which are thought to be chemically defended (Norris and Fenical 1982), appear on the Hydrolithon boergesenii-coated rubble substratum.

We were surprised by the diverse and complex nature of the algal communities at Looe Key, particularly within the previously undescribed Back-Reef habitat. It would be beneficial to future ecological studies if a high level of taxonomic effort were undertaken by specialists to thoroughly inventory the algal resources within the entire Sanctuary system. Expertise in dealing with microfilamentous and coralline algae would be required in the Fore-Reef and Reef-Flat habitats in particular.

A broad scale quantitative description of permanent transects would be useful to document algal community structure in selected reef habitats at Looe Key. Because the major habitats and biotic zones have now been identified by qualitative means and aerial photography (Figs. 2 and 4, Appendix A), they can be subsampled appropriately. Initially, the unique Back-Reef ecosystem would seem to justify a more detailed inventory and baseline effort from which to ascertain dynamic patterns due to upwelling episodes. Seasonal studies would be required, particularly involving biomass flux determinations in the case of the dominant Back-Reef algae, in conjunction with studies of nutrient-related events such as periodic upwelling. The understanding of such factors must be considered of paramount importance because of their potential relationship to the stability of the Looe Key Sanctuary.

Because, in our opinion, herbivory is such a dominant direct controlier of algal standing stocks throughout the Looe Key Reef-Flat and Fore-Reef habitats (Fig. 8), limited manipulative studies of fish populations (involving small, closely monitored, exclosure cages) would yield predictive insights into the effects of fish demographics on the structure of the various reef communities. If coupled with factorial experiments utilizing nutrient diffusers to simulate upwelling or anthropogenically increased eutrophication, predictive information having considerable management potential would be forthcoming.

The particularly high resistance of the Back-Reef alga Meristiella (=Eucheuma) gelidium to grazing fishes (Fig. 8) is probably due to its structural toughness (e.g., carageenan gels) and not toxic secondary compounds. Although we can not rule out the possibility of chemical defense, no toxic compounds are known from Eucheuma (Fenical, personal communication) even though a number of species have been screened. If, as we suspect, the primary defense is structural, then the disproportionately large losses this plant suffered on the Reef Flat was probably due to

the particularly large populations of Scaridae (parrotfishes) in this habitat (see Bohnsack et al., Chap. 7). Parrotfishes have relatively large and powerful mouth parts capable of taking bites from the tougher coarse forms of algae (Lewis and Wainwright in press); whereas the Acanthuridae (surgeonfishes) that dominate Fore-Reef habitats are adapted to grazing primarily the weaker algal forms (e.g., filaments). In the cases of Laurencia and Dictyota, their high resistances to herbivory have been noted by others (Hay, 1981c; Littler et al. 1983; Hay 1984; Lewis 1985) and attributed to chemical defense compounds (Norris and Fenical 1982).

In terms of net apparent photosynthetic rates on both a weight (Fig. 9) and area basis (Fig. 10), the values for Looe Key algae fall within the range reported (Littler 1973; Wanders 1976; Connor and Adey 1977; Bach 1979; Rogers and Salesky 1981; Littler et al. 1983, 1985) for other tropical reefs. As expected, those forms having the greatest surface area/volume ratios tended to show the highest weight-based primary productivities, with the grazer resistant crustose and calcified forms producing at much lower rates. The forms dominating the Back Reef, because of their larger standing stocks and high photosynthetic rates, contribute substantially to the primary production of the Looe Key system.

The growth and net production rates of the brown macroalgae (Dictyota divaricata, Sargassum pteropleuron and Sargassum hystrix) and the red macroalgae (Meristiella gelidium and Gracilaria tikvahiae) were not appreciably stimulated by nitrogen and phosphorus enrichment, suggesting a high flux of these elements at Looe Key prior to and during this study (i.e., June-September). These findings contrast with similar studies conducted with Gracilaria tikvahiae in nearshore waters of Pine Channel where phosphorus (but not nitrogen) severely limited both growth and net photosynthesis during the same time of year (Lapointe and Miller 1985). These results also contrast with our parallel data set from Curlew Cay, Belize (Fig. 14) and previous reports from the Great Barrier Reef (Kinsey and Domm 1974; Hatcher and Larkum 1983), both of which found growth and/or photosynthesis to be highly nutrient-limited. Accordingly, the macroalgae at Looe Key appeared to be particularly well-nourished compared to algae in nearshore environments such as Pine Channel during summer 1984, which could partly explain the striking abundance of macroalgal biomass during this period of time in the Back-Reef habitat (where herbivory is low).

The relatively enriched nutritional state of macroalgae at Looe Key is supported further by their high tissue percentages of nitrogen and phosphorus. The nitrogen content of the red algae Laurencia poitei and Chondria sp. were both ca. 2.0% of dry weight at Looe Key--a nitrogen content sufficient to sustain non-nitrogen-limited growth in the related red alga Gracilaria tikvahiae (Lapointe and Duke 1985). These levels are also greater than those found in the same species in nearshore areas of Pine Channel, which averaged ca. 1.0-1.5% of dry weight. However, the differences in phosphorus content between the Looe Key algae and the Pine Channel algae are even more dramatic; phosphorus averaged ca. 0.15% of dry weight in Laurencia and Chondria at Looe Key compared to about five-fold lower levels, ca. 0.03%, in these same algae in Pine Channel. We suspect that the elevated phosphorus content of the Looe Key macroalgae may be the key factor in determining their well nourished physiological state, because this element severely limits growth of Gracilaria tikvahiae in the nearshore waters in Pine Channel during summer months (Lapointe and Miller 1985). Thus, nutrient flux, particularly that of phosphorus, appears to be elevated in Looe Key waters, compared to nearshore waters, during summer months.

Analyses of seawater at Looe Key suggests that the high nutrient flux implicated in these studies may be due to summertime shelf-break upwelling. Elevated levels of NO_3^- and PO_4^{3-} occurred on the lower portion of the Spur-and-Groove zone, ca. 2.5 uM and 0.40 uM, respectively, compared to lower surface concentrations, ca. 1.0 uM and 0.17 uM, respectively. Even these relatively low surface nutrient quantities are well above concentrations typical of blue oceanic water (levels that approach analytical detection limits), because even under stratified nutrient conditions, some degree of vertical mixing

and upward diffusion of nutrients occurs.

The nutrient concentrations at Looe Key lie roughly in the middle of the range reported for coral reef systems of the world; reactive phosphate ranges from undetectable (<15uM) to approximately 0.6 uM, while nitrate (NO_3^-) ranges from undetectable to 6 uM (Pilson and Betzer 1973; Smith and Jokiel 1975; Marsh 1977). Contrastingly, these compounds at Curlew Cay, Belize are so low as to approach the limits of resolution of standard analytical procedures. The stratified nutrient conditions found at Looe Key in summer 1984 are typical of shelf break upwelling that occurs through the summer months along Florida's east coast (Atkinson et al. 1984). During such stratified conditions, dense water upwelled at the shelf break can penetrate onto and across the continental shelf, usually as a response to wind-driven Ekman flow (Atkinson, 1977). Apparently this process is enhanced off northeast Florida where southeast winds (Green 1944; Taylor and Stewart 1957), and diverging isobaths can amplify upwelling (Blanton et al. 1981). However,the potential importance of upwelling as a source of nutrients to Looe Key National Marine Sanctuary is clearly implicated by this study; further studies are now needed to quantify the nutrient flux associated with these upwelling events because such nutrient inputs may dominate all other nutrient sources to the Looe Key system, as they do in the whole of the South Atlantic Bight (Atkinson et al. 1984)

Although upwelled waters have previously been observed on coral reef systems (Glynn and Stewart 1973; Glynn 1977; Birkeland 1977), such upwelling conditions have generally been considered detrimental to coral reef growth. Inhibition has been attributed to the reduced temperatures associated with upwelling (Glynn and Stewart 1973; Glynn 1977) that reduce coral growth rates (Shinn 1966; Weber et al. 1975). However, Dodge and Vaisnus (1975) found that coral growth in Bermuda bears an inverse relationship to temperature, which they interpreted as being due to increased nutrient supply with intrusions of cooler upwelled waters. Recent studies on the great Barrier Reef (Andrews and Gentian 1982) have also implied an importance of upwelled nutrients to sustaining coral reef development. We believe that because the upwellings at Looe Key during summer 1984 coincided with the seasonal maxima in surface water temperatures (ca 30°C) in the Florida Current, the cooler upwelled source waters were sufficiently ameliorated so as to not cause temperature stress in Looe Key corals. Alternatively, if upwellings were to occur during winter when continental shelf water temperatures are reduced, low temperature stress would undoubtedly occur. Thus, in the absence of low temperature stress during summer conditions, we believe that the increased nutrient flux due to upwelling must be beneficial to the Looe Key ecosystem in relieving nutrient limitation.

However, elevated concentrations of phosphate are known to reduce coral growth. Kinsey and Davies (1979) found that phosphate enrichment to 2 uM caused greater than 50% suppression of reef calcification and suggested that this was the reason for poor coral growth on reefs adjacent to upwellings (e.g., Glynn 1977). This inhibition is due to blockage of carbonate crystal formation in the presence of high phosphate (Simkiss 1964). Considering that the mild upwellings that occurred at Looe Key during summer 1984 produced phosphate concentrations that were five-fold lower than those in the experiments of Kinsey and Domm (1974), the elevated phosphate concentrations observed at Looe Key were probably not detrimental to coral growth and in the long run, were most likely stimulatory. It is clear, however, that Looe Key would be most susceptible to phosphate pollution and resultant coral toxicity during summer months when anthropogenic phosphate inputs, coupled with upwelled phosphate, could result in concentrations sufficient to reduce coral growth rates.

It appears that the abundant macroalgae in the Back-Reef area of Looe Key during summer 1984 represent an important source of rapidly cycling biomass that may provide indirect sources of particulate enrichment (i.e., detritus) for coral growth. On many occasions, we have observed herbivorous fish schools (Kyphosidae and Acanthuridae mostly) literally attacking allochthonous patches of drift algae (Fig. 3C) en masse on the Looe Key Fore Reef. Our results suggest that the

Back Reef macroalgae respond to the recurring, summertime input of nutrients due to upwelling by achieving maximal growth rates that ultimately result in high turnover of algal biomass. Observations throughout the year (by B. Lapointe) indicate that the large macroalgal biomass which develops in the Back Reef in conjunction with summertime upwelling (Atkinson et al. 1984, Lapointe and Smith, unpublished NOAA report) persists into the fall and diminishes by midwinter. Such seasonal patterns suggest that the residual macroalgae may support organic nutrient demands of reef metabolism by rapidly assimilating and storing inorganic nutrients derived from summertime upwelling as algal biomass that persists through the fall and winter. This is of special ecological significance in that the biomass developed by the Back Reef macroalgae becomes available as drift organic matter (Fig. 3C) transported to the Reef Flat and Fore Reef, thereby possibly sustaining metabolism during periods of low nutrients--i.e. fall, winter and early spring when blue water (low nutrient) conditions prevail(Lapointe, unpublished data). Such an ecological mechanism of uptake and storage of pulses of nutrients by reef macroalgae during summer upwelling, and subsequent growth, senescence and detrital production during the extended months of low nutrient input may partially explain why highly productive coral reefs, such as Looe Key, can flourish in what are usually considered nutrient-depauperate oceanic waters. Corals are known to require particulate nutrition for healthy growth (D'Elia and Muscatine, 1977), but ecological mechanisms for sustaining such modes of coral reef growth have not been previously elucidated. Our studies clearly show the potential importance of relatively short-term events (e.g., upwellings) to the ecology of Looe Key and suggest that future studies are needed to determine the seasonal and annual variability in these events.

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Figure 1. Oblique view of Looe Key from the southeast showing the location of the study transects and major macroalgal habitats (identified on Fig. 2. Photograph by Aerial Photos International, courtesy of NOAA.

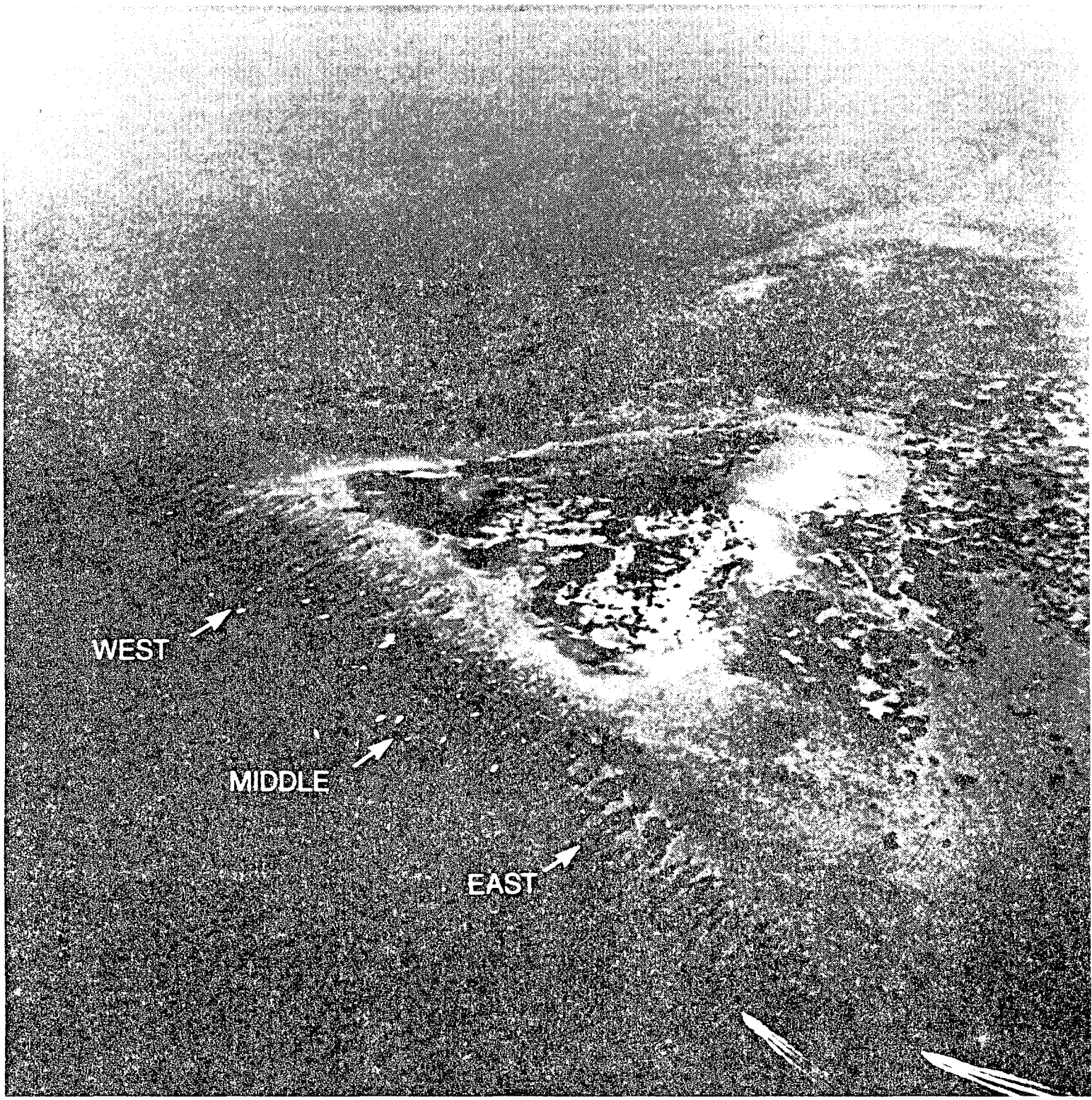

WEST
MIDDLE
EAST

Figure 2. Aerial perspective of the five major macrophyte habitats for the Looe Key system. Based on aerial photography, line-intercept transects (in areas indicated) and observations by towed divers. For within-habitat detailed descriptions, see RESULTS (Floristic Overview and Major Plant Cover) and Appendix A).

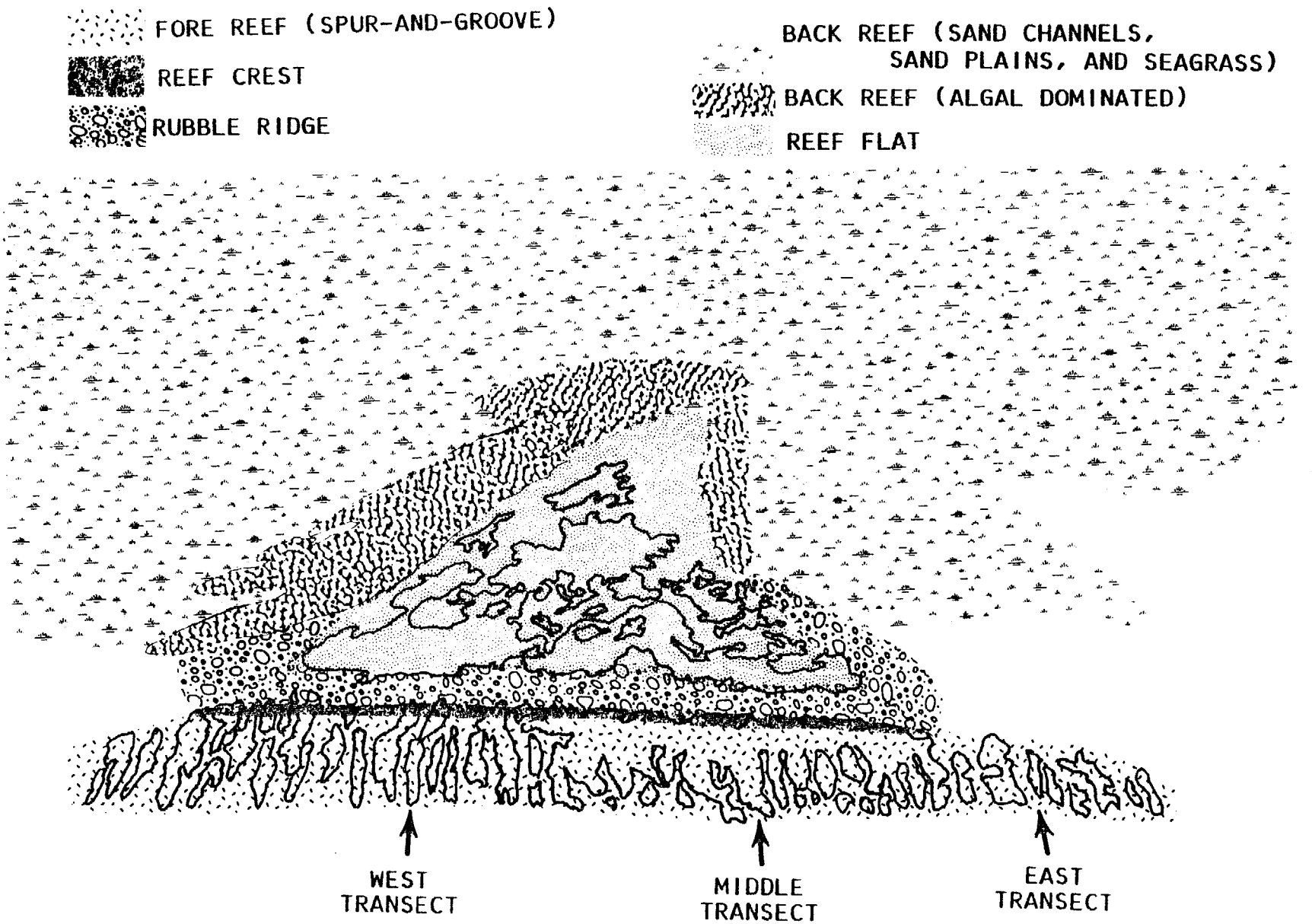

FORE REEF (SPUR-AND-GROOVE)
REEF CREST
RUBBLE RIDGE
BACK REEF (SAND CHANNELS, SAND PLAINS, AND SEAGRASS)
BACK REEF (ALGAL DOMINATED)
REEF FLAT
WEST TRANSECT
MIDDLE TRANSECT
EAST TRANSECT

Figure 3. A - Porolithon pachydermum at Looe Key showing fresh grazing scars from parrotfish. B - Wrangelia argus turf from Spur-and-Groove habitat, C - Sargassum sp. adrift over Fore Reef, D - Diver recording macroalgal abundances on east study transect in area dominated by Palythoa and gorgonians.

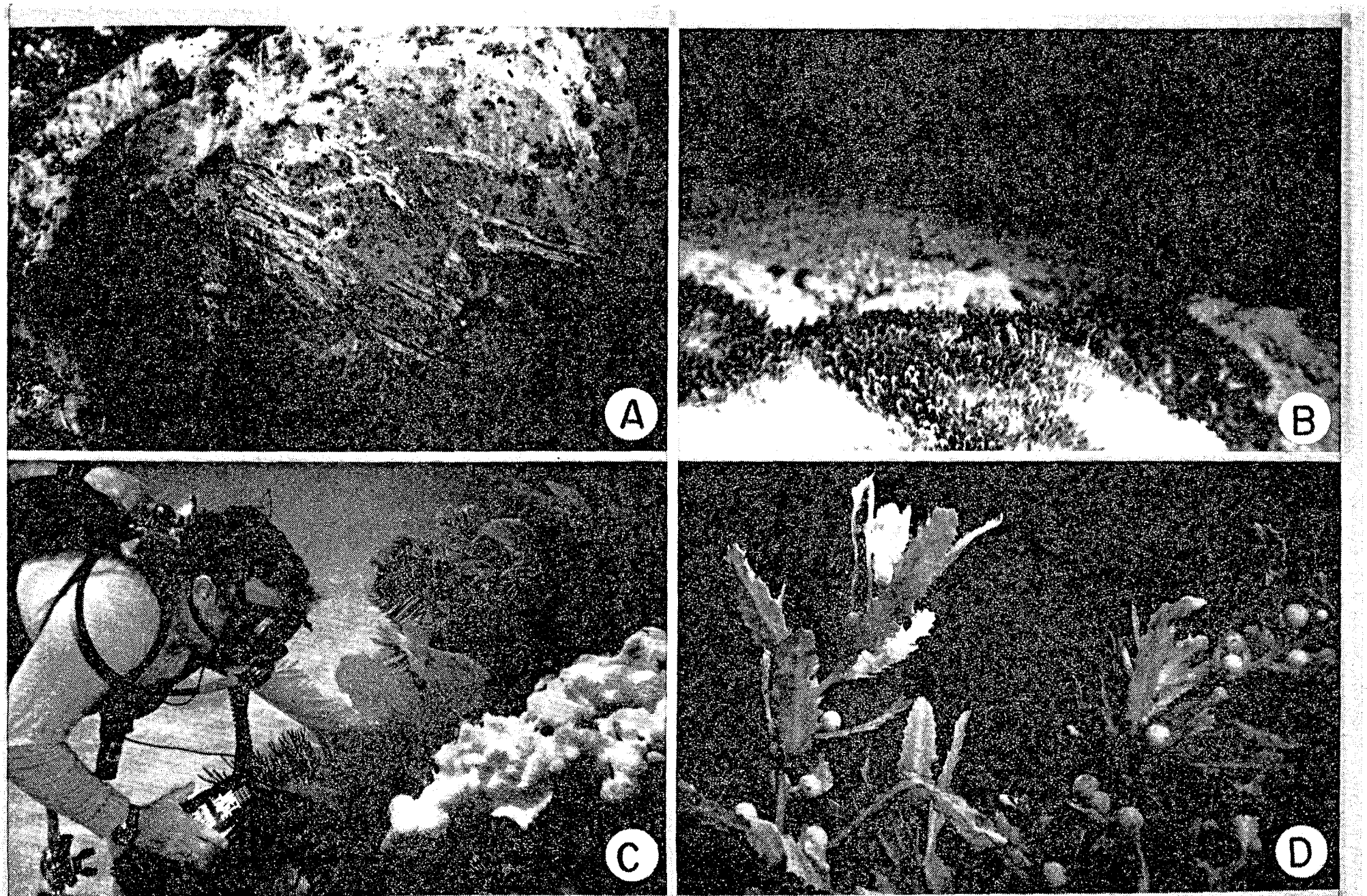

A
B
C
D

Figure 4. Diagrammatic representation of detailed data given in Appendix A showing dominant plant cover by major habitat type (scale of vertical axis is expanded).

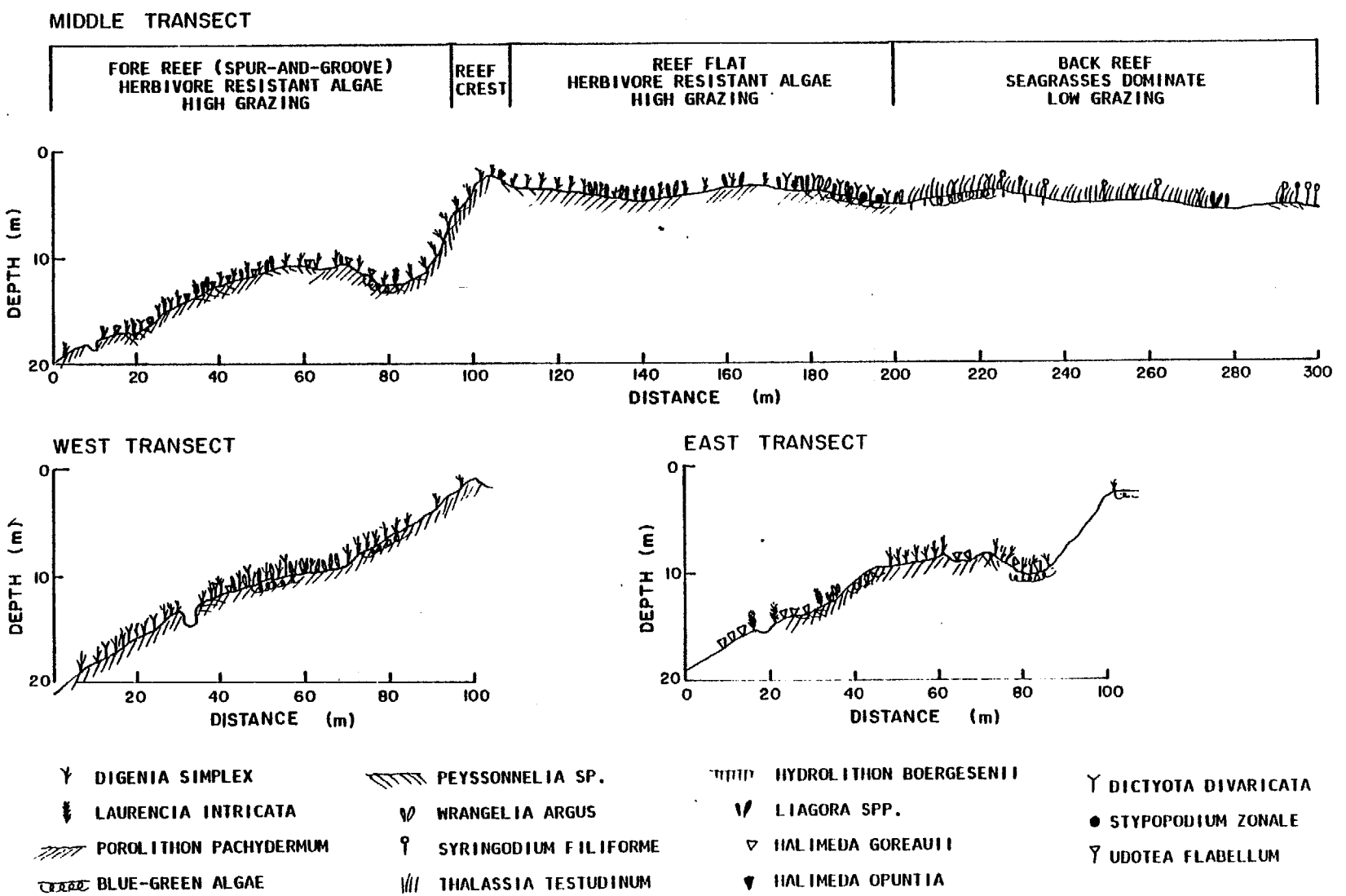
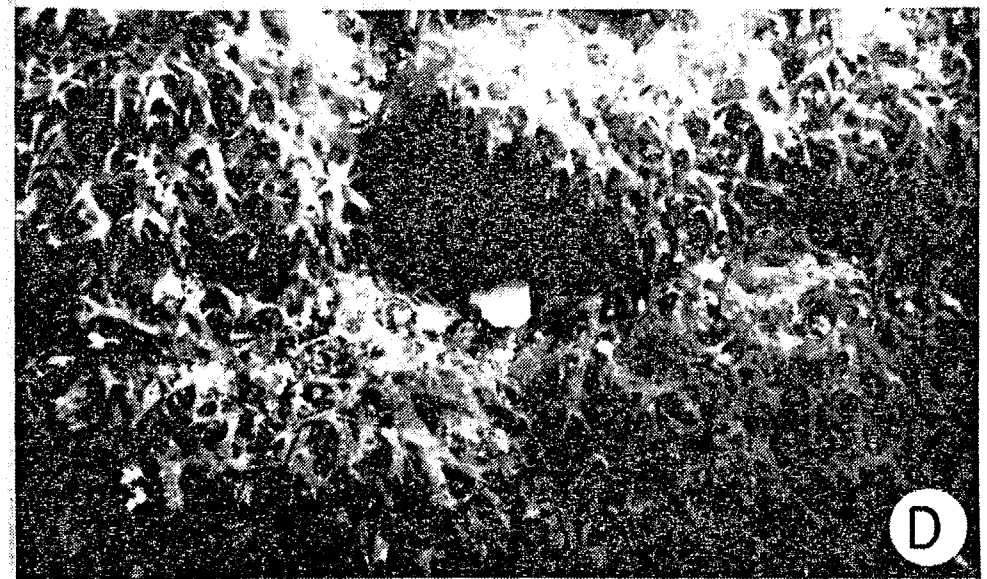

MIDDLE TRANSECT
FORE REEF (SPUR-AND-GROOVE)
HERBIVORE RESISTANT ALGAE
HIGH GRAZING
REEF CREST
REEF FLAT
HERBIVORE RESISTANT ALGAE
HIGH GRAZING
BACK REEF
SEAGRASSES DOMINATE
LOW GRAZING
DEPTH (m)
DISTANCE (m)
WEST TRANSECT
EAST TRANSECT
DIGENIA SIMPLEX
LAURENCIA INTRICATA
POROLITHON PACHYDERMUM
BLUE-GREEN ALGAE
PEYSSONNELIA SP.
WRANGELIA ARGUS
SYRINGODIUM FILIFORME
THALASSIA TESTUDINUM
HYDROLITHON BOERGESENII
LIAGORA SPP.
HALIMEDA GOREAUII
HALIMEDA OPUNTIA
DICTYOTA DIVARICATA
STYPOPODIUM ZONALE
UDOTEA FLABELLUM

Figure 5. A - Sargassum polyceratium (Back Reef), B - Halimeda opuntia (Spur and Groove), C - Neogoniolithon strictum (Reef Flat), D - Dictyota sp. (Spur and Groove), E - Padina jamaicensis (Reef Flat).


A


B

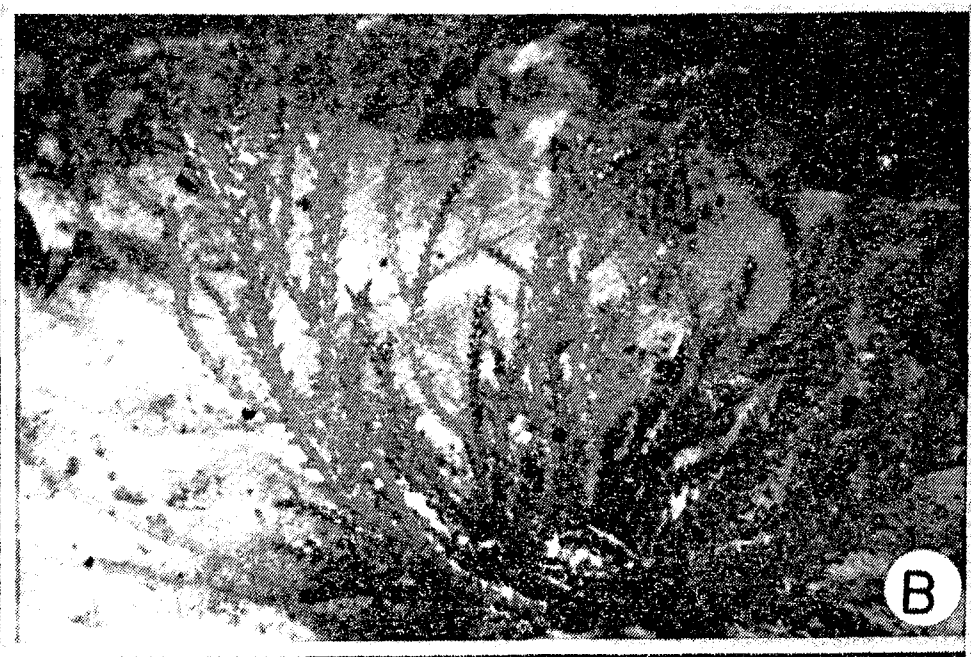

C

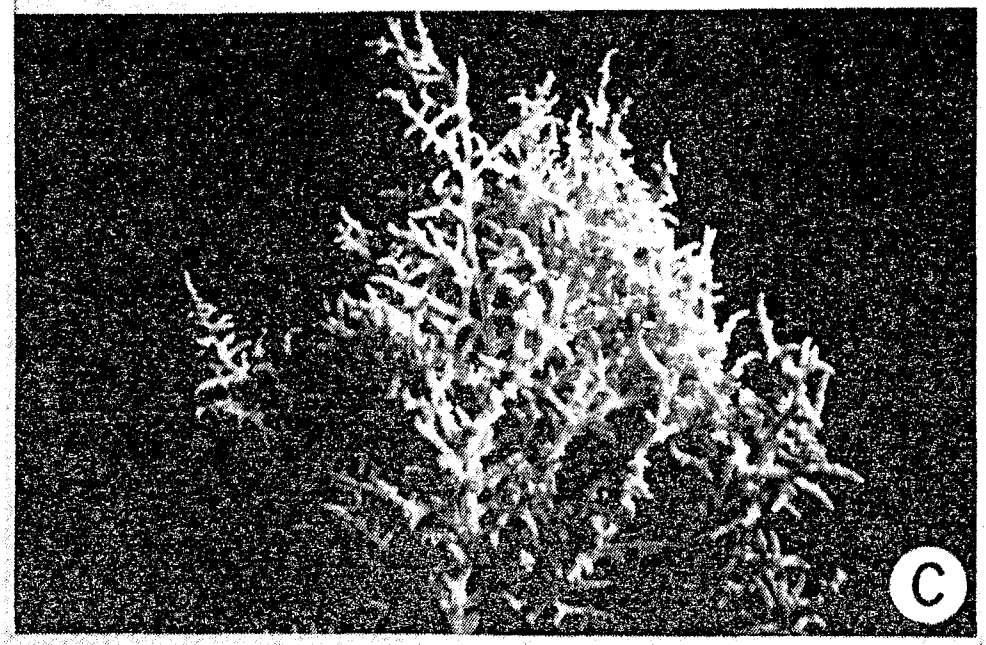

D


E

Figure 6. A - Rhipocephalus phoenix (Back Reef), B - Acanthophora spicifera (Back Reef), C - Udotea flabellum (Back Reef), D - Liagora sp. (Reef Flat).


A


B


C

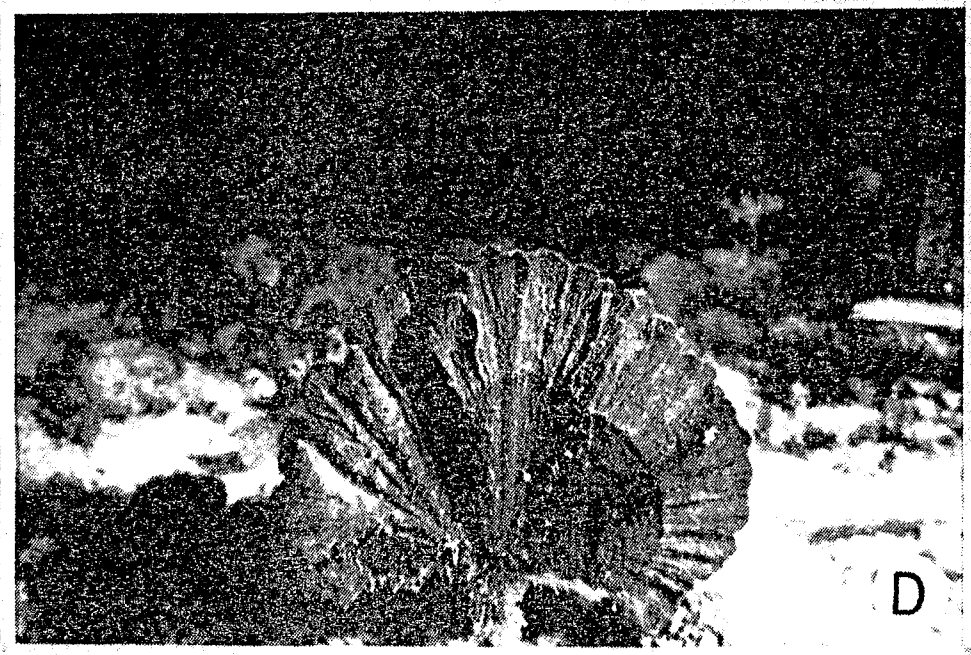

D

Figure 7. Oblique view of Looe Key from the north showing (black arrows) the rich area of large frondose macroalgae. The darkest patches in the photograph are seagrass beds, whereas the light patches are sand pockets. Photograph by Aerial Photos International, courtesy of NOAA.

Figure 8. Comparison of the four major habitats in terms of overall herbivory, and grazer susceptibility of 16 macroalgal species, in order from highest to lowest means (N = 24) for all habitats.

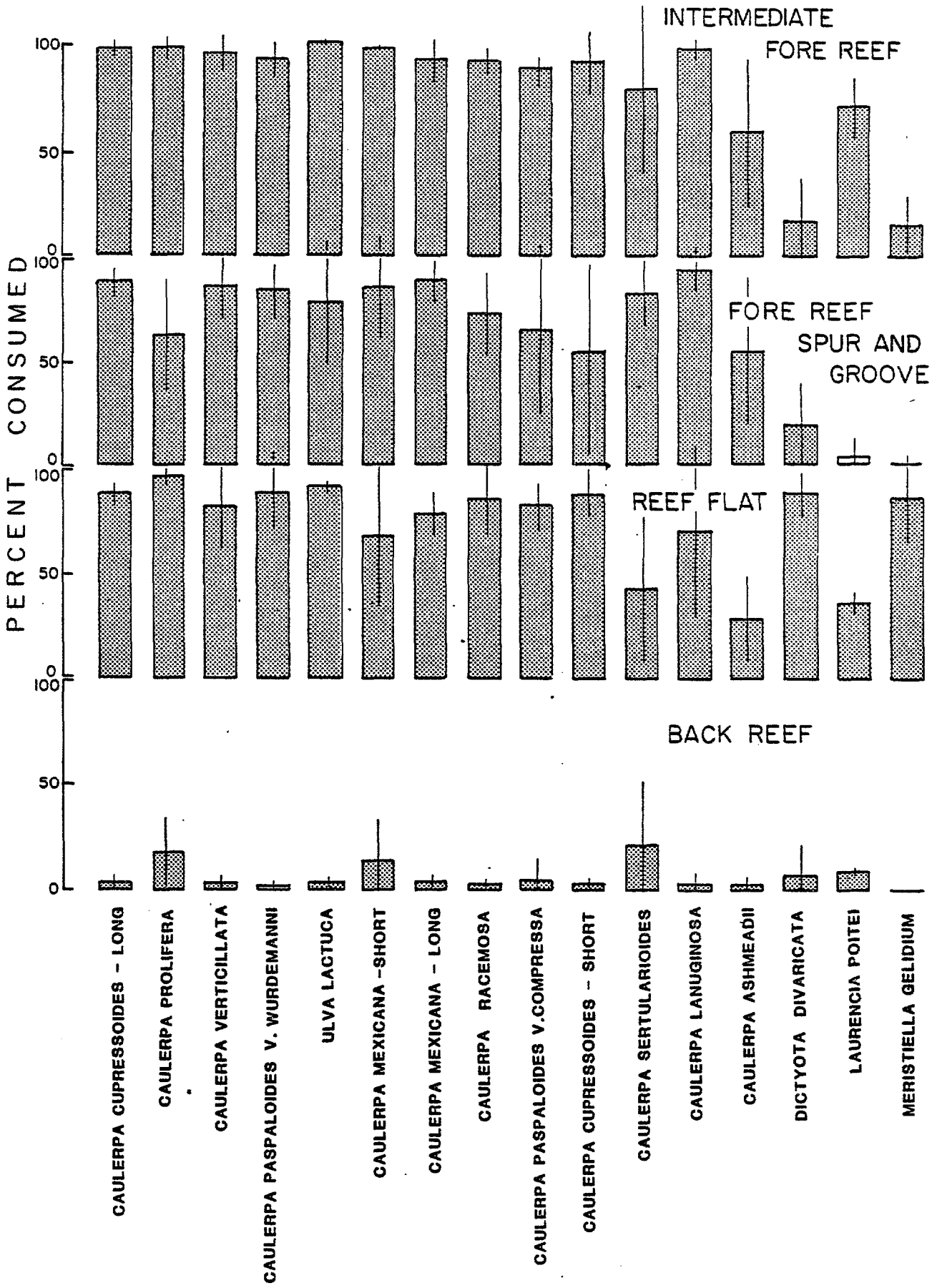

PERCENT CONSUMED
100
50
0
INTERMEDIATE
FORE REEF
FORE REEF
SPUR AND
GROOVE
REEF FLAT
BACK REEF
CAULERPA CUPRESSOIDES - LONG
CAULERPA PROLIFERA
CAULERPA VERTICILLATA
CAULERPA PASPALOIDES V. WURDEMANNI
ULVA LACTUCA
CAULERPA MEXICANA -SHORT
CAULERPA MEXICANA - LONG
CAULERPA RACEMOSA
CAULERPA PASPALOIDES V.COMPRESSA
CAULERPA CUPRESSOIDES - SHORT
CAULERPA SERTULARIOIDES
CAULERPA LANUGINOSA
CAULERPA ASHMEADII
DICTYOTA DIVARICATA
LAURENCIA POITEI
MERISTIELLA GELIDIUM

Figure 9 . Mean net primary productivity of abundant algal taxa at Looe Key on an organic biomass basis (N = 6).

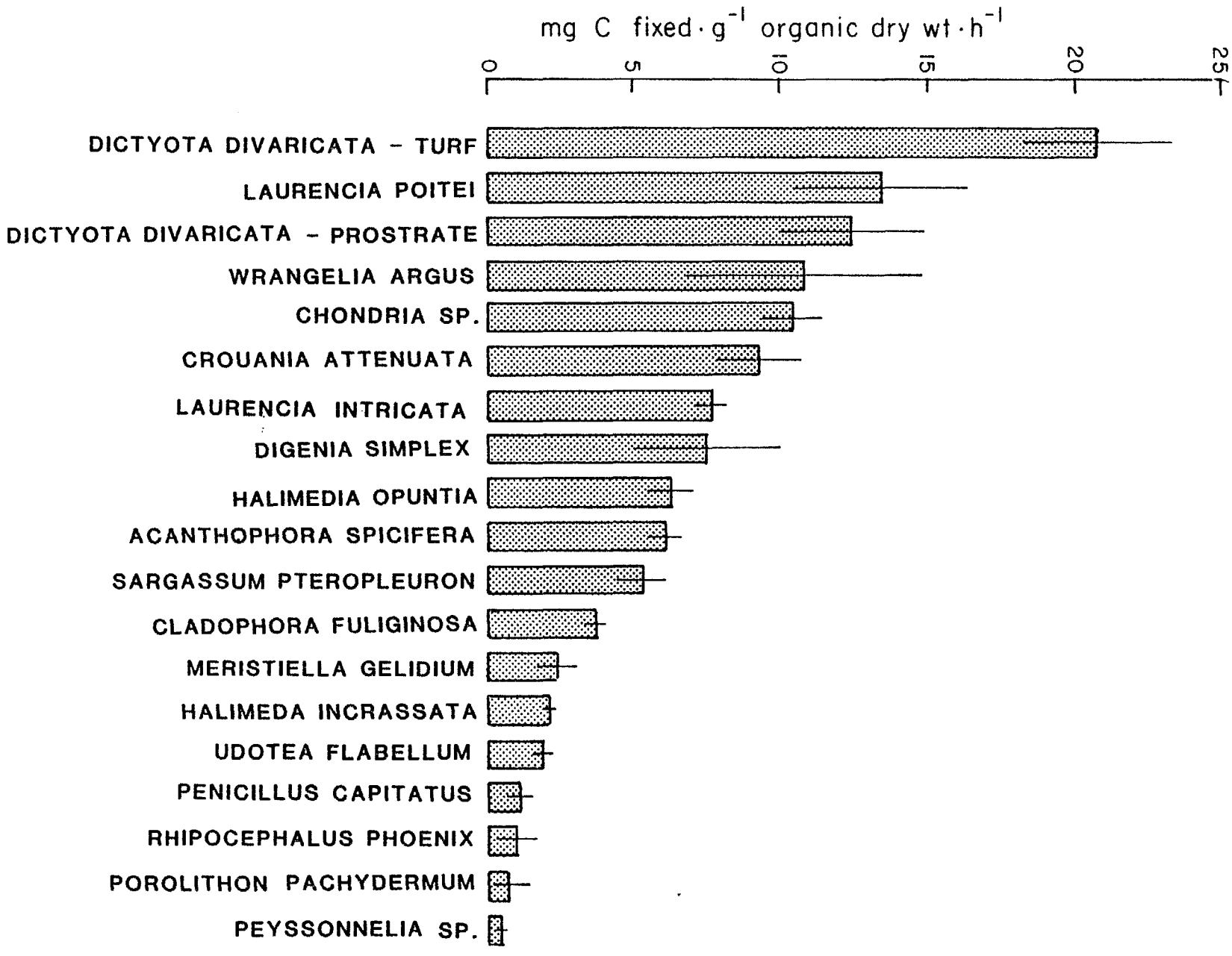

mg C fixed · g⁻¹ organic dry wt · h⁻¹
0
5
10
15
20
25
DICTYOTA DIVARICATA - TURF
LAURENCIA POITEI
DICTYOTA DIVARICATA - PROSTRATE
WRANGELIA ARGUS
CHONDRIA SP.
CROUANIA ATTENUATA
LAURENCIA INTRICATA
DIGENIA SIMPLEX
HALIMEDIA OPUNTIA
ACANTHOPHORA SPICIFERA
SARGASSUM PTEROPLEURON
CLADOPHORA FULIGINOSA
MERISTIELLA GELIDIUM
HALIMEDA INCRASSATA
UDOTEA FLABELLUM
PENICILLUS CAPITATUS
RHIPOCEPHALUS PHOENIX
POROLITHON PACHYDERMUM
PEYSSONNELIA SP.

Figure 10. Mean net primary productivity of abundant algal taxa at Looe Key on a projected (two-dimensional) surface-area basis (N = 6).

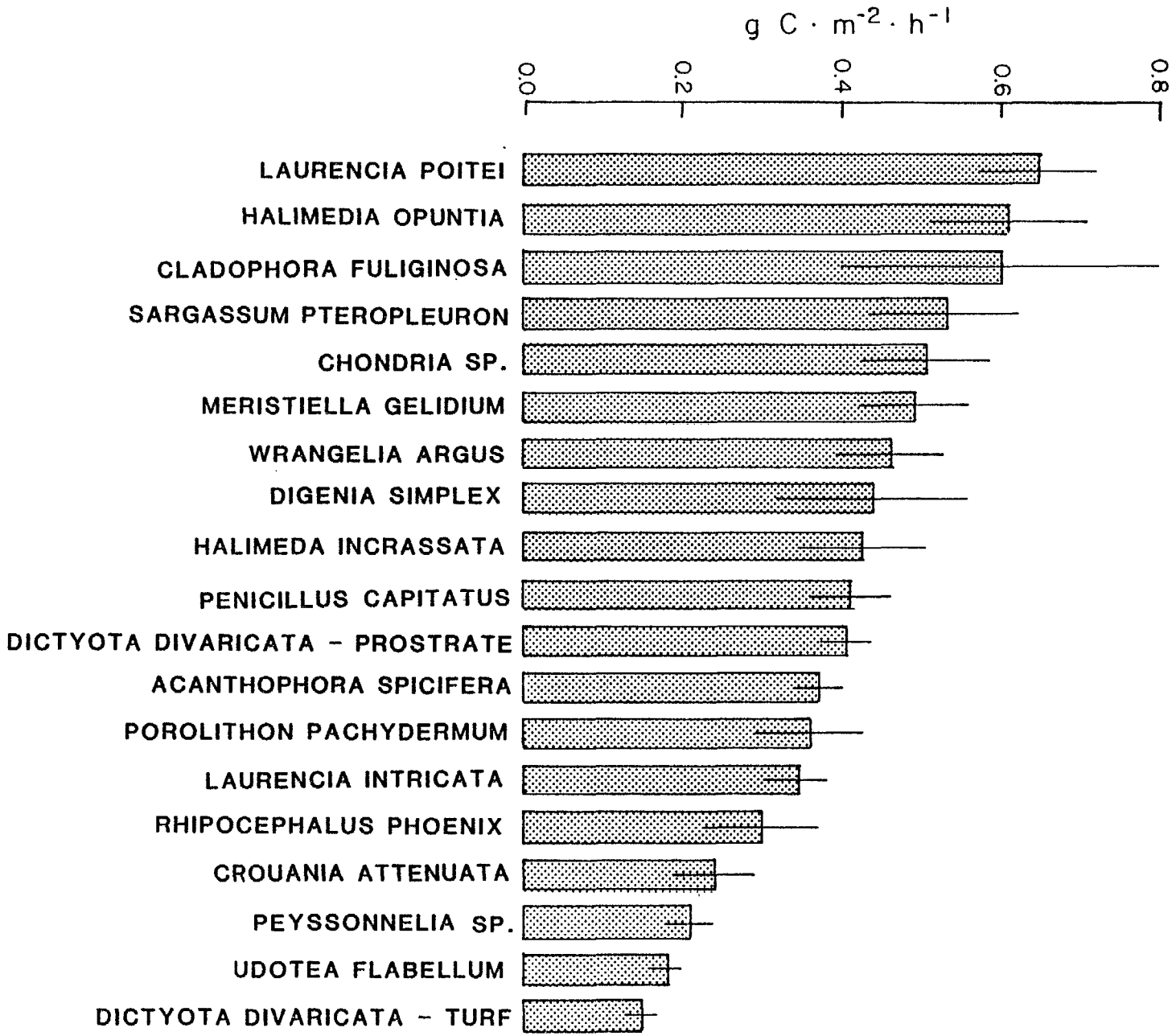
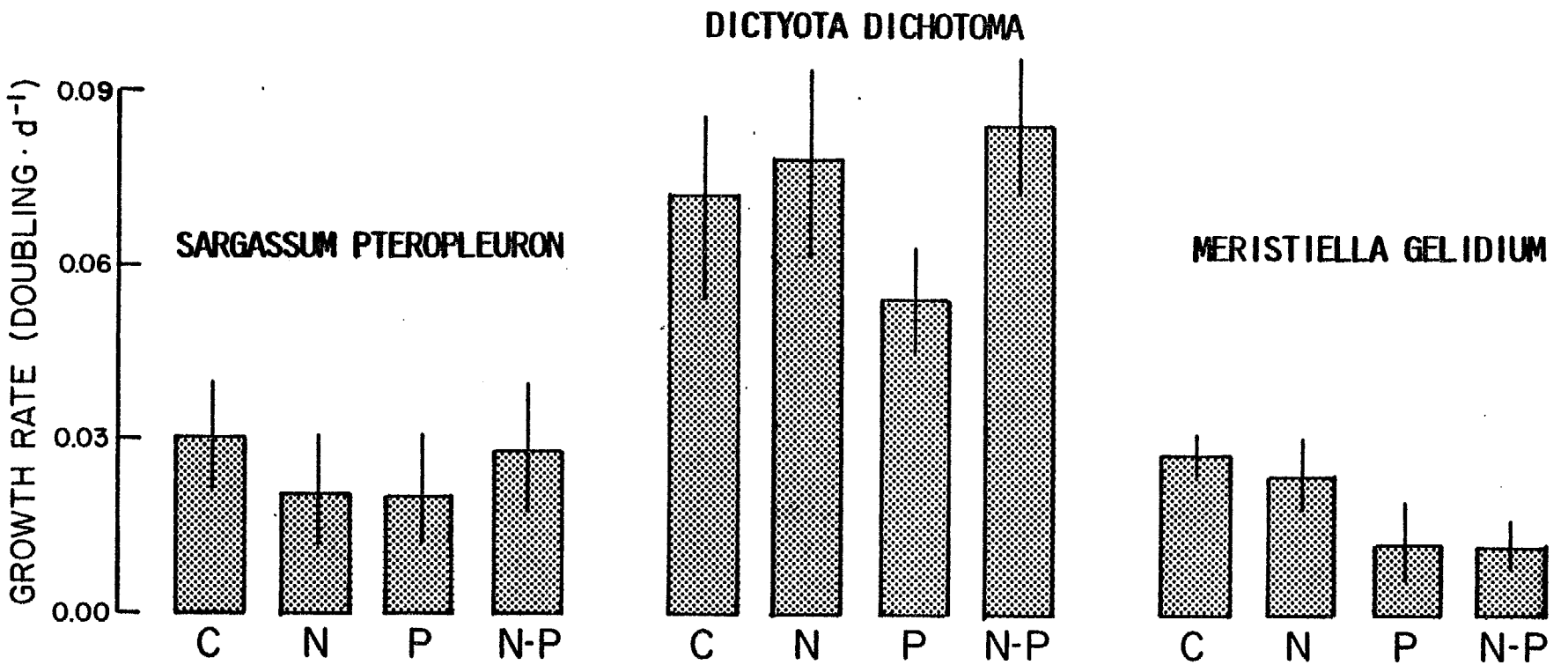

g C · m-2 · h-1
0.0
0.2
0.4
0.6
0.8
LAURENCIA POITEI
HALIMEDIA OPUNTIA
CLADOPHORA FULIGINOSA
SARGASSUM PTEROPLEURON
CHONDRIA SP.
MERISTIELLA GELIDIUM
WRANGELIA ARGUS
DIGENIA SIMPLEX
HALIMEDA INCRASSATA
PENICILLUS CAPITATUS
DICTYOTA DIVARICATA - PROSTRATE
ACANTHOPHORA SPICIFERA
POROLITHON PACHYDERMUM
LAURENCIA INTRICATA
RHIPOCEPHALUS PHOENIX
CROUANIA ATTENUATA
PEYSSONNELIA SP.
UDOTEA FLABELLUM
DICTYOTA DIVARICATA - TURF

Figure 11. In situ growth rates of three species of dominant macroalgae (from 25 June to 1 July 1984) on the Back Reef of Looe Key in response to diffuser enrichment by either N (NO_3^-), P (PO_4^{3-}), N and P (NO_3^- and PO_4^{3-}) or no enrichment (C). Results of two-way ANOVA are also shown.

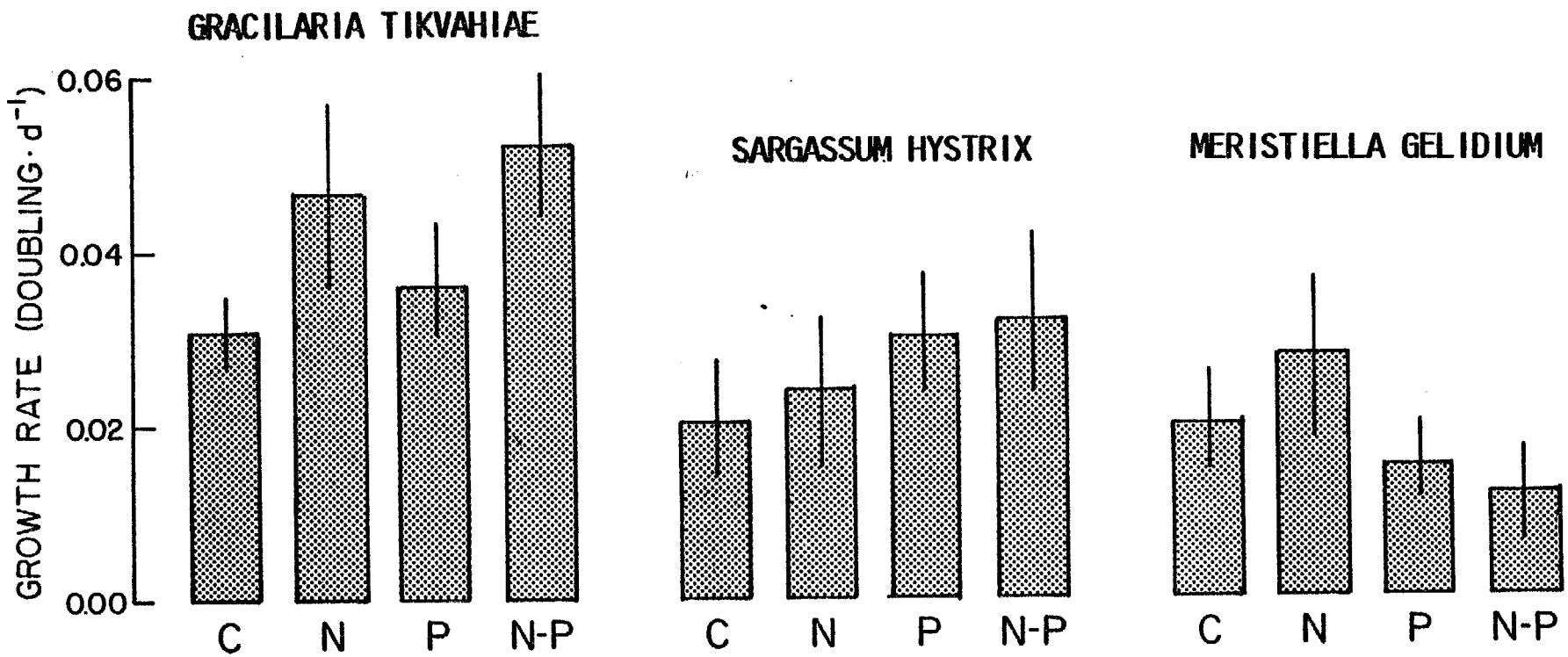


FACTOR	% VAR	P
N	<1	N.S.
P	<1	N.S.
N&P	3.6	N.S.

FACTOR	% VAR	P
N	1	N.S.
P	<1	N.S.
N&P	<1	N.S.

FACTOR	% VAR	P
N	<1	N.S.
P	7	N.S.
N&P	<1	N.S.

Figure 12. In situ growth rates of three species of macroalgae (from 6-12 September 1984) on the Back-Reef habitat of Looe Key in response to diffuser enrichment by either N (NO_3^-), P(PO_4^{3-}), N and P (NO_3^- and PO_4^{3-}) or no enrichment (C). Results of two-way ANOVA are also shown.

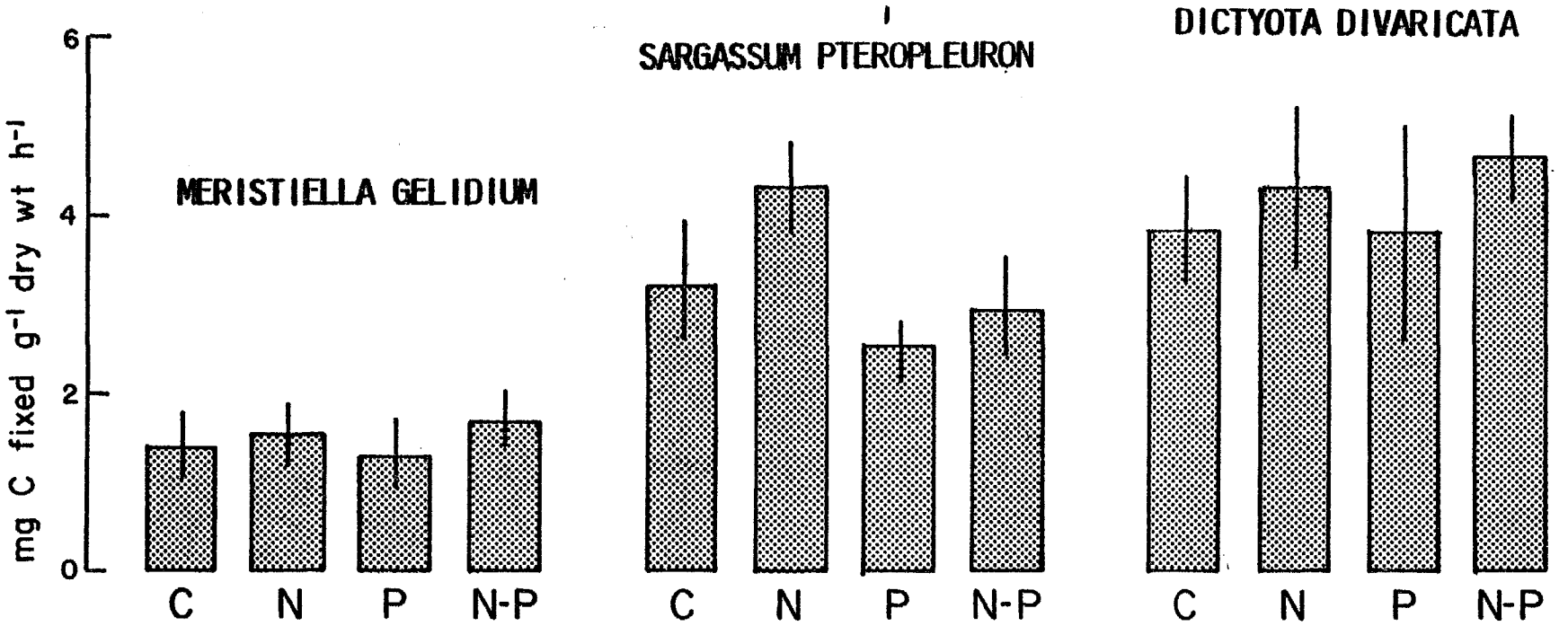


FACTOR	% VAR	P
N	2	N.S.
P	<1	N.S.
N&P	<1	N.S.

FACTOR	% VAR	P
N	<1	N.S.
P	1	N.S.
N&P	<1	N.S.

FACTOR	% VAR	P
N	<1	N.S.
P	5	N.S.
N&P	<1	N.S.

Figure 13. Photosynthetic rates (per gram dry wt) under full natural sunlight in three species of dominant macroalgae from the Back Reef of Looe Key National Marine Sanctuary following a 10 h factorial design nutrient pulse of either N (NO_3^-, 200 uM), P (PO_4^{3-}, 20 uM), both N and P (NO_3^- and PO_4^{3-}, 200 and 20 uM, respectively) or no nutrients (C). Results of two-way ANOVA are also shown (N = 6).

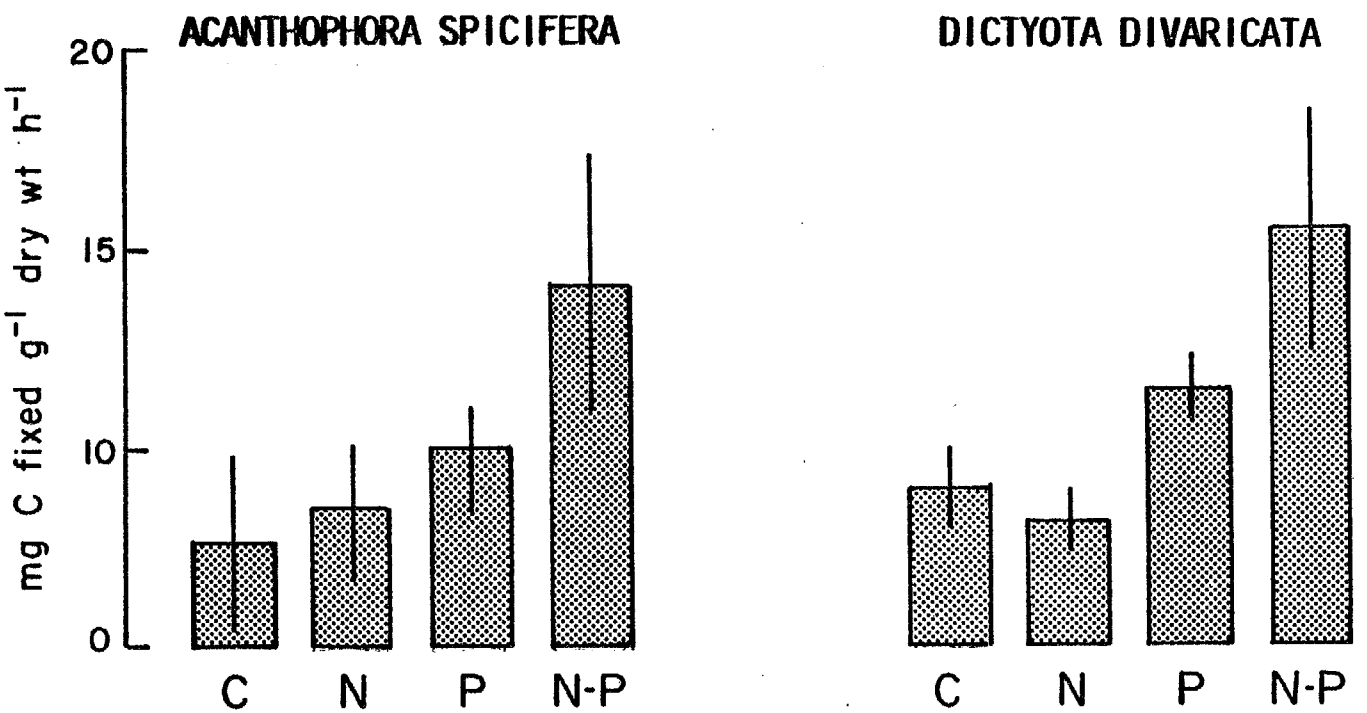


FACTOR	% VAR	P
N	1	0.62
P	<1	0.89
N&P	<1	0.94

FACTOR	% VAR	P
N	<1	0.86
P	1	0.66
N&P	1	0.65

FACTOR	% VAR	P
N	<1	0.63
P	2	0.75
N&P	1	0.70

Figure 14. Photosynthetic rates (per gram dry wt) under full natural sunlight in two species of dominant macroalgae from the Back Reef of Curlew Cay, Belize following a 10 h factorial design nutrient pulse of either N(NH_4^+, 200 uM), P (PO_4^{3-}, 20 uM), both N and P (NO_3^- and PO_4^{3-}, 200 and 20 uM, respectively) or no nutrients (C). Results of two-way ANOVA are also shown (N = 6).



FACTOR	% VAR	P
N	20	<0.05
P	40	<0.01
N&P	7	N.S.

FACTOR	% VAR	P
N	11	<0.01
P	61	<0.01
N&P	19	<0.01