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RECOLONIZATION OF ALGAL COMMUNITIES FOLLOWING THE
GROUNDING OF THE FREIGHTER WELLWOOD ON
MOLASSES REEF, KEY LARGO NATIONAL MARINE SANCTUARY

M.M. Littler, D.S. Littler, J.N. Norris, K.E. Bucher

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

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INTRODUCTION

On 4 August 1984, the 396-foot Cyprian-registered freighter Wellwood ran aground off the Florida Keys on Molasses Reef in the Key Largo National Marine Sanctuary and remained aground until 16 August 1984. The vessel was carrying a cargo of pelletized animal feed from Louisiana to Portugal. While the vessel received relatively little damage and no fuel or oil was spilled, the coral reef was physically impacted over a total area of 75,000 m² (Jaap 1984).

Molasses Reef lies inside the southeastern boundary of the Sanctuary (25°00.7'N, 80°22.4'W) and is one of the most highly visited reefs in the region. Dozens of recreational divers and fishermen, numerous charter diveboats, and two glass bottom boats use the site on a daily basis. The 12-day grounding and associated efforts to remove the Wellwood from the reef resulted in multiple forms of environmental damage (e.g., crushing, scraping, shading, cable shearing and abrasion, prop wash) at a scale of unprecedented proportion to the Sanctuary (Bright and Andryszak 1984; Fig. 1). Large areas of coral formations were totally destroyed where the vessel's hull cut into the reef framework. Other parts of the reef suffered partial destruction and may be further stressed by secondary effects of the grounding. Impacts range from complete habitat destruction in an approximate 4430-m² area to sheared and wounded sessile organisms and disturbed substrata on the periphery (Jaap 1984). The damage sustained is expected to have long-term ecological and economic effects.

Phase 1, a damage assessment conducted immediately following the grounding of the Wellwood, was made by Sanctuary personnel (see Jaap 1984). NOAA's Sanctuary Programs Division (SPD) has developed a research plan (covering phases 2-8) to address management and legal questions concerning the extent and severity of resource damage and rates of recovery and recolonization of dominant reef biota. This final report, a survey of algal damage and recovery, constitutes the initial component of Phase 2 of the research plan and establishes a format for further work in cooperation with other scientists and NOAA personnel.

Few studies of this nature have been conducted. It will be necessary to investigate not only the immediate effects of the grounding, but also the long-term ecological implications. Reef regeneration is expected to occur, although it may take decades in badly damaged areas for the reef to return to pre-wreck conditions in terms of coral and perennial algal cover and diversity, and even then scars may remain.

The recent literature contains accounts of damage to biotic reefs caused by natural events (e.g., hurricanes, typhoons, red tides, low tides, thermal stress, volcanic activity, and earthquakes) and man-made disturbances [e.g., dredging, blasting (including nuclear explosions), oil pollution, deleterious coastal development, sewage, and anchoring] (Johannes 1975; Endean 1976). There are very few accounts in the literature, however, that describe damages caused by major ship groundings

(Dustan 1977; Jaap 1984; Hatcher 1984; Halas unpublished reports). Even fewer sources document the recovery of plant and animal communities following these disturbances (Pearson 1981; Hatcher 1984).

The factors that affect the rate of recovery of devastated reefs are discussed by Endean (1971) and Pearson (1981). In the case of a major ship grounding, recovery is primarily through recolonization, rather than regeneration. Substratum conditions, reproductive cycles, environmental factors, competition, predation, and rates of growth and survival of successful colonizers are likely to be particularly important. The solid reef surface at Molasses Reef is now partly covered with blocks of fragmented dead coral colonies and a rubble of coral stocks, which will offer differing degrees of substratum types and stability to recruits. Algae, notably microalgal turfs, calcareous forms, and sheet forms such as Enteromorpha and Dictyota, as well as gorgonians, are the more common organisms that are expected to be early colonizers on damaged reefs, but too little is known of the roles of these and of grazing animals (Dart 1972; Sammarco, 1980, 1982) on patterns and rates of reef recovery. The literature indicates that regeneration of a biotic reef following man-made disturbance may be prolonged or prevented altogether because of permanent change to the environment (Lighty 1982; Hatcher 1984) and/or continuation of chronic, low-level disturbance (Pearson 1981; Rose and Risk 1984).

Continued study of reef recovery is clearly needed before conclusions can be drawn. Specific objectives of the study reported here (1- 4 September 1984) were as follows:

(1) Survey the damaged area and select appropriate strata for quantitative sampling of algal distributions and abundances.

(2) Select methodology and design a statistically suitable sampling regime to accurately assess algal changes due to the physical impact of the Wellwood's grounding and to enable further monitoring of subsequent algal community re-establishment and development.

(3) Establish a number of experimental plots in order to manipulate the timing of recruitment to assess the feasibility of accelerating the diversity, rates, and final products of the recolonization process to predisturbance levels.

Description of the Impacted Area

Selected features of Molasses Reef have been described by Shinn (1963; geology); Jones and Thompson (1978; reef fish); Bohnsack and Bannerot (1982; reef fish), Bohnsack (1983); Schmale and Bannerot (1984; reef fish); Dustan (1977; coral recruitment and mortality); Halas and Jaap (1983; stony coral); and Voss (1984; species inventory). Molasses Reef is located on the margin of the reef tract at the southeastern end of the Sanctuary and receives the full force of waves from open water seaward of the reef (Shinn 1963). The reef has an extensive spur and groove system with a narrow crest zone of elkhorn coral (Acropora palmata) and crustose algae (Porolithon, Hydrolithon, Lithophyllum) extending downward to approximately 7 m in depth. The system contains at least 30 species of corals (mainly A. palmata, Montastrea annularis, Gorgonia ventalina) and several times this number of macroalgal taxa. Below this, the forereef

is sloped, dropping from the 7-m water depth to about 17 m, and composed of hard bottom on which are found green, brown, blue-green, and red algae, scattered alcyonarians, sea feathers and sea whips, vase sponges, and occasional small colonies of finger coral (Porites), brain coral (Meandrina), and star corals (Montastrea). Landward of the reef crest is a broad flat formed of extensive rubble areas that contain abundant large macroalgae and numerous alcyonarians. Seagrasses grow close to the rubble area on the shoreward side.

METHODS AND MATERIALS

Modern ecological sampling represents a quantitative discipline designed to produce statistically interpretable analyses of biotic distribution and abundance patterns within defined habitats. An adequately large number of samples must be taken for proper statistical treatment and this requires that the method be simple and rapid to use. Non-destructive sampling, by utilizing permanently-marked sampling locations that can be precisely relocated and reassessed, provides a powerful tool for quantification of natural and anthropogenic changes in macroalgal standing stocks. The principal method of non-destructive recording of standing stocks is the photogrammetric technique of undisturbed sampling (first developed for seaweeds by Littler 1968, 1971) that yields parallax-free samples. This method has become the standard required for large-scale macroalgal studies contracted by the United States Department of the Interior (e.g., Bureau of Land Management, U.S. National Park Service, Minerals Management Service) for nearly a decade. One purpose of the

photogrammetric technique is to produce a permanent historic record of photosamples that depict the status of the biota at a given time. Additionally, changes (e.g., due to human disturbance) can easily be documented by direct comparison of photo-samples taken of the same quadrats at different times. Seasonality can also be demonstrated by direct comparisons of photo-samples taken of the identical quadrats over different sampling periods. This system also permits a high degree of quality control because photo-samples scored by various individuals can be reviewed by the total research staff, including senior taxonomic personnel, to ensure standardization and accuracy in the quantification process. Such samples can be used to generate precisely-detailed and highly-reproducible quantitative information, i.e., cover and frequency (percentage of sample plots in which a given species occurs). Since the first time photographic sampling was alluded to as a possibility for ecological studies in the marine environment (Ernst 1957), it has been developed independently (e.g., Littler 1968, 1971, 1980; Johnston *et al.* 1969; Connell 1970); and undergone diffuse application (Lundälv 1971; Vadas and Manzer 1971; Dayton *et al.* 1974; Laxton and Stablum 1974; Torlegård 1974; Wilson 1974; Paine 1974; Ott 1975; Drew 1977; Vance 1979; George 1980; Karlson 1980; Bright *et al.* 1984). The method now represents one of the most widespread and sophisticated techniques for permanently recording marine algal standing stocks.

Random sampling (determined by some mechanical means) is theoretically required to obtain unbiased results (Southwood 1966). Randomness is usually achieved by means of a line transect laid out along a predetermined compass bearing, using a table of random numbers to determine the precise sampling locations. Although bias is eliminated by random sampling, it is not always desirable for subtidal reef work because of the marked patchiness typically present. Systematic assessment at fixed intervals within a given area has the advantage that the array of samples is relatively easy to achieve and relocate for repetitive study. In addition, this arrangement of plots may give a more accurate picture of macrophyte distributions and abundances because samples are spread over the entire area to be analyzed (Greig-Smith 1964; Poole 1974; Loya 1978); e.g., patchy randomized sample arrays superimposed on patchily-distributed organisms contain a relatively greater potential for under- or overestimation. Uniform intervals cannot be used if the biota itself is distributed in a systematic pattern (coincident to that of the sample array), such as a linear arrangement within a narrow zone related to depth or along a rock fissure. Haphazard techniques, such as throwing a marker or dropping a quadrat without looking at the sample area, are not random and should be avoided because marginal areas are prone to be undersampled and plots tend to become arrayed inadvertently at fixed distances, often with undetected bias.

Based upon maps of the region, aerial photographs taken by NOAA, data on pre-wreck conditions at Molasses Reef (Voss 1984), and the findings from the initial damage assessment surveys (Jaap

1984), a reconnaissance SCUBA effort was conducted during 1-4 September 1984 by a team of six experienced professional phycologists (M. Littler, D. Littler, J. Norris, K. Bucher, S. Blair, R. Sims) to survey the grounding site. The initial effort required five days of field time (approximately 100 person hours of bottom time).

As a result of the field reconnaissance by our team, six separate algal habitat types were recognized in close association with the site of the Wellwood grounding (Table 1). Five lines were deployed along predetermined compass headings (100° magnetic) from a randomly selected origin (to avoid bias) so as to transect the six habitat types. The stratified array along these five transects (Table 1, Fig. 2) resulted in thirty-three replicate samples deployed along three of the transect lines in the undisturbed control area dominated by stony corals (Fig. 3A), thirteen among the undisturbed area intercepted by transect A that was dominated by gorgonian corals and algae (Figs. 3B and 4A), thirty-seven quadrats on three lines within the area scraped to solid reef framework (Fig. 4B), nineteen quadrats within the scraped cobble system (transected by three of the lines, Fig. 5A), twenty-one samples within the area primarily affected by prop wash (intercepted by two transects), and thirteen quadrats deployed along the boulder wall (associated with three lines, Figs. 5B and 6A,B). Thirty-five additional experimental successional plots were established by two independent transect

lines (Table 1, Fig. 2). Since the six habitats were subjectively determined to have the potential to lead to different successional trends or patterns, we have chosen to treat them separately in this report.

Because we elected to use systematic sampling at fixed intervals for reasons given earlier (see also Greig-Smith 1964, Poole 1974; Loya 1978 for additional justification), an analysis was made comparing mechanically randomized methods for the two major areas (i.e., damaged solid substratum and undisturbed stony coral/algal control). The results of the two tests, comparing 20 samples taken randomly with 20 samples serially spaced at 1.0-m intervals (Tables 2 and 3), yielded surprisingly similar results given the relatively small sample size. All dominant taxa had similar means, reasonably narrow confidence intervals, and showed no significant ($P < 0.05$, ANOVA, Duncan's multiple range test) differences among means. Obviously, there were also no statistical differences for uncommon species because of the large confidence intervals involved. This test indicates that bias due to sample uniformity was not a problem in either system and supports the use of systematic assessments at fixed intervals.

Using two teams of phycologists, the permanent transects were established so as to intercept undisturbed coral/algal communities as well as portions of the substrata physically impacted by the grounding. The precise location of the upper end of each transect was determined optimally by consensus of our group of marine biologists along a biologically representative part of the substratum. Several transect tapes (Leitz "Synlon" fiber glass tapes, Ben Meadows Co.), positioned within the

representative areas and as dictated by the steepness of the substratum and topography, were laid parallel by means of a sighting compass (Suunto Fast-Accuracy Compass, Ben Meadows Co.) at each study site from immediately adjacent to the grounding area and transecting through it, thus providing locations for a minimum of at least 10 samples per community type. To establish permanent sample locations, holes were drilled and eyebolts cemented into the substratum at the upper, middle, and lower ends of the transect lines; this enables the precise replacement of the transects during subsequent studies. 136 rectangular quadrats were placed along five transect lines at 1.0 m intervals providing permanent, stratified plots for sampling temporal and spatial distributions of organisms. Additional samples were added at 1.0 m intervals to the right and left where the lines transected the narrow boulder-wall zone. Quadrat locations were marked permanently with metal studs, stainless steel washers, and marine epoxy (Sea Goin' Poxy Putty Multi-Purpose - 1324, Permalite Plastics Corp.). The numerical deployment of permanently-marked quadrats is given in Table 1. Length of transects and spacing of quadrats was determined on site with consideration of the various damaged areas and equivalent, but undamaged, controls.

A large number of small quadrats is usually preferable to a lesser number of large plots per unit of equal area sampled (Green 1979), since greater sample numbers permit a better assessment of between-sample variability. The size of the plots should be commensurate with the size of the organisms themselves

and their density (Kershaw 1973). The number of quadrats sampled must be sufficient to include the majority of species present in the study area. In quadrat assessments, the plot should be no smaller than the largest individual organism to be sampled. We have found a rectangular 0.15-m² quadrat to be optimal for sampling most tropical marine macrophytes. Rectangular quadrats have the advantage over square or circular plots of equal area because they tend to incorporate a greater diversity of populations, since it is less probable that a rectangle will fall completely within a given clump or patch of organisms. In this regard, a number of studies (Clapham 1932; Pechanec and Stewart 1940; Bormann 1953) have shown that elongate rectangular quadrats may furnish a more accurate analysis of the composition of a population or community than an equal number of square or circular plots having the identical area. We also designed our labelled quadrats for photogrammetric sampling (30 x 50 cm) to coincide with the proportions of the 35-mm film used for recording the data. These dimensions permit framing of the sample at a close distance (~15 cm) without having to resort to overly distortive lenses, excessively long quadrapods, or suspended divers for holding the camera.

The team of D. Littler and S. Blair swam the same transects and photographed quadrats at right angles to the substratum using NOAA's Nikonos underwater cameras with 15-mm lenses and 4 Oceanic Products 3004 strobes, mounted on two specially-constructed compact quadrapods. In the case of vertically stratified communities, lower layers were photographed after upper canopies had been gently moved aside. Each quadrat had a numbered

counter and plastic label affixed to the upper right corner that was marked with a wax pencil to identify permanently each of the photosamples. Miniature tape recorders in waterproof housings (Wet-Tape, Sound-Wave Systems, Inc.) and plastic (polyethylene) coated paper (PolyPaper, Nalge Company) were used as a rapid method of taking field notes on the contents of the photosamples. The team of J. Norris and K. Bucher slowly swam the transects and made sketches of species and substratum type and detailed areas of algal coverage within each of the 0.15-m² quadrats. The understory was estimated at this time where present. The only organisms removed from the permanent undisturbed quadrats were small voucher samples taken by M. Littler and R. Sims for taxonomic purposes. However, this was done rarely and only when adequate voucher material was unavailable elsewhere. The recorded in situ information was used in the laboratory for cryptic organisms, dense understory layering, and to minimize taxonomic and other problems encountered while interpreting the photo-samples.

It is worthwhile noting that many studies stop at this level of quantification (by estimation in situ). We have found (Littler 1980) that such approximations usually cannot be repeated precisely (i.e., often exceeding $\pm 25\%$ for dominant organisms) because of parallax and variability between and within observers. Observer differences are influenced by varying degrees of field distractions and stresses, which can be pronounced during cold, heavy surge, and turbid conditions.

In the laboratory, the developed transparencies (Kodachrome 25) were projected onto a sheet (27 x 35 cm) of fine-grained white bristol paper. The paper contains a grid pattern of dots at an average of 2.0-cm randomized intervals on the side of the reflected light; this has been shown (Littler 1980) to be an appropriate density (e.g., ~ 0.5 per cm^2) for consistently reproducible estimates of cover. Sousa (1979) presents a discussion of the advantages of the placement of dots at uniform fixed intervals versus mechanically randomized placement of dots. Briefly, uniform arrangements are easier to locate and faster to score, but can over- or under-estimate linearly-arranged organisms. Random dot placements are confusing to score, can over- or under-estimate clumped organisms, but are technically required for statistical analysis. A stratified-random arrangement (utilizing a random numbers table) was employed as a compromise. The photographs were aligned and focused without regard to the field of dots to assure unbiased assessments. The percentage cover values were expressed as the number of "hits" for each species divided by the total number of dots contained within the quadrats. Reproducibility is consistently high by this technique and seldom varies more than $\pm 5\%$ for a given taxon (Littler 1980). Species not abundant enough to be scored by the replicated grid of point intercepts were assigned an arbitrary cover value of 0.1%, or the field estimates were used.

The method as applied here does not allow for the complete quantification of microalgae, endolithic flora, and infauna when they occur in low abundances. Their analysis requires special techniques and expertise that comprise separate problems outside

the scope of this study. For this reason, the present discussion is restricted to macro-epiflora that can be discerned in the field with the unaided eye. However, it was straightforward to quantify microbiota (e.g., turfs of filamentous algae) when it was uniform and present in high abundance. Abundant turf-forming microalgae were extensively sampled and component species were identified microscopically to the lowest taxonomic category feasible. Estimates of their average abundances were made and incorporated in our analysis.

Analyses of data

Information obtained by the photogrammetric method (undisturbed) provides quantitative information on the distribution of standing stocks in relation to depth, distance along transect lines, environmental gradients, or between the physically damaged areas and control habitats before and during recovery. The raw transect data were summed and means, standard deviations, and indices of dispersion were calculated to interpret differences in populations and communities between sites. These statistics can be used in the future to compare experimental treatments as well as seasonal within-site changes. Species cover fluctuations were calculated as a function of various depth or horizontal gradients throughout the habitats transected. Quantitative comparisons among populational means and variances between habitats were made using nonparametric (one-way ANOVA) and parametric (Duncan's multiple range test, DMRT) comparative statistical analyses (Sokal and Rohlf 1981; Steel and Torrie 1980). In both of these analyses, assumptions of normality and

homoscedasticity were met without transforming the percent cover data. In the analysis of variance (ANOVA), we tested the null hypothesis that the means of all data sets from the six different habitats (Fig. 2) were derived from the same population (i.e., equal at the 95% confidence level). Habitat by habitat comparisons (Table 4) were also made by DMRT to examine which of the means differed from one another at the $P < 0.05$ level.

To characterize objectively between-habitat groupings in an unbiased manner, the undisturbed cover data for every macrophyte species from each quadrat were subjected to hierarchical cluster analyses (flexible sorting, unweighted pair-group method) by the Bray and Curtis (1957) percentage distance statistic (Smith 1976). The product of this analysis was a dendrogram of quadrat assemblages (Fig. 7) that were then interpreted according to their dominant taxa and environmental affinities. This cluster method, utilizing non-destructive sampling of the identical permanently marked quadrats, is among the most powerful for identifying subtle temporal changes in patchy biotas and should be employed in subsequent recovery studies.

RESULTS

Floristic Overview and Major Plant Cover

This completion report represents an initial examination of the damage and establishment of a sampling strategy and experimental design. Consequently, analyses of subsequent photo-samples and time-dependent interpretations must await further research efforts. However, we have obtained enough information and insight to (1) draw several conclusions, (2) make

recommendations concerning monitoring of recovery by plant life, and (3) suggest small-scale pilot experiments to examine potential strategies for the enhancement of natural recovery processes. Algae were the first organisms to colonize the denuded and partially impacted areas. Because the plant life proved to be surprisingly diverse, a major portion of this initial effort has been devoted to taxonomic endeavors. Consequently, we will begin by presenting our floristic analyses based on the extensive initial collections of voucher material given in Table 5.

I. Undisturbed Areas Adjacent to the Wellwood Grounding

A diverse tropical marine flora resides among the hard corals and calcareous algae forming Molasses Reef (Table 5). Based on only this initial effort, a total of 73 taxa were collected, of which 13 represent new records (Table 6) for the state of Florida. The long-lived calcified greens, e.g., Halimeda opuntia, H. goreaui, and Udotea verticillosa, and calcified reds, e.g., Galaxaura oblongata, G. cylindrica, and Amphiroa tribulus, are sparsely distributed but conspicuous components of the natural flora, due to their relatively large size.

A. Stony Coral/Algal Area (SC)

In all, 40 taxa of benthic marine algae were recognized in this undisturbed "control" habitat (Fig. 2). Total macrophyte cover averaged 49.8% (overstory plus understory), of which none included the weedy yellow-turf assemblage (Table 7). Turfs, usually less than 3-cm tall, are the dominant algae in terms of

percent coverage (14%), consisting of patchy complex assemblages of perennial species often growing together or entangled (Fig. 3A); the major components are Gelidium pusillum, Amphiroa fragilissima, Wurdemannia miniata, Jania capillaceae, Laurencia spp., and Polysiphonia spp. These turf assemblages often grow on or through an understory layer of smooth crustose coralline algae (13% cover). Relatively unialgal stands of Wrangelia argus are also common (2%). Filamentous species of Ceramium, Centroceras, Polysiphonia, and Herposiphonia form broad expanses of delicate turfs and the foliose browns Dictyota bartayresii and D. divaricata are present in low abundances (3%). Red-orange peyssonnelid crusts are also conspicuous here. Occasionally, Valonia ventricosa and Anadyomene saldanhae are found, the latter often occurring in depressions (A. saldanhae was originally described from Brazil, and represents a new distributional record for Florida). A small and cryptic species of Botryocladia, B. spinulifera (a new distributional record for Florida) was discovered on the undersides of coral rubble.

B. Gorgonian/Algal Area (GA)

The algal flora of this environment is quite rich, totaling 54 species, including Dictyopteris delicatula and occasional small, juvenile Sargassum (possibly S. hystrix and S. acinarium ?). Total macrophyte cover in this habitat (Figs. 2, 3B, and 4A) averaged 58.9% coverage, with the opportunistic yellow turf being quite minor (2% cover, Table 7). Crustose coralline algae and mixed turfs again predominate (25% and 14% mean coverage, respectively) with a similar assemblage of species as found in

the "Stony Coral/Algal Area"; including Gelidium pusillum, the small articulated corallines Amphiroa fragilissima and Jania capillaceae, Chondria polyrhiza, and Wurdemannia miniata. Large clumps of the foliose browns, Dictyota bartayresii and D. divaricata (12% coverage), and dense turfs of the purple-red Wrangelia argus (0.8%) also characterize this gorgonian/algal habitat. Clumps of Halimeda opuntia, H. goreauii, Amphiroa tribulus, Galaxaura oblongata, and G. cylindrica are common here and host a multitude of epiphytes (i.e., Griffithsia, Ceramium, Polysiphonia, encrusting corallines). Other common macroalgae include the wiry-red Gelidiella acerosa, Hypnea spinella, and the iridescent blue-colored Coelothrix irregularis. A dwarf form of Digenia simplex, less than 0.5 cm tall above a broad expanding base, is apparent here that is known to be indicative of intense grazing pressure (S.M. Lewis & J.N. Norris, personal observation). An unusual Gloioderma, G. cf. atlantica, is epiphytic or entangled on various macroalgae. Other encrusting algae present are the red peyssonnelids, and the brown encrusting form of Lobophora variegata. Yellow-green turfs (3% cover) composed of Enteromorpha chaetomorphoides, Cladophora brasilana, and Cladophora laetevirens and reddish brown turfs of Sphacelaria, Ceramium, and Centroceras also contribute to the algal cover. Two species of Botryocladia, B. shanksii and B. spinulifera, occur here (both new records for Florida).

II. Damaged Reef Study Sites

A. Solid Substratum Area (SS)

This solid substratum area contains by far the most impoverished flora (Figs. 2 and 4B), with only 10 taxa. Total macrophyte cover is 60.5%, which is higher than undamaged sites due to the dramatic increase in the early successional yellow-turf species (54% cover) which had replaced live corals, gorgonians, sponges, macroalgae, etc. that had been scraped away (evidenced by streaks of ship paint, see photographs in Jaap 1984). This area was the most severely impacted by the grounding of the Wellwood. Here the reef is now more or less flat, virtually homogeneous, consisting of scraped coral substratum and sand, looking almost barren except for the short (less than 0.5 cm high) "yellowish turf" (54% coverage). Based upon microscopic assessments, the major element (41% of this turf) is the green alga Trichosolen parva (new to Florida) that was only found in the disturbed quadrats, and which appears to be an opportunistic or early colonizing species indicative of environmental disturbance. Other components of this "yellowish turf" are the similar sized green Enteromorpha chaetomorphoides (29%), the red Polysiphonia (18%) and the green Cladophora (12%). Occasional dark tufts of the blue-green Calothrix are present. Polysiphonia, Digenia simplex (dwarf form), Herposiphonia, other blue-greens, and Chondria polyrhiza compose the occasional reddish creeping turfs seen here (2.5% cover). Crustose coralline algae are common in this area (2.5% cover); however, these plants are not newly-settled but remnants attached to broken coral fragments. The Chlorophyta comprise the main cover in this damaged site while in undisturbed habitats Rhodophyta dominate.

B. Boulder Wall (BW)

A new more or less vertical rubble-wall habitat consisting of smashed and packed coral blocks was formed along one side of the two flattened areas (solid substratum) as the ship ploughed into the reef (Figs. 1 and 2). Damsel fish already have established territories among the nooks and crannies (Figs. 5B and 6A,B) throughout this wall. In all, 31 species of macrophytes were encountered, covering 67.9 % of the substratum. The yellow-turf assemblage contributed 32.4% of the total cover (Table 7) and characterizes the flora of this habitat, the major elements again being small but luxuriant plants of Trichosolen parva, Enteromorpha chaetomorphoides, Polysiphonia, and Cladophora. Gelidium turfs (11% coverage) and similar associated species as found the "gorgonian area", with the additions of Corallina cubensis and Digenia simplex (dwarf form), are frequent here as well. As in the other sites, these often occur over an understory of coralline crusts (5% coverage). Also present are the filamentous tetrasporic "Falkenbergia" stage of Asparagopsis, Champia parvula, Chondria, and numerous other small filamentous reds such as Polysiphonia, Dasya, Ceramium, Antithamnion, Antithamnionella, and Herposiphonia, as well as blue-green turfs (filamentous and reddish in color), Sphacelaria, and some dark green-blackish Calothrix crustacea clumps. Botryocladia shanksii was encountered closely adhering to the coral rubble.

C. Prop-Wash Area (PW)

A total of 22 taxa of marine algae were found in the prop-washed environment, with 63.9 % mean coverage. The green alga Trichosolen parva, Enteromorpha chaetomorphoides, Polysiphonia and Cladophora, all components of the dominant "yellowish turf", comprise the major algal cover (24%) in this habitat along with two species of crustose coralline algae (20% cover). Also common (17% cover), are mixed species turfs composed of Gelidium pusillum, Jania capillaceae, Amphiroa fragilissima, Polysiphonia, and Chondria. Present in lower abundances are small clumps of the dark blue-green Calothrix crustacea, Gelidiella acerosa, and Hypnea spinella. Other blue-greens, are occasionally present along with sporadic clumps of Dictyota bartayresii.

D. Cobble Area (CA)

There are, including the trace species, 18 taxa present, representing 67.4% mean algal cover in this habitat (Figs. 2 and 5A), with the majority of this (64.3%) comprised of the opportunistic yellow turf (Table 7). However, the turf here is dominated by Trichosolen parva and the two Cladophora species. The crustose corallines account for about 3% cover [purple crust (Hydrolithon) 2.1% and pink crust (Porolithon) 0.6%]. Present also are occasional tufts of Gelidium and Calothrix.

Quantitative Interpretation

The quantitative data (Tables 4 and 7) clearly show a statistically greater ($P < 0.05$, ANOVA, DMRT) abundance of dominant long-lived perennial algal species in the two undisturbed areas (coral/algal and gorgonian algal) relative to the solid substratum area and the cobble habitat. For example, total algal cover, excluding opportunistic yellow-turf forms, averaged 49.8% in the stony coral/algal control area and 56.7% in the gorgonian/algal control area. In marked contrast, these species were reduced to only 5.8% cover in the solid substratum area, that had been crushed and scraped to reef framework by the ship, and 3.0% cover in the scoured cobble habitat. The prop-washed and boulder-wall areas, which had received an intermediate level of scraping or physical shearing, showed a reduction to about half the natural level of algal species coverage (21.0% and 32.4% cover, respectively, Table 7). These values were significantly greater ($P < 0.05$ ANOVA, DMRT) than those from the disturbed solid substratum and cobble areas but not statistically ($P > 0.05$, Table 4) different from the control areas.

Conversely, the opportunistic successional species comprising the yellow turf (i.e., Trichosolen parva, Enteromorpha chaetomorphoides, Polysiphonia sp., and Cladophora sp.) were absent in the stony coral/algal control area and covered only 2.2% in the gorgonian/algal control area. These species showed dramatic increases in the disturbed solid substratum habitat (54.7% cover), the scraped cobble area (64.3%), the prop-washed area (21.0%), and the boulder wall (32.4%). All of the differences between the mean

cover of yellow turf in undisturbed versus damaged habitats were statistically significant (Table 4) at the $P < 0.05$ level of probability (ANOVA, DMRT). Dominant algae in the surrounding natural communities that were eliminated or reduced significantly ($P < 0.05$) include species of Dictyota, Gelidium pusillum, Polysiphonia, the unidentified red turf, and Wrangelia argus (Table 7). Gelidium turf and the purple crustose coralline (Hydrolithon) were also markedly reduced in all disturbed habitats except in the prop-wash area, due to the tough wiry nature of the former and the stony texture of the latter, which resisted hydrodynamic shearing effects (i.e., prop wash) but not mechanical scraping. Both of these two taxa also persisted in the boulder-wall habitat because numerous large fragments that were moved remained in an upright position and tended to retain some of the normal community components (Figs. 5B and 6A,B). However, this boulder-wall community will predictably become altered with time because it represents excellent damselfish habitat. Damselfish are known (Montgomery 1980; Brawley and Adey 1977; Hixon and Brostoff 1982; Sammarco, 1983) to exert strong influences on algal community development by eliminating certain large forms, while enhancing and guarding other species within their territories.

This initial assessment of the 136 samples relies heavily on the cluster patterns revealed in Figure 7, based on the plant species composition and percentage cover. It is interesting to compare the sample assemblages in view of their locations within the six different areas transected. When all of the sample plots were subjected to hierarchical cluster analysis (Bray-Curtis similarity coefficient, unweighted pair-group method), the resultant dendrogram

(Fig. 7) statistically corroborated the findings based on the parametric and nonparametric analyses just described (Tables 4 and 7). The most conspicuous feature is that the quadrats within the undisturbed control areas (both the stony coral/algal and gorgonian/algal communities) clustered tightly together, but at relatively variable levels of coefficients of similarity (Fig. 7). This variation is due to the patchy nature of the natural undisturbed environment, which is rich but very non-uniform in terms of the predominant plant cover. Contrastingly, all but one of the quadrats within the disturbed solid substratum and cobble habitats clustered separately at a much higher coefficient of similarity (Fig. 7), due to their more uniform domination by the yellow turf's early successional species.

In agreement with the statistical comparison tests, the prop-wash and boulder-wall disturbed quadrats were dispersed (Fig. 7) among both the undisturbed and physically-scraped quadrat assemblages owing to the varying degree of impact that they experienced. For example, a number of plots within these last two habitats retained some of the long-lived species characteristic of the undisturbed habitats, whereas others received disturbances sufficient to cause domination by the weedy yellow-turf forms. As mentioned, because of the relatively high spatial heterogeneity and concomitant rapid colonization by damselfishes, we anticipate that successional patterns will differ greatly within the boulder-wall substrata, unless dispersion by unpredictable storm activity occurs.

Based on the cluster array (Fig. 7), an argument could be made for grouping the undisturbed stony coral/algal and gorgonian/algal habitats as a single control system, and the scraped solid substratum and cobble zones as a single extreme physically disturbed system. This would increase the sample size and narrow the statistical confidence intervals accordingly. However, it may be necessary during recolonization studies to maintain the separate autonomies of these systems, because we cannot yet predict what successional events may occur owing to inherent microhabitat differences. The prop-wash and boulder-wall systems clearly will continue to warrant separate treatment due to their varying degrees of intermediate disturbances.

CONCLUSIONS

1. The effects of the grounding by the freighter Wellwood caused extensive alterations in the distribution and abundance patterns of algal communities on the shallow spur system of Molasses Reef, Key Largo Marine Sanctuary.

2. The natural algal communities of the shallow forereef, although dominated by small perennial forms indicative of high grazing activity, were surprisingly rich in species (73 taxa, 13 of which were previously unknown in Florida waters).

3. Long-lived perennial plants were almost totally removed in those areas scraped by the Wellwood's hull; whereas, all but the wiry and stony forms were sheared away in prop-washed areas not directly contacted by the ship. The abundances of long-lived forms in adjacent areas not affected (controls) were statistically greater ($P < 0.05$, ANOVA, DMRT) than those in the two areas physically scraped by the grounding.

4. Conversely, all four of the mechanically-disturbed habitats had significantly greater ($P < 0.05$) abundances of a weedy microfilamentous yellow-turf assemblage (Trichosolen parva, Enteromorpha chaetomorphoides, Polysiphonia sp., and Cladophora sp.) that had already become extensive (up to 64.3% mean cover) within two weeks following the grounding.

5. The number of replicate samples in the physically scraped areas probably can be decreased as a cost-saving measure during future studies because of their relatively high level of similarity. This is not the case in the more patchy natural habitats containing abundant stony coral/algal and gorgonian/algal communities.

RECOMMENDATIONS

1. Due to the surprisingly diverse and complex nature of the algal communities at Molasses Reef, a high level of taxonomic effort needs to be sustained. This would primarily necessitate expertise in dealing with microfilamentous algae.

2. A broadscale quantitative description of permanent photo-transects should be made to document algal community structure throughout the major zonal habitats of Molasses Reef. Major habitats and biotic zones should be determined by aerial photography and then subsampled appropriately. This would provide a much-needed inventory and baseline from which to ascertain changing patterns of the reef biota, including possible human-induced alterations.

3. Because of the high degree of patchiness in the algal communities of Molasses Reef, the same permanent, fixed-plot,

non-destructive methods should be utilized to monitor recovery patterns. Consideration should be given to lumping the stony coral/algal and gorgonian/algal control quadrats as well as the scraped solid and cobble areas to improve the statistical confidence limits during future analyses. However, microhabitat differences and subsequent successional events may preclude this.

4. Experimental manipulations involving the timing of recruitment would provide powerful predictive insights into seasonal patterns and availability of spores as well as examine the efficacy of enhancing recovery to predisturbance levels by controlling recolonization events. This type of study has considerable potential for providing managers with useful information and is strongly recommended.

5. Consideration should also be given to conducting limited controlled transplant experiments within the physically damaged habitats. This would examine the feasibility of directly re-establishing long-lived slow-recruiting organisms as well as augmenting the number of viable recruits for species that disperse over relatively short distances.

6. Because the natural algal assemblages are indicative of herbivore-controlled systems, consideration should be given to monitoring, and possibly manipulating, the patterns of fish recruitment and grazing intensity in undisturbed vs. damaged habitats during the recovery process.

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Table 1. Molasses Reef permanent sample deployment (1-4 September 1984).

Transect	Undisturbed Areas		Disturbed Areas		Experimental/Successional (Disturbed Solid Substratum Area)		
	Stony Coral/Algal Area	Gorgonian/Algal Substratum Area	Cobble Prop Wash Area	Boulder Wall			
A	9	13	14	1	11	6	
B	17		16	16		6	
C	7		7	1	10	1	
D						23	
E						12	
Total Replicates	33	13	37	19	21	13	35

*Total permanent samples = 171; 46 undisturbed, 90 disturbed, and 35 experimental.

Table 3. Comparison of serial and random quadrats for the solid substratum disturbed area (N=20).

Taxa	Serial Array	Random Array
Yellow turf	54.650	52.565 Mean Value
	11.052	7.304 95% Confidence Interval
	5.281	3.490 Standard Error
Purple crustose coralline (<u>Hydrolithon</u>)	0.285	3.490
	0.586	4.167
	0.280	1.991
<u>Gelidium</u> turf	0.300	2.580
	0.340	2.418
	0.163	1.155
Pink crustose coralline (<u>Porolithon</u>)	0.430	0.550
	0.667	1.140
	0.319	0.545
<u>Calothrix</u>	0.060	0.010
	0.105	0.014
	0.050	0.007
<u>Gelidium pusillum</u>	0.020	0.010
	0.019	0.014
	0.009	0.007
<u>Crustose coralline</u>	0.010	0.005
	0.014	0.010
	0.007	0.005
<u>Dictyota</u>	0.005	0.005
	0.010	0.010
	0.005	0.005
<u>Gelidium</u> red turf	0.000	0.005
	0.000	0.010
	0.000	0.005

Table 4. Duncan's multiple range test (DMRT) results for all six areas sampled. Significant differences at the 95% confidence level are indicated by asterisks. (A) represents DMRT for the dominant yellow turf present in most areas. (B) represents DMRT for all other taxa present in the samples.

Areas	Yellow turf only (A)						All other taxa (B)					
	Areas						Areas					
	SC	GA	SS	CA	PW	BW	SC	GA	SS	CA	PW	BW
Stony coral/algal	SC						SC	*	*			
Gorgonian/algal	GA						GA	*	*			
Solid substratum	SS	*	*			*	SS					
Cobble	CA	*	*	*		*	CA					
Prop wash	PW	*	*				PW		*	*		
Boulder wall	BW	*	*			*	BW		*	*		

Table 5. Marine algae in the vicinity of the Wellwood grounding, molasses reef: undisturbed (control) sites (SC = stoney coral/algal area, GA = gorgonian/algal area) vs. disturbed (damaged) sites (SS = solid substratum area, BW = boulder wall, PW = prop wash area, CA = cobble area).

CHLOROPHYTA	SC	GA	SS	BW	PW	CA
<u>Enteromorpha chaetomorphoides</u>		x	x	x	x	x
<u>Cladophora brasilana</u>		x			x	x
<u>Cladophora laetevirens</u>		x		x		x
<u>Chaetomorpha</u>		x				x
<u>Valonia ventricosa</u>	x	x				
<u>Anadyomene saldanhae</u>	x	x				
<u>Neomeris mucosa</u>	x					
<u>Caulerpa ambigua</u>		x				
<u>Trichosolen parva</u>			x	x	x	x
<u>Halimeda goreauii</u>	x	x		x		
<u>Halimeda opuntia</u>	x	x		x		x
<u>Udotea verticillosa</u>	x					
PHAEOPHYTA						
<u>Ectocarpus cf. elachistaeformis</u>			x			
<u>Sphacelaria novae-hollandiae</u>	x	x		x		x
<u>Dictyota bartayresii</u>	x	x			x	x
<u>Dictyota divaricata</u>	x	x			x	x
<u>Dictyopteris delicatula</u>		x				
<u>Lobophora variegata</u>		x		x		
"Vaughaniella" stage of <u>Padina</u>		x				
<u>Sargassum ? acinarium</u>		x				
<u>Sargassum ? hystrix</u>		x				

RHODOPHYTA	SC	GA	SS	BW	PW	CA
<u>Acrochaetium</u>	x	x				
<u>Galaxaura cylindrica</u>	x	x				
<u>Galaxaura oblongata</u>	x	x				x
"Falkenbergia" stage of <u>Asparagopsis</u>	x	x		x		
<u>Gelidiella acerosa</u>		x			x	x
<u>Gelidium pusillum</u>	x	x		x		x
<u>Wurdemannia miniata</u>	x	x				x
<u>Peyssonnelia</u>	x	x				x
crusts		x				x
<u>Amphiroa fragilissima</u>	x	x		x	x	x
<u>Amphiroa tribulus</u>	x	x				
<u>Jania capillacea</u>	x	x		x	x	x
<u>Fosiella</u> or <u>Lithoporella</u>						
coralline crust (purple, <u>Hydrolithon</u>)	x	x	x	x	x	x
coralline crust (pink, <u>Porolithon</u>)	x	x	x	x	x	
<u>Corallina cubensis</u>				x		
<u>Hypnea spinella</u>	x	x			x	x
<u>Hypnea</u>		x				
<u>Botryocladia shanksii</u>		x		x		
<u>Botryocladia spinulifera</u>	x	x				x
<u>Gloioderma c.f. atlantica</u>		x				
<u>Chrysymenia</u>	x	x		x		
<u>Champia parvula</u>	x	x		x		x
<u>Coelothrix irregularis</u>	x	x				
<u>Anotrichium tenue</u>				x		
<u>Antithamnion ogdeniae</u>				x		
<u>Antithamnionella breviramosa</u>	x			x		

	SC	GA	SS	BW	PW	CA
<u>Centroceras</u>		x		x		
<u>Centroceras clavulatum</u>	x	x			x	
<u>Ceramium flaccidum</u>	x	x		x	x	x
<u>Ceramium</u>						
<u>Ceramium</u>						
<u>Ceramium</u>						
<u>Crouania pleonospora</u>					x	
<u>Diplothamnion sp.</u>						
<u>Griffithsia globulifera</u>	x	x				
<u>Gymnothamnion elegans</u>		x				
<u>Wrangelia argus</u>	x	x			x	x
<u>Branchioglossum ?</u>	x					
<u>Hypoglossum tenuifolium v. carolinianum</u>	x			x		
<u>Myriogramme-Nitophyllum</u>						
<u>Taenioma nanum</u>	x	x				
<u>Dasya rigidula</u>				x		
<u>Halodictyon mirabile</u>		x				
<u>Chondria polyrhiza</u>		x				
<u>Chondria</u>	x	x	x	x	x	x
<u>Digenia simplex "dwarf form"</u>		x	x	x		
<u>Herposiphonia secunda</u>	x	x		x	x	x
<u>Herposiphonia tenella</u>	x					
<u>Polysiphonia</u>	x	x	x	x	x	x
<u>Laurencia</u>	x	x	x	x	x	x
<u>Laurencia</u>						
CYANOPHYTA						
<u>Calothrix crustacea</u>		x	x	x	x	x
<u>Blue-greens</u>	x	x			x	x

Table 6 . List of marine algae new to Florida.

CHLOROPHYTA

Anadyomene saldanhae Joly & Olivera

Neomeris mucosa Howe

Trichosolen parva (Dawson) Taylor 1962

Udotea verticillosa A. & E.S. Gepp

PHAEOPHYTA

Sphacelaria novae-hollandiae Sonder

"Vaughaniella" stage of Padina

RHODOPHYTA

Botryocladia shanksii Dawson

Botryocladia spinulifera Taylor & Abbott 1973

Gloioderma ??

Antithamnion ogdeniae Abbott

Antithamnionella breviramosa

Diplothamnion ?

Branchioglossum ?

Table 7. Mean Percent Cover(+standard error) for the predominant habitats sampled on Molasses Reef 31 August - 4 September 1984.

Taxa	Undisturbed		Disturbed			
	Stony Coral /Algal	Gorgonian /Algal	Solid Substratum	Disturbed Cobble	Prop Wash	Boulder Wall
<u>Gelidium</u> turf	14.027(3.143)	14.431(1.803)	2.346(0.856)	0.147(0.096)	17.733(3.867)	10.062(4.270)
Purple crustose coralline	12.788(3.163)	24.200(3.158)	2.424(1.099)	2.116(0.761)	18.914(2.914)	3.677(1.463)
<u>Polysiphonia</u> turf	5.188(2.325)					0.223(0.223)
<u>Gelidium/Dictyota</u> turf	4.097(2.404)					
<u>Polysiphonia/Gelidium</u> turf	3.600(1.853)	0.346(0.346)	0.246(0.246)			
<u>Wrangelia argus</u>	2.127(0.825)	0.823(0.596)	0.062(0.059)		0.076(0.076)	0.031(0.013)
Red turf	1.815(1.806)		0.046(0.041)			0.015(0.010)
Crustose coralline	1.339(0.574)		0.005(0.004)			0.077(0.077)
<u>Dictyota</u>	1.203(0.503)	7.962(2.517)	0.003(0.003)		0.005(0.005)	0.115(0.083)
Green turf	0.752(0.546)	1.685(0.869)		0.074(0.074)	3.867(2.740)	17.792(5.876)
<u>Peyssonnelia</u>	0.670(0.473)			0.058(0.053)	0.014(0.008)	0.285(0.181)
<u>Dictyota bartayresii</u>	0.421(0.287)	5.754(2.392)			0.081(0.076)	0.008(0.008)
<u>Gelidium pusillum</u>	0.403(0.321)		0.011(0.005)			0.500(0.352)
Brown turf	0.273(0.273)					
<u>Coelothrix</u>	0.206(0.128)	0.008(0.008)				0.008(0.008)
<u>Halimeda goreauii</u>	0.185(0.132)	0.146(0.138)				
<u>Polysiphonia</u>	0.127(0.121)				0.071(0.067)	
Bluegreens	0.097(0.088)			0.016(0.009)	0.010(0.007)	0.015(0.010)
<u>Hypnea</u>	0.085(0.085)					
Pink crustose coralline	0.073(0.070)	1.238(0.601)	0.530(0.336)	0.605(0.293)	1.514(1.281)	1.569(1.275)
<u>Falkenbergia</u>	0.073(0.073)					
<u>Amphiroa triloba</u>	0.061(0.033)	0.023(0.012)			0.010(0.007)	0.108(0.100)

Trichosolen parva. 29% Enteromorpha chaetomorpha. 18% Enteromorpha sp. and
by Gladstone

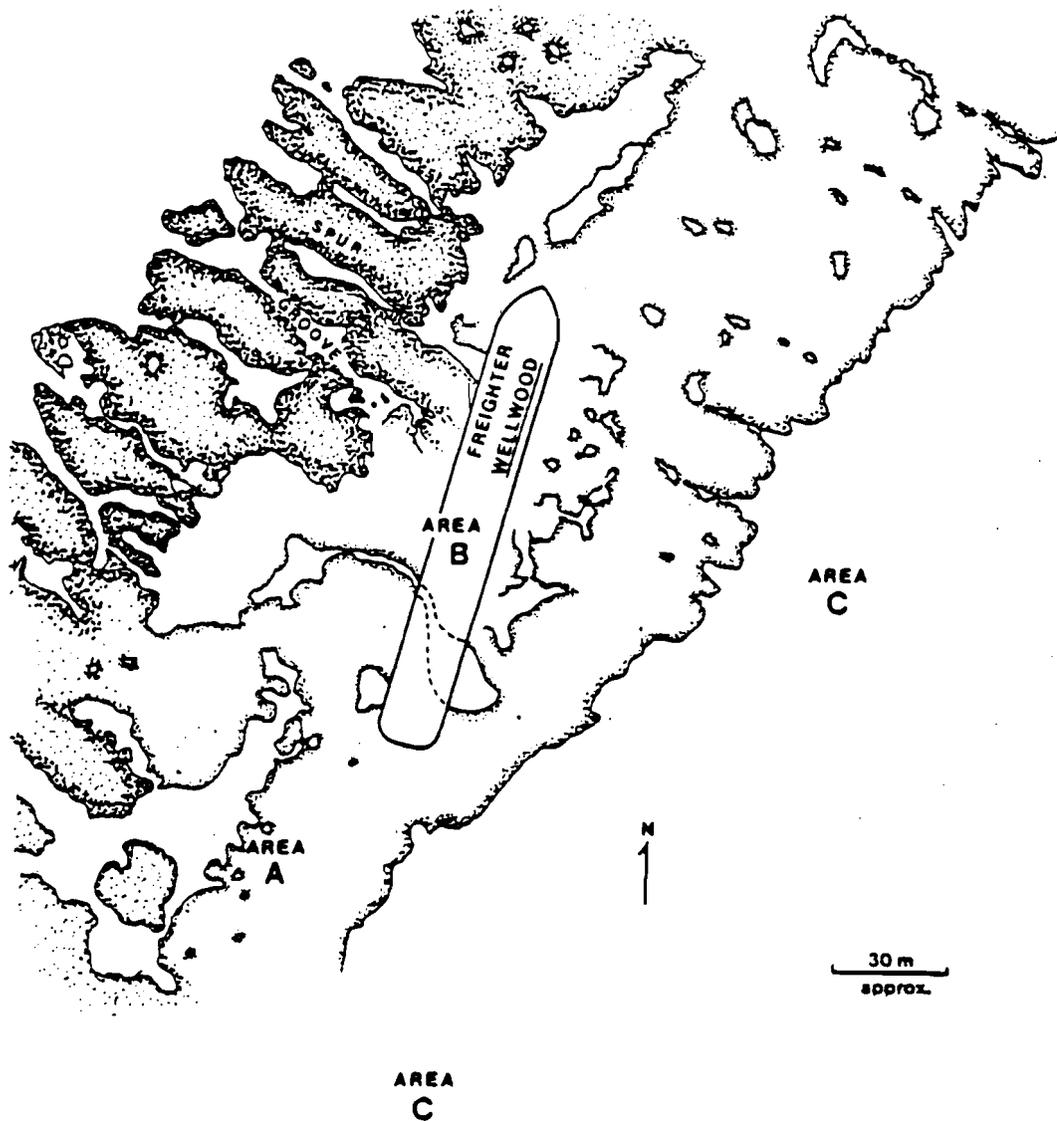


Figure 1. Location of the Wellwood grounding site (4-16 August 1984) on the shallow forereef of Molasses Reef, Key Largo National Marine Sanctuary (modified from Bright and Andryszak 1984). Area A is the path of the ship during initial grounding. Area B is the major grounding site. Area C is the area of damage by towing cables. See Fig. 1 for detail of algal study area.

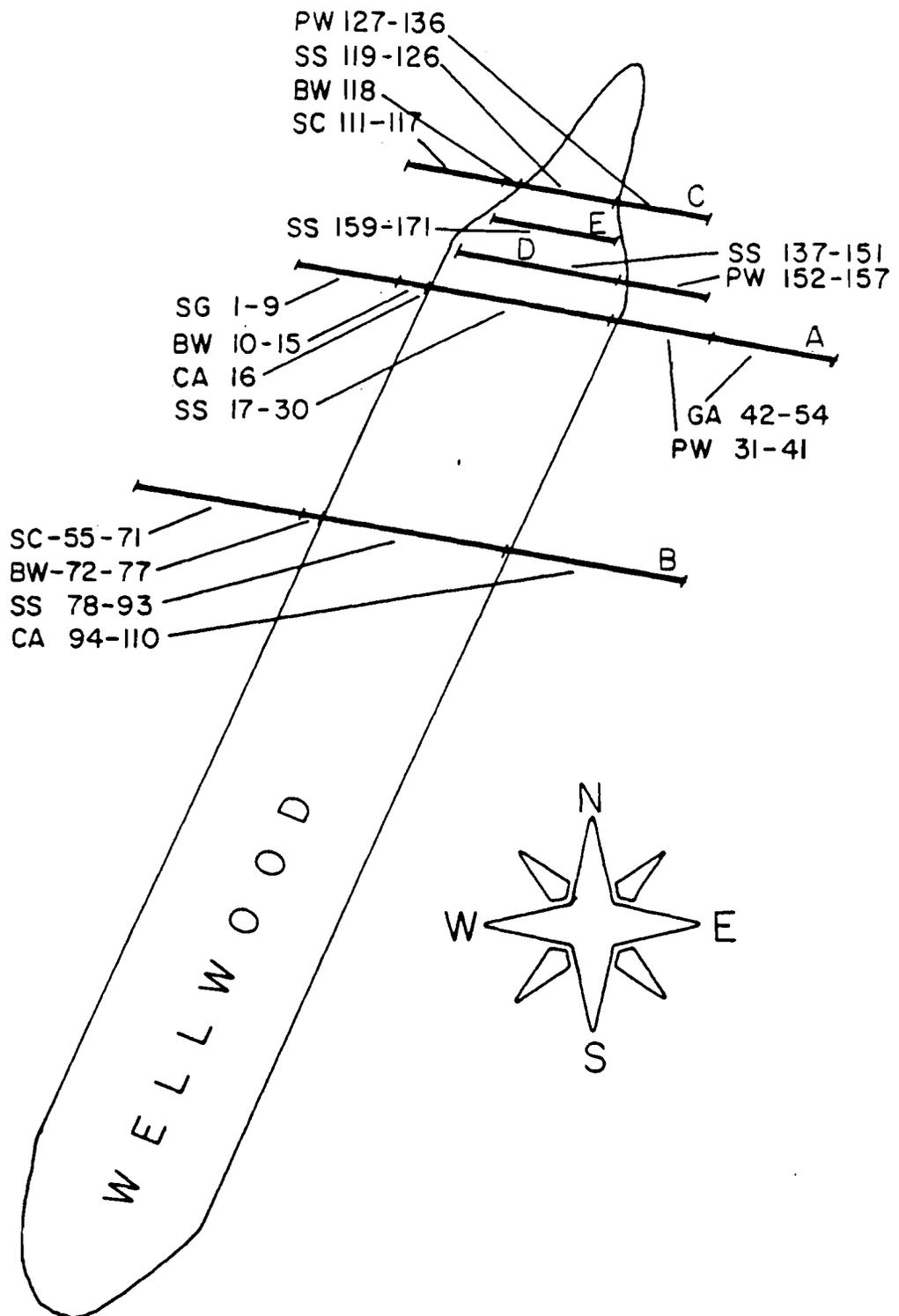
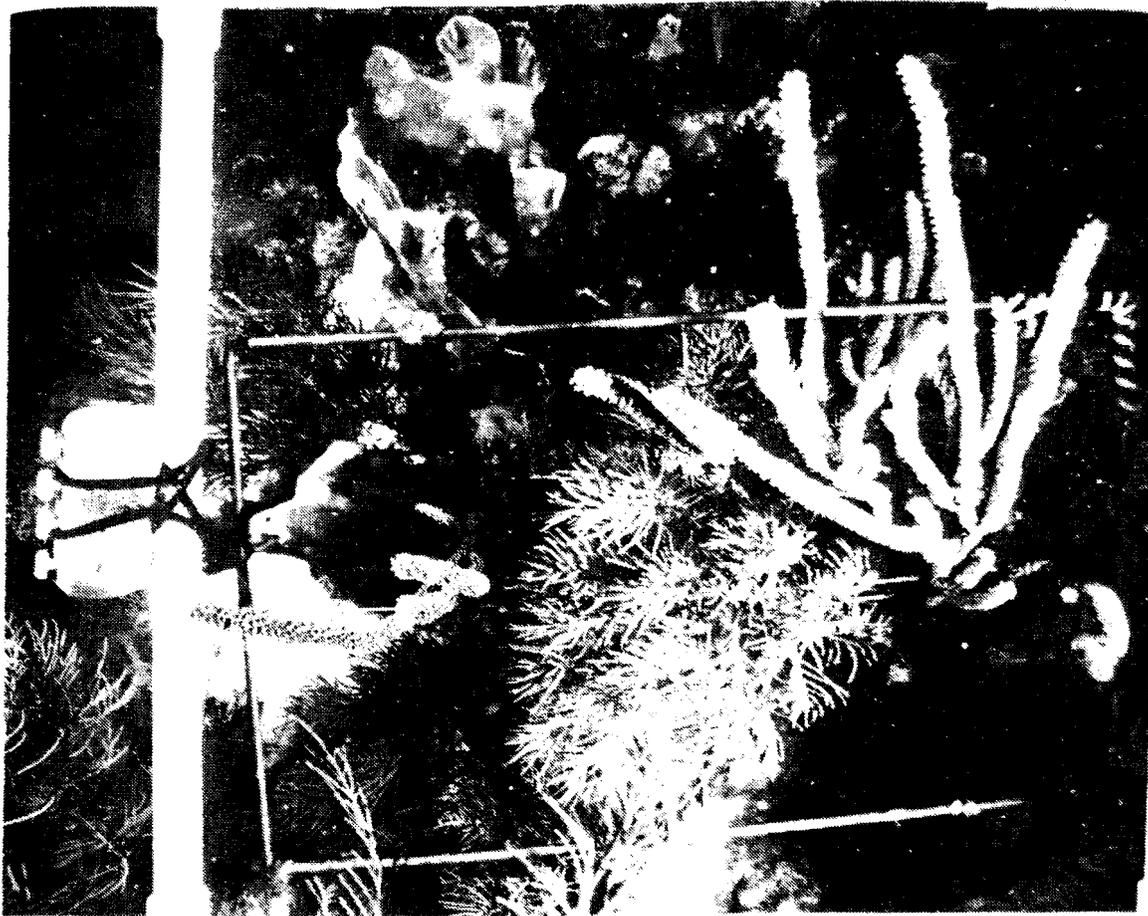


Figure 2. Approximate transect and quadrat locations (SC - undisturbed stony coral/algal area; GA - undisturbed gorgonian/algal area; SS - disturbed solid substratum area; CA - disturbed cobble area; PW - disturbed prop wash area; BW - disturbed boulder wall area) relative to the grounding site of the freighter Wellwood. Transects D and E are experimental successional quadrats.

Figure 3. Representative 0.15-m² photo-quadrats taken in (A) the undisturbed stony coral/algal area and (B) the gorgonian/algal area. Rephotographed and enlarged from color transparencies.



A



B

Figure 4. Representative 0.15-m² photo-quadrats taken in (A) the gorgonian/algal area and (B) the disturbed solid substratum area. Rephotographed and enlarged from color transparencies.



A



B

Figure 5. Representative 0.15-m² photo-quadrats taken in (A) the disturbed cobble area and (B) the disturbed boulder wall area. Rephotographed and enlarged from color transparencies.

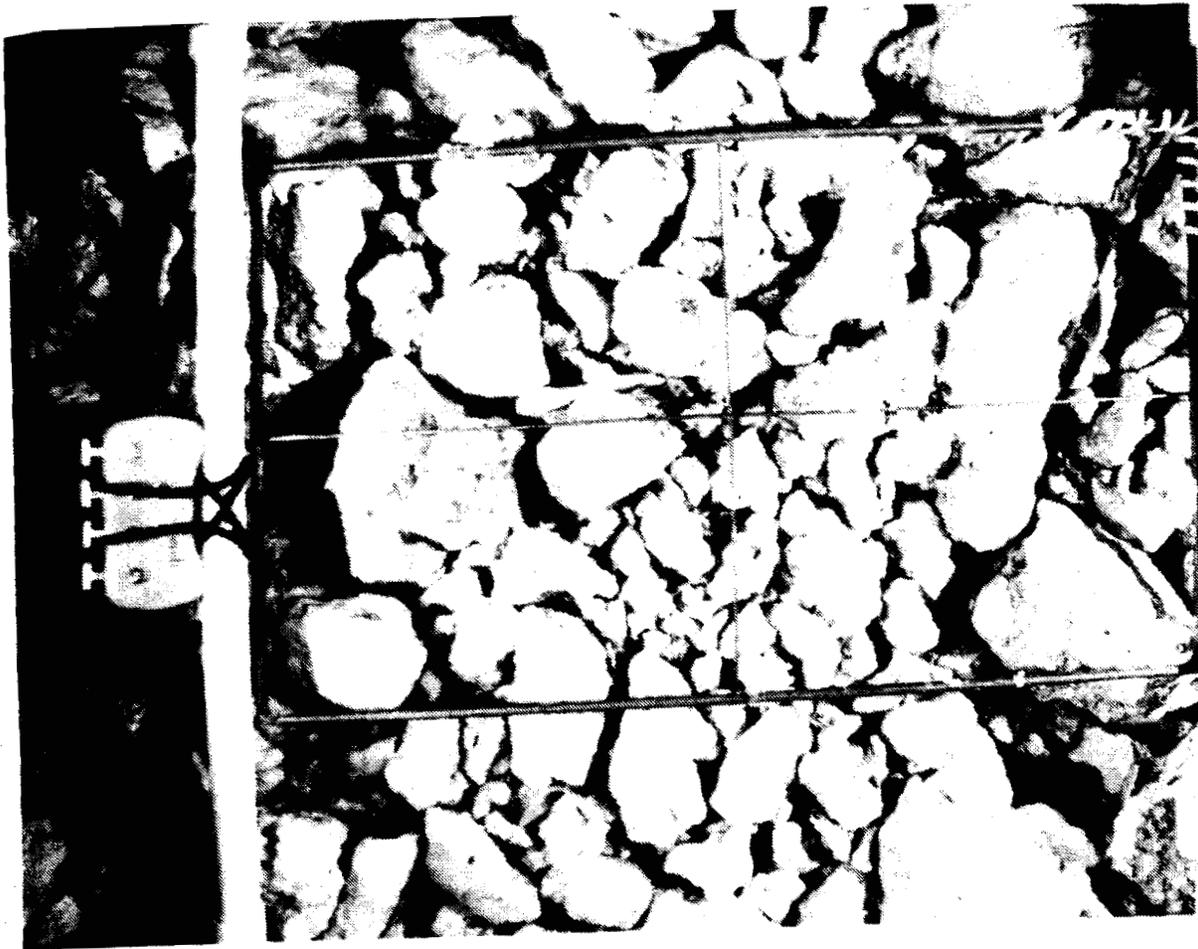
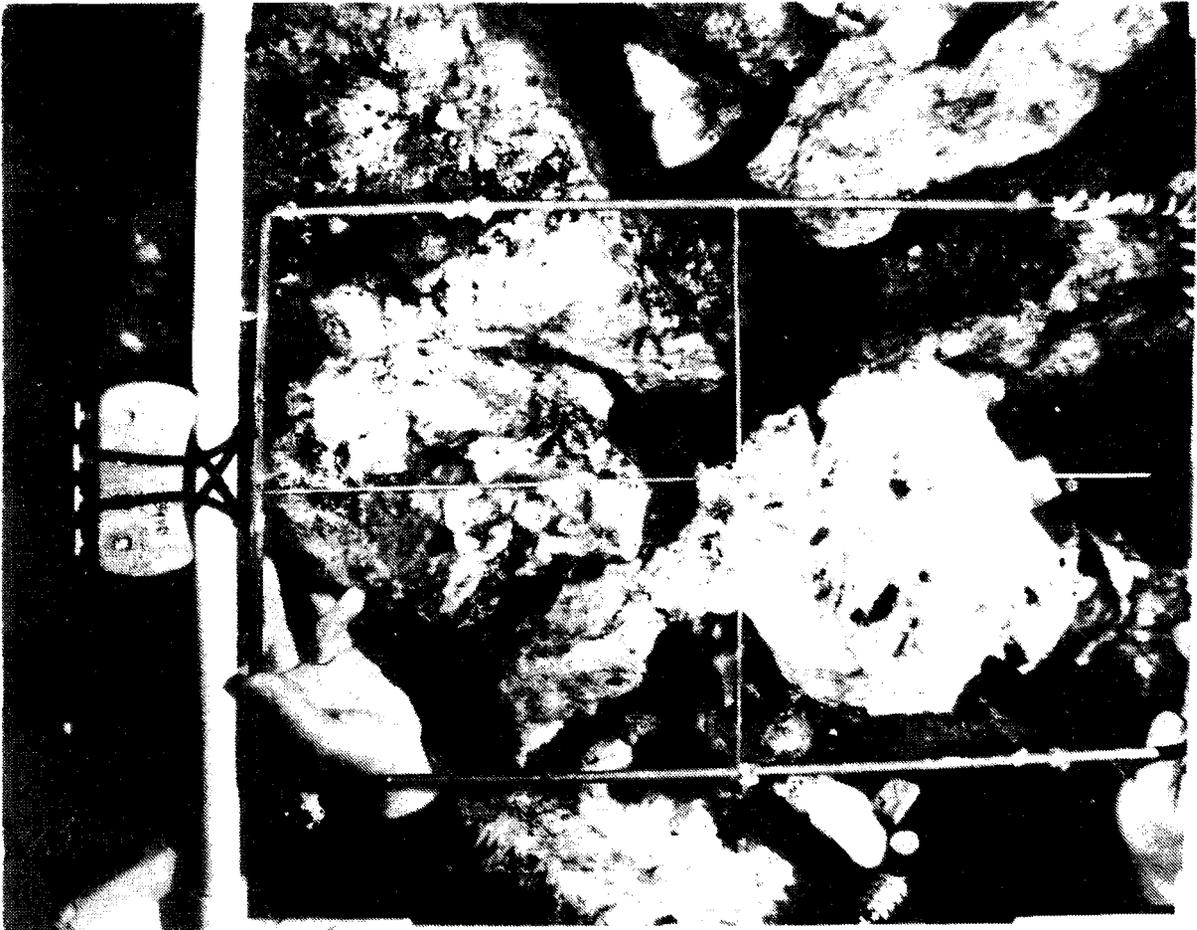
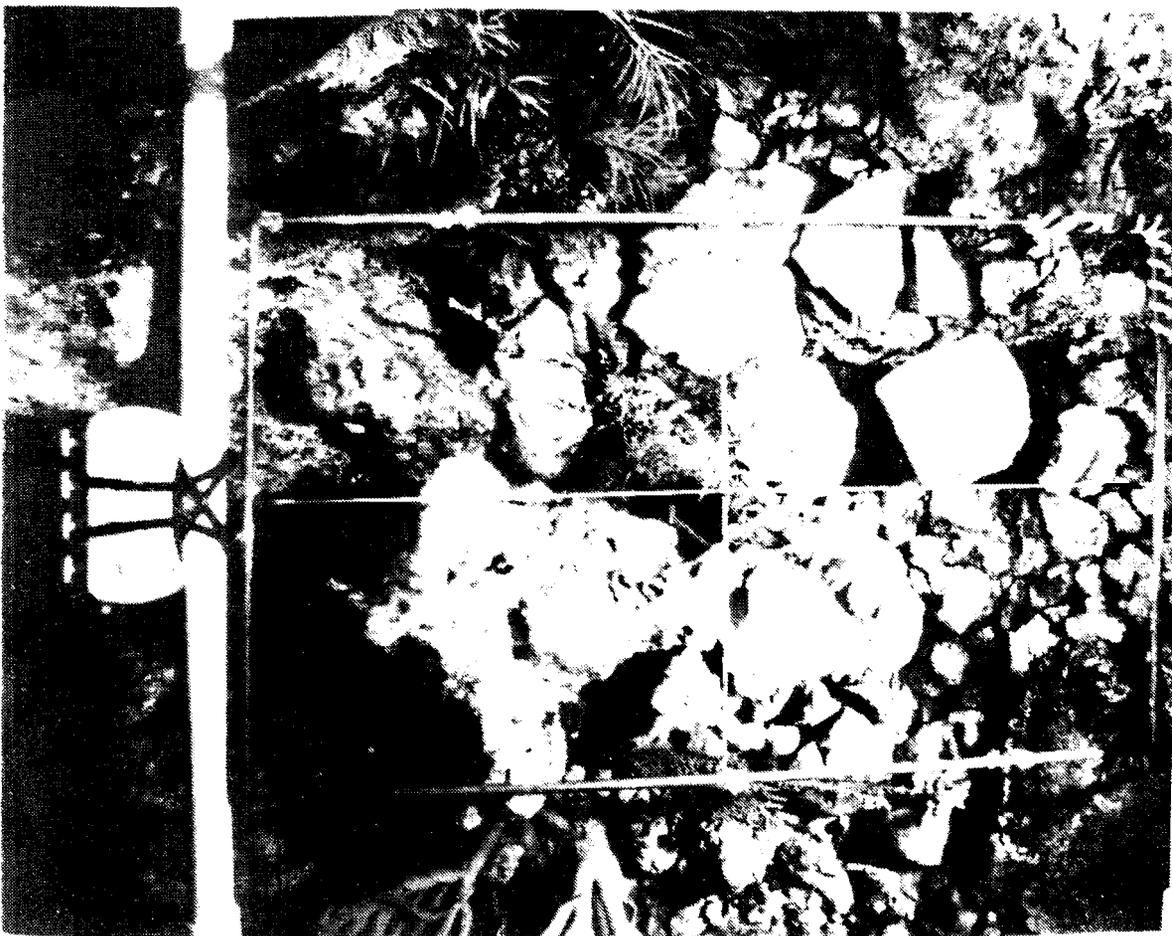


Figure 6. Representative 0.15-m² photo-quadrats taken in (A and B) the disturbed boulder wall area. Rephotographed and enlarged from color transparencies.



A



B

Figure 7. Dendrogram display of differential clustering of the 136 photo-quadrats based on cover abundances of the various species during the 1-4 September 1984 assessment. Numbers at the bottom represent area designation (1-6), hyphen, and quadrat number. Deployment of the sample array is referenced in Table 1 and Fig. 2.

SIMILARITY COEFFICIENT

1.0 0.8 0.6 0.4 0.2 0.0

