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SURVEY OF MARINE COMMUNITIES IN PANAMA AND EXPERIMENTS WITH OIL



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SURVEY OF MARINE COMMUNITIES IN PANAMA
AND EXPERIMENTS WITH OIL

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PREFACE

This report presents the results of a three-year study on the intertidal marine communities near the Galeta Point Laboratory following the spill of approximately 20,000 barrels of Bunker C and marine diesel oil during the breakup of an oil tanker about three miles from the laboratory. Since the laboratory was new and still unoccupied at the time of the spill, no baseline data on marine organisms were available for comparison so the damage caused by the spill on the local marine communities could not be evaluated precisely. It was apparent from the literature that adequate data were not available for any Caribbean intertidal reef flats. We accordingly had to devote the first two years of the study primarily to compiling baseline data for the marine community on the reef flat to provide background information for experimental tests of effects of oil. This base of information is presented in the appendices and is discussed in the first half of the report. The second half of the report is concerned with the experiments testing the effects of oil.

Throughout the study, we often observed patches of oil about 15 to 60 cm in diameter wash up against the foundation of the laboratory at high tide or during onshore winds and other patches which stuck to the algae and animals in the reef community at low tide and during calm seas. These oil patches presumably were coming from ships clearing ballast tanks or perhaps sometimes from accidents in operations at the nearby refinery or Panama Canal fuel piers. Visitors to the laboratory from other parts of the world would sometimes comment on these irregular but not infrequent oil patches or "blobs" as being of more immediate and personal concern to them than were the less frequent major oil spills. They would ask whether these small patches had significant effect on the intertidal marine communities. Because the small patches of oil were of more frequent concern and yet perhaps have received less attention in previous studies than the massive oil spills, our field studies were set up as experiments with controls using one meter square quadrats as the size of the replicates. We also used one meter square quadrats rather than larger ones in order to prevent undue damage to the reef from our experimental procedures and to protect other on-going research projects.

Therefore, because of the frequent occurrence of small oil patches, the widespread interests in their effects, the agreement with authorities to release only a small amount of oil into the environment, and for the general condition of the study sites near the laboratory, our field was restricted to experimental quadrats of one square meter in size as was outlined in the contracted program.

In addition to the field studies on entire communities, experiments were performed which were designed to concentrate on specific effects of oil,

e.g., on the growth rates of corals or on recruitment of sessile marine invertebrate larvae and algal sporelings. The experiments were not set up to make trivial demonstrations of mass mortality under a thick coating of oil, but to perform accurate quantitative measurements of effects detectable only through comparisons with controls in the experiments.

ABSTRACT

Baseline surveys were conducted on both the Caribbean and Pacific coasts of Panama. The structure of macroinvertebrate communities along the Caribbean transect are presented from data collected for over 500 identified species in 108 samples including a total of over 50,000 specimens. Recruitment to benthic communities was investigated with settling plates. The Caribbean was found to be seasonal in species occurrence while the Pacific was seasonal in productivity.

The effects of oil pollution on tropical intertidal marine communities were tested by precisely controlled experiments utilizing tarry Bunker C and volatile marine diesel oils. Field experiments were performed on a Caribbean intertidal reef flat community, a Pacific rocky shore community, settling plates in both oceans, mangrove trees sprayed with oil on the leaves and/or stilt roots and on coral growth. Bunker C oil had a greater detrimental effect than did marine diesel oil on coral growth. Marine diesel oil had a greater detrimental effect than did Bunker C oil on fouling communities of settling plates. When comparing experimentals with controls, growth rates were used as an indicator of the presence of unobserved physiological stress or damage and a quantitative index of the cost of repair. Susceptibility to oil pollution varied significantly between individuals. The growth rates of corals differed significantly with location and time of year so that very precise controls were required in the experiments.

This report was submitted in fulfillment of Program Element Number 1BA022, Contract Number 14-12-874 to the Smithsonian Tropical Research Institute, P. O. Box 2072, Balboa, Canal Zone, under the (partial) sponsorship of the Water Quality Office, Environmental Protection Agency.

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During this entire project, the Smithsonian Tropical Research Institute made available all facilities of the Caribbean coast marine laboratory at Galeta Point. STRI also provided so many other facilities, we could not possibly name them all. We are especially grateful to Peter W. Glynn, Ira Rubinoff and Edward Kohn, who aided us with advice, encouragement and administrative assistance. Peter Glynn suggested the field experiment on the effect of oil pollution on coral growth and Ira Rubinoff suggested the field experiment on the effects of pollution on mangrove trees. Deborah M. Dexter provided particularly valuable instructions and suggestions on the survey of the sand beach habitat. We also appreciate the advice and suggestions of David L. Meyer, coordinator of the Environmental Sciences Program at Galeta. Joyce Redemske Young provided identifications of the algae presented in Appendices A, E and F. Peter W. Glynn, Neal G. Smith, Henk Wolda and Egbert G. Leigh read an earlier draft of the manuscript and gave suggestions for improvements.

Almost every animal species in this report was identified by taxonomic authorities, each of whom devoted many hours to our assistance even though all had many other research and/or teaching commitments. The polychaetes and crabs were sent to the Allan Hancock Foundation, where Kristian Fauchald identified all the polychaetes in this report and is preparing some publications on the material. John S. Garth and Janet Haig, at the same foundation, identified the species of six families of crabs with incredible promptness. The other great source of aid was the National Museum of Natural History. C. Allan Child always quickly sent identifications of pycnogonids and returned some specimens for our reference collection. The stomatopods were identified by Raymond B. Manning, who also send us a reference collection. Mary E. Rice tutored us in sipunculan identification and left a good reference collection at the Galeta laboratory. Joseph Rosewater identified our gastropods and bivalves and confirmed or corrected the identifications we attempted. Helen Hayes helped with the species of *Isognomon*. G. Arthur Cooper identified our brachiopod.

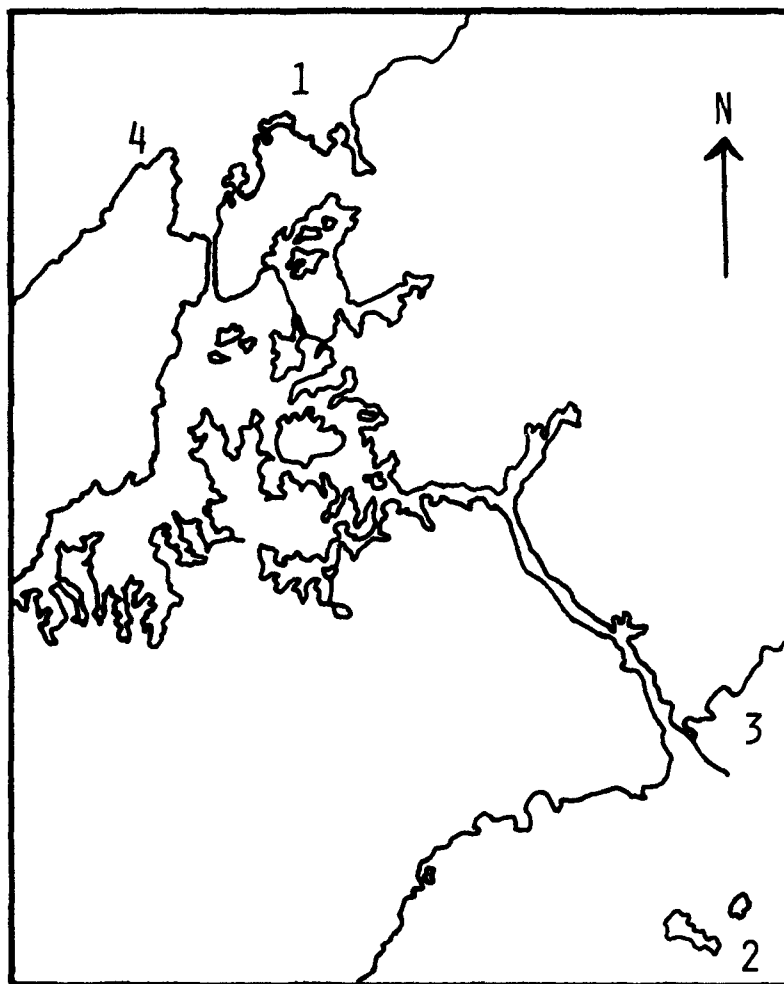
The associates of STRI also provided considerable taxonomic assistance. Lawrence G. Abele provided all our shrimp identifications, the alpheidids being a particular challenge. He is also publishing the description of a new species of crab. Peter W. Glynn has identified our isopods and in the process of identification found several species new to science. David L. Meyer made up a labeled collection of ophiuroids for us to use as a reference in sorting our samples. Because the amphiurid ophiuroids were tiny, numerous, diverse and practically indistinguishable from each other, Michael Kyte of Marine State Sea and Shore Fisheries sorted and identified each of our collections for us.

Cirripeds were identified by Dora P. Henry, Department of Oceanography, University of Washington, and Peter R. Bacon, of the University of the West Indies, Trinidad. Bryozoans are being worked on by William C. Banta, The American University, Washington, D.C., and tunicates by R. H. Miller, Dunstaffnage Marine Research Laboratory, Oban, Scotland. Robert C. Bullock, of Florida Technological University, identified our chitons.

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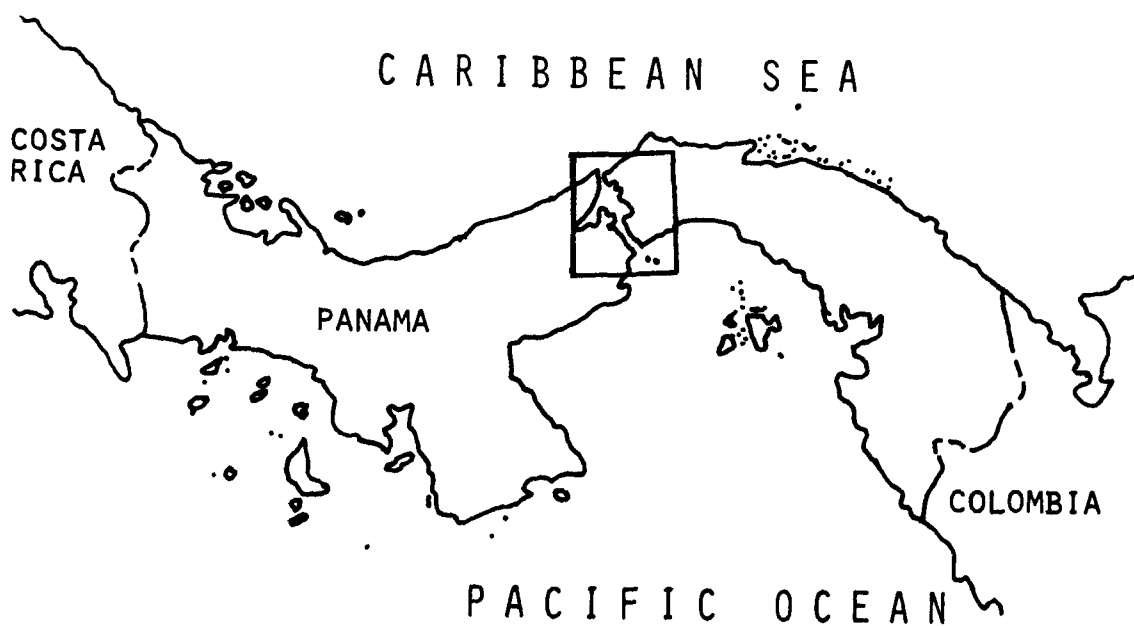
A MAP OF PANAMA,
INDICATING THE
MAJOR STUDY SITES
DISCUSSED IN
THIS REPORT.

1 = STRI MARINE
LABORATORY,
GALETA POINT

2 = ISLA TABO-
GUILLA

3 = PUNTA PAITILLA

4 = SHIMMEY BEACH



SECTION I

CONCLUSIONS

1. Growth rates provide an indicator of the presence of unobserved physiological stress or damage and a quantitative index of the cost of repair. Although appearing to be in good health after one day in the field following 2.5 hours of exposure to Bunker C oil, the mean growth increments of the hermatypic corals *Porites furcata* were significantly smaller than those of the controls during the following 61 days.
2. The mean growth of branches making up heads of *Porites furcata* did not differ significantly between heads used as controls, while the mean growth of *P. furcata* branches in heads subjected to Bunker C oil differed significantly between heads. An individual variation of heads or colonies in susceptibility to oil pollution at low levels is implied.
3. Precise controls are required for low-level pollution experiments. The mean growth increments of both control and experimental coral heads varied significantly in the field over 3-meter distances at the same depth and during time periods of the same length but 2 months apart. Location and time of year each had a great enough effect that tests involving 2.5 hours exposure of corals to Bunker C oil need controls set very close by to observe growth during recovery. Growth rates from literature cannot be accurately used for comparison.
4. In laboratory experiments, Bunker C oil had a more damaging effect than did marine diesel oil on *Porites furcata*, *Pocillopora damicornis*, *Pavona gigantea* and *Psammocora stellata*. After short exposures of 0.5, 1.0, and 30 minutes, the rate and extent of tissue death depended on coral species and did not appear until about 2 weeks after the exposure to oil.
5. Marine diesel oil had a clearly toxic effect on fouling communities. Dry weight measurements of production showed that plates coated with marine diesel oil had a significantly lower biomass of fouling organisms than did the control plates. Surface coverage measurements showed less space occupied by algae and animals on settling plates coated with marine diesel oil than on control plates.
6. The percent surface coverage of algae on settling plates was significantly higher on plates coated with Bunker C oil than on plates coated with marine diesel oil or on control plates. Five aquaria previously containing Bunker C oil each grew more algae than any of five aquaria previously containing marine diesel oil and each grew three to five times as much algae as any of the five control aquaria. After spraying intertidal quadrats in the field with Bunker C oil, the number of algal species in the quadrats

increased significantly while the number of species in quadrats sprayed with marine diesel oil and control quadrats did not increase significantly.

7. The spraying of leaves of mangrove trees (*Rhizophora mangle*) with the volatile marine diesel fuel oil was correlated with reduced leaf coverage or no growth of the trees during the following year. Coating the stilt roots with tarry Bunker C oil was of less definitive effect. This may explain why the most obvious defoliation of mangrove trees following the wreck of the *SS Witwater* was in a band along the windward edge of the forest facing the sea from the other side of a causeway. As Rützler and Sterrer (1970) noted, "high winds caused a spray of mixed seawater and oil to cover mangrove trees . . . to a height of 2 m above mean tide level" and that the oil had ". . . already killed many of these plants." However, the trees were probably not killed but were greatly defoliated.

8. Each class or category of motile animal species on the Caribbean reef flat at Galeta has its own pattern of community structure. There is a general trend for the number of species of epifaunae to correlate positively with spatial heterogeneity.

9. No matter how many species of a class of motile animals are found in a zone and no matter how abundant the total class is in the area, there are usually about two "relatively abundant" species making up 50 percent of the total individuals in each zone. Only sipunculans and gastropods require four species to make up 50 percent of the total number of individuals in certain zones.

10. Sipunculans are a particularly "packed" group of species on the intertidal limestone reef flat, having a high diversity, by far the highest species per genus ratio, a high number of common species on both a relative basis and an absolute areal basis, but not a particularly large number of species per zone.

11. A predominant intertidal red algae, *Laurencia papillosa*, undergoes significant changes in dry weight biomass, but the population does not vary seasonally on the Galeta transect to the extent that it does in Florida.

12. On the andesite rock shore at Paitilla on the Pacific coast, the barnacle *Tetraclita stalactifera panamensis* provides a series of space niches for 32 species of mollusks, 37 species of polychaetes and several species of crustaceans, anemones, turbellarians, nemerteans and other invertebrates. When a *Tetraclita* dies, invertebrates colonize the empty test within a month. The abundance and diversity of these associates increases steadily for six months, then continues about a mean with slight fluctuations.

13. Drift logs hinder the spread of the mangrove forest across the intertidal reef flat by destroying isolated advancing recruits. The logs then

drift up against the solid outer bands of stilt roots of the forest and stop, not doing any apparent damage to the standing forest itself.

14. The Caribbean sand beach faunae varied greatly between wet and dry seasons in terms of species composition and abundances. This was probably due to changes in substratum composition and/or grinding action of the sand brought about by heavier wave action during the windy dry season.

15. Animals settle on plexiglass plates in a pattern indicating that recruitment is seasonal in different ways in the two oceans. A larger portion of the Caribbean species were restricted to a specific portion of the year, but the total dry weight of the fouling community on each plate varied less obviously with season than it did in the Pacific.

SECTION II

RECOMMENDATIONS

It is obvious that an extensive treatment with oil will kill animals, but it is not safe to conclude a lack of harmful effects if the creatures appear to be in good health following an oil spill. The presence and cost of repair of unseen physiological damage must be determined and measured with an objective, quantitative indicator. Decrease in growth rate is an indicator of the general cost of repair and should be utilized as a standard measure. The balance in many populations, especially in corals, between rates of growth and grazing or other factors of deterioration are of basic importance.

Mass mortality is not an unusual occurrence in marine communities, but most natural communities are stable in that they respond with a predictable pattern of recovery to natural catastrophes. Mortality itself should not be the main subject of interest in pollution studies. Of greater importance is the effect of pollution on recruitment. The eventual final stage in succession may be modified by an alteration of relative success of different organisms in the earlier stages.

We learned that experiments concerned with the effects of oil on whole communities cannot be conducted on one meter square experimental and control quadrats because of the constant washing with fresh seawater. Each experimental and control quadrat should be much larger, a program that is not a recommended way to treat the shoreline because of potential damage to surrounding areas, the possibility of interfering with other studies, consideration of local people and difficulty in obtaining permission from authorities. Instead, we recommend concentrating on specific questions for which experimental tests with precise controls can be designed, e.g., growth rate or recruitment experiments. Examining the effects of pollution on entire communities required too large an experimental area, and precise controls are difficult to obtain.

For all experimental studies on the effects of oil pollution, experimental controls should be emphasized because of natural variation between local areas for physiological events in tropical species. A horizontal distance of 3 m or periods of time 2 months apart had greater effect on the growth of corals than 2.5 hours exposure to Bunker C oil, although the effect of oil was statistically significant. The latter was determined by comparison with very precise controls.

In order to evaluate the effects of unpredicted events on community structure and to provide a foundation for understanding the communities with which we are working, baseline studies should be performed in regions of

high probability of future subjection to pollution. In these surveys, the pattern and relative magnitudes of the variances are of far greater interest than the values of the means or averages. For instance, recruitment to settling plates varied seasonally in biomass in the eastern Pacific but not in the Caribbean. However, recruitment varied seasonally in species composition more in the Caribbean than in the Pacific. These sorts of distinctions in patterns of variation provide more power and insight for analyzing results of experiments and observations than do descriptions of community structure.

SECTION III

INTRODUCTION

On 13 December 1968, the 35,000-barrel oil tanker *SS Witwater* broke apart about three miles from the Smithsonian Tropical Research Institute (STRI) Marine Laboratory on the Caribbean coast of Panama and released approximately 20,000 barrels of Bunker C and marine diesel oil which spread over the shoreline. The STRI staff, with aid from US armed forces personnel and the conditions of high water, cleared much of the oil from the water around the laboratory and apparently reduced the potential damage to the natural marine communities (Rützler and Sterrer, 1970). The marine communities on the reef flat do appear normal now, and did when the project started two years after the oil spill. The amount of damage could not be evaluated quantitatively because the Galeta Point laboratory was set up only a short time before and no baseline data were available for comparison. In considering the problem of evaluating the effects of such occurrences on tropical marine systems, it became clear that it was not just a matter of gaining baseline data for the local reef flat. Adequate information was not available for any Caribbean intertidal reef flat communities.

Although the effects of increasing spillage of hydrocarbon oils into the sea have been reported since the early 1920's (US Public Health Service, 1924; Lane, 1924, 1925; Orton, 1925), it was not until a major disaster as the 1967 Torrey Canyon incident that the concern about oil pollution received intense and world-wide attention. It then became apparent that it was very difficult, if not impossible, to evaluate the effects of oil pollution in marine ecosystems, due to the sparsity or complete lack of prepollution ecological data. Until the beginning of this study, the only comprehensive account of pre- and postpollution distribution of intertidal organisms is that of Nelson-Smith (1968) who worked in Milford Haven, Britain. Most of the current information is from studies in temperate regions (Carthy and Arthur, 1968; Pollution Abstracts, 1970-1973). On tropical marine shores, the sparsity of ecological knowledge has been particularly eminent. Very little information was available on the structure of undisturbed intertidal communities in the Caribbean. The information available was either qualitative or concerned with a narrow subject. Consequently, the Environmental Protection Agency (EPA) contracted the Smithsonian Institution to undertake a project on (1) the normal variations in structure of Caribbean intertidal communities, and (2) the effects of oil on these communities.

The research sponsored by EPA at STRI consisted of a 3-year program. During the first year, a baseline of information on community structure and recruitment patterns on both the Caribbean and Pacific coasts was established.

Studies of the rocky intertidal, reef flat intertidal, sandy beach, and mangrove habitats were included. During the second and third years, normal temporal variability in both community structure and recruitment were evaluated by comparing data taken over the three-year period. During the second year, controlled experiments were begun on the effects of oil pollution at both the levels of tropical marine communities and physiology of individual organisms.

The oil pollution experiments were not set up to make trivial demonstrations of mass killoffs under a heavy coat of oil, but to perform a quantitative analysis of oil effects detectable only by comparisons with controls in the experiments. The report is presented in two separate parts, the baseline surveys (Sections IV through VIII) followed by the oil pollution experiments (Sections IX through XIII).

A reference collection for the species listed in this report is kept at the STRI Marine Laboratory at Galeta to confirm identifications in future projects at the same locality and to assist in verifications of the records in this report. A few species which are represented by only a few specimens have been submitted to the organizations of the taxonomic authorities that provided the identifications. These locations can be found in the acknowledgments section.

PART I

BASELINE SURVEYS OF THE MARINE COMMUNITIES

SECTION IV

SURVEY OF THE CARIBBEAN INTERTIDAL REEF FLAT AT GALETA

The baseline survey program of the Galeta laboratory was organized around a consideration of the intertidal as consisting of five distinct zones. Although the extreme range in tidal fluctuations covers only 0.7 m, the five communities of organisms from the laboratory (Acanthophora Zone) to the surf (Coralline Zone) was obvious on the first view of the reef flat (Table 1). The composition of occupation of primary substrata in the five zones was measured through the contact made by the fall of 25 point-set quadrats in positions located by coordinates obtained from tables of random numbers. The actual data consist of independent counts, not measures or percentages, although data are transformed into percentages for presentation and discussion for easier comparisons.

DISTRIBUTION AND ABUNDANCES OF INVERTEBRATES

The main purpose of the baseline study was to acquire a quantitative estimate of the community structure of a tropical intertidal reef flat. In this section we will discuss the communities of motile epifaunal and infaunal macroinvertebrates collected along an intertidal transect at the Galeta Marine Laboratory. Macroscopic invertebrates are operationally defined as those we could sort out with forceps in trays without requiring a dissecting microscope. This means the animal is at least 2 millimeters in length or width.

During the sampling program, approximately 50,000 specimens were sorted for 520 different species which were identified to genus or species. The descriptive data in a catalog of species for the Caribbean intertidal reef flat transect at Galeta would disrupt the text, so the data are organized in Appendices A through D. Although the data are summarized at the level of order and class in Tables 2 through 6, the information for each species is presented in the appendices in order to provide the reader with the opportunity to derive answers to original questions he might have. This also allows for more accurate and extensive comparisons with communities or specific groups of intertidal organisms in other localities or long-term changes in populations of selected species on the Galeta transect.

For conveniently and accurately making comparisons, we have attempted to design the appendices in an efficient format that perhaps could serve as a standardized form of data presentation. In the Results section below, the explanations and justifications for the statistics and format used in the appendices are presented. If the reader does not wish to spend time with explanations of procedures, but mainly wishes a summary of the findings, then the reader may skip the Methods and Results sections below and move straight to the Discussion section on page 20.

TABLE 1. DESCRIPTION OF ZONATION ON THE CARIBBEAN INTERTIDAL REEF FLAT AT GALETA IN TERMS OF PERCENT SURFACE COVERAGE. Variance is defined as $\chi^2/\text{d.f.}$, each sample consisting of about 250 or 500 points. For easy reading and comparisons, all data were transformed to percentages after analysis. Red algae and anthozoans were vastly predominant. In order to provide quick class or phylum recognition for those unfamiliar with local species, the names are followed by the following letters: R = Rhodophyta, C = Chlorophyta, P = Phaeophyta, A = Anthozoa, S = Porifera.

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
TOTAL SAMPLE SIZE IN RANDOM POINTS	2491	1750	3000	1750	2250
crustose coralline algae R	53.43±0.48	15.20±1.88	7.30±0.34	0.57	1.20±0.18
<i>Halimeda opuntia</i> C	14.89±0.28	8.57±1.80	5.23±1.05	3.03±1.51	2.22±0.27
<i>Laurencia papillosa</i> R	1.08±1.08	59.37±1.17	1.40±0.58	0.11	14.22±1.06
<i>Acanthophora spicifera</i> R		1.83±0.27		1.03±0.33	21.06±0.74
<i>Zoanthus sociatus</i> A		0.80	65.43±0.31	0.05	
<i>Zoanthus solanderi</i> A	9.03±0.37				
<i>Thalassia testudinum</i>			0.16	26.17±1.65	5.86±0.49
<i>Millepora complanata</i>	4.42±0.32	0.80	0.33		0.04
<i>Porites furcata</i> A	4.18±0.20	0.29			
<i>Porites astreoides</i> A	1.04±0.10				
<i>Palythoa caribaeorum</i> A	3.09±0.10		0.06		
branching coral- line algae R	1.12±0.42	1.77±0.37	0.40	0.34	0.97
short filamentous green algae C	2.41±1.86	1.26±0.27	2.23±0.90		2.04±1.43
<i>Phyllactis floculifera</i> A	0.08	0.29	2.80±0.11		
<i>Erythropodium caribaeorum</i> A	0.92±0.16		0.06		

TABLE 1 continued. DESCRIPTION OF ZONATION ON THE CARIBBEAN INTERTIDAL REEF FLAT AT GALETA IN TERMS OF PERCENT SURFACE COVERAGE.

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Dichocoenia stokesii</i> A	0.24	0.06			
filamentous brown algae R & P	0.16				
<i>Trididemnum solidum</i>	0.12				
<i>Agaricia agaricites</i> A	0.08				
<i>Caulerpa racemosa</i> C	0.08	0.11	0.26		
<i>Caulerpa sertularioides</i> C			0.06	0.28	
<i>Peyssonnelia nordstedtii</i> R	0.08	0.06			
<i>Dictyosphaeria cavernosa</i> C	0.04		0.16		
<i>Wrangelia argus</i> R	0.04		0.03		
<i>Hypnea spinella</i> R	0.04				0.35
brown sponge S	0.04				
anemone spp. A	0.04				0.04
<i>Isaurus duchassaingi</i> A		0.06			
<i>Gelidiella acerosa</i> R		0.46	0.10		
<i>Penicillus capitatus</i> C				0.68	0.13
<i>Anthosigmella varians</i> S				0.22	0.75
<i>Craniella</i> sp. S					0.17
gray sponge S					0.04
bare rock, sand or detritus	3.33±0.22	8.86±1.32	13.93±0.42	67.49±1.09	50.84±0.97

TABLE 2. NUMBER OF GENERA/NUMBER OF SPECIES IN EACH OF 15 CATEGORIES OF ORGANISMS IN EACH OF 5 INTERTIDAL REEF FLAT ZONES AT THE GALETA MARINE LABORATORY ON THE CARIBBEAN COAST OF PANAMA.^a

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
CHLOROPHYTA	14/17	13/17	11/12	11/15	13/18
PHAEOPHYTA	5/5	4/4	2/2	4/4	2/2
RHODOPHYTA	21/41	19/35	13/20	18/27	18/29
ZOANTHINIARIA	3/4	3/5	2/2	2/2	1/1
ACTINIARIA	5/6	6/8	6/8	5/5	5/6
OPHIUROIDEA	11/18	9/18	9/11	9/11	8/12
ECHINOIDEA	6/7	6/7	5/6	6/7	6/7
AMPHINEURA	6/10	5/10	4/8	4/8	3/7
GASTROPODA	28/43	23/31	20/25	15/15	22/27
BIVALVIA	14/17	17/21	10/13	10/13	15/18
SIPUNCULA	5/25	6/29	5/22	7/20	6/35
POLYCHAETA	51/80	48/75	33/42	39/54	32/46
PYCNOGONIDA	7/9	8/11	8/10	3/3	7/10
NATANTIA	9/22	5/18	4/7	4/7	9/14
REPTANTIA	18/35	17/22	12/14	10/13	11/14
TOTAL ALGAE	40/63	36/56	26/34	33/46	33/49
TOTAL ANIMALS	146/276	153/255	118/158	114/158	125/197

^a The data for numbers of genera and species include all those recorded in samples along with others seen in the immediate area in which samples were taken, but not actually in the samples.

TABLE 3. NUMBER OF SPECIES NECESSARY TO MAKE UP 50% OF THE INDIVIDUALS IN EACH ZONE FOR EACH OF 11 CATEGORIES OF MACROINVERTEBRATES ON THE INTERTIDAL CARIBBEAN REEF FLAT AT GALETA MARINE LABORATORY.

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
ACTINIARIA	2	2	2	1	1
OPHIUROIDEA	3	2	1	1	1
ECHINOIDEA	1	2	1	1	2
AMPHINEURA	2	1	2	1	3
GASTROPODA	3	3	4	2	4
BIVALVIA	2	1	2	2	2
SIPUNCULA	4	4	3	2	2
POLYCHAETA	3	1	2	2	2
PYCNOGONIDA	2	3	2	2	2
NATANTIA	2	2	2	2	2
REPTANTIA	2	2	3	2	2

TABLE 4. SHANNON-WIENER INDEX OF DIVERSITY CALCULATIONS FOR EACH OF TEN CATEGORIES OF MOTILE MACROINVERTEBRATES IN EACH OF THE FIVE INTERTIDAL ZONES ON THE CARIBBEAN REEF FLAT AT GALETA MARINE LABORATORY. The formula used to calculate the indices was $-\sum_i p_i \log_2 p_i$.

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
OPHIUROIDEA	3.02	2.20	0.88	1.75	1.22
ECHINOIDEA	0.90	1.73	0.14	1.86	1.84
AMPHINEURA	2.71	2.15	2.49	2.25	2.70
GASTROPODA	3.72	3.04	3.80	2.72	3.52
BIVALVIA	2.34	1.93	3.89	2.64	2.51
SIPUNCULA	3.50	3.95	3.20	2.74	2.45
POLYCHAETA	3.74	2.37	3.10	3.52	3.04
PYCNOGONIDA	2.51	2.63	2.52	1.39	2.61
NATANTIA	2.91	3.08	1.76	2.30	2.66
REPTANTIA	2.81	2.40	3.10	2.33	2.45
MEAN DIVERSITY OF ALL TEN CATEGORIES	2.82	2.55	2.49	2.35	2.50

TABLE 5. MEAN NUMBER OF INDIVIDUALS PER M² FOR ALL MEMBERS OF EACH OF 12 CATEGORIES OF MACROINVERTEBRATES ALONG THE CARIBBEAN INTERTIDAL REEF FLAT TRANSECT AT GALETA MARINE LABORATORY.

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
ZOANTHINIARIA	4346	1366	4830	50	33
ACTINIARIA	129	79	110	117	36
OPHIUROIDEA	334	166	294	53	323
ECHINOIDEA	34	42	10	13	3
AMPHINEURA	65	149	48	13	14
GASTROPODA	72	60	34	22	28
BIVALVIA	134	288	150	37	198
SIPUNCULA	175	352	265	209	633
POLYCHAETA	2697	5914	1201	640	1073
PYCNOGONIDA	25	34	37	4	38
NATANTIA	270	31	30	10	64
REPTANTIA	471	153	46	40	79
Average ^a total number of macro- invertebrates per m ² (excluding coelenterates and sponges)	4323	7297	2137	1087	2498

^a From Appendix B.

TABLE 6. NUMBER (AND PERCENT) OF "COMMON" SPECIES, DEFINED AS OCCURRING IN AVERAGE ABUNDANCES GREATER THAN $1/m^2$. Twelve categories of macroinvertebrates are considered separately for each of five intertidal Caribbean reef flat zones at Galeta marine laboratory.

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
ZOANTHINIARIA	3(75)	4(80)	2(100)	2(100)	1(100)
ACTINIARIA	6(100)	6(75)	6(75)	5(100)	4(67)
OPHIUROIDEA	12(67)	8(44)	6(55)	7(64)	9(75)
ECHINOIDEA	3(43)	4(57)	3(50)	3(43)	1(17)
AMPHINEURA	9(90)	9(90)	6(75)	4(50)	6(86)
GASTROPODA	14(33)	13(42)	7(28)	4(27)	6(22)
BIVALVIA	8(47)	12(57)	9(69)	6(46)	10(56)
SIPUNCULA	16(64)	20(69)	16(73)	13(65)	16(46)
POLYCHAETA	52(65)	52(69)	30(71)	31(57)	30(65)
PYCNOGONIDA	6(67)	6(55)	7(70)	2(67)	7(70)
NATANTIA	14(64)	5(28)	3(43)	2(29)	9(64)
REPTANTIA	24(69)	10(45)	8(57)	5(38)	6(43)
	167	149	103	84	105

Methods

The transect line extended from the northeast corner of the Galeta Marine Laboratory (Acanthophora Zone) to the furthest and lowest point in the intertidal (Coralline Zone) and was divided into 5 segments according to the pattern described in Table 1. The boundaries were marked by iron concrete-reinforcing rods which were hammered into the reef top and, surprisingly, are still in good condition after three years. The specific location of each quadrat sample in each zone was determined by selecting two coordinates from a table of random numbers: the first representing those paces taken directly along the transect line perpendicular to shore; the second representing paces taken perpendicular to the transect line at that point.

A sledge hammer and chisel were used to dig up all the material to a depth of 6 to 8 cm that lay within a 0.125 m² frame tossed on the sample site. The dead coral fragments, large pieces of dead coral and plants were then rinsed in seawater while the sand and silt were sieved. The silt, sand, and rinse water were then each carefully examined for small faunal species. The macroscopic fleshy algae, *Thalassia*, crustaceans, mollusks, echinoderms and some worms were removed from the dead coral fragments and separated. Further examination of dead coral fragments and rocks for sponges, tunicates and other faunal species followed. The coral fragments and macroscopic fleshy algae were examined under a dissecting scope for smaller cor-alphytic and epiphytic algal species. Finally the large pieces of dead coral were broken down into smaller ones in order to facilitate the search for burrowing sipunculans, bivalves, and crevice-inhabiting polychaetes.

The small pieces of coral were then placed in the refrigerator in a tray of fresh seawater. Many polychaetes emerged after this treatment and all polychaetes and sipunculans were relaxed more effectively by cooling overnight rather than by utilizing MgSO₄.

Results

Findings from the survey are summarized and presented in the tables of Appendices A through D and Tables 2 through 6. In many descriptions of the spatial and temporal structures of communities, only abundances of each species in terms of mean plus standard deviation are presented. In contrast, we believe that statistics concerning frequency, predominance, and dispersion should be presented in addition to abundance and that for the vast majority of intertidal invertebrate species, tropical or temperate, mean plus standard deviation are not the best statistics. Further, we placed each of these statistics for each species in the same location in the table in order to give the reader the ability to make quick comparisons of these different measurements for a single species in the same location. To extend this comparison within the species to different zones, the reader shifts laterally in the table; to compare these measurements of different species within the zone, the reader moves vertically. The main

criticism against this tabular presentation of descriptive statistics may be that the pile of 5 numbers in each species-zone unit is bulky. But having it in one location is more efficient than in 5 sets of tables. The table is basically similar to that of E. W. Fager on the invertebrates in decaying oak wood (1968) or plankton (1963). The 5 statistics are briefly discussed from top to bottom in order of their organization in Appendices B, C, and D.

The first line in each set of statistics refers to frequency, the number of samples in which collections of the species were obtained over the total number of samples sorted for this species. Frequency is a very important index with which to judge the spread of the species within the zone, to evaluate its significance in the zone and to evaluate the reliability of other statistics such as "fidelity."

"Fidelity" is a measure of the degree to which a species is confined to one zone. This is not presented directly as an additional line to the unit of statistics because it can be easily observed by comparing the frequency figures of the species through the zones. For instance, note that *Paraliomera* is quite restricted to the Coralline Zone, each polychaete species is distributed through all zones but each is particularly abundant in one zone and *Arca* is fairly uniformly distributed through all zones. Fidelity is an indication of an ecological characteristic of each species which is very important for both the baseline and pollution studies. For most species, each zone is a physically and biologically different environment. If a species is generally restricted to one zone it may be regarded as a specialist, while if found fairly uniformly throughout most zones it may be regarded as adapted to a wide range of conditions. It may be hypothesized that wide-ranging species may be more tolerant to oil pollution than highly localized species. This definition of degree of generalization of a species based on fidelity to a zone is also of particular interest to our baseline studies. The baseline studies are, in part, a comparison of the structure of intertidal communities in mild but unpredictable environments (Caribbean, Galeta) with those in harsh but predictable environments (Pacific, Paitilla). The degree to which the predominant species are generalists or the proportion of species which are of restricted range in the communities occupying these environments of opposite physical characteristics is of theoretical interest for several reasons. Further, these same comparisons will be extended to inspect the species characteristics between the zones within each of the intertidal ranges under study.

Abundance is described in the second and third lines in two manners, in median plus quartiles (second line) and in mean plus standard error of the mean (third line). Since most intertidal invertebrates are quite aggregated in their dispersion, the abundance count data do not resemble a normal distribution. Thus the mean plus standard error is not an appropriate abundance statistic and the median plus quartiles is much more informative because it provides a more precise record of aggregation. Examples demonstrating the definitive superiority of the median and quartiles in terms of

clarity, informativeness and reality are *Ophiactis* in the Zoanthus Zone and *Perinereis* in the Acanthophora Zone.

Although not a realistic statistic for most species of intertidal invertebrates, the most usual presentation of abundance counts in the literature are in terms of mean and standard error of the mean. Therefore, these numbers are included for easy comparison with other surveys in the literature. The number is in parenthesis because the calculations are made to conform to the square meter area standard in the literature while the other lines are on a one-eighth square meter to conform to our sample size.

The relative abundance of a species to others within its class in a zone is of more direct and immediate value as information pertinent to functional characteristics of a species than is absolute abundance. The majority of theoretical essays on community structure have been based on this form of information. Data presented at the class level summarize the degree to which a few species are predominant and whether most are rare. However, predominance (a large relative abundance) does not necessarily imply dominance (importance of functional role in the community).

Dispersion pattern is a very important description category for species in both the pollution and baseline work. The vast majority of invertebrate species are clumped in distribution. This, of course, is responsible for the requirement of extensive sampling in following the fate of most species. Morisita's index of dispersion is of primary interest in raising questions on the physical and biological environmental factors which affect the distribution patterns of each species. For instance, if the index of dispersion of a species drops below unity as it becomes more abundant, then an increase in intraspecific competition may be suspected. If a species is more clumped in one zone than in others, reproductive behavior or certain predators may be restricted to these zones or the physical environment relevant to the particular species, though not obvious to us, may be more patchy.

Discussion

For the convenience of the reader, the specific data in the appendices are summarized at the level of classes or orders for the communities of each zone (Tables 2 through 6). The number of identified species and genera living together in each zone are summarized in Table 2. For most classes, there is usually an average no higher than 2 species per genus. For the sipunculans, however, there is an average of 4 to 6 species per genus except in the Thalassia Zone. Although there are often 2 or 3 times as many species of polychaetes in an area, the sipunculans appear more tightly "packed." For instance, terebellid, nereid, sabellid and amphinomid polychaetes are very different in their morphology while most sipunculans appear relatively similar to each other. Because of this, more species tend to fall into fewer genera and this may serve as a rough index of "packing."

The lowest numbers of species that constitute over 50 percent of the individuals in each zone are summarized in Table 3 for each of 11 classes of animals. Curiously, no matter how many species are in the area and no matter how abundant or numerous the total class is in the area, there seems to be most often 1 "relatively abundant" species making up 50 percent of the total. For invertebrate communities in general, some as remote as those in decaying oak logs in an English forest (Fager, 1968), at least half the individuals are made up of about 2 species. The calculated diversity indices (Table 4) correlate with the number of "relatively abundant" species in a rather imprecise manner. This may lead us to wonder whether nearly all communities (or zones) are organized around a similar pattern of common species while certain areas or classes with higher diversity have only additional rare species. For instance, compare pycnogonids and polychaetes. The polychaetes are represented by about 4 to 18 times as many species (Table 2), usually over 100 times as many individuals as pycnogonids (Table 5) and usually a higher diversity (Table 4), but over 50 percent of the individuals in both classes are usually made up by about 2 species.

A vague correlation does exist between diversity and the number of species required to make up 50 percent of the individuals in a class. Gastropods and sipunculans are the only classes that sometimes require 4 species (Table 3) and are usually the 2 classes with the highest diversities (Table 4). Sipunculans are a particularly "crowded" group of species on the Caribbean intertidal reef flat whether considering species "packing" (Table 2), the number of "relatively abundant" species (Table 3) or species diversity (Table 4).

Tables 2, 3, and 4 are concerned with summarizing relative abundances; Tables 5 and 6 with absolute abundances. Table 5 compares the average number of individuals per m^2 for twelve taxonomic categories of animals in each of the zones. On the intertidal reef flat, polychaetes are clearly the numerically predominant class of motile animals and the Laurencia Zone is the most heavily populated region. However, the greatest number of "common" species is found in the Coralline Zone (Table 6) when we arbitrarily define "common" in the absolute sense as having an abundance greater than $1/m^2$.

The spatial pattern of the reef flat biota at Galeta is summarized in Table 1 for sessile species and in Figure 1 for the abundance and variety of motile animals in relation to sessile species. Spatial heterogeneity of different zones of the reef flat is defined and measured as diversity of surface coverage by sessile species and categories of substrata. The numbers of common animal species ($>1/m^2$) and the mean diversities of the 10 major categories of motile animals have the same general comparative relationships in magnitude between zones as do the measurements of spatial heterogeneity. However, the numbers of algal species and of animal species differ from the other trends and correlate with each other in that they reach their lowest values in the Zoanthus Zone. This may be because of

Codes and ordinate scale units are as follows:

- Spatial heterogeneity. Shannon-Wiener measure of counts of sessile species and substratum categories contacted by the fall of random points obtained from a random number table. Each unit on the ordinate axis = 0.5 bits per individual.
- Shannon-Wiener diversity measurements in each zone averaged over the 10 major categories of macroscopic motile invertebrates. Each unit on ordinate = 0.5 bits per individual.
- No. individuals/m² for 10 categories of macroscopic motile invertebrates combined. Each unit on ordinate = 2000 individuals/m².
- - - - - Total number of species in all categories of macroscopic invertebrates. Each unit on ordinate = 50 species.
- - - - - Total number of algal species. Each unit on ordinate = 25 species

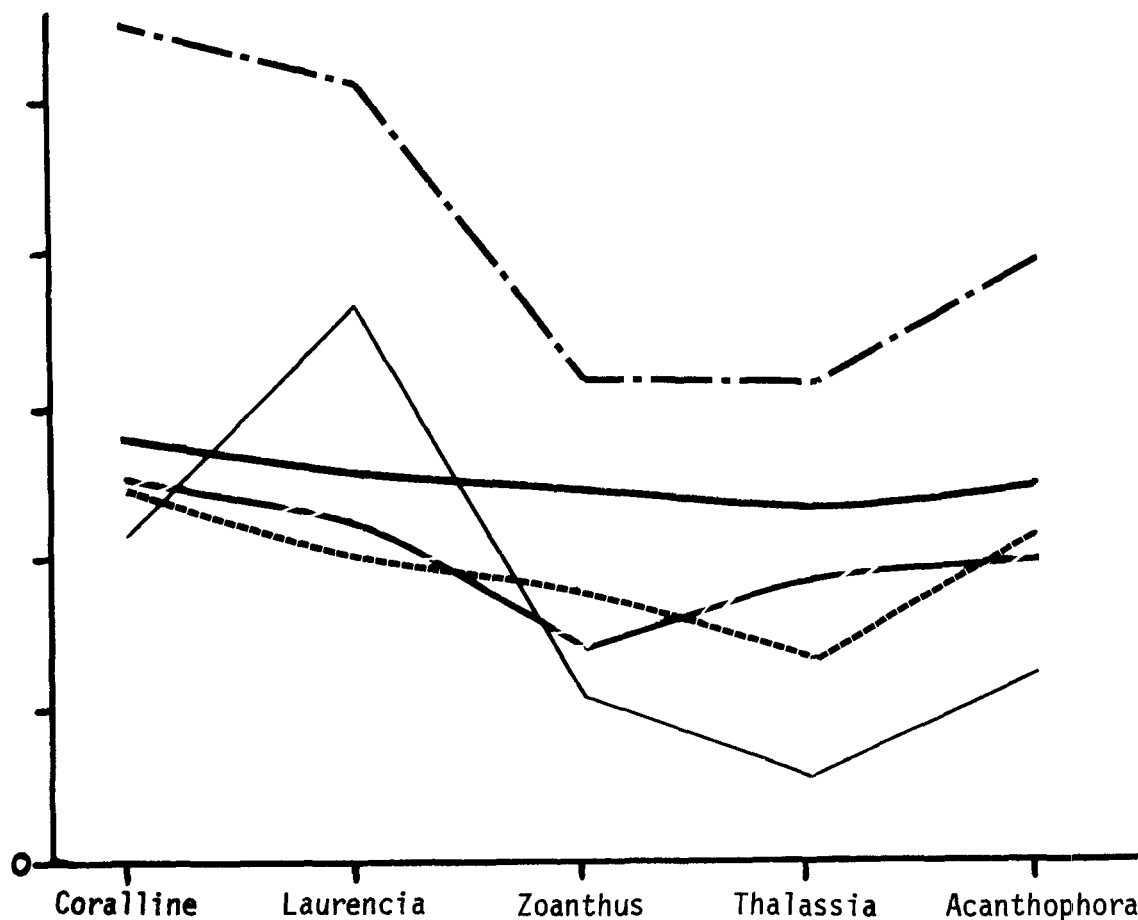


Figure 1. A comparison of the total abundance, number of species and diversity of macroscopic invertebrates with the pattern of spatial heterogeneity in the communities of encrusting organisms on intertidal zones at Galea.

the unpredictability of the survival of the predominant species in the zone, *Zoanthus sociatus*. In Caribbean intertidal areas occupied mainly by sessile animals, mostly anthozoans or sponges, the surface coverage patterns tend not to fluctuate regularly but to undergo unpredictable catastrophes, usually because of desiccation. The greatest variability with time and seasonal change is found in zones in which algae are the predominant space-holders. A study of the patterns of variation in time of the biotic communities on the Galeta reef flat and its influence on adaptive strategies of the resident species and on community structure was begun during this EPA study and is being continued as part of the Environmental Sciences Program of the Smithsonian Institution.

VARIATION IN BIOMASS OF THE PREDOMINANT RED ALGA, *Laurencia papillosa*

Our survey of the intertidal reef flat at Galeta was begun with the expectation of disproving the stereotypic picture of a tropical marine community as a system with very small fluctuations in abundances of the predominant species. To our surprise, we indeed found no gross seasonal changes in numbers or surface coverages of predominant species. The observed seasonal variations were not large enough to change the general appearance of the area and the irregular variation between years was more obvious than the seasonal changes. [The data and information on these temporal variations in the reef flat community are available as photo-offset copies from the Smithsonian Tropical Research Institute. One should ask for pages 227 to 231 of Environmental Monitoring and Baseline Data compiled under the Smithsonian Institution Environmental Sciences Program (1973)] It appeared, however, that the biomass may be changing on a larger scale than the surface coverage data indicated. That is, the *Laurencia* looked as if it were becoming flatter and thinner while still occupying most of the space previously occupied. In order to test and quantify this observation, we decided to take samples and measure the dry weights. *Laurencia papillosa* was selected because of its predominance on the reef flat, especially in the *Laurencia* Zone (Table 1) and because its seasonal variation in spatial occupation was the most pronounced.

Methods

Thirty-six permanent markers were placed along the seaward edge of the *Laurencia* Zone, 2 meters apart (railroad spikes, 18 to the left and 18 to the right of our transect line). These markers served as reference points from where a distance in the numbers of centimeters acquired from tables of random numbers were measured along the zone's edge. Another distance value, measured at a right angle inward to the first gave a point in the center of a 0.06 m² quadrat. Distances were measured very accurately in centimeters and placement data for all quadrats collected were kept in order to avoid sampling the same spot twice. If a placement fell on a tide pool or on a patch with over 50 percent *Halimeda* coverage, a new placement for that quadrat was found.

All the *Laurencia* and *Halimeda* present within the 0.06 m² frame was picked up by hand or by using a paring knife. Samples were placed in bottles identified with their placement numbers. In the laboratory, *Halimeda* and *Laurencia* were separated and washed in running seawater over a screen to removed any sediment or organisms caught in the blades. The algae were fixed in 5 percent formalin in seawater for 2 days, dried to constant weight and weighed in a Mettler balance.

Results and Discussion

Four collections were made (Table 7); the first collection was taken after a period of continuous coverage of seawater at high tide levels for at least 1 week previous to the sampling, the other three after a period of at least 1 week of prolonged midday exposures. An analysis of variance on the biomass of *Laurencia* found in the four collections showed that there was a significant difference in biomass (Table 7). For some reason the *Laurencia* biomass to the left of the transect line seemed more sparce than the lush growth to the right of the line. A test applied to the 36 samples of the May 2nd collection showed the difference to be insignificant ($t = 1.57$, $P > 0.05$).

Although the changes in biomass of *Laurencia papillosa* were statistically significant, the changes would not be obvious without careful quantitative sampling. Our results are in striking contrast to those of Thompson (1969) and Bernatowicz (1952) who found marked seasonal changes in biomass and surface coverage of many algal species in Florida and Bermuda. Although technically the Florida and Bermuda studies were in the temperate zone (above the Tropic of Cancer) while ours were done in the tropics, most of the species are common to our studies. It suggests that the same community may have different dynamic properties in different regions. A part of this difference may also be due to our studies not being comparable with theirs. Casual observations on species outside our transect (e.g., *Padina* sp.) suggest that other species show more temporal change than those we studied. Further, the data of Croley and Dawes (1970) indicate much less seasonal change in Florida than those of Thompson (1969).

Other aspects of the biology of organisms in our studies, such as reproduction and larval settlement, often show more periodicity than biomass or surface coverage (Section VIII). The Caribbean fouling organisms were found to be significantly more "seasonal" than those in the Pacific by this comparison.

TABLE 7. BIOMASS OF PREDOMINANT ALGAE IN THE LAURENCIA ZONE, GALETA REEF FLAT, ON FOUR DIFFERENT COLLECTION DATES.

Collection date	No. of samples of <i>Laurencia</i>	Average dry weight of <i>Laurencia</i> (in gms)	No. of samples with <i>Halimeda</i>	Average dry weight of <i>Halimeda</i> (in gms)
February 9, 1972	36	16.6	15	no data
March 22, 1972	20	15.0	3	no data
May 2, 1972	36	10.4	20	37.36
June 15, 1972	20	14.2	17	26.68

Analysis of variance for the biomass of *Laurencia papillosa* and *Halimeda opuntia* from February thru June 1972.

	d.f.	F	Significance
<i>Laurencia papillosa</i>	3, 90	6.83	P < 0.001
<i>Halimeda opuntia</i>	1, 36	0.69	n.s.

SECTION V

SURVEY OF THE PACIFIC INTERTIDAL ANDESITE ROCK BEACH AT PAITILLA

DISTRIBUTION AND ABUNDANCE OF INVERTEBRATES

The Pacific coast of Panama is made up predominantly of sand or andesite rock substrata with a pronounced vertical zonation of the biota and extreme tidal fluctuations. Because of the differences in substrata, hydrography and the much wider but more regular fluctuations of parameters such as temperature, nutrient upwelling and salinity, it was of interest to survey a Pacific locality and to investigate the effects of oil pollution on that locality. Because of adaptation to a more widely fluctuating but predictable environment, the Pacific coast communities may respond to pollution in a different way than the communities on the reef flat on the Caribbean coast.

At first sight, Paitilla beach appeared to be rather barren of organisms and very simple in the structure of its invertebrate communities. It is characterized by an upper intertidal zone of littorinids, a very wide expanse where the dominant species was the barnacle *Tetraclita stalactifera panamensis*, an area dominated by *Chthamalus panamensis*, and a lower Abietinaria Zone of hydroids and bryozoans. The paucity of organisms and simplicity of structure were, however, only apparent. As an example, the sorting to major taxonomic categories of a 0.125 m² sample from the Abietinaria Zone required 80 hours of labor. The *Tetraclita* Zone had an extremely rich fauna of mollusks and polychaetes associated with the barnacle tests. Because of the tremendous amount of time required for the sorting of samples, our work on the Pacific shore was very limited and only represents a preliminary study of the area.

Methods

The study area was located at Paitilla, an eastern suburb of Panama City, directly southeast of the Club Union de Panama (Via Italia and Tomas G. Duque Street). A transect line was determined by walking with a compass southwest from the back steps of the Club Union de Panama along the reef. Four zones were evident along the intertidal portion of the beach. They were named the Littorina, *Tetraclita*, *Chthamalus*, and Abietinaria Zones, according to the most conspicuous species present in each zone.

Once a particular zone was reached along the transect line, four 0.125 m² samples were taken at positions determined from a table of random numbers. In the Abietinaria Zone the samples were obtained by two methods: scraping the rocks and chipping off and collecting the rocks. In the *Chthamalus*

Zone, samples were scraped from the rocks. In the *Tetraclita* Zone, barnacles were removed from the rock and areas covered with a mat of algae were scraped. In the *Littorina* Zone, animals within a 1 m² frame were counted in the field.

Two sets of 4 samples each were collected in the *Abietinaria* Zone, one on 29 October 1970 and one on 26 April 1971. One set of 2 samples was collected in the *Chthamalus* Zone on 29 January 1971. Three sets of 4 samples each were collected in the *Tetraclita* Zone: one on 31 December 1970; one each on 26 and 27 April 1971, and one on 31 January.

To study the succession of organisms that settle on or in the tests of dead barnacles, *Tetraclita stalactifera panamensis*, an area 4.7 meters by 0.7 meters was marked in the *Tetraclita* Zone with Sea Goin' Pox Putty. Within the area, 532 *Tetraclita* were killed and the tests were left in place. The test of *Tetraclita* which were dead before the experiment began were removed. A map of the area showing position and size of each *Tetraclita* was made from photographs taken with a 4 x 5 view camera. The fate of individual barnacles, the settling of new *Tetraclita* and the colonization of the tests by invertebrates were followed periodically for 16 months.

Collections of the experimentally killed barnacles were preserved with formalin in the field. They were sorted by scraping and counting all the organisms attached to the external and internal surfaces of each barnacle, then the test was examined for animals that had settled in the parietal canals. Separation to species was done under a dissecting microscope.

Results and Discussion

The findings of the survey are summarized for the four intertidal zones at Paitilla in Appendix E. Observations from other areas in the eastern tropical Pacific indicate that the Paitilla beach fauna is depauperate by comparison. Several usually predominant species are missing. This probably is due to human activity in the area, such as the collection of oysters, large *Siphonaria* and other mollusks for food.

The oil pollution experiments discussed later in this report were performed in the *Tetraclita* Zone so this zone will be examined in detail. The information on organisms in the *Tetraclita* Zone will be presented in two sections. First a description of the structure of the *Tetraclita* community will be given. This is followed by an examination of an important aspect of the dynamics of the *Tetraclita* community, the succession of boring organisms and the eventual clearing of space by the weakening of the structure of *Tetraclita* tests.

COMMUNITY COMPOSITION OF THE TETRACLITA ZONE

The *Tetraclita* Zone occupies a wide expanse of the beach on the upper shore near and above mean sea level. The dominant organism is the barnacle *Tetraclita stalactifera panamensis*. Twelve samples, 0.125 m² each, gave an

average of 284 barnacles per m². Of these, 51 or 18 percent were dead and harbored a rich fauna of some 32 species of mollusks, 37 species of polychaetes, 3 species of sea anemones, 2 species of sipunculans and several species of crustaceans, nemerteans and turbellarians (Appendix E). Live and dead *Tetraclita* together occupy an average 28 percent of the surface area available in the zone (Table 8). The rest of the surface area is mostly bare rock except for a few anemones, patches of *Membranipora tuberculata*, *M. hastingsae* and sponges. The algae present in the zone (Appendix E) are very small and densely packed and grow close to the substratum. At first sight the zone appears almost barren at low tide. Aside from the barnacles and some crabs (*Pachygrapsus transversus*) which move about in and out of dead *Tetraclita* tests or crevices in the rocks, there are apparently no other animals in the zone. If a collection is taken and examined with care, over 4,000 specimens belonging to about 90 different species can be found in an 1 m² area (Appendix E).

Table 9 shows the number and abundance of taxa, their distribution among live and dead barnacles, and their physical position with reference to the barnacles. The first number gives the density or number in a taxon found per test of dead or live *Tetraclita*. The second number represents the percentage of the specimens of a particular taxon that are found in any particular niche. In the case of *Balanus*, 34 percent are associated with the external surface of live barnacles, 37 percent with the external surface of dead barnacles and 29 percent with the internal surface of dead barnacles. The third number in the table indicates the importance of each taxon on every niche relative to the total number of specimens of all species found in the samples. The last number in the table indicates the number of species found in each niche.

Dead *Tetraclita* offer several space niches to associated invertebrates: the external surface of the test; the base of the parapet or largest circumference of the barnacle where the test is attached to the substratum; the internal surface of the empty test; the parietal canals, which start with a large diameter at the base of the test and taper off to a point at the upper end. Most niches are occupied by a very diverse and abundant fauna which includes over 50 species. On dead barnacles the number of specimens associated with a particular niche is greatest on the internal surface. In order of decreasing importance, other niches are the external surface and the parietal canals. The number of species, however, is largest in parietal canals and decreases in the internal surface. The most important animals in terms of abundance and frequency of occurrence are three species of *Balanus*: *B. tintinnabulum*, *B. inexpectatus* and *B. amphitrite* which were not distinguished to species but counted together. They are found preferentially on the external surface (Table 9) where they represent 17.3 percent of the entire fauna associated with dead barnacles. They are also found on the internal surface of dead barnacles and there they make up 14 percent of the faunal associates.

TABLE 8. NUMBERS OF LIVE AND DEAD BARNACLES AND AREAS THEY OCCUPY IN THE TETRACLITA ZONE, PAITILLA BEACH.

Sample No.	No. of live <i>Tetracilita</i> /m ²	Per cent of area covered by live <i>Tetracilita</i> a	No. of dead <i>Tetracilita</i> /m ²	Per cent of area covered by dead <i>Tetracilita</i>	Per cent of area covered by both dead and live <i>Tetracilita</i>
1	376	20.21	120	8.33	28.54
2	264	20.22	96	3.50	23.72
3	368	32.33	48	3.98	36.31
4	680	33.91	104	7.62	41.53
5	104	15.30	24	3.72	19.02
6	176	16.58	40	4.67	21.25
7	136	14.84	24	3.12	17.96
8	312	31.82	56	6.77	38.59
9	120	no data	40	no data	no data
10	80	" "	40	" "	" "
11	88	" "	0	" "	" "
12	96	" "	16	" "	" "
TOTALS	2800	185.21	608	41.71	226.92
AVERAGE/m ²	233	23.15	51	5.21	28.36

a The number of barnacles actually on the substratum is from 87 to 100% of the total present. The rest are attached to other live or dead *Tetracilita*.

TABLE 9. RELATIVE IMPORTANCE OF DIFFERENT SURFACES OF LIVE (LT) AND DEAD (DT) *TETRACLITA STALACTIFERA PANAMENSIS* TO INVERTEBRATE POPULATIONS IN THE INTER-TIDAL. The data are based on eight 0.125 m² samples, including a total of 238 live *Tetraclita* and 29 dead *Tetraclita*. Four descriptive statistics are as follows, from top to bottom in each unit:

1. Number in a taxon found per dead or live *Tetraclita* test.
2. Per cent of each taxon found on the particular surface type.
3. Per cent of total fauna on the surface type represented by the taxon.
4. Number of species found on the surface type.

TAXA	External surface		Base of parapet (exterior)		Internal surface		Parietal canals		Fallen from barnacles	
	LT	DT	LT	DT	LT	DT	LT	DT	LT	DT
<i>Balanus</i> (3 spp.) ^a	33.40 34 18.2 3	31.70 37 17.3 3				26.00 29 14.0 3				
Mollusca (32 spp.)	2.05 4 1.1 12	2.80 5 1.5 6	2.94 6 1.6 3	1.52 3 0.8 2	0.02 -- -- 2	12.24 24 6.7 13	0.21 -- 0.1 3	4.68 9 2.5 12	10.29 20 5.6 26	14.08 28 7.6 26
Polychaeta (37 spp.)	0.26 1 0.1 14	0.58 2 0.3 6	0.17 1 0.1 2	1.29 4 0.7 3		8.61 28 4.7 10	0.16 1 0.1 7	12.03 39 6.5 16	0.45 1 0.2 16	7.50 24 4.0 8
Actiniaria (3 spp.)	0.28 3 0.2 2	0.20 4 0.1 1	1.29 19 0.7 2	1.52 22 0.8 2		0.41 6 0.2 2		0.31 5 0.2 2	0.44 6 0.2 2	2.50 35 1.4 1
Isopoda (4 spp.)							0.03 1 -- 1		0.39 12 0.2 2	2.83 87 1.5 4
Nemertinea						0.03 43 -- --		0.03 43 -- --	0.01 14 -- --	
Turbellaria						0.08 32 -- --		0.13 52 -- --	0.04 16 -- --	
Total Fauna	35.99 42 19.6 31	35.28 48 19.2 16	4.4 26 2.4 7	4.3 29 2.3 7	0.02 -- -- 2	47.4 162 25.6 28	0.37 1 0.2 10	17.21 149 9.3 33	11.62 69 6.2 46	26.91 174 14.5 39

^a Numbers for *Balanus* spp. are calculated from only two 0.125 m² samples which include 95 live and 10 dead *Tetraclita*. Of the *Balanus* counted, 36% were dead.

Live *Tetraclita* also have an important number of species associated with the external surface of the test. With the exception of the mollusks *Hipponix panamensis* (only found on dead barnacles) and *Siphonaria maura* (only found on live barnacles), the same species are found associated with live and dead *Tetraclita* (Table 10). However, the variety of the fauna associated with each dead barnacle is far greater than that of the fauna associated with each live one (Table 10). In terms of abundance of specimens, the tests of dead *Tetraclita* support 74 percent of the animals (Table 11) although only 18 percent of the tests are of dead *Tetraclita* (Table 8).

SUCCESSION OF INVERTEBRATES IN TESTS OF DEAD *TETRACLITA*

The first animals to invade and occupy the empty tests of dead *Tetraclita* were the crabs, *Pachygrapsus transversus*. No other animals colonized the spaces during the first 14 days after the barnacles were killed.

Colonization of empty tests started within 32 days and the abundance of the fauna increased steadily for about 6 months. From then on it fluctuated slightly. If some of the more abundant species are considered separately, each had a different pattern of change with time (Figure 2). The polychaete *Pseudonereis gallapagensis* showed sharp fluctuations in abundance. The mollusk *Sphenia fragilis* increased slowly, reaching a maximum abundance after 9.8 months, then decreased but maintained itself for the rest of the period for which data is available. Serpulid polychaetes appeared in the collections at the same time as *Sphenia*, but their abundance increased at a more rapid rate, then decreased more dramatically. The *Balanus* species were the first to achieve dense populations, but their abundances fluctuated from then on.

The number of species found in each collection is given at the bottom of Table 12 and in Figure 3. The diversity was quite low initially, but it increased rapidly to reach a peak after 9.8 months. The diversity dropped considerably in the next collection taken during the same month. The latter collection gave the largest number of species and the drop in diversity was due to a drastic change in the relative abundance of the species, mostly because of a predominance of *Balanus* spp. The diversity increased again and reached a maximum after 13 months and at this point it also approached the theoretical maximum. If only the number of different species was taken into account (Figure 3), the highest diversity was reached after 9.8 months and then there was a drop. From Table 12 it can be seen that the species that drop out are the rare ones, with relative abundances below 1 percent.

After *Tetraclita* tests are heavily colonized by a mixed fauna, they are structurally weakened by the burrowing animals, especially by the bivalve *Lithophaga aristata*, and are broken by wave shock and washed away. Space is thereby cleared for settlement of new *Tetraclita*. Boring organisms force a pattern of repeated succession or cyclic changes in the communities dominated by barnacles. The data in Table 13 demonstrate that the

percentage of barnacles lost over a period of 15 months was as high as 62 percent of the initial experimental set. The same table indicates that settlement of new *Tetraclita* in the area occurs throughout the 16 months and also that there is considerable mortality of young *Tetraclita* between collections.

TABLE 10. DISTRIBUTION OF THE COMMON AND ABUNDANT INVERTEBRATE SPECIES IN SPACE NICHES PROVIDED BY LIVE (LT) AND DEAD (DT) *TETRACLITA STALACTIFERA PANAMENSIS*.

	Number of specimens per <i>Tetracelita</i>						Percentage of <i>Tetracelita</i> in which species were found				
	External surface		Internal surface		Parietal canals			TOTAL	Percent- tage of relative abundance		
	LT	DT	LT	DT	LT	DT	LT			DT	
<i>Balanus</i> spp. (3 species)	29.45	33.10	--	14.20	--	6.10	29.45	53.40	76.63	100	100
<i>Sphenia fragilis</i>	0.29	2.33	0.02	7.00	--	1.33	0.31	10.66	4.02	16	80
<i>Brachidontes semilaevis</i>	0.86	0.25	--	0.50	0.001	--	0.86	0.75	3.15	15	60
<i>Serpulid</i> sp. 1	0.31	0.25	--	4.16	--	0.41	0.31	4.82	2.36	9	60
<i>Boccardia proboscidea</i>	0.03	0.08	--	0.16	0.03	6.33	0.06	6.57	2.04	8	60
<i>Lithophaga aristata</i>	0.02	1.08	--	0.41	0.05	2.16	0.07	3.65	1.28	2	40
<i>Syllis gracilis</i>	0.04	--	--	0.75	--	1.91	0.04	2.66	0.89	2	70
<i>Anthopleura dowii</i>	0.17	--	0.02	0.50	--	0.08	0.19	0.58	0.82	13	20
<i>Pseudonereis gallapagensis</i>	0.08	0.58	0.006	0.50	0.01	0.58	0.09	1.66	0.82	13	50
<i>Siphonaria maura</i>	0.23	--	--	--	--	--	0.23	--	0.80	15	--
<i>Autolytus</i> cf. <i>magnus</i>	0.18	--	--	--	--	--	0.18	--	0.59	1	--
<i>Isognomon recognitus</i>	0.08	0.40	--	0.58	--	0.08	0.08	1.06	0.55	5	30
<i>Hippomix panamensis</i>	--	--	--	1.66	--	--	--	1.66	0.46	--	30
nemerteans	--	1.00	--	--	--	0.41	--	1.41	0.39	--	20
<i>Onchidella hildae</i>	0.01	0.33	--	0.33	--	0.42	0.01	1.07	0.34	3	30
<i>Diadumene leucolena</i>	0.01	--	0.02	0.66	--	--	0.03	0.66	0.32	13	20
turbellarian	0.02	--	--	0.50	--	0.33	0.02	0.83	0.29	2	20
<i>Onchidella ?binneyi</i>	0.02	--	--	0.16	0.006	0.50	0.03	0.66	0.29	1	20
<i>Nereis callaona</i>	0.02	--	--	0.16	0.006	0.33	0.03	0.49	0.23	1	30
<i>Boccardia triaupa</i>	--	--	--	0.08	0.02	0.25	0.02	0.33	0.16	1	30
<i>Platynereis dumerilii</i>	--	--	--	--	0.02	0.25	0.02	0.25	0.13	--	10
<i>Opisthosyllis brunnea</i>	0.03	--	--	0.08	--	--	0.03	0.08	0.13	2	20
<i>Perinereis elena casoi</i>	0.006	--	0.006	--	--	--	0.01	--	0.05	1	--
<i>Lysidice ninetta</i>	--	--	--	--	--	0.08	0.06	0.08	0.05	1	--
species diversity H	0.160	0.294	--	0.724	--	0.783	0.163	0.678	0.05	1	10

TABLE 11. RELATIVE IMPORTANCE OF DIFFERENT SPACE NICHES FOR COMMON SPECIES ASSOCIATED WITH *TETRACLITA STALACTIFERA PANAMENSIS*. Calculations are based on Table 10.

Niche		Per cent of total fauna	Per cent of total fauna (<i>Balanus</i> excluded)	Per cent of common species present
External surface	live	25	6	79
	dead	32	15	42
Internal surface	live	0.2	0	21
	dead	25.8	43	80
Parietal canals	live	0	0	37
	dead	17	36	71
All niches	live	26	6	92
	dead	74	94	87

Figure 2. Density (expressed as number of individuals per *Tetraelita*) of the community associated with *T. atalactifera panamensis* tests and of its most abundant components over a period of 15 months. Note scale is different for each diagram.

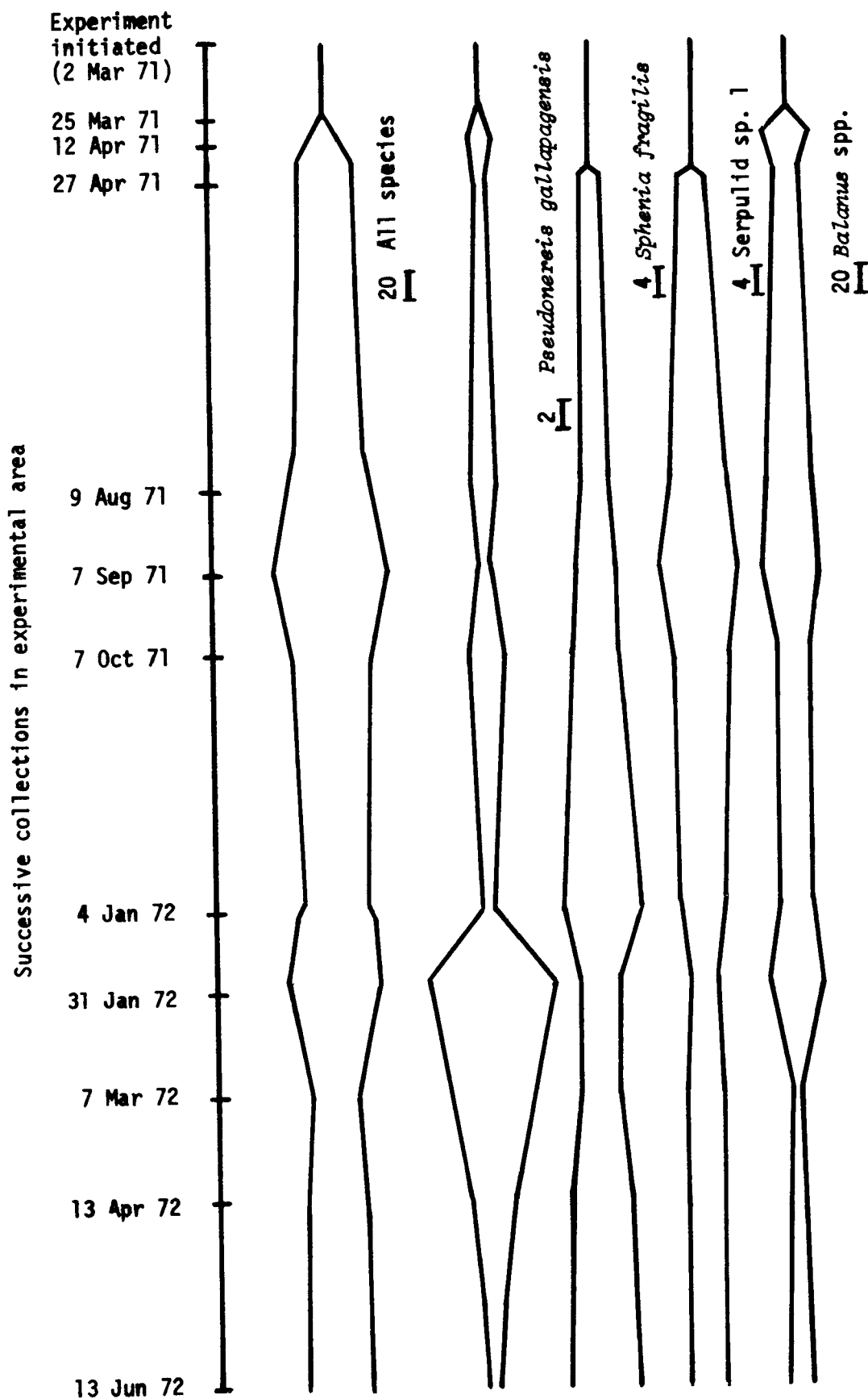


TABLE 12. SPECIES ASSOCIATED WITH *TETRACILITA STALACTIFERA PANAMENSIS* IN SUCCESSIVE COLLECTIONS OVER A PERIOD OF 15 MONTHS. Species are ordered by abundance and frequency of occurrence in the collections. (C = crustacean; M = mollusk, P = polychaete, N = nemertean, A = anemone, Ar = arthropod, T = turbellarian, S = sipunculan)

	25 Mar 71	12 Apr 71	27 Apr 71	9 Aug 71	7 Sep 71	7 Oct 71	4 Jan 72	31 Jan 72	7 Mar 72	13 Apr 72	13 Jun 72
	Number of specimens per barnacle										
(C) <i>Balanus</i> spp.	-	33.0	24.4	30.9	38.4	18.8	17.0	38.2	5.1	9.6	14.0
(M) <i>Sphenia fragilis</i>	-	-	2.4	2.8	5.8	7.5	9.6	7.4	5.6	6.8	11.6
(P) <i>Serpulid</i> sp. 1	-	-	3.4	8.4	11.4	9.8	5.1	2.6	4.2	4.6	6.6
(P) <i>Pseudonereis gallapagensis</i>	-	2.0	0.8	0.8	0.4	2.3	-	8.3	6.3	3.3	-
(P) <i>Boccardia proboscidea</i>	-	-	-	0.1	-	-	2.0	1.9	1.1	7.3	4.6
(N) nemerteans	-	-	-	-	0.5	2.0	1.2	4.8	1.8	1.0	-
(M) <i>Lithophaga aristata</i>	-	-	-	0.8	0.4	0.3	-	0.4	2.4	2.5	-
(M) <i>Brachidontes semilaevis</i>	-	-	0.2	0.04	0.4	1.3	-	1.3	-	1.5	1.2
(P) <i>Syllis gracilis</i>	-	0.6	0.2	0.1	0.3	-	1.3	0.4	0.5	2.2	0.2
(M) <i>Onchidella hildae</i>	-	-	-	-	0.5	1.5	1.4	1.0	1.4	-	-
(M) <i>Hippomix panamensis</i>	-	0.3	0.6	-	0.4	0.3	2.0	0.1	0.1	0.7	-
(A) <i>Diadumene laucolena</i>	-	-	1.0	-	-	-	-	-	1.6	0.8	0.6
(M) <i>Siphonaria maura</i>	-	0.6	1.4	-	0.1	-	-	0.3	0.8	-	0.6
(M) <i>Isognomon recognitus</i>	-	-	-	0.3	0.1	0.3	0.8	-	-	1.8	0.2
(M) <i>Crepidula striolata</i>	-	-	-	0.1	-	1.0	0.6	0.1	0.3	0.7	-
(T) turbellarians	-	0.6	-	-	-	-	-	1.7	0.3	-	-
(P) <i>Nereis callaona</i>	-	-	-	0.3	-	1.0	0.3	0.1	-	-	0.6
(M) <i>Fissurella virescens</i>	-	-	-	0.2	0.4	-	0.6	-	-	0.2	-
(M) <i>Ostrea iridescens</i>	-	-	-	-	-	0.3	-	0.1	-	-	1.0
(P) <i>Typosyllis aciculata</i>	-	-	-	-	-	1.3	-	-	-	-	-
(P) <i>Opisthosyllis brunnea</i>	-	-	-	0.1	-	-	-	-	0.3	0.7	-
(P) <i>Lepidonotus crosslandi</i>	-	0.2	-	-	-	-	-	0.1	-	-	0.6
(M) <i>Onchidella binneyi</i>	-	-	-	0.1	-	-	0.3	-	-	-	0.4
(A) <i>Anthopleura dowii</i>	-	-	-	-	-	-	-	-	-	0.2	0.6
(P) <i>Serpulid</i> sp. 9	-	-	-	-	-	-	0.7	-	-	-	-
(P) <i>Cirriformia luxuriosa</i>	-	-	0.2	-	0.1	-	0.1	-	0.2	-	-
(M) <i>Ostrea conchaphila</i>	-	-	-	-	0.1	-	0.2	0.1	-	0.5	-
(Ar) Insect larvae	-	-	-	0.1	-	-	-	-	-	-	-
(P) <i>Platynereis dumerilii</i>	-	-	-	-	-	-	-	-	-	-	0.6
(M) <i>Brachidontes puntarenensis</i>	-	-	-	-	-	-	-	-	-	-	0.6

TABLE 12 (continued). SPECIES ASSOCIATED WITH *TETRACLITA STALACTIFERA PANAMENSIS* IN SUCCESSIVE COLLECTIONS OVER A PERIOD OF 15 MONTHS.

	25 Mar 71	12 Apr 71	27 Apr 71	9 Aug 71	7 Sep 71	7 Oct 71	4 Jan 72	31 Jan 72	7 Mar 72	13 Apr 72	13 Jun 72
(M) <i>Nerita funiculata</i>	-	-	-	-	-	-	0.2	0.1	-	0.2	-
(P) <i>Lysidice ninetta</i>	-	-	-	0.1	0.1	-	0.2	-	-	-	-
(M) <i>chiton</i>	-	-	-	0.1	-	-	0.2	0.1	-	-	-
(M) <i>Lasaea</i> sp.	-	-	-	-	-	-	0.3	-	0.1	-	-
(M) <i>Fossarus atratus</i>	-	-	-	-	-	-	0.3	0.1	-	-	-
(C) <i>Pachygrapsus transversus</i>	+	-	0.4	-	-	-	-	-	-	-	-
(M) <i>Acanthina brevidentata</i>	-	-	0.4	-	-	-	-	-	-	-	-
(M) <i>Ostrea tubulifera</i>	-	-	-	0.1	0.1	-	-	0.1	-	-	-
(M) <i>Anachis rugosa</i>	-	-	-	-	-	-	-	0.1	-	0.2	-
(S) <i>Phascolosoma perlucens</i>	-	-	-	-	-	-	-	-	0.3	-	-
(P) <i>Phyllodoce</i> sp. 1	-	-	-	-	0.1	-	-	0.1	-	-	-
(P) <i>Eulalia</i> cf. <i>viridis</i>	-	-	-	-	-	-	-	-	-	-	0.2
(M) <i>Lasaea rubra</i>	-	-	-	-	-	-	-	-	0.2	-	-
(P) <i>Haplosyllis spongicola</i>	-	-	0.2	-	-	-	-	-	-	-	-
(M) <i>Fatelloida semimibida?</i>	-	-	-	-	-	-	-	0.1	-	-	-
(P) <i>Serpulid</i> sp. 12	-	-	-	-	-	-	0.1	-	-	-	-
(M) <i>Fissurella microtrema</i>	-	-	-	-	0.1	-	-	-	-	-	-
(M) <i>Cardita radiata</i>	-	-	-	-	0.1	-	-	-	-	-	-
(M) <i>Ostrea palmula</i>	-	-	-	-	-	-	-	0.1	-	-	-
(P) <i>Cirriformia tentaculata</i>	-	-	-	-	-	-	0.1	-	-	-	-
Average no. of specimens per barnacle		37.3	35.6	45.44	60.3	47.7	44.6	69.7	32.6	35.4	44.2
Total no. of species		0	13	18	20	14	22	26	19	20	17

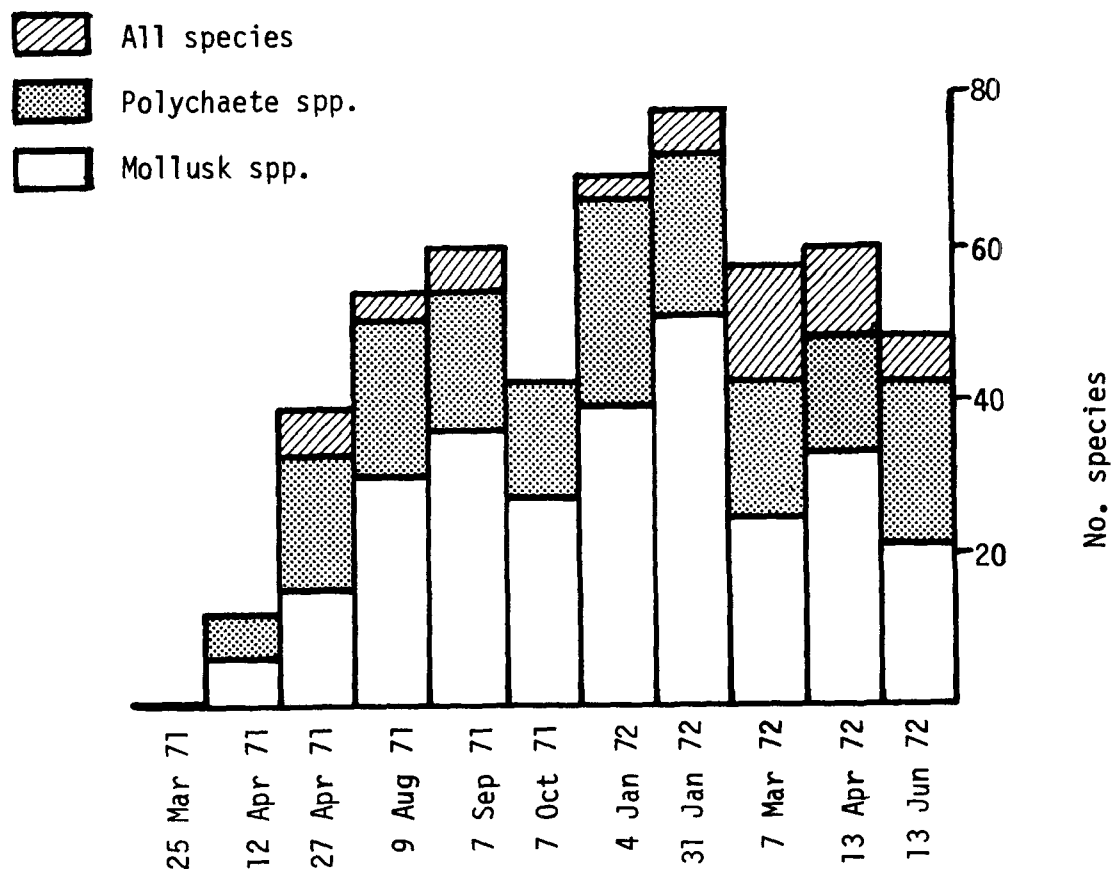


Figure 3. Number of species in collections of invertebrates associated with *Tetraclita stalactifera panamensis* over a period of 15 months.

TABLE 13. COLLECTION, NATURAL LOSS OF TESTS, AND RECRUITMENT OF YOUNG *TETRACLITTA STALACTIFERA PANAMENSIS* IN AN AREA OF 4.7 X 0.7 METERS FOLLOWING AN EXPERIMENTAL KILL OF BARNACLES.

Collection No.	No. of dead <i>Tetracelita</i>	Accumulative percentage of <i>Tetracelita</i> collected	Accumulative percentage of <i>Tetracelita</i> lost other than by collecting	Young <i>Tetracelita</i> on rock/on <i>Tetracelita</i>	Percent mortality of young <i>Tetracelita</i> between collecting on rock/on <i>Tetracelita</i>		
2 Mar 71 (initial)	545	0.0	0.0	6	12	--	
1. 25 Mar 71 (23 days after)	530	2.7	0.0	121	612	--	
2. 12 Apr 71 (32 days after)	517	3.6	1.9	no data	412	--	32.0
3. 27 Apr 71 (47 days after)	480	4.5	7.6	no data	261	--	36.2
4. 9 Aug 71 (150 days after)	361	7.0	26.5	no data	138	--	45.5
5. 7 Sep 71 (179 days after)	301	9.5	34.7	no data	84	--	38.8
6. 7 Oct 71 (207 days after)	223	10.2	49.4	66	no data	--	--
7. 4 Jan 72 (295 days after)	202	12.3	51.0	53	66	18.5	--
8. 31 Jan 72 (322 days after)	129	14.6	60.8	29	32	33.6	21.0
9. 7 Mar 72 (359 days after)	120	16.2	60.8	no data	no data	--	--
10. 13 Apr 72 (396 days after)	110	17.2	61.5	no data	no data	--	--
11. 13 Jun 72 (457 days after)	107	18.1	62.2	498	150	--	--

SECTION VI

SURVEY OF AN INTERTIDAL MANGROVE COMMUNITY AT GALETA

The study of the effects of oil on mangrove forests is particularly important because they occupy nearly 25 percent of the world's coastline in the tropics (25°N to 25°S) and serve as important "nursery" areas for many species of invertebrates and fishes (MacNae, 1968). The mangrove forest adjacent to the Galeta Marine Laboratory was visited by Klaus Rützler and Wolfgang Sterrer approximately two months after the Witwater oil spill. They observed that the mangrove community suffer the most damage from the oil spill of any of the marine communities at Galeta (Rützler and Sterrer, 1970). *Crassostrea* sp., *Brachidontes* sp., sponges, tunicates and bryozoans were covered with oil and nearly eliminated in all exposed areas.

In order to provide background information on the composition and characteristics of the mangrove community, we conducted a survey that included the intermittently submerged floor, aerial vegetation, and permanently submerged prop roots.

Methods

Ten 0.125 m² samples were collected from locations along the edge of the mangrove shore at the south side of the Galeta Road causeway. The samples were located by selecting coordinates from a table of random numbers and pacing the distances. A 0.125 m² frame with an open end was laid on the selected spot and placed on the substratum by sliding it in among the aerial roots through the open end. The aerial roots were sawed off at a distance of one foot above the level of the substratum. Pieces of coral rubble and the mat of algae laying on the surface of the substratum were collected by hand. The substratum (composed mainly of sand, root hairs, and continuations of the aerial roots) was collected to a depth of about three inches with a shovel and diving knives. These two communities were kept in separate buckets.

The sample was analyzed as follows:

1. The aerial prop roots were stripped of epiphytic algae and animals and their surface area calculated by measuring the length and determining an average diameter for each root.
2. The extraordinarily dense mat of root hairs was carefully examined for possible dwellers. After having been cleaned of sediment by repeated washings in seawater, the root hairs were measured for volume and wet weight.

3. The epiphytic algae from the prop roots, the pieces of coral rubble and the mat of algae that covers the substratum were examined for small faunal species.

Results and Discussion

The intertidal habitats resulting from the structure of mangrove trees, *Rhizophora mangle*, form a topographically heterogeneous region. Attention was given to characterizing the several habitats for marine organisms produced by the *Rhizophora mangle* (Table 14). One habitat is formed by the prop roots which support a typical association of algae: *Bostrychia binderi*, *Catenella repens*, *Caloglossa leprieurii* and *Murrayella pericladus*. These grow as dense masses with each plant attached to others by holdfasts. Several species of amphipods and some xanthid and oxypodid crabs are usually found associated with the epiphytic algae of the prop roots. The roots themselves are almost barren of animal life except for some epizoic barnacles and a few polychaete worms which build tubes in cracks and galleries.

Another mangrove habitat is the ground between the prop roots which consists of fine sand or mud and is usually covered by a dense mat of algae (Table 14). Large numbers of mollusks such as *Batillaria minima* and hermit crabs of the genus *Clibanarius* move around on this algal mat. In the sand or mud underneath there are few polychaetes, some sipunculans of the genus *Golfingia*, and some crustaceans.

A third habitat of the mangrove is the submerged roots which were completely barren of organisms in all our samples. Another probably habitat is the dense mat of root hairs which weighed an average of 6.6 kg (wet weight) per m² (Table 15). Here only *Batillaria minima* and *Clibanarius* were found. Coral fragments washed from the Galeta reef constitute perhaps the richest habitat for animal species, but these cannot be considered typical of the mangroves. For example, most of the polychaetes and sipunculans found in quadrats 6 and 9 (Appendix F) were collected from coral fragments and are also present in the Galeta reef. The coelenterate *Zoanthus sociatus* and the algae *Laurencia papillosa*, crustose red coralline, creeping Gelidiales and *Halimeda opuntia* are also typical reef inhabitants and are only found in the mangroves on coral fragments washed from the reef.

The most striking characteristic of the mangrove community shown by our data is the variability in the species composition, in the relative abundance of species and in proportions of habitat surfaces available to plants and animals. Because of the tremendous habitat diversity or spatial heterogeneity involved for invertebrates in the mangrove forest, the abundance and association data of Appendix F must be compared for each sample with the data in Tables 14 and 15. The variation between samples precludes summarization. The large differences in species composition and relative abundances between samples taken during the same periods of time also preclude definite conclusions about seasonal variations. Table 16 gives an

TABLE 14. CHARACTERISTICS OF THE MANGROVE SAMPLES FROM GALETA POINT. A description of the degree of spatial heterogeneity which is too large for our sampling program to cope with capably.

Sample number, location ^a and date	Ground coverage		Algae epiphytic on aerial roots	No. algal species	Weight (gm) of <i>Bostrychia-Catenella</i> ^b association	No. animal species	No. animal specimens (all species combined)
	algal mat	Coral fragments					
1 (?) 23 Nov 70	<i>Cladophoropsis</i> (abundant)	none	none	2	---	13	870
2 (38-4) 24 Nov 70	<i>Caulerpa fastigiata</i> (abundant)	few with some <i>Laurencia papillosa</i>	<i>Bostrychia-Catenella</i> (abundant)	-	11.12	11	105
3 (84-4) 20 Apr 71	none	none	no prop roots	0	---	4	6
4 (49-1) 21 Apr 71	<i>Cladophoropsis</i> (common to abundant)	none	<i>Bostrychia-Catenella</i> (common to abundant)	4	1.90	16	365
5 (55-4) 21 Apr 71	none	few with no fleshy algae	<i>Bostrychia-Catenella</i> (abundant)	8	19.02	25	341
6 (77-2) 22 Apr 71	Filamentous blue-green	few	<i>Catenella</i> (sparse)	5	---	24	336
7 (25-1) 29 Jul 71	<i>Cladophoropsis</i> , <i>Caulerpa</i> (some)	few with sparse but typical coral reef algae	<i>Bostrychia-Catenella</i> (abundant)	10	2.96	12	73
8 (65-1) 11 Aug 71	<i>Cladophoropsis</i> (common to abundant)	none	<i>Bostrychia-Catenella</i> (common to abundant)	4	4.36	15	99
9 (75-1) 23 Aug 71	Filamentous blue-green	few	no aerial roots	7	---	44	1500
10 (61-3) 25 Aug 71	<i>Cladophoropsis</i> (abundant)	few with some <i>Laurencia papillosa</i>	<i>Bostrychia-Catenella</i> (abundant)	6	4.90	22	335

^a Location is given in parenthesis, the first number representing paces along the shore, the second representing paces into the mangrove forest perpendicular to the shore.

^b The *Bostrychia-Catenella* association includes some or all of the following algae: *Bostrychia binderi*, *Catenella repens*, *Caloglossa leprieurii*, *Murrayella pericladus*, *Chaetomorpha brachygonia* and *Chaetomorpha clavata*.

TABLE 15. SIZE ESTIMATES OF PROBABLE HABITATS AVAILABLE TO PLANTS AND ANIMALS IN FIVE 0.125 m² MANGROVE SAMPLES.

Sample No.	Surface area of aerial roots ^a (cm ²)	Wet weight of submerged roots (g)	Wet weight of root hairs (g)	Settled volume of root hairs (ml)
1	899.1	36.4	741	650
2	1414.3	260.9	1135	965
7	767.2	537.0	1024	1970
8	936.5	142.0	368	803
10	400.8	360.0	871	2090
Average of 5 Samples	883.6	267.2	827.8	1295
Average per m ²	7068.8	2137.6	6622.4	1036.0

^a Aerial roots were sawed off at a distance of 1 foot above the level of the substratum.

TABLE 16. THE MEAN FREQUENCY OF OCCURRENCE IN TEN 0.125 m² INTERTIDAL QUADRATS TAKEN AT THE SEAWARD EDGE OF A MANGROVE FOREST ADJACENT TO THE GALETA MARINE LABORATORY.^a

Taxa	No. genera/ No. species	Mean frequency for each species in 0.125 m ² samples (n = 10)
Chlorophyta	6/7	0.24
Rhodophyta	11/11	0.32
Anthozoa	2/2	0.25
Sipuncula	4/13	0.17
Polychaeta	19/22	0.16
Crustacea	19/26	0.22
Gastropoda	15/16	0.19
Bivalvia	9/11	0.25

^a For detailed species list and data, refer to Appendix F.

average density of each species, but it should be remembered that there is great patchiness in animal distribution and a large number of species are not typical of mangrove habitats but can survive in the area if suitable substrata such as coral rubble are available.

As is indicated in Table 16, the fauna of *Crassostrea* sp., *Brachidontes* sp., sponges, tunicates and bryozoans reported by Rützler and Sterrer (1970), as covered with oil, has not returned to the area after 33 months. On nearby mangrove root communities (Bocas del Toro to the west and San Blas to the east), a typically lush fauna of sponges, tunicates and oysters is still present. Old, dried, patches of oil are still present on the mangrove roots in our study area. This, along with the observed presence of a lush encrusting community on nearby mangroves and the presumed presence of a lush encrusting community at Galeta previous to the oil spill (Rützler and Sterrer, 1970), implies that the Witwater spill may have had a long-term impact (33 months+) on the Galeta mangrove community. Unfortunately, this conclusion is invalidated by the lack of quantitative data before the spill and confounded by other possible causal factors. For instance, Army Malaria Control has been spraying the mangroves of Galeta Point intensively for 15 to 20 years. Information obtained from the Navy Office of Public Works indicates that roughly 1200 gallons of Malathion has been sprayed around the Navy recreation area bordering to our mangrove study area. Previous to this, DDT was used rather than Malathion. These chemicals were sprayed by means of a fogging machine. Roughly 300 to 400 gallons per year of Dalapon (a herbicide) is applied directly to the ground around the Navy's antenna site approximately 0.8 km upstream from our mangrove study area.

However, Navy Office of Public Works informed us that an intensive mosquito and sand-fly control program has been underway for 15 to 20 years. If anything, the efforts have been reduced over the last 5 years. In contrast, the devastation of the mangrove root epifaunal communities appeared to take place during the Witwater oil spill (Rützler and Sterrer, 1970). If this is correct, then the spill has had a major influence which has continued for better than 33 months.*

* At the time of this rewriting of the report (June 1974), 66 months after the Witwater oil spill, the state of the epifaunal communities on the mangrove roots still appears to remain in the same condition.

SECTION VII

SURVEY OF A SAND BEACH COMMUNITY

Studies of the Torrey Canyon disaster showed that white sandy beaches which appear clean after an oil spill are not necessarily free from pollution (Nelson-Smith, 1968). Due to the paucity of the beach fauna in the immediate vicinity of the laboratory, a survey of beaches was made east of Galeta Point along the road to the town of Portobelo. Beaches to the west of Galeta had been sampled by Dr. Deborah Dexter, San Diego State University, who was our advisor in the sandy beach program. The beach selected was Shimmey Beach at Fort Sherman (west of Galeta Point) which had the richest macroscopic fauna of the beaches sampled and had been intensively surveyed from June through August of 1969 (Dexter, 1972).

Methods

In order to locate the sample quadrats, pairs of numbers were obtained from a table of random numbers. From the first number of each pair, which represented the number of paces from the high tide line, the quadrat could be located in one of the following three intertidal "zones": upper (range 0-5 paces), middle (range 6-10), and lower (range 11-15). The second number in each pair represented the paces to be taken parallel to the shoreline and these fell within a range from 0 to 99. Eight samples were taken from each zone, using either of the following two methods, depending on whether or not the quadrat area was exposed by the tide:

1. Exposed quadrat area. An 0.1 m^2 frame was placed on the area to be sampled and all the sand within the frame to a depth of two inches was troweled into a 500μ sieve.

2. Water-covered quadrat area. A coring device, consisting of a stainless-steel cylinder with a valve on the upper (closed) end, was pushed into the sand with the valve open. After closing the valve, the coring device was pulled up and the sample placed in the 500μ sieve.

According to Dr. Dexter, one frame sample (0.1 m^2) is equivalent to four core samples (0.025 m^2 each) and there is no significant difference between samples taken with the frame and those taken with the core.

The majority of the sand was washed through the 500μ sieve. The remainder of the sample, consisting of animals and large sand particles, was troweled and washed into a labeled (by its pair of location numbers) plastic bag. A series of 24 samples (8 in each intertidal zone) was collected in December 1970 and April and August 1971.

The infauna was separated from the large sand particles by pouring an entire sample into a saturated sugar solution. As the sand sunk to the bottom, the animals floated on the surface where their activity made them readily observable. Using a pipette, the animals were then washed in seawater and transferred into vials containing 10 percent formalin. Since the larger mollusks do not float, the remaining sand particles were examined for them.

Results and Discussion

The results of our sandy beach studies are summarized in Tables 17 and 18. In Table 17 we compare the abundances of macroscopic infaunal species found in our study in December, April, and August with each other and with the abundances found by Dr. Deborah Dexter in the summer of 1969 (Dexter, 1972). Most species (16, or 76 percent) were rare (averaged from all samples as less than 2 per m²). The abundances of *Ancinus brasiliensis*, *Excirolana salvadorensis* and *Cyclaspis* sp., the three most common animals found during the summer of 1969, were different in each sampling period. We have no suggestions to explain these differences except that certain populations may fluctuate not only with period of the year but perhaps with the time of day and stage of the tide.

It is clear from these data that the surf-swept intertidal sandy beach supports a fauna with great temporal variability in species composition and abundance. A possible cause of this temporal variability was suggested to us by Dr. Dexter. She observed that the sand on several of the beaches during our sampling in December was composed of coarser grains than during her sampling period in the summer of 1969. We had an opportunity to confirm this later since our samples of December and April contained at least five times more sand than those taken in August with the same sieve (500 μ mesh).

Dr. Dexter suggested that the grinding action of large sand particles in heavy surf probably creates a very hostile environment for soft-bodied infaunal animals such as nerinid polychaetes. This is quite possible. However, our data cannot separate this grinding action from other important factors such as water retentive capacity of the sand, its absorptive capacity, its capillarity and porosity to gases and water, all of which depend on the sand grade and could affect the organisms living in the beach.

Table 18 shows that the largest diversities and abundances of organisms are found throughout the year in the middle and lower intertidal zones, both of which harbor a number of rare species that are not found in the high intertidal zone. This last zone is characterized throughout the year by the isopod *Excirolana salvadorensis*. The abundance of another isopod, *Ancinus brasiliensis*, shifts from the middle and low intertidal zones in April to the high intertidal zone in August. *Scoelelepis agilis* occurs throughout the beach during the year with the highest abundances in the lower intertidal zone.

TABLE 17. TEMPORAL CHANGE IN COMMUNITY STRUCTURE OF MACROSCOPIC INFAUNA AT SHIMMEY BEACH. For discussion, see text.

TAXA	Average Number/m ²			
	June - August 1969 ^a	21 December 1970 ^b	19 April 1971 ^b	13 August 1971 ^b
<i>Ancinus brasiliensis</i>	80.25	6.3	32.9	10.8
<i>Excirolana salvadorensis</i>	67.88	17.5	13.8	1.2
<i>Cyclaspis</i> sp.	44.75	0.8	--	--
<i>Scolecopsis agilis</i>	20.00	7.5	52.1	19.5
<i>Donax</i> spp.	7.75	0.8	1.7	0.4
<i>Exosphaeroma diminutum</i>	2.63	--	--	--
<i>Lepidopa</i> spp.	1.25	--	--	--
<i>Atylus minikoi</i>	1.25	--	--	--
<i>Microprotopus</i> sp.	1.00	--	--	--
<i>Emerita brasiliensis</i>	0.50	--	--	0.4
nemertean	0.50	--	--	--
<i>Dispio</i> sp.	0.13	--	--	--
<i>Trichophoxus floridensis</i>	0.13	--	--	--
amphipod	--	1.2	--	--
magelonid polychaete	--	0.8	--	0.4
polychaete sp. 3	--	--	7.5	--
polychaete sp. 4	--	--	0.4	0.8
polychaete sp. 5	--	--	--	0.4
<i>Hippa</i> sp.	--	--	0.4	--
sipunculan	--	--	--	0.8
ophiuroid	--	--	--	0.8

^a Average of 80 samples, 0.1 m² each, taken by Dexter (1972).

^b Average of 24 samples, 0.12 m² each, taken by FWQA staff.

TABLE 18. ABUNDANCES OF MACROSCOPIC ORGANISMS (NUMBER/m²) FOUND IN THREE ZONES (HIGH, MIDDLE AND LOW) OF A SANDY BEACH (SHIMMEY BEACH, FORT SHERMAN, CANAL ZONE). The zones are defined as 0 to 5, 6 to 10 and 11 to 14 paces, respectively, seaward from the high tide drift line. Numbers are averages of eight quadrats in each zone so that the average in each zone is based on 72 quadrats. Each quadrat is 0.1 m² in area and about 2 inches deep.

TAXA	High			Ave.	Middle			Ave.	Low			Ave.
	Dec. 1970	Apr. 1971	Aug. 1971		Dec. 1970	Apr. 1971	Aug. 1971		Dec. 1970	Apr. 1971	Aug. 1971	
<i>Excirolana salvadorensis</i>	51.2	25.0	3.8	26.7	1.2	16.2	--	5.8	--	--	--	--
<i>Scolecopsis agilis</i>	1.2	1.2	1.2	1.2	3.8	35.0	7.5	15.4	17.5	120.0	50.0	62.5
<i>Donax</i> spp.	--	2.5	--	0.8	--	2.5	1.2	1.2	2.5	--	--	0.8
<i>Hippa</i> sp.	--	1.2	--	0.4	--	--	--	--	--	--	--	--
<i>Ancinus brasiliensis</i>	--	--	13.8	4.6	13.8	75.0	5.0	39.1	5.0	23.8	13.8	14.2
ophiuroid	--	--	1.2	0.4	--	--	1.2	0.4	--	--	--	--
amphipod	--	--	--	--	3.8	--	--	1.3	--	--	--	--
polychaete sp. 3	--	--	--	--	--	1.2	--	0.4	--	21.2	--	7.1
polychaete sp. 4	--	--	--	--	--	1.2	--	0.4	--	--	2.5	0.8
polychaete sp. 5	--	--	--	--	--	--	1.2	0.4	--	--	--	--
<i>Cyclaspis</i> sp.	--	--	--	--	--	--	--	--	2.5	--	--	0.8
magelonid polychaete	--	--	--	--	--	--	--	--	2.5	--	1.2	1.2
sipunculan	--	--	--	--	--	--	--	--	--	--	2.5	0.8
<i>Emerita brasiliensis</i>	--	--	--	--	--	--	--	--	--	--	1.2	0.4
Total number of species	6				9				9			
Average number of individuals/m ²	34.1				64.4				88.6			

The great temporal variability in species composition and abundance indicate that a study of effect of oil on the organisms inhabiting the beach would require a very intensive sampling program and that an after-the-fact assessment of the effects of pollution in this environment would be extremely difficult. Identification of changes brought about by pollution would be confounded by natural changes. For this reason we eliminated the sandy beach habitat from our study on the effects of oil pollution and confined this to the reef and andesite rock communities which have a more predictable species composition.

SECTION VIII

RECRUITMENT PATTERNS IN CARIBBEAN AND EASTERN PACIFIC BENTHIC COMMUNITIES

In benthic marine habitats, recruitment is probably one of the most important processes in understanding the functional organization of the community (Thorson, 1957, 1966; Loosanoff, 1964). The scheduling of the reproductive processes is an indication of how natural selection on the species in question is guided by the predictability or periodic harshness of the physical environment (Murphy, 1968) or the periodic changes in the condition of competitors or predators (Thorson, 1960, 1966). Although over 99 percent of the mortality for most marine organisms with pelagic larvae occurs during the planktonic stage of development and full-grown adults often have an exceptionally high probability for survival, the "bottle-necks," or controlling factors, for a benthic species are usually found during the processes of settling and metamorphosis. (The distinction between destruction and control should be kept in mind—cf. Nicholson, 1933.) The larvae of benthic animals are very selective in location and timing of settlement (Wilson, 1960; Thorson, 1957, 1966; Birkeland, Chia and Strathmann, 1971) which attests to the importance of settlement in natural selection. It is not merely a numbers game to the extent of their planktonic life. In the communities of adult benthic organisms, the disturbance factors are often haphazard in timing and the pattern of succession may depend on which species sets in the cleared space first. Since the basic patterns of recruitment are of fundamental importance in understanding the functional organization of benthic communities, we conducted settling plate experiments on both the Caribbean and Pacific coasts of Panama. It would also be of great interest to compare the data with results obtained in other geographical regions. To enhance the validity and ease of the comparisons, the methods and materials used should be the same; consequently, we have outlined the methods in detail. Those not wishing to conduct similar studies will probably prefer to skip the methods section and move ahead to Results and Discussion, page 52.

Methods

Settling plates were made of 0.6 cm thick plexiglas cut into rectangular pieces 5 cm wide by 15 cm long. The plates were roughened on both upper and lower surfaces by rubbing with "coarse" grade sandpaper, with at least 10 strokes along the length and 10 strokes along the width. Plexiglas was chosen for settling plates in this study in preference to natural substrata for several reasons. First, since the coasts of Panama differ in the prevalence of different kinds of natural substrata, e.g., basalt is far more prevalent in the eastern Pacific and limestone is more prevalent in the Caribbean, a direct comparison of the communities using either of these substrata was originally considered to be a potential source of bias

which may confound comparative measurements. For example, the diversity or complexity of temporal organization could have been expected to be greater in the eastern Pacific if basalt was used or greater in the Caribbean if limestone was used. Therefore, we decided to use plexiglass, a more standardized material with less bias biologically. Also, the surfaces of natural substrata vary more in microtopography and texture between replicates than plexiglass plates roughened by scraping in a standard pattern. The standardized plexiglass plates were made to fit well under the dissecting microscope for examination. For further explanation of our choice of plexiglass, refer to paragraph 2, page 91.

Each line and box set was suspended from a styrofoam float and anchored with a cement construction block. The blocks were placed at depths of about 8 m in both the Caribbean (Galeta Marine Laboratory) and Pacific (Isla Taboguilla). It must be remembered that the depth varies through a tidal range of 6 m in the Pacific and 0.5 m in the Caribbean. The plates were suspended approximately 1 m above the bottom in either case. The Galeta plates were situated on a coral reef; the Taboguilla plates on a rocky "reef."

For recruitment periodicity studies, two lines (a total of eight plates) were collected for each of 1- and 2-month intervals. One-month sets were collected and replaced each month. At the same time, four sets of 2-month plates were set out and collected in pairs on alternate months. The intervals were as near as logistics and weather permitted to one and two months in length. For the productivity studies, pairs of lines were left out for different periods ranging between 31 and 148 days.

When the plates were collected, they were examined under 12-power magnification. Plates were held under a dissecting scope by placing them on non-toxic modeling clay supports while emersed in seawater in a Pyrex baking dish. Surface coverage counts were made by tallying the substrata or organisms under the 13 points along the line in the ocular micrometer of the microscope eyepiece. The surface of the plate was covered by 8 positions when shifting the plate under the microscope. This gave a total of 104 data points for surface coverage on each surface of each plate. Both upper and lower surfaces were examined and the data were recorded separately. To facilitate both recording and analyzing the data, labeled data forms were mimeographed.

After noting the species present and quantifying surface coverage patterns, the plates were placed in an oven at 85°C for at least two days to dry for weighing. To prevent added weight from crystallization and accumulation of salts, the plates were rinsed gently in fresh water before drying.

Results and Discussion

The distribution of lengths of recruitment periods for benthic animals in the Pacific and the Caribbean were estimated from the records of animals settling on plexiglass plates. The data were classified into four categories

and tallied into the categories in Table 19 by assuming only one period per year for each species. The longest possible period for each species in which no recruitment was observed during the year was subtracted from 12 months and the remainder was considered the recruitment period. If the longest break was only three months, recruitment was considered to be continuous throughout the year. The greatest possible break was always used in the calculations, e.g., records from a single set of 1-month settling plates and a single set of 2-month settling plates would each be considered as one month of recruitment since we could not be certain that recruitment had occurred during both months on plates left out for two months. The presence of a species is, of course, a solid observation while its absence may be due to sampling error.

The eastern tropical Pacific is a more "seasonal" environment in terms of magnitude of yearly (and other) fluctuations in several physical parameters of the environment (temperature, salinity, nutrients, tide levels) and plankton productivity than is the Caribbean. In view of this, it is most interesting to compare the degree to which the recruitment of benthic organisms in these two environments differ in uniformity, "seasonality" and "unpredictability." In order to do this we first need operational definitions of these terms. So, for the purpose of these comparisons alone and in order that workers in other latitudes may compare their organisms with ours, we make the following ad hoc definitions:

Where n_1 = the number of species recruiting to plates in a given month of one year (M_1) but not on the same month in the next year (M_2),

n_2 = the number of species recruiting to plates in M_2 but not M_1 ,

n_t = the number of species recruiting to plates in both M_1 and M_2 ,

n_j = the number of species recruiting to plates in a given month (M_1) but not in the sixth month following (M_6),

n_f = the number of species recruiting to plates in M_6 but not M_1 ,
and

n_g = the number of species recruiting to plates in both M_1 and M_6 ,

$$\text{"seasonality"} = \frac{n_j + n_f}{n_j + n_f + n_g} \quad \text{and}$$

$$\text{"year-to-year variation"} = \frac{n_1 + n_2}{n_1 + n_2 + n_t} .$$

These comparisons are given in Table 20 and analyzed statistically in Table 21.

TABLE 19. A COMPARISON OF LENGTHS OF RECRUITMENT PERIODS FOR BENTHIC ANIMALS ON THE PACIFIC VERSUS THE CARIBBEAN AS ESTIMATED FROM ANIMALS SETTLING ON PLEXIGLAS PLATES.

Location	Maximum length of recruitment period in months				Total number of species
	1 - 3	4 - 6	7 - 9	year-round	
Taboguilla (Pacific)	32	16	19	16	83
Galeta (Caribbean)	66	29	19	3	117
Per cent of grand total	49.0	22.5	19.0	9.5	200

$\chi^2 = 19.23$ with 3 d.f.: $P < 0.001$

Reject H_0 : conclude that probability of an animal species being found recruiting over a given period differs between Taboguilla (Pacific) and Galeta (Caribbean).

TABLE 20. DEGREE OF "SEASONALITY" AND "YEAR-TO-YEAR VARIATION" IN RECRUITMENT OF ANIMALS TO SETTLING PLATES IN CARIBBEAN AND PACIFIC PANAMA. The definitions of the indices are given in the text.

Index	Pacific (Taboguilla)	Galeta (Caribbean)
Seasonality	0.42	0.65
Year-to-year variation	0.68	0.66

TABLE 21. CHI-SQUARE TEST OF THE SIGNIFICANCE OF DIFFERENCES BETWEEN TABOGUILLA AND GALETA SETTLING PLATE COMMUNITIES IN TERMS OF CATEGORIES INVOLVED IN CALCULATIONS OF "SEASONALITY" AND "YEAR-TO-YEAR VARIATION" INDICES.

a. Seasonality.

Location	$n_j + n_f$	n_g	Total number of species
Taboguilla (Pacific)	30	41	71
Galeta (Caribbean)	56	30	86
% of grand total	54.8	45.2	157

$$\chi^2 = 8.23 \text{ with 1 d.f.: } P < 0.01$$

Reject H_0 : conclude that seasonality index differs for Taboguilla and Galeta settling plate communities.

b. Year-to-year variation.

Location	$n_1 + n_2$	n_t	Total number of species
Taboguilla (Pacific)	41	29	70
Galeta (Caribbean)	59	31	90
% of grand total	62.5	37.5	160

$$\chi^2 = 0.819 \text{ with 1 d.f.: not significant}$$

Fail to reject H_0 : conclude that year-to-year variation index is not different for Taboguilla and Galeta settling plate communities.

It can be seen that when using our definition of seasonality, there is much less seasonality in the Pacific. It is surprising in view of the greater amplitude of seasonal fluctuations of physical parameters in the Pacific. But these differences between Pacific and Caribbean seasonality are shown to be statistically significant in Table 21 and this conclusion is also corroborated by the significantly greater proportion of animal species which recruit throughout the year in the Pacific (Table 19) and by the comparisons in Table 22 which indicate a greater total number of animal species, but no more in any given month, in the Caribbean. Although the total number of animal species recorded on settling plates is 41 percent greater in the Caribbean, the average number of animals recorded in any given comparable settling plate collection or on any given month is not significantly different (Table 22). There tends to be more "repeats" from month to month in the Pacific. A significantly greater proportion of Pacific species than Caribbean species can be found recruiting throughout the year.

A confounding factor exists in this analysis. Rather than being more seasonal, individual species could merely be more common at Taboguilla. Since observed presence is hard data, while absence of a species could be due to sampling error, common species would be recorded more regularly than rare species and would thus be less likely to be regarded as "seasonal." While we cannot disregard this possibility, a number of species do appear to be seasonal. Even those species which are found to be present throughout the year in our qualitative analysis appear to have definite quantitative seasonal trends in abundance of recruitment. *Balanus trigonus* is thus found to recruit throughout the year but shows a tremendous increase in abundance each late dry season (February through April). The quantitative patterns of other presumably continuous settlers do not show evidence of such a regular pattern.

In a few instances, we have what appear to be identical species on the settling plates in both oceans. In these cases, they appear to have similar reproductive periods in spite of the great differences in their physical environments. As examples, the brachiopod *Discinisca strigata* appears to set only in December through February in both oceans, while the tunicate *Diplosoma macdonaldi* sets throughout the year. There is a statistically significant predominance of bryozoan species on the Pacific settling plates and ascidian species on the Caribbean settling plates (Table 23). This reflects the clear prevalence of this pattern in the surrounding community.

While recruitment is restricted to certain times of the year for a larger portion of the species in the Caribbean than in the eastern Pacific, the total dry weight production does not show a significant change with season (Table 24). In contrast, there are extreme seasonal changes in dry weight production of the fouling community on the Pacific plates (Table 24), but the predominant species are present throughout the year. Thus, recruitment is seasonal in the benthic communities in both oceans, but in opposite ways: seasonal in organization or quality in the Caribbean in contrast with production or quantity in the eastern Pacific.

TABLE 22. SUMMARY AND COMPARISON OF SOME OF THE CHARACTERISTICS OF THE COMMUNITIES OF ORGANISMS FOULING PLEXIGLAS PLATES ON THE PACIFIC AND CARIBBEAN SIDES OF THE ISTHMUS OF PANAMA.

	Taboguilla (Pacific)	Galeta (Caribbean)
Total No. animal spp.	83	117
Ave. No. animal spp. per month ^a	27.0±8.43 S.D.	23.9±12.6 S.D.
Total No. tunicate spp.	13	28
Ave. No. tunicate spp. per month ^b	2.8±1.3 S.D.	4.4±3.8 S.D.
Total No. bryozoan spp.	22	15
Ave. No. bryozoan spp. per month ^c	8.1±3.1 S.D.	2.8±2.9 S.D.

^a $t = 0.085$ with 36 d.f.: not significant

^b $t = 0.909$ with 36 d.f.: not significant

Fail to reject H_0 : the number of animal species seen on any single monthly or bimonthly collection of settling plates does not differ significantly between the Taboguilla and Galeta sites.

^c $t = 11.28$ with 36 d.f.: $P < 0.01$

Reject H_0 : conclude that the number of bryozoan species seen on any single monthly or bimonthly collection of settling plates differs significantly between the Taboguilla and Galeta sites.

TABLE 23. COMPARISONS OF PREDOMINANCE OF CERTAIN BRYOZOANS AND TUNICATES IN PACIFIC AND CARIBBEAN FOULING COMMUNITIES.

a. Bryozoa, ascidians and other animals; tally of number of species.

Location	Bryozoa	Tunicata	Other animals	Total
Taboguilla	22	13	48	83
Galeta	15	28	74	117
% of grand total	18.5	20.5	61.0	200

$$\chi^2 = 6.78 \text{ with 2 d.f.: } P < 0.05$$

Reject H_0 : conclude that bryozoa and/or ascidians and/or other animals together differ in importance in Pacific and Caribbean communities.

b. Bryozoa and ascidians, tally of number of species.

Location	Bryozoa	Tunicata	Total
Taboguilla	22	13	35
Galeta	15	28	43
% of grand total	47.4	52.6	78

$$\chi^2 = 6.06 \text{ with 1 d.f.: } P < 0.02$$

Reject H_0 : conclude bryozoa are relatively predominant and/or ascidians relatively unimportant in terms of number of species on Taboguilla settling plates.

TABLE 24. RATES OF INCREASE IN DRY WEIGHT OF THE COMMUNITIES OF FOULING ORGANISMS ON PLEXIGLAS PLATES. Both sides of the flat plates are 75 cm² in area, for a total of 150 cm² per plate. Weights were taken from communities between 27 and 148 days old. To calculate the power regression and to statistically test the relationships between dry weight of the fouling community and the number of days over which the community has been developing in the ocean, the original data were all transformed to natural logarithms.

Location	Time of year	No. of plates	Regression of dry weight per day ^a	Coefficient of determination (r ²)
Taboguilla (Pacific)	Dry season Dec 16 to Apr 15	113	$y = 0.0003 x^{2.23}$	0.62
	Wet season Apr 16 to Dec 15	113	$y = 0.0004 x^{2.04}$	0.61
Galeta (Caribbean)	Dry season Dec 16 to Apr 15	119	$y = 0.0001 x^{1.91}$	0.53
	Wet season Apr 16 to Dec 15	95	$y = 0.0007 x^{1.61}$	0.33

^a y is dry weight of fouling community on 150 cm² plate; x is number of days the plate was in the ocean.

Analysis of variance on common regression; H₀ is that $\beta = 0$

$$F = \frac{\text{variance due to regression}}{\text{deviations from regression}} \begin{cases} \text{(Pacific)} & F = 338 \text{ (1,224 d.f.) } P < 0.005 \\ \text{(Caribbean)} & F = 180 \text{ (1,212 d.f.) } P < 0.005 \end{cases}$$

Reject H₀ in both cases; conclude there is a significant linear relationship.

Analysis of variance on individual regression lines from each season (wet and dry seasons); H₀ is that the data from the two seasons fit a common regression line.

$$F = \frac{\text{variance due to common regression}}{\text{deviations from individual regression lines}} \begin{cases} \text{(Pacific)} & F = 9.741 \text{ (2,222 d.f.) } P < 0.005 \\ \text{(Caribbean)} & F = 6.406 \text{ (2,210 d.f.) } P < 0.005 \end{cases}$$

Reject H₀ in both cases; conclude the regressions from the data from the two seasons differ significantly in both oceans.

PART II

EXPERIMENTAL STUDIES ON THE EFFECTS
OF OIL POLLUTION

SECTION IX

FIELD EXPERIMENTS WITH THE EFFECTS OF EXPOSURE TO BUNKER C OIL

ON THE GROWTH RATE OF THE HERMATYPIC CORAL, *PORITES FURCATA*

A number of studies are cited in the literature in which both field and laboratory studies have been made with the effects of oil on hermatypic corals (Johannes, Maragos and Coles, 1972). Very few of these indicate signs of damage and almost none show definite evidence. Since hermatypic corals are very important in the ecology of reef communities, providing habitat as well as entering importantly into community metabolism, it is important to assess as thoroughly as possible the effects of oilspills on the health of corals. When mortality does not occur, rate of growth is probably the best quantitative, objective measure which integrates a variety of physiological effects. Further, much of a coral's success in a community, e.g., its strength in competition with other species for space or its ability to tolerate grazing and predation, depends in part upon its rate of growth (Glynn, Stewart and McCosker, 1972).

Methods

In brief, *Porites furcata* heads were collected, stained to mark the size at the initiation of the experiment, experimentally subjected to Bunker C oil or placed in pure seawater as a control, then replaced in the *Porites* bed where originally collected. After 61 days, the amount of growth added since the staining process was compared between the controls and those treated with oil. The procedures are described in detail in the following passages. Those who are interested mainly in the results and discussion may wish to skip directly to that section.

The experiment was repeated over two 61-day intervals, 25 January 1973 to 27 March 1973 and 4 April 1973 to 5 June 1973. Heads of *Porites furcata*, all of about the same size (about 10 or 12 branches), were each collected from a depth of 4.6 m (15 ft) near the Galeta laboratory. They were placed in plastic bags with Alizarin red S bone stain, sealed closed, and left for 6 hours (1100 to 1700) in shallow water 0.3 m (1 ft) in depth. After 6 hours of staining, they were placed overnight in an outside fiberglass tank with running seawater.

The next morning, two coral heads were placed in each of six buckets with just enough seawater to cover them. One hundred milliliters of Bunker C oil was poured into each of 4 buckets. When poured, the oil reached the bottom of the buckets but immediately floated to the surface through the branches of the corals. The water surface was 23 cm in diameter so the film was 2.4 mm thick. In the first experiment, four corals in two buckets

were left with Bunker C oil for 1 hour, four in the other two buckets were left with Bunker C oil for 2.5 hours and the remaining four corals were left in two buckets with pure seawater as controls for 2.5 hours. Since no significant difference was found between the growth of corals exposed for 1 hour and 2.5 hours, all corals were exposed for 2.5 hours during the second experiment.

When removed from the buckets, the corals were replaced in the *Porites* bed at a depth of 4.6 m near the laboratory. In order to distinguish between the experimentals and controls, wire bag fasteners were twisted about the base of each coral head, 1 on each of those from 1 hour in oil, 2 on each from 2.5 hours in oil, and 3 on each of the controls. Except for the last step in the entire process, the corals were transferred between containers within water, never breaking the surface. In the last step, however, the oil was poured off and the corals, coated with a film of oil, were placed in buckets of seawater by being lifted through air. The controls were also transferred through air.

Twenty-four hours later, the corals were observed in their field location. All corals appeared quite healthy, including those treated with Bunker C. All polyps were expanded to the same degree as those of the surrounding natural population. Effects of oil treatment were not apparent upon casual observation.

After 61 days in the field, both controls and experimentally treated *Porites* were collected and sprayed with water to remove the living tissue. The tips of the branches were filed by hand down to the center to that a flat, longitudinal section was provided for growth measurement. The measurement was made with vernier calipers to the nearest 0.1 mm of the distance between the apex of the pink-stained portion and the tip of the branch.

Before designing the experiment to test the effects of Bunker C oil on *Porites furcata*, we had already anticipated that growth increments of coral would vary greatly from location to location and from month to month. This variability could not be separated from the differences due to the effects of oil if all the data from controls were lumped together and compared with the data from all corals treated with Bunker C oil. Therefore, the statistical design of the growth experiment was a simple randomized block design and the data were analyzed by a paired difference test. A comparison of growth increments between corals used as controls and corals treated with Bunker C oil were made for each location and time period to eliminate the effects of variations between time periods and locations and to yield more accurate information on the mean difference in growth due to stress from treatment with Bunker C oil. Three difference measurements were utilized to test the null hypothesis that the average difference is equal to zero. This is equivalent to stating that the mean growth increments are the same.

Results and Discussion

The effects of Bunker C oil on the hermatypic coral *Porites furcata* were especially interesting in view of the lack of apparent damage upon casual observation. In brief, the *Porites* subjected to Bunker C for 1 or 2-1/2 hours appeared quite healthy during the next 61 days, but the difference in growth increments between corals subjected to Bunker C and controls was significant (Tables 25 and 26) and there was a significantly greater proportion of branches which failed to grow at all (Table 27). Thus, although exposure to Bunker C oil was not fatal to the *Porites*, it had some negative effect on its physiology which was reflected in its growth. As was previously mentioned, much of a sessile organism's success in a community, e.g., its strength in competition with other sessile species or its ability to tolerate grazing or predation, depends in part upon its rate of growth. It is quite conceivable that a decrease in growth rate of the predominant corals could affect the reef community as a whole.

A comparison of the growth increments of *Porites furcata* treated with Bunker C oil and of those used as controls is given in Table 25. The branch tips that did not grow at all were not included in this analysis but were treated separately (Table 27). When combined, these analyses amplify the significance of our conclusion (Table 26) that the growth rate of *Porites* was impaired by contact with Bunker C oil. When the corals were collected each time after 61 days' growth and cleaned, they appeared to have not differed in their growth rates. In fact, the single branch which increased in length the most (12.4 mm) was on a *Porites* subjected to Bunker C oil. It was only through statistical treatment that the reduced rate of growth of corals treated with oil became apparent. Because of the subtleness of the effect of oil on coral to the casual observer, the experiment was repeated a second time in spite of the significant results of the first trial. However, this is an example of how the minimal effects of an oil spill cannot be adequately judged on the basis of mortality or apparent condition of the resident populations.

Each *Porites* head consisted of several branches. An analysis of variance was made on the differences in mean growth increments on different heads between the 5 controls and also between the 10 experimentals in the first trial. The mean growth of control *Porites* heads did not differ significantly ($F = 1.96$ with 4, 55 d.f.; $P > 0.10$). The mean growth rate of *Porites* heads subjected to Bunker C did differ significantly ($F = 5.51$ with 9, 108 d.f.; $P < 0.005$). Since controls and experimentals were treated at the same time in the same manner except for the treatment with Bunker C, it would appear that there is much individual variation in susceptibility to oil pollution.

Although no difference in growth increments was found between the branches of controls growing in the same areas during the same periods, the growth

TABLE 25. THE EFFECT OF EXPOSURE TO BUNKER C OIL ON THE GROWTH RATE OF *PORITES FURCATA*. The growth took place during 61 days following exposure to Bunker C. Each *Porites* head had ten to twenty branches.

Cate- gory	Treatment	Experi- mental area ^a	No. <i>Porites</i> heads	Total no. branch tips that grew	Mean and standard error of the growth increment (mm/61 days)
(25 Jan 73 to 27 Mar 73)					
A.	Control	1	5	60	4.97 ± 0.03
B.	Exposed to Bunker C	1	10	118	4.25 ± 0.02
(4 Apr 73 to 5 Jun 73)					
C.	Control	1	4	74	7.5 ± 0.3
D.	Exposed to Bunker C	1	5	76	6.6 ± 0.4
E.	Control	2	3	31	5.5 ± 0.3
F.	Exposed to Bunker C	2	3	37	4.7 ± 0.3

^a Area 2 was located 3 m away from Area 1 at the same depth.

TABLE 26. THE STATISTICAL SIGNIFICANCE OF PHYSIOLOGICAL STRESS OF BUNKER C OIL ON *PORITES FURCATA* AS MEASURED BY DIFFERENCE IN GROWTH INCREMENTS OVER 61-DAY PERIODS. Also compared are differences in growth increments with season and with location.

Categories in Table 25 compared	Difference in growth increment (mm/61 days)	Mean difference in growth increments (\bar{d}) (mm/61 days)	Standard deviation of growth difference increments (S_d)	t^a (paired difference test)	d.f.	95% confidence intervals for differences in growth increments (mm/61 days)
A-B	0.72)					
C-D	0.90)	0.807	0.0902	15.496	2	0.807+0.224
E-F	0.80)					
C-E	2.00)	1.95	0.0707	39.006	1	1.95+0.64
D-F	1.90)					
C-A	2.53)	2.44	0.1273	27.107	1	2.44+0.11
D-B	2.35)					

Conclusions: Reject H_0 : conclude that the mean growth increments differ significantly between *Porites* subjected to Bunker C oil and *Porites* used as controls.

Reject H_0 : conclude that the mean growth increments of *Porites* colonies subjected to the same treatment but placed in different locations can differ significantly.

Reject H_0 : conclude that the mean growth increments of *Porites* colonies subjected to the same treatment in the same location differ significantly with time of year.

$$^a t = \frac{\bar{d} - 0}{S_d / \sqrt{n}}$$

rates of corals varied both in space (a distance of 3 m at the same depth) and time (two different 61-day periods). The effects of location (3 meter distance at same depth) and time of year (about two months apart) were each greater than the effect of 2.5 hours exposure to Bunker C oil (Table 26). Therefore, it is very important that the effects of oil be judged by accurately situated controls.

TABLE 27. A COMPARISON BETWEEN CONTROLS AND EXPERIMENTALS OF THE PROPORTION OF LIVE BRANCH TIPS THAT FAILED TO GROW DURING THE 61 DAYS FOLLOWING INITIATION OF THE EXPERIMENT. One *Porites* head of 10 branches subjected to Bunker C oil failed to grow at all although it appeared quite healthy to superficial observation. In case this occurred due to a factor other than exceptional individual susceptibility to Bunker C oil, a Fisher exact probability test was performed on all data (given in the table) then performed a second time disregarding this one *Porites* head (29 rather than 39 oil-subjected branch tips producing no growth).

<i>Porites</i>	No. branches that grew	No. branches with no growth	Total
Control	60	4	64
Subjected to Bunker C	118	39	157
Total	178	43	221

For all data in table: Fisher exact probability: $P = 0.0006$

Disregarding one head with 10 branches, none of which grew:

Fisher exact probability: $P = 0.0064$

Reject H_0 : conclude that the proportion of live branch that failed to grow during the 61-day period was greater than in those *Porites* heads subjected to Bunker C oil.

SECTION X

LABORATORY EXPERIMENTS WITH THE EFFECTS OF OIL ON HERMATYPIC

CORALS FROM THE EASTERN PACIFIC AND FROM THE CARIBBEAN

To compare the effects of different oils on several species of hermatypic corals, controlled experiments were performed in aquaria. The species used were: *Pocillopora* cf. *damicornis*, collected at a depth of 9 meters off Saboga, Perlas Islands, Pacific Panama; *Pavona gigantea* and *Psammocora* (*Stephanaria*) *stellata*, collected at a depth of 9 meters off Isla Chapera, Perlas Islands, Pacific Panama; *Porites furcata*, collected in intertidal open pools at Galeta Point, Caribbean Panama.

Methods

Experiments with *Pocillopora* cf. *damicornis*.—Two colonies of *Pocillopora* cf. *damicornis* were placed in a dish without water. The size range of the first colony was 6.0 cm (largest height) by 3.6 cm (largest width), and the second colony was 5.9 cm by 3.1 cm. Marine diesel oil was poured into the dish to cover them for 30 minutes. After 30 minutes, the colonies were rinsed in several changes of seawater and then placed in a well-aerated 5-gallon aquarium. Control colonies were subjected to the same manipulations, using seawater to replace oil, and were placed in a different well-aerated 5-gallon aquarium.

Next, two colonies of *P. cf. damicornis* were submerged in marine diesel oil (size ranges of the colonies were 2.5 by 3.0 cm and 5.5 by 4.5 cm), three colonies in Bunker C oil (size ranges of 2.9 by 2.2 cm to 4.0 by 4.2 cm) and three controls (size ranges of 4.5 by 3.7 cm to 4.5 by 4.2 cm) in seawater, all for 1-minute exposures to the test substance.

A third experiment was performed as follows. Colonies of *Pocillopora* with two distinct branches (Figure 4) were used for experiments in which 1 branch was exposed for 0.5 minutes to marine diesel oil in three colonies ranging in size between 4.0 by 2.5 cm and 4.0 by 4.0 cm, or to Bunker C oil for 0.5 minutes in three colonies ranging in size between 4.5 by 6.9 cm and 6.8 by 6.8 cm; the second branch in each colony was left untouched by oil. Three control colonies ranging in size between 4.0 by 4.6 cm and 5.0 by 5.2 cm were handled in the same manner but were exposed to seawater instead of oil.

In all of the experiments oil was removed from the colonies by submerging them in seawater and allowing the oil to float to the surface, from where it was removed by soaking it into Kimwipes. Next, the colonies were placed in a different container and exposed to running seawater for one-half hour.

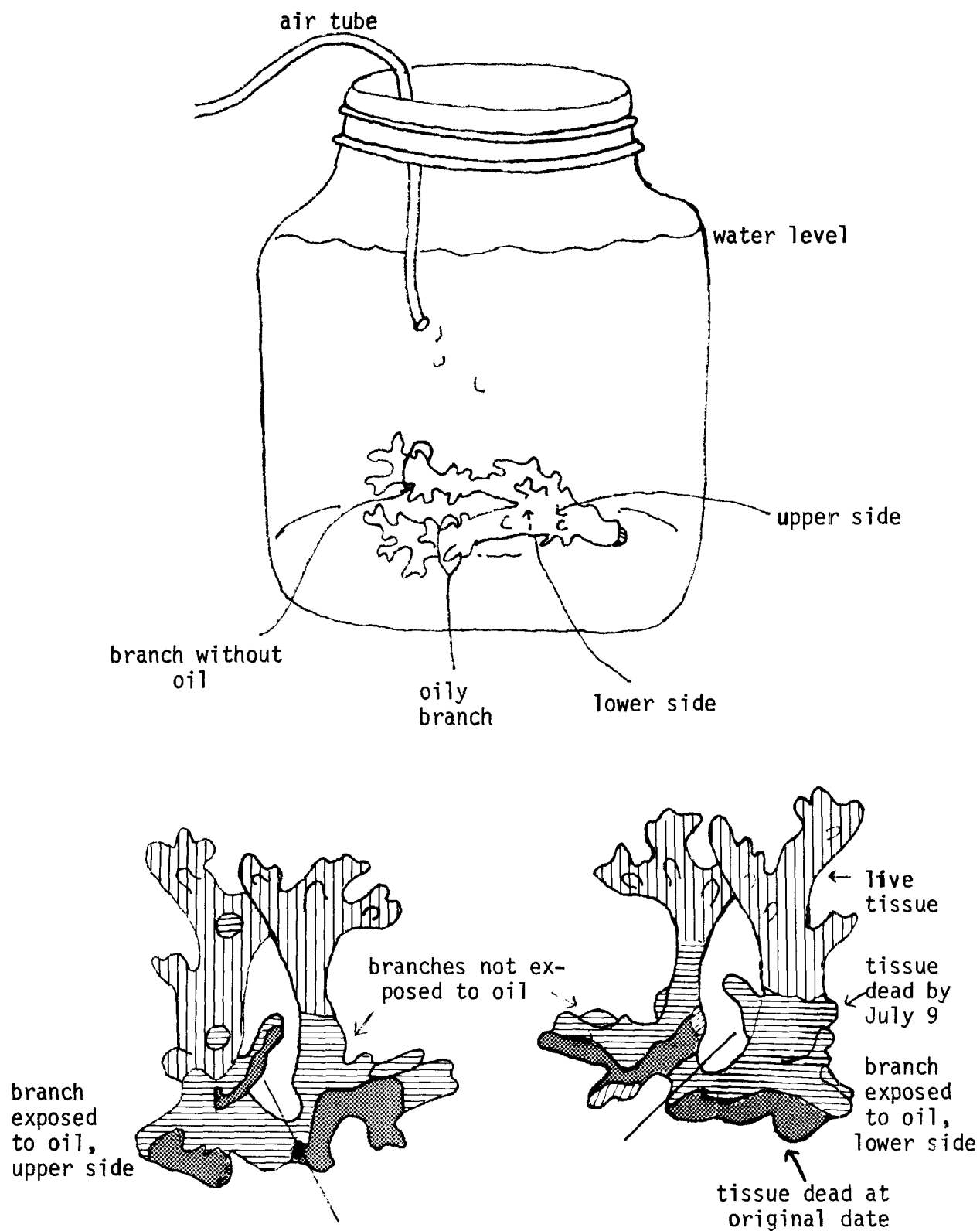


Figure 4. Experimental methods for investigating the effects of oil on *Pocillopora* cf. *damicornis* in the laboratory. For explanation see text, experiment 3.

All colonies in the second and third experiments were finally placed in well-aerated 3-liter containers under cool white fluorescent light for 12 hours daily.

The upper and lower surfaces of the colonies (Figure 4) were outlined on millimeter-lined paper and the surface area occupied by live tissue was calculated by counting the number of squares within the outline of the colony. The complicated topography of the branches provided many useful reference points to check the regression or addition of live tissue. This procedure does not take into account the three dimensional character of the colonies, but, since the changes in live tissue are expressed as a percentage of the original, based on two-dimensional drawings, the method is useful and accurate enough. Percentages of bleached (loss of color because of massive loss of symbiotic zooxanthellae) and dead tissue were calculated periodically.

Experiments with other corals.—Branches and small colonies of *Pavona*, *Psammocora* and *Porites* were exposed to experimental conditions similar to those described for *Pocillopora* in the second experiment.

Results and Discussion

Table 28 summarizes the data obtained for three different experiments. The first experiment shows that the colony tested was able to survive an exposure to pure marine diesel oil for 30 minutes and that it displayed the same tissue death rate as the control for about one month.

In the second experiment, all the colonies had similar degrees of tissue death for the first week, but after 13 days there was a very obvious difference between the control colonies and those that were exposed to oil. The colonies in marine diesel oil lost almost all of their living tissue within 13 days; those in Bunker C oil lost from 70 to 84 percent of their living tissue in the same period. After 16 days, both marine diesel and Bunker C colonies lost a large portion or all of their living tissue while the control colonies sustained over 95 percent of it. The third experiment showed that except for colony 1 in marine diesel oil the rest behaved in much the same way for almost one month. Some sharp differences between the colonies appeared after 71 days although there was no evident trends for colonies treated in a particular way. After 109 days, all of the colonies treated with Bunker C oil and one colony of the controls were dead. The rest of the control colonies and the colonies treated with marine diesel oil had comparably low percentages of living tissue left. The instances in which the percentage of tissue at one date was greater than at a previous one (e.g., colony 6, control for experiment 3 between 31 March and 6 April; colony 4, control for experiment 3 between 5 April and 13 April; colony 1, marine diesel oil between 27 April and 10 June) represents actual growth of new tissue covering areas that were originally dead. In all cases this new tissue covered small isolated dead patches towards the tips of the

TABLE 28. PERCENTAGE OF LIVE TISSUE LEFT ON *POCILLOPORA* CF. *DAMICORVIS* AFTER TREATMENT WITH MARINE DIESEL (M.D.) OR BUNKER C (B.C.) OILS ("NONE" INDICATES CONTROLS, DETAILS ON EXPERIMENTAL SETUP ARE IN METHODS SECTION).

Date	Type of oil	Ex-periment #	Col-ony #	Original live tissue (mm ²)	First obser- vation after	%	Second obser- vation after	%	Third obser- vation after	%	Fourth obser- vation after	%	Fifth obser- vation after	%
26 February 1972	M.D.	1	1	2043	18 hrs.	97	19 days	62	26 days	0				
	none	1	2	1836	18 "	98	19 "	67	26 "	20	32 days	2	35 days	0
16 May 1972	M.D.	2	1	2839	7 days	86	13 "	1	16 "	0				
	M.D.	2	2	5468	7 "	91	13 "	16	16 "	0.8	20 "	0		
	none	2	3	3102	7 "	97	13 "	96	16 "	96	20 "	95		
	none	2	4	2967	7 "	99	13 "	99	16 "	99	20 "	97		
	B.C.	2	5	1076	7 "	82	13 "	53	16 "	8	18 "	0		
	B.C.	2	6	4105	7 "	92	13 "	30	16 "	6	18 "	0		
	B.C.	2	7	1450	7 "	92	13 "	16	16 "	0				
31 May 1972	M.D.	3	1	2491	5 "	63	13 "	63	27 "	44	71 "	45	109 "	35
	M.D.	3	2	2517	5 "	95	13 "	95	27 "	95	71 "	76	109 "	21
	M.D.	3	3	1897	5 "	94	13 "	94	27 "	94	71 "	82	109 "	18
	none	3	4	2272	5 "	100	13 "	101	27 "	100	71 "	95	109 "	29
	none	3	5	4149	5 "	91	13 "	85	27 "	86	71 "	58	109 "	0.38
	none	3	6	3180	5 "	103	13 "	103	27 "	96	71 "	83	109 "	32
	B.C.	3	7	2206	5 "	100	13 "	100	27 "	100	71 "	33	109 "	0
	B.C.	3	8	2514	5 "	100	13 "	100	27 "	99	71 "	51	109 "	0
	B.C.	3	9	4803	5 "	100	13 "	100	27 "	100	71 "	93	109 "	0

colonies. Colony 1 in marine diesel oil, for instance, showed a 2.94 percent increase between 27 April and 10 June, and this represents a growth of tissue to cover 64 mm^2 of surface.

Several colonies in the third experiment showed extensive "bleaching" (loss of their characteristic brown color) due to a massive loss of symbiotic zooxanthellae. Most bleaching occurred within 5 to 13 days of the experimental setup and, except for colony 3 in marine diesel oil and which was bleached towards the end of the experiment, all the others recovered by the third observation time, 27 days after experiments were initiated. Colony 3 in marine diesel oil was also unusual in that bleaching disappeared in the lower oil-treated side by the second observation, but it recurred by the fifth observation and then it affected both sides and all the branches of the colony. Although bleached polyps seemed to regress in size (evident especially in the smaller tentacles) there was only one instance where previously bleached tissue was dead at the next observation.

Table 29 details the percentages of live and bleached tissue remaining on upper and lower branches which were exposed to oil and on upper and lower branches not exposed to oil. The purpose of this table is to permit several analyses to find the effects of, and interactions between, the factors of oil and light in their effect on corals. Seventy-one days after being exposed to oil for 0.5 minutes, corals do not display a significant difference in living tissue left on upper and lower branches ($t = 1.33$, d.f. 16, $P > 0.05$) or on oily and nonoily branches ($t = 0.14$, d.f. 13, $P > 0.05$).

If an analysis of variance (Table 30) is conducted on the percentage of tissue bleached within five days after 0.5 minutes exposure to marine diesel or Bunker C oils, it becomes clear that the variation between the colonies is greater than the differences due to treatment. The factors analyzed are the presence or absence of oil and the different amount of light received by upper and lower surfaces of the branches. The variance ratios are smaller than expected for both colonies and treatments and therefore the percentage of tissue bleached is not significantly different ($P > 0.05$) between colonies or between treatments. The same analysis applied to the percentage of live tissue present on the coral after 109 days of the oil application (Table 30) produces similar results.

The results of similar experiments performed on other species of hermatypic corals are given in Table 31. *Psammocora stellata* is not clearly affected by Bunker C or marine diesel oils, but physiological stress or unseen damage was not measured by growth increments in comparison with controls. The effects of Bunker C and marine diesel oils on *Pavona gigantea* and *Porites furcata* did not appear until after a period of about two weeks following the exposure to the oil. After 93 days, both Bunker C and marine diesel oils were seen to have detrimental effects on both *Pavona* and *Porites*. As with *Pocillopora*, both *Pavona* and *Porites* were more severely harmed by Bunker C oil than by marine diesel oil.

TABLE 29. PERCENTAGE OF LIVE AND "BLEACHED" (LOSS OF ZOOXANTHELLAE) TISSUE ON *POCILLOPORA* CF. *PAMPCORPUS* ON APRIL 5 (1), APRIL 13 (2), APRIL 27 (3), JUNE 10 (4), AND JULY 9 (5); AFTER AN INITIAL (MARCH 31) TREATMENT WITH BUNKER C (B.C.) AND MARINE DIESEL (M.D.) OILS. In each pair the lower number represents "bleached" tissue; when no value is given, the percentage of bleached tissue is 0.00.

	Upper Side, Oil					Upper Side, No Oil				
	(1)	(2)	(3)	(4)	(5)	(1)	(2)	(3)	(4)	(5)
B.C., colony 1	100	100	89.50	46.10	0	100	100	96.85	61.83	0
B.C., colony 2	100	100	67.00	31.75	0	$\frac{100}{6.60}$	100	70.41	68.53	0
B.C., colony 3	$\frac{100}{18.00}$	100	100	99.70	0	100	100	98.10	74.40	0
M.D., colony 1	$\frac{100}{88.06}$	$\frac{100}{88.06}$	86.98	98.89	97.33	$\frac{100}{27.36}$	$\frac{100}{27.36}$	27.56	80.50	80.42
M.D., colony 2	100	100	100	94.00	45.30	100	100	93.84	94.40	54.50
M.D., colony 3	100	97.34	97.30	91.22	$\frac{85.94}{100}$	100	100	80.64	63.70	65.44
Control 1	$\frac{90.88}{6.48}$	90.88	94.10	98.60	17.15					
Control 2	$\frac{81.32}{10.80}$	81.74	77.25	56.95	0.95					
Control 3	100	103.29	97.34	89.78	59.71					

TABLE 29 (continued). PERCENTAGE OF LIVE AND "BLEACHED" (LOSS OF ZOOXANTHELLAE) TISSUE ON *POCILLOPORA* CF. *DAMICORNIS* ON APRIL 5 (1), APRIL 13 (2), APRIL 27 (3), JUNE 10 (4), AND JULY 9 (5); AFTER AN INITIAL (MARCH 31) TREATMENT WITH BUNKER C (B.C.) AND MARINE DIESEL (M.D.) OILS.

	Lower Side, Oil					Lower Side, No Oil				
	(1)	(2)	(3)	(4)	(5)	(1)	(2)	(3)	(4)	(5)
B.C., colony 1	$\frac{100}{64.89}$	100	49.68	46.62	0	$\frac{100}{58.80}$	100	97.36	57.04	0
B.C., colony 2	100	100	59.08	26.86	0	$\frac{100}{27.60}$	$\frac{97.24}{9.60}$	65.92	50.08	0
B.C., colony 3	$\frac{100}{71.68}$	100	98.58	86.56	0	$\frac{100}{29.60}$	100	99.04	80.64	0
M.D., colony 1	$\frac{100}{26.04}$	$\frac{100}{26.04}$	100	95.68	70.75	$\frac{100}{25.08}$	$\frac{100}{25.08}$	65.83	65.00	35.40
M.D., colony 2	$\frac{100}{100}$	$\frac{100}{100}$	93.60	95.12	5.60	$\frac{100}{100}$	$\frac{100}{100}$	94.56	53.44	2.56
M.D., colony 3	$\frac{100}{100}$	$\frac{100}{100}$	97.62	97.90	$\frac{89.65}{100}$	100	100	97.62	82.12	73.48
Control 1	$\frac{93.85}{48.84}$	$\frac{93.85}{48.84}$	94.39	92.20	7.08					
Control 2	100	94.50	90.28	13.34	0					
Control 3	101.40	102.50	95.70	77.90	5.91					

TABLE 30. ANALYSIS OF VARIANCE FOR A 2^2 FACTORIAL ON THE AMOUNT OF TISSUE BLEACHED WITHIN 5 DAYS AND ON THE AMOUNT OF LIVE TISSUE AFTER 109 DAYS TREATMENT OF *POCILLOPORA* CF. *DAMICORNIS* WITH OIL (FACTORS ARE OIL AND QUANTITY OF OIL, NS = NOT SIGNIFICANT). For experimental design see text, experiment 3 and Table 29.

	Per cent of tissue bleached within 5 days in colonies treated with Bunker C or marine diesel	Per cent of live tissue left after 109 days on colonies treated with Bunker C or marine diesel
Variance ratio for colonies	0.33	1.43
d.f. colonies	5, 15	2, 11
F at P = 0.05	4.62	5.14
Significance	NS	NS
Variance ratio for treatments	1.33	0.97
d.f. treatments	3, 15	3, 11
F at P = 0.05	8.70	4.76
Significance	NS	NS
Effect:		
Upper oil	+61.97 NS	+117.66 NS
Upper no oil	+16.13 NS	+14.00 NS
Lower oil	-38.63 NS	+25.33 NS
Lower no oil	-4.11 NS	-4.3 NS
5 per cent point	±521.01	±455.77

TABLE 31. EFFECT OF A 1-MINUTE EXPOSURE TO BUNKER C (B.C.) OR MARINE DIESEL (M.D.) ON *PSAMMOCORA STELLATA*, *PAVONA GIGANTEA* AND *PORITES FURCATA*.

Type of oil	# of colonies and their size range (in cm.)	Species	State of colony after 12 days	State of colony after 93 days	State of colony after 114 days
M.D.	1 (5.0 X 2.9)	<i>Psammocora</i>	no change	no change	no change
B.C.	5 (1.1 X 1.4 to 3.0 X 3.9)	<i>Psammocora</i>	no change	no change	no change
none	2 (3.0 X 2.7 to 3.8 X 3.0)	<i>Psammocora</i>	no change	no change	2 mm ² new tissue
M.D.	1 (4.7 X 0.7)	<i>Pavona</i>	no change	12% tissue dead	12% tissue dead
B.C.	1 (4.0 X 2.5)	<i>Pavona</i>	no change	50% tissue dead	100% tissue dead
none	1 (5.5 X 5.5)	<i>Pavona</i>	no change	18 mm ² new tissue	new tissue maintained
M.D.	2 (2.0 X 1.7 to 3.1 X 2.3)	<i>Porites</i>	no change	15-37% tissue dead	15-32% tissue dead (colony 2 shows 50% of tissue recovered)
B.C.	3 (2.4 X 1.3 to 4.0 X 2.5)	<i>Porites</i>	no change	no change	100% tissue dead in all three colonies
none	1 (8.1 X 5.3)	<i>Porites</i>	no change	1% tissue dead	18% tissue dead

All corals used in these experiments had filamentous algae associated with them around the bases of the colonies and branches at the time the experiments were begun. In the five control aquaria not subjected to Bunker C oil, the algae maintained itself at about the same levels. In each of the five aquaria previously treated with marine diesel oil, the algae grew more lush. The five aquaria previously containing Bunker C oil each grew strands of algae, especially blue-green algae (Cyanophyta), three to five times as lush as any of the control aquaria or aquaria previously containing marine diesel oil.

SECTION XI

FIELD EXPERIMENTS WITH THE EFFECTS OF OIL POLLUTION ON CARIBBEAN AND EASTERN PACIFIC INTERTIDAL COMMUNITIES

On the basis of the baseline data presented in Part I of this report on intertidal communities of the Caribbean and Pacific coasts of Panama, two zones, one on each coast, were selected for the tests of the long-term effects of an oil spill on the fauna and flora. These zones were selected for several reasons: they were the most easily sampled zones on each coast, they were relatively high in the intertidal zone so that the oil could be applied safely, they were characterized by a diversity of species so that we could obtain data on the effects of oil on a variety of organisms, they were relatively uniform in composition in comparison with other zones so that our replicates and controls would have some validity and, perhaps most importantly, they were zones selected for special studies in addition to our regular sampling program. These additional studies are hoped to provide further insight in interpreting any effects or lack of effects of the oil pollution. The zones selected were the *Tetraclita* Zone, Pacific side, at Paitilla Beach, and the Laurencia Zone, Caribbean side, on the Galeta Point reef flat.

Methods

Since Bunker C and marine diesel are the oils most commonly spilled in the areas under study, we conducted experiments with each of them. Bunker C and marine diesel oils were mixed in a 1:1 ratio while marine diesel was used pure. They were applied to the substratum during low tide, while the area was exposed, with an X-Pert 2-gallon professional sprayer (D-Hudson Manufacturing Company, Illinois). The flow rate of the sprayer was measured just before each experiment. The substratum was sprayed evenly, from a distance of about 0.3 m above the substratum, for the length of time necessary to release 250 ml of oil. Areas surrounding the pollution quadrats were protected from oil spray by a continuous wall of moist paper towels about 30 cm wide. The paper towels were placed around the outside of quadrats treated with oil, not in any quadrats, for the brief period of the actual spraying operation.

Experiments were set up in the *Tetraclita* Zone, Paitilla Beach, as follows. A total of six experimental quadrats were selected on a horizontally flat top ridge of andesite rock standing about 1.8 m above mean sea level which offered a typically abundant standing crop of *Tetraclita stalactifera panamensis*. The quadrats were marked with Sea Goin' Poxxy Putty. Three quadrats about 1 meter apart were used to study the possible effects of oil on a community of live *Tetraclita*. The other three quadrats, standing

a few meters from the first triplet, and also places at 1 meter intervals, were used to study the effects of oil on the recruitment of invertebrates to empty *Tetraclita* tests. For the latter study, all the barnacles in a quadrat were killed and the tests were washed thoroughly with seawater to clean out the remains of the animal. In each triplet one quadrat was sprayed with a 1:1 mixture of Bunker C:marine diesel, one was sprayed with marine diesel and one was left as control. In order to have an idea of the flora and fauna present in the study site at the time of pollution, two 0.10 m² samples were scraped from the rock, and two clumps of *Tetraclita* (7 barnacles each) were collected in the neighborhood of the experimental quadrats. The experiments were carried out at low tide. The area remained exposed for about 5 hours. Examination of the area on the next day showed no visible traces of oil on the surface of rocks or *Tetraclita* tests. Periodic samples were taken in order to evaluate long-term changes in the quadrats.

The experiments in the Laurencia Zone on the Galeta reef were set up as follows. Six 1 m² quadrats, 100 meters northwest from the Laurencia Zone marker of our transect zone, were staked with railroad spikes at 1 meter intervals. The two extreme quadrats (1 and 6) were controls; quadrats 2 and 4 were sprayed with a 1:1 mixture of Bunker C and marine diesel oils; quadrats 3 and 5 were sprayed with marine diesel oil. Three days previous to the experimental pollution a series of twelve 0.10 m² samples (2 from each quadrat) were collected and sorted. The quadrats were observed continuously for 1 hour after pollution. A series of four 0.10 m² samples (1 each from quadrats 2 to 5) were taken after 1-1/2 hours. Another series of twelve 0.10 m² samples (2 from each quadrat) were collected after 48 hours of the pollution experiment. The experiment was carried out at low tide. The pollution quadrats were completely exposed for 2 hours. Monthly collections were taken to detect any long-term changes.

Results and Discussion

The number of species of algae in the Laurencia Zone quadrats underwent a significant increase following pollution with Bunker C:marine diesel oil mixture (Table 32). The four 0.01 m² samples each contained fewer than the four samples taken one week following treatment with the oil ($P = 0.014$, Mann-Whitney U test). During the following three weeks, the number of algal species increased significantly further ($P = 0.029$, Mann-Whitney U test). The samples taken in control quadrats and quadrats treated with straight marine diesel oil varied greatly and in no particular pattern (Table 32). The small number of samples and the variation in the control quadrats cast a warning of caution on acceptance of the significance of the Bunker C effects. However, a similar pattern of effects of Bunker C oil on algae is found in the significant results of increased algal production on settling plates coated with Bunker C oil to a much greater extent than in the aquaria not exposed to oil (Section X).

TABLE 32. NUMBER OF ALGAL SPECIES FROM EXPERIMENTAL QUADRATS SPRAYED WITH BUNKER C:MARINE DIESEL OIL MIXTURE (1:1 RATIO) OR STRAIGHT MARINE DIESEL OR CONTROL QUADRATS NOT SPRAYED WITH OIL IN THE LAURENCIA ZONE, GALETA REEF. ^a The first number refers to total number of species, the second number refers to the average number of species per 4 quadrats in each time-place-treatment combination.

	Before oil treatment	7 days after	28 days after
Control	33/18	32/16	26/16
Bunker C:Marine Diesel	20/10	24/14	28/16
Marine Diesel	29/14	19/12	26/14

^a Algal identifications were provided by
Joyce Redemske Young.

It is interesting to note that algae recovers (in fact, expands dramatically) after heavy oil spills such as that following the breakup of the TAMPICO MARU (North, Neushul and Clendenning, 1965). The expansion of kelp was assumed to be caused by the failure of the populations of herbivorous echinoids to recover for more than seven years following the spill. This is probably correct, but confounded by the apparent influence of certain oils, such as Bunker C, on algal recruitment.

The animal communities, on the other hand, showed no evidence of a long-term effect of oil pollution (Tables 33, 34, and 35). Thousands of amphipods were seen to be killed immediately by the oil spray at Galeta and many crabs ran out of the area when the experimenters approached. Both groups of crustaceans had reinvaded the polluted areas within one week.

Table 34 shows the number of species and specimens found in controls and treated quadrats of the Tetraclita Zone during a series of collections following the oil treatment. The number of species and their abundances show no clear trends following the experimental pollution. Variations in the controls were just as great as those in the treated quadrats and are probably a reflection of the great patchiness of the community rather than of the effects of oil. The same is evident in the area where barnacles had been killed and cleaned in order to study effects of the oil on the recruitment and succession of invertebrates to the barnacles' tests. Table 35, where these results are presented, shows no trend of increase or decrease in the number of species or in their abundances. Furthermore, there are no changes in the kinds of species present in either the regular Tetraclita Zone or the recruitment and succession experiment.

The same situation is apparent in animals from our experiments in the Laurencia Zone on the Galeta reef. Table 33 shows no significant changes in number of species or in abundances between control and experimental quadrats.

A factor that may account for the survival of organisms in the experimental quadrats is the size of areas involved. One square meter quadrats subjected to each treatment were separated and placed between quadrats subjected to other treatments. An isolated square meter could be supplied with unaffected plankton and nutrients as surrounding water washes across. It may be necessary to test this factor by experimental pollution on the scale of hectares rather than square meters, but this is not a reasonable field experiment for a marine laboratory to undertake.

Another important factor is the toxicity of the particular oils involved. The fuel oils, Bunker C and marine diesel, were chosen because they were the types most commonly involved in local oil spills and because they represent two opposite categories of volatility. Mr. Eugene Lau, Chief Chemist of the local Refineria de Panama, S.A., gave us technical information on the contents of these oils when the oils were supplied. This information is given in Table 36 so the reader can judge potential toxicity

TABLE 33. NUMBER OF SPECIES AND AVERAGE TOTAL NUMBER OF INDIVIDUALS OF ALL SPECIES PER 0.01 m² FROM EXPERIMENTAL QUADRATS IN THE LAURENCIA ZONE, GALETA REEF. Quadrats were treated with Bunker C:Marine Diesel oil mixture (1:1 ratio, noted as BC:MD in the table) or straight marine diesel oil; the control quadrats were not sprayed with oil. Each first number refers to number of species, the second numbers refer to average total abundance of all species per 0.01 m² for four quadrats in each time-place-treatment combination category.

	Before oil treatment	7 days after	28 days after
Polychaeta			.
Control	19/26	22/73	23/82
BC:MD (mixture)	14/56	16/56	14/44
Marine Diesel	17/35	17/58	21/86
Sipunculida			
Control	8/8	9/17	7/9
BC:MD (mixture)	6/5	8/8	8/12
Marine Diesel	8/6	5/6	10/8

TABLE 34. NUMBER OF SPECIES (FIRST NUMBER) AND INDIVIDUALS (SECOND NUMBER) FOUND IN 0.01 m² SAMPLES FROM: UNTREATED, BUNKER C:MARINE DIESEL (1:1 RATIO), AND MARINE DIESEL SPRAYED QUADRATS IN THE TETRACLITA ZONE, PAITILLA BEACH. Number of species represents the total found in each sample. Since number of specimens found in dead barnacles is 5.9 times that found in live ones, a standardization factor was calculated by dividing the number of live barnacles by 5.9 in each sample and adding it to the number of dead barnacles present in the same sample. Essentially, then, the number of specimens indicated is per barnacle and not per sample.

	Pre-pol- lution	26 days after	61 days after	98 days after	129 days after	159 days after
Coelenterates						
Control	2/11	1/13	2/15	2/42	1/5	1/30
BC:MD		2/29	2/15	1/13	1/21	1/1
Marine Diesel		2/4	1/8	--	3/27	1/53
Polychaetes						
Control	7/16	2/2	8/12	10/13	8/34	8/38
BC:MD		7/18	8/13	9/16	8/14	7/24
Marine Diesel		14/42	8/12	4/12	9/21	7/17
Mollusks						
Control	8/39	1/<1	10/7	6/58	8/17	9/12
BC:MD		6/43	6/25	8/30	4/36	7/74
Marine Diesel		9/9	7/17	4/16	8/35	6/52
Barnacles						
Control	2/97	2/428	2/60	2/9	2/23	2/23
BC:MD		2/89	2/59	2/89	2/50	2/80
Marine Diesel		2/52	2/94	2/57	2/15	2/88
Arthropods (other than barnacles)						
Control	6/48	5/6	4/21	5/8	2/1	4/41
BC:MD		4/17	5/7	6/9	3/8	1/1
Marine Diesel		13/10	2/11	--	5/7	1/2
ALL TAXA						
Control	39/224	8/458	23/189	26/132	22/92	24/308
BC:MD		22/168	25/94	23/159	29/105	18/180
Marine Diesel		38/117	23/147	11/87	21/134	18/303

TABLE 35. NUMBER OF SPECIES (FIRST NUMBER) AND INDIVIDUALS (SECOND NUMBER) FOUND IN 0.01 m² SAMPLES OF KILLED, CLEANED *TETRACLITA* TESTS FROM UNTREATED, BUNKER C:MARINE DIESEL = 1:1, AND MARINE DIESEL SPRAYED QUADRATS IN THE TETRACLITA ZONE, PAITILLA BEACH. Number of species represents the total found in each sample. Since number of specimens found in dead barnacles is 5.9 times that found in live ones, a standardization factor was calculated by dividing the number of live barnacles by 5.9 in each sample and adding it to the number of dead barnacles present in the same sample. Essentially, then, the number of specimens indicated, is per barnacle and not per sample. BC:MD is an abbreviation for the term Bunker C:Marine Diesel sprayed quadrats.

	Pre-pol- lution	26 days after	61 days after	98 days after	129 days after	159 days after
Coelenterates						
Control	2/11	2/5	1/<1	2/1	2/3	1/2
BC:MD		2/14	1/<1	2/4	3/4	--
Marine Diesel		1/2	--	2/3	--	1/<1
Polychaetes						
Control	5/12	14/15	9/6	10/5	7/7	11/7
BC:MD		2/10	3/4	7/14	6/8	9/10
Marine Diesel		8/10	7/4	13/3	7/7	6/7
Mollusks						
Control	6/106	11/30	10/5	15/16	6/18	9/19
BC:MD		11/64	5/5	7/9	7/11	8/12
Marine Diesel		14/20	3/4	13/30	12/22	9/21
Barnacles						
Control	2/145	2/83	2/61	2/93	2/32	2/67
BC:MD		2/23	2/57	2/96	2/55	2/99
Marine Diesel		2/208	2/126	2/165	2/64	2/50
Arthropods (other than barnacles)						
Control	7/114	3/3	5/1	3/1	1/7	3/4
BC:MD		5/14	1/<1	1/2	1/2	3/2
Marine Diesel		6/12	3/1	4/15	2/<1	2/2
ALL TAXA						
Control	26/369	34/137	27/74	35/115	20/93	28/99
BC:MD		24/116	13/66	21/126	27/85	22/122
Marine Diesel		33/254	17/135	36/246	25/103	20/90

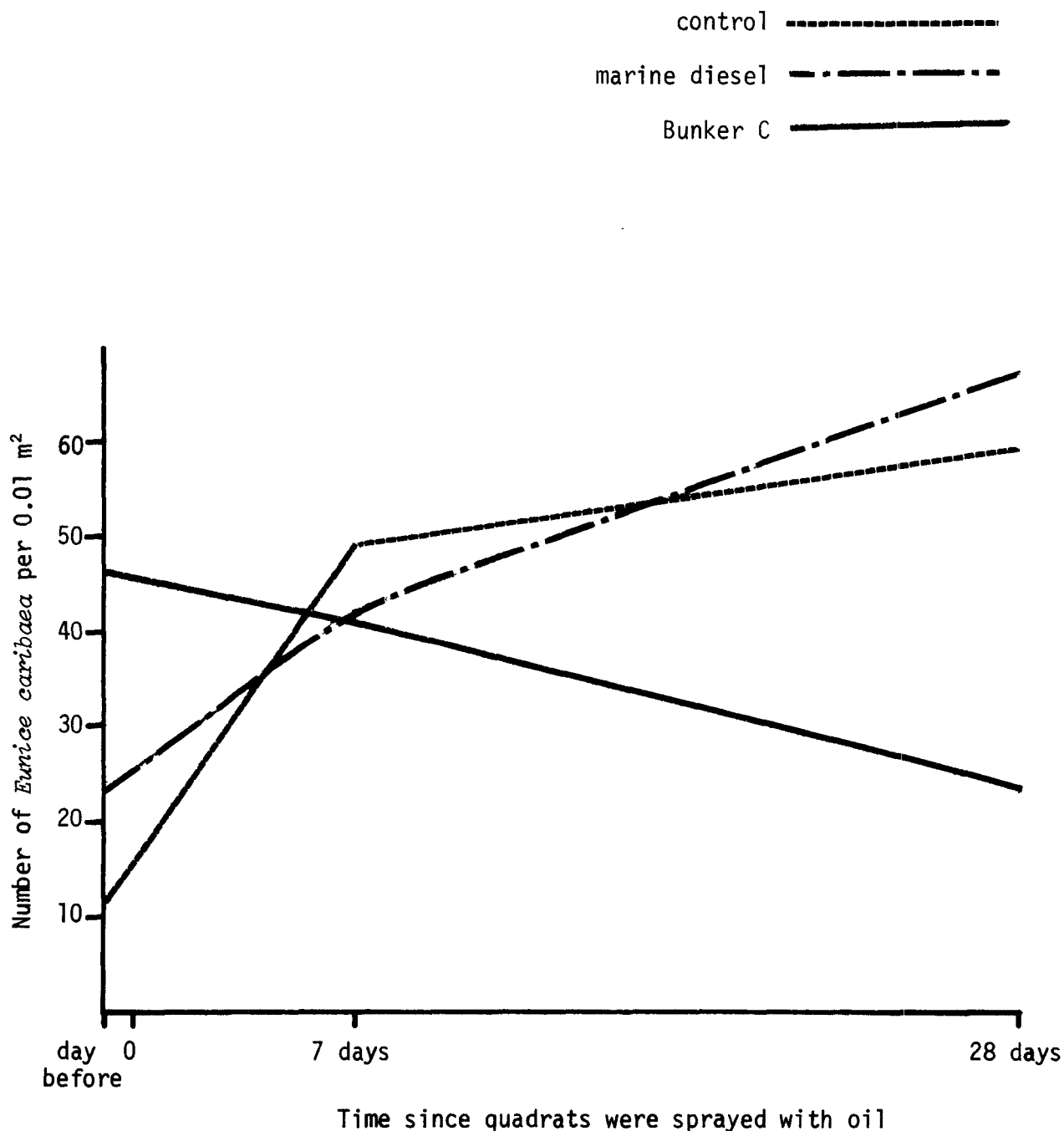
TABLE 36. CHARACTERISTICS OF THE FUEL OIL SAMPLES USED IN POLLUTION EXPERIMENTS IN THIS REPORT.

	Bunker C	Marine Diesel
Specific gravity	0.9646	0.8767
Density (API at 15.5°C)	15.2	29.9
Viscosity (SFS at 50°C)	161.0	49.0
Flash point, °F (PM)	162	194
Pour point, °F	+25	+30
Sulphur total, % weight	2.33	0.93
Water and sediment, % volume	0.05	trace
Ashes, % weight	0.05	0.005
Calorific value, BTU/lb (gross)	18,800	--
Explosivity, %	40	--

or compare with oils involved in other situations.

Perhaps the most important single criterion for judging the effects of an oil spill is comparative data from control quadrats. If no change occurs with respect to extensive background data for the area, this does not necessarily imply a lack of effect of oil. As an example, consider the changes in *Eunice caribaea* populations in the three quadrat sets (Figure 5). *Eunice caribaea* was previously regarded as the polychaete species most accurately evaluated in our pollution experiments because of its relatively regular, nonclumped, consistently abundant distribution (Appendix B). Although the populations in quadrats treated with Bunker C oil underwent a significant decrease between the period before the oil spray and 28 days after ($P < 0.05$, t -test or $P = 0.057$, Mann-Whitney U test), during the same period populations in both the control quadrats and quadrats sprayed with marine diesel oil increased significantly in abundance ($P < 0.01$, t -test or $P = 0.01$, Mann-Whitney U test). The increase in control quadrats and quadrats subjected to marine diesel oil alone did not differ significantly. Thus, marine diesel oil apparently had no effect on *Eunice caribaea* populations, while Bunker C oil had a significant effect. From baseline data the *Eunice caribaea* populations would not have been expected to undergo an increase. The decrease in Bunker C oil populations would have been far less noticeable and it may even have been hypothesized that marine diesel oil encouraged the increase in *Eunice caribaea*. This implies that, even though no gross changes in diversity or abundance are apparent, subtle changes in certain populations do occur and may in the end have significant effects on the ecology of the area. This points to the need of extensive controls for a reliable interpretation of the effects of an oil spill on a marine community.

Figure 5. Change in average abundance of *Eunice caribaea* in quadrats for experimental control and for quadrats sprayed with Bunker C or marine diesel. Two samples were taken on each date for two spatially separated quadrats for each treatment so $n = 4$ for each point. The populations in quadrats subjected to marine diesel or left untreated did not differ significantly and both underwent a significant increase. The populations in quadrats treated with Bunker C, separated from each other, but located between quadrats treated in the other ways, decreased significantly.



SECTION XII

FIELD EXPERIMENTS WITH THE EFFECTS OF OIL ON THE

MANGROVE TREE, *RHIZOPHORA MANGLE*

Rützler and Sterrer (1970), in observations made two months after the wreck of the 35,000-barrel oil tanker *SS Witwater*, noted that "high winds caused a spray of mixed seawater and oil to cover mangrove trees and shrubs in the supra-littoral zone to a height of 2 m above mean tide level" and that the oil had "already killed many of these plants." Although oil flowed in through tide channels and covered the stilt roots of mangroves a good distance in from the open sea, Ira Rubinoff pointed out two years later that the most obvious defoliation was in a band of mangrove trees at the edge of the sea and possibly could be a result of the spray of oil onto the leaves rather than the coating of the stilt roots. We set up the experiment to test this hypothesis.

Methods

Thirteen small *Rhizophora mangle* trees were sprayed with oil. All were 0.6 to 2 meters tall, except for one which was 3 meters tall. They were growing at the edge of the forest but isolated so their sizes could clearly be determined by planimetry from photographs taken with a scale included. Four trees were sprayed on the leaves from the direction of the wind with 300 ml of marine diesel oil (trees 5-8, Figure 6). Three trees were evenly sprayed on the stilt roots with 300 ml of marine diesel and Bunker C oils in a 1:1 ratio (trees 9-11, Figure 6). (Pure Bunker C oil is too viscous for the sprayer to handle, so it had to be diluted with marine diesel oil.) Trees 12 and 13 were sprayed both on the roots with 300 ml of mixture and on the leaves with 300 ml of marine diesel oil. Four trees were not sprayed and left as controls (trees 1-4, Figure 6). All trees were sprayed and photographed on 17 January 1972. The same spraying procedure was repeated 22 days later. After 372 days, the trees were again photographed from the same angle with the same scale. Measurements of leaf coverage were made with a Gelman planimeter.

Results and Discussion

All trees that had leaves sprayed with oil had fewer leaves and more bare branches than the year before and showed no growth of the trunk or branches (Table 37). Two of the control trees grew and seemed quite healthy, but a third did not show a change in size. Of those sprayed on the roots with Bunker C oil, a small individual (0.6 m tall) deteriorated to about half its original size in terms of leaf coverage, while the largest (3 m tall) apparently remained in fine health. Both were sprayed with 300 ml of oil,

Figure 6. Map of the relative positions of *Rhizophora mangle* trees involved in oil pollution experiments. Galeta Marine Laboratory is located near the pier. The numbers refer to the trees used in the experiment. The treatment of each numbered tree is given in Table 44. "X" refers to a small *R. mangle* not used in the experiment or photographed as a control.

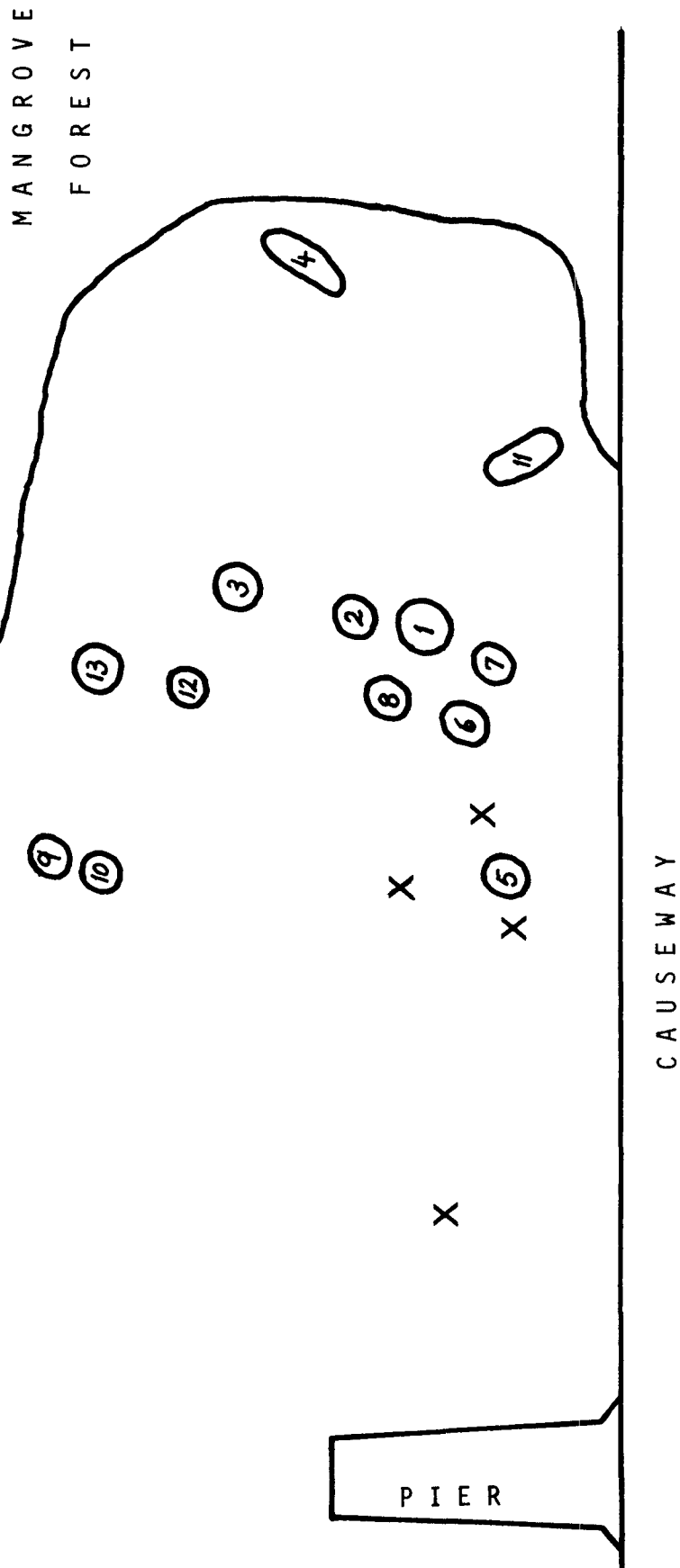


TABLE 37. CONDITION OF SMALL *RHIZOPHORA MANGLE* AFTER HAVING BEEN SUBJECTED TO OIL POLLUTION ON TWO OCCASIONS, 22 DAYS APART. All trees were isolated and between 0.6 and 2 m tall except for tree number 11 which was 3 m tall.

Experimental Procedure	Mangrove No. (Fig. 6)	Change in Condition after 372 Days
Control	1	Increased by 3 per cent in side view area, apparently in fine health.
	2	Increased by 5 per cent in side view area, apparently in fine health.
	3	Removed by a drift log.
	4	Same size in side view area.
300 ml of marine diesel sprayed on leaves	5	Reduced in leaf coverage by 67 per cent, bare branches.
	6	Reduced in leaf coverage by 30 per cent.
	7	Reduced in leaf coverage by 11 per cent.
	8	Reduced in leaf coverage by 26 per cent.
300 ml of half marine diesel and half Bunker C sprayed on roots	9	Reduced in leaf coverage by 55 per cent, many bare branches.
	10	Gone--removed by a drift log.
	11	Apparently in fine health.
300 ml of marine diesel sprayed on leaves <u>and</u> 300 ml mixture sprayed on roots	12	Completely dead, bare branches, but still standing.
	13	Carried away by a drift log.

so that the larger tree received a thinner coating. It seems quite likely that spraying leaves with marine diesel oil caused at least temporary deterioration in the health of the small *Rhizophora mangle*.

It was also striking that three of the 13 trees were removed by large drift logs which were carried across the reef flat during the windy dry seasons. The logs rip away or roll across the small recruiting trees, then drift up against the outer edge of the forest and stop, piled up against the solid outer band of stilt roots. The drift logs were not seen to do any obvious damage to the forest itself, but could quite possibly greatly hinder the spread of the forest across the intertidal reef flat by destroying isolated advancing recruits. Drift logs are recognized as an important disruptive factor in the rocky intertidal zone of temperate zones (Dayton, 1971); they could well be important in the tropics as well. The drift logs observed were the trunks of large trees with the base of the branches and root systems still attached, which indicates the logs were probably natural and not due to logging operations.

SECTION XIII

EFFECTS OF OIL ON THE RECRUITMENT OF ORGANISMS TO

PLEXIGLAS SETTLING PLATES

There is a variety of natural factors that cause mass mortality in marine intertidal communities, e.g., unusual water temperature changes, current changes, severe storms, dinoflagellate blooms (Brongersma-Sanders, 1957), drift log battering (Dayton, 1957), or desiccation (Glynn, 1968). Oil spills, of course, are a cause of mass mortality to which organisms have not evolved adaptive response. But the mortality caused by the oil spill is not as great an interest as is the influence of oil on the pattern of recruitment and succession following the catastrophe. That is, we are especially interested in the effect of oil on the ability of the community to recover. To approach this problem, we investigated the effects of relatively volatile (marine diesel) and relatively viscous (Bunker C) oils on the recruitment of organisms to settling plates.

Plexiglas settling plates were selected for this study because the basic substratum material of the experimental and control samples are precisely standardized with uniform surface, area, shape, location and exposure time. Also, the samples could be collected and analyzed intact under a dissecting microscope. Because of the standardization benefits of this sampling process, growth rates, productivity and species composition of communities of fouling organisms are used as indicators of the amount of pollution in local waters (Anonymous, 1970).

Methods

The settling plates were prepared and set out in the same manner and at the same stations as the plates for the regular recruitment study discussed in Section VIII. See that section for details of the methods and materials involved. The controls for this experiment also provide data for the program described in Section VIII.

To coat plates with oil for the experiment, 24 plates were set for 24 hours in a large jar of Bunker C oil and another 24 plates were set in marine diesel oil for 24 hours. The plates were then set out in air, propped up on the work bench until dry, then tied in sets of 4 on settling plate lines. After 126 days in the ocean, the Bunker C-treated plates were still coated with oil. Films of oil formed on the surfaces of the trays of water containing marine diesel-treated plates which had been in the ocean for 126 days and then preserved in 10 percent formalin for nearly a year. We can assume there was enough oil present to measure its effects on recruitment.

Two experiments were set out in the Caribbean in 1972 on 14 April and left for 59 and 92 days, respectively. In 1972, experiments were set out in the Pacific on 4 April and left for 59 and 126 days. The Caribbean experiment was repeated in 1973. The plates were set out on 9 April and left for 60 days.

The surface coverage counts and dry weights were taken by the same procedures as described in Section VIII. The surface coverage counts consisted of 104 points per side (208 per plate) and 4 plates per line. Each control average is based on 8 plates from 2 lines and each experimental average is based on 4 plates.

Results and Discussion

The upper surfaces of Galeta settling plates which were coated with Bunker C oil had a significantly greater percent coverage of algae than did the controls (Table 39). This corroborates the tendency for algae to increase in the presence of Bunker C oil more than in controls which was found in the Galeta reef flat field experiments (Section XI) and noted in laboratory aquaria experiments (Section X). Two factors are possibly involved with the Bunker C effect on algae, viscosity and nutrient supply. In the field experiments on the Laurencia Zone which is washed by surf and on the sub-tidal settling plates, animal larvae and algal spores may have a difficult time attaching to smooth surfaces in surging water. The viscosity of Bunker C oil may facilitate the attachment of algal spores. However, the same benefits of Bunker C oil to algae appear to occur in the still water in aquaria, which implies some aspect other than viscosity. The most unexpected result of all was the significantly greater coverage of algae on the undersides of the Bunker C-treated plates than on the undersides of the control plates. The coating of the plates with the thick black, tarry Bunker C oil must have reduced light to a much lower level than that available to the algae on the undersides of the translucent control plates.

Increased algal growth is not so clearly associated with Bunker C oil on the Pacific plates. The much more rapid productivity of Pacific fouling communities (Section VIII) implies that nutrients may be more limiting to algal growth in the Caribbean and so additional nutrients from Bunker C oil may have a greater effect. Secondarily derived carbohydrates or hydrocarbons may be a possible source of nutrients for organisms. This hypothesis, of course, needs further testing, but it seems to be the best explanation to fit the results to date.

Unlike Bunker C oil, marine diesel oil appears to have a toxic effect on fouling communities. Dry weight measurements of production showed that neighboring lines of plates coated with marine diesel oil had significantly less (about half) biomass of fouling organisms than the nearby controls (Table 38). If the error of oil added to the measured weight of the community could be corrected, it would further increase the differences. We did not attempt to measure the weights of the fouling communities from

TABLE 38. COMPARISON OF THE DRY WEIGHTS OF CARIBBEAN FOULING ORGANISMS WHICH GREW OVER A 60-DAY PERIOD ON CONTROL PLEXIGLAS PLATES AND PLEXIGLAS PLATES COATED WITH MARINE DIESEL OIL. ^a

Treatment	Dry weight (gms/plate)	t	d.f.	P
Control	1.03 ± 0.17			
		2.79	14	<0.02
Marine Diesel	0.55 ± 0.04			

^a Each sample is composed of four plates on each of two lines.

TABLE 39. DIFFERENT PATTERNS OF SURFACE COVERAGE BY FOULING ORGANISMS ON CLEAN SCRAPED PLEXIGLAS PLATES (CONTROLS) IN COMPARISON WITH PLATES COATED WITH BUNKER C (BC) OR MARINE DIESEL (MD) OIL. All plates were set out in April for lengths of periods noted in the first column. Results of analysis by *t*-test between controls and oil-coated plates are given. Data on coralline algae are not included in the table so the per cent coverages do not always total 100.

	Period (days)	Average per cent sur- face coverage of plates		<i>t</i>	d.f.	P
		controls	oil coated			
GALETA (Caribbean)						
Upper Surface						
Algae - 1973	60	58.4	BC - 79.0 MD - 20.1	3.98 8.13	14 14	<.01 <.001
- 1972	59	38.1	BC - 68.8 MD - 35.8	2.25 0.13	10 10	<.05
- 1972	92	62.8	BC - 86.5 MD - 66.2	1.95 0.28	10 10	<.1
Open space - 1973	60	6.2	BC - 19.5 MD - 41.9	2.47 5.04	14 14	<.02 <.001
- 1972	59	20.4	BC - 20.2 MD - 23.2	0.02 0.41	10 10	
- 1972	92	17.8	BC - 11.2 MD - 15.2	0.84 0.31	10 10	
Under Surface						
Algae - 1973	60	16.6	BC - 40.1 MD - 17.6	3.93 0.21	14 14	<.01
- 1972	59	8.5	BC - 12.0 MD - 4.0	0.42 1.00	10 10	
- 1972	92	8.6	BC - 18.2 MD - 5.8	1.26 0.39	10 10	
Animals - 1973	60	42.1	BC - 31.2 MD - 27.9	0.89 0.82	14 14	
- 1972	59	17.9	BC - 43.2 MD - 15.0	3.51 0.45	10 10	<.01
- 1972	92	24.4	BC - 39.8 MD - 42.0	1.71 1.69	10 10	
Open space - 1973	60	39.0	BC - 28.7 MD - 39.4	0.60 0.04	14 14	
- 1972	59	66.5	BC - 44.8 MD - 69.8	3.85 0.45	10 10	<.01
- 1972	92	55.9	BC - 29.2 MD - 45.2	1.86 0.81	10 10	<.1

TABLE 39 (Continued). DIFFERENT PATTERNS OF SURFACE COVERAGE BY FOULING ORGANISMS ON CLEAN SCRAPED PLEXIGLASS PLATES (CONTROLS) IN COMPARISON WITH PLATES COATED WITH BUNKER C (BC) OR MARINE DIESEL (MD) OIL.

	Period (days)	Average per cent sur- face coverage of plates		t	d.f.	P
<hr/>						
TABOGUILLA (Pacific)						
Upper Surface						
Algae - 1972	59	52.5	BC - 63.8	0.72	10	
			MD - 34.5	1.22	10	
- 1972	126	53.5	BC - 43.2	0.65	10	
			MD - 24.0	2.11	10	<.1
Animals - 1972	59	35.6	BC - 19.8	1.78	10	
			MD - 52.2	1.22	10	
- 1972	126	45.1	BC - 51.0	0.41	10	
			MD - 74.0	2.08	10	<.1
Under Surface						
Algae - 1972	59	18.9	BC - 11.8	0.99	10	
			MD - 0.2	2.69	10	<.05
- 1972	126	1.8	BC - 2.0	0.14	10	
			MC - 3.8	0.93	10	
Animals - 1972	59	6.15	BC - 47.4	1.81	10	
			MD - 95.0	6.36	10	<.001
- 1972	126	97.0	BC - 89.0	0.72	10	
			MD - 95.2	0.90	10	
Open space - 1972	59	19.2	BC - 40.8	5.80	10	<.001
			MD - 4.5	3.71	10	<.01
- 1972	126	1.2	BC - 9.0	2.53	10	<.05
			MC - 1.0	0.31	10	

plates with Bunker C oil because including much of the thick tarry oil would have been a large error. The toxic effects of marine diesel oil are also implied by the surface coverage measurements from Galeta plates (Table 39). During the first 59 or 60 days, there was always more bare space, i.e., less coverage by algae and animals, on both upper and lower surfaces of plates coated with marine diesel oil than on control plates.

In summary, marine diesel oil appeared to have toxic effects on fouling organisms while an increase in algal production appeared to be associated with Bunker C oil. However, the effect of Bunker C oil on algae may upset the usual organization of intertidal communities. For instance, the algae may be better able to compete with sessile animals for space. It is interesting to consider the outcome of the wreck of the oil tanker TAMPICO MARU. The kelp expanded dramatically and this phenomenon was explained as a result of the failure of the echinoid populations of herbivorous grazers to recover for over seven years (North, Neushul and Clendenning, 1965). This explanation is probably correct. A more direct effect of the oil to algae may have been an additional factor.

SECTION XIV

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SECTION XV

APPENDICES

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APPENDIX A

Frequency of macroscopic plants in the intertidal reef at the Galeta marine laboratory. Species found only below spring tide low water are not included. Frequency is given as the number of samples in which the species were present divided by the total number of 0.125 m² samples sorted for plants. Joyce Redemske Young provided the identifications and the data for this table.

TAXA	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
CHLOROPHYTA					
<i>Acetabularia crenulata</i>				1/16	
<i>Acetabularia pusilla</i>	15/20	9/20	6/16	7/16	7/16
<i>Anadyomene stellata</i>	2/20	8/20	2/16		
<i>Bryopsis plumosa</i>	14/20	6/20	1/16	1/16	1/16
<i>Caulerpa cupressoides</i>			1/16		
<i>Caulerpa sertularioides</i>		1/20		1/16	1/16
<i>Caulerpa vickersiae</i> v. <i>furcifolia</i>	4/20	3/20		1/16	
<i>Caulerpa racemosa</i>		1/20			
<i>Chaetomorpha brachygona</i>					1/16
<i>Chaetomorpha</i> sp.				9/16	5/16
<i>Cladophora</i> sp.	14/16	16/16	12/12	12/12	10/12
<i>Cladophoropsis membranacea</i>	16/20	2/20	2/16		2/16
<i>Codium isthmocladum</i>	2/20				
<i>Derbesia</i> sp. (bushy)	10/20	14/20	2/16	9/16	5/16
<i>Derbesia</i> sp. (unbranched)	5/20	2/20	3/16	1/16	1/16
<i>Dictyosphaeria cavernosa</i>					1/16
<i>Dictyosphaeria vanbosseae</i>	3/20	4/20	9/16	1/16	5/16

TAXA	Coraline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Enteromorpha</i> sp.	5/20	11/20	5/16	11/16	8/16
green crust	2/20	1/20		9/16	1/16
<i>Halocystis</i> <i>osterhoutii</i>	10/20	1/20			2/16
<i>Halimeda opuntia</i>	16/20	15/20	15/16	13/16	10/16
<i>Halimeda tuna</i>	9/20				2/16
<i>Penicillus</i> <i>capitatus</i>				4/16	6/16
<i>Struvea</i> <i>anastomosans</i>	6/20	4/20	1/16	2/16	5/16
<i>Valonia</i> <i>utricularis</i>		1/20			
<i>Valonia</i> <i>ventricosa</i>	1/20				
PHAEOPHYTA					
brown crust				5/16	
<i>Dictyota</i> sp.	3/20	1/20	1/16		
<i>Dictyopteris</i> <i>delicatula</i>	2/20	3/20		1/16	2/16
<i>Giffordia indica</i>	1/20	2/20		2/16	
<i>Sphacelaria</i> <i>tribuloides</i>	6/20	5/20	8/16	10/16	7/16
<i>Lobophora</i> <i>variegata</i>	2/20				
RHODOPHYTA					
<i>Acanthophora</i> <i>spicifera</i>		14/20		4/16	14/16
<i>Amphiroa</i> <i>brasiliensis</i>	5/20	5/20			
<i>Amphiroa</i> <i>fragilissima</i>	7/20	2/20	2/16	3/16	4/16
<i>Amphiroa rigida</i> v. <i>antilliana</i>	8/20	8/20	2/16		
<i>Amphiroa</i> sp.	8/20	9/20			
Antithamnion-type	2/20	3/20		1/16	

TAXA	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Astracystis ramosa</i>				2/16	2/16
<i>Centroceras clavulatum</i>	3/20		1/16	4/16	7/16
<i>Ceramium cruciatum</i>	3/20	8/20		2/16	
<i>Ceramium fastigiatum</i>				1/16	
<i>Ceramium leutzelburgii</i>	6/20	2/20		4/16	1/16
<i>Ceramium</i> sp.	10/20	10/20	7/16	5/16	7/16
<i>Champia parvula</i>	1/20	1/20			
<i>Chondria floridana</i>		2/20			
<i>Chondria tenuissima</i>	1/20				
crustose coralline spp.	20/20	20/20	15/16	14/16	10/16
Crustose coralline sp. B	14/14	5/12	2/12		1/12
Crustose coralline sp. C	14/14	6/12		1/12	2/12
Crustose coralline sp. D	14/14	7/12		1/12	
Crustose coralline sp. E	5/14				
Crustose coralline sp. F	2/14	12/12	6/12	3/12	4/12
Crustose coralline sp. G	12/14				1/12
Crustose coralline sp. H	3/14	2/12	1/12	1/12	5/12
<i>Eucheuma echinocarpum</i>	1/20				
fleshy red crust	11/14	9/12	8/12	12/12	8/12

TAXA	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Fosiella</i> sp.	7/20	16/20	4/16	12/16	13/16
<i>Gelidiella</i> <i>acerosa</i>		6/20			2/16
<i>Gelidium pusillum</i>	19/20	13/20	8/16	5/16	7/16
<i>Goniotrichium</i> <i>alsidii</i>				1/16	
<i>Gracilaria</i> <i>mammillaris</i>			1/16		1/16
<i>Griffithsia</i> <i>radicans</i>	8/20				
<i>Griffithsia</i> <i>globifera</i>	1/20				
<i>Herposiphonia</i> <i>secunda</i>	1/20	1/20	3/16	3/16	3/16
<i>Herposiphonia</i> <i>tenella</i>	20/20	15/20	13/16	11/16	10/16
<i>Hypnea</i> sp.	6/20	4/20		1/16	2/16
<i>Hypnea cervicornis</i>	5/20	3/20			1/16
<i>Hypnea spinella</i>	1/20	1/20			3/16
<i>Jania</i> sp.	13/20	18/20	13/16	10/16	10/16
<i>Jania adherens</i>	5/20	3/20	2/16	1/16	1/16
<i>Laurencia</i> <i>papillosa</i>	9/20	20/20	8/16	2/16	13/16
<i>Lophosiphonia</i> sp.	1/20	1/20			
<i>Peyssonnelia rubra</i>	1/20				
<i>Peyssonnelia</i> <i>amorica</i>	9/20	11/20	10/16	9/16	8/16
<i>Peyssonnelia</i> <i>nordstedtii</i>	2/20	8/20	2/16		1/16
<i>Polysiphonia</i> sp.	9/20	5/20		6/16	3/16
<i>Polysiphonia</i> <i>subtilissima</i>	1/20	1/20			
<i>Taenioma macrourum</i>	6/20				
<i>Wrangelia argus</i>	13/20	1/20	1/16	1/16	1/16
PTEROPHYTA					
<i>Thalassia testudinum</i>				16/16	7/16

APPENDIX B

Catalog of the larger invertebrates from the intertidal reef at the Galeta marine laboratory (tidal depth range 0.7 m). Species found only below spring tide low water or in the Littorina-Nerita "splash" zone are not included. Important species definitely observed in a zone but not actually encountered in a quadrat sample are indicated by "+". Five descriptive statistics are as follows, from top to bottom in each unit:

1. Frequency (0.125 m² samples): no. of samples in which the species were present/total no. of samples sorted for this species.

2. Abundance (0.125 m² samples): median plus quartiles of abundance counts.

3. Abundance (1 m² calculated): mean plus standard error of the mean in samples including those in which the species was not present.

4. Relative abundance: per cent of class within the zone numerically represented by this species. (The Coelenterata are analyzed as per cent of order and decapod crustaceans as per cent of suborder.)

5. Dispersion: Morisita's index of dispersion, unity indicates random dispersion, larger values indicate greater aggregation and smaller values indicate more even distributions.

If the species is encountered in less than 6 samples, only the upper 3 statistics are given.

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<hr/>					
COELENTERATA					
Order Hydroida					
<i>Millepora complanata</i>	8/24			1/20	
Order Ceriantharia					
<i>Cerianthus</i> sp.				3/20 1-1-2 (1.6)	
Order Gorgonacea					
<i>Erythropodium caribaeorum</i>	7/24				
Order Zoanthiniaria					
<i>Palythoa variabilis</i>	7/24 12-64-520 (350±194) 7.4 192.445	2/24 14-16 (10.0)	2/20 17-29 (18.4)	1/20 13 (5.2)	

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Palythoa caribaeorum</i>	5/24 1-1-2063 (784)	3/24 1-5-12 (6.0)			
<i>Isaurus duchassaingi</i>	+	+			
<i>Zoanthus sociatus</i>		3/24 1-2-44 (15.7)	20/20 1847-4305-7492 (4812±1364) 99.9 1.012	6/20 1-2-103 (45.2±41.0) 89.2 16.627	1/20 82 (32.8)
<i>Zoanthus solanderi</i>	19/24 13-247-2333 (3212±963) 67.5 3.059	19/24 1-91-2155 (1334±694) 80.0 7.196			
Order Actiniaria					
<i>Aiptasia tagetes</i>	11/24 1-6-15 (30.0±10.3) 22.5 3.481	9/24 1-4-10 (13.7±4.8) 17.2 3.307	10/20 1-7-63 (55.2±28.9) 49.6 5.141	8/20 1-1-19 (16.0±8.2) 13.6 5.717	8/20 1-3-41 (24.8±16.0) 68.8 9.032
<i>Anthopleura krebsi</i>	3/24 1-3-4 (2.6)	5/24 2-2-3 (4.0)	8/20 1-3-4 (8.4±1.8)	1/20 4 (1.6)	1/20 1 (0.4)
<i>Anthopleura</i> sp.	12/24 1-3-13 (20.0±4.1) 15.0 2.922	10/24 1-3-8 (12.3±3.9) 15.5 2.378	6/20 1-1-5 (5.6±2.5) 5.0 3.736		
<i>Epiphellia</i> n. sp.		1/24 7 (1.7)	1/20 1 (0.4)	15/20 1-7-91 (97.2±38.5) 82.6 3.916	7/20 1-2-8 (7.6±0.8) 21.1 4.093
<i>Phyllactis floculifera</i>	8/24 1-3-91 (59.6±32.3) 44.8 7.630	12/24 1-4-12 (16.3±5.2) 21.4 2.837	11/20 2-6-18 (33.6±8.8) 30.2 2.088	2/20 1-2 (1.2)	
<i>Phymanthus crucifer</i>	4/24 1-3-4 (4.0)	1/24 1 (0.3)	1/20 1 (0.4)		

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Telmatactis americana</i>		2/24 1-2 (1.0)	1/20 5 (2.0)		1/20 1 (0.4)
<i>Telmatactis roseni</i>	13/24 1-3-7 (13.0±3.2) 9.8 1.846	17/24 1-4-14 (29.6±6.6) 35.7 1.989	5/20 1-2-5 (4.8)	2/20 1-2 (1.2)	2/20 2-2 (1.6)
anemone sp. (unknown)					2/20 1-2 (1.2)
Order Scleractinia					
<i>Agaricia agaricites</i>			2/20		
<i>Astrangia solitaria</i>	1/24				
<i>Dichocoenia stokesii</i>	1/24				
<i>Favia fragum</i>	3/24				
<i>Porites astreoides</i>	3/24				
<i>Porites furcata</i>	7/24	1/24	3/20		
<i>Siderastrea radians</i>				1/20	
<i>Siderastrea siderea</i>					1/20
TURBELLARIA					
turbellarian spp. (number of species unknown)	6/24 1-1-2 2.6	13/24 1-2-19 (18.6±6.8)	5/20 1-2-10 7.2	4/20 1-1-2 2.4	4/20 1-2-3 3.2
NEMERTINA					
nemertean spp. (number of species unknown)	11/24 1-3-11 (12.3±7.1)	10/24 1-3-6 (10.8±3.0)	12/20 1-2-5 (10.4±5.2)	8/20 1-3-4 (7.6±0.4)	7/20 1-2-4 (6.8±5.1)
BRACHIOPODA					
<i>Discinisca strigata</i>	6/24 1-1-1 (2.3±0.9) -- 1.143	4/24 1-1-1 (1.3)	1/20 1 (0.4)		

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<hr/>					
ASTEROIDEA					
<i>Oreaster</i>				+	
<i>reticulatus</i>					
<i>Ophidiaster</i>		+			
<i>gouldingii</i>					
OPHIUROIDEA					
<i>Ophiolepis</i>	8/24	6/24	6/20	5/20	8/20
<i>paucispina</i>	1-1-2 (4.3±1.6) 1.3 2.462	1-2-2 (3.3±1.4) 2.0 2.667	1-1-2 (3.2±1.2) 1.1 1.429	1-1-2 (2.8±1.2) 5.4 1.905	2-2-3 (7.6±2.4) 2.4 1.988
<i>Ophiocoma</i>	18/24	7/24	2/20	1/20	4/20
<i>echinata</i>	2-3-4 (20.3±4.0) 6.1 1.522	1-1-3 (3.7±1.4) 2.2 2.618	1-1 (0.8)	1 (0.4)	1-1-1 (1.6)
<i>Ophiocoma</i>	7/24	1/24	2/20		
<i>pumila</i>	1-1-4 (6.7±3.5) 2.0 6.568	1 (0.3)	1-1 (0.8)		
<i>Ophiocoma</i>		+			
<i>wendti</i>					
<i>Ophionereis</i>	3/24	1/24	1/20	1/20	
<i>reticulata</i>	1-1-1 (1.0)	4 (1.3)	2 (0.8)	1 (0.4)	
<i>Ophioderma</i>	1/24	2/24			
<i>appressum</i>	1 (0.3)	1-1 (0.7)			
<i>Ophioderma</i>	3/24	3/24			
<i>brevicaudum</i>	1-1-1 (1.0)	1-1-1 (1.0)			
<i>Ophioderma</i>				1/20	
<i>brevispinum</i>				1 (0.4)	
<i>Ophioderma</i>		2/24	3/20		3/20
<i>cinereum</i>		1-1 (0.7)	1-3-3 (2.8)		2-2-2 (2.4)
<i>Ophiodermatid</i>	2/24	1/24			
<i>sp.</i>	1-1 (0.7)	1 (0.3)			

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Ophiactis savignyi</i>	17/24 3-9-16 (74.3±22.5) 22.3 3.009	15/24 2-4-14 (64.7±35.3) 38.4 7.761	10/20 1-9-70 (253.2±151.1) 86.1 7.748	8/20 2-2-3 (9.6±4.1) 18.5 3.913	18/20 3-12-26 (252.4±92.4) 78.2 3.522
<i>Amphiura</i> (<i>Nullamphiura</i>) sp.	10/24 3-5-10 (33.0±14.5) 9.9 5.259	3/24 1-1-2 (1.3)			1/20 1 (0.4)
<i>Amphiura</i> (<i>Monamphiura</i>) sp.	10/24 2-2-3 (9.0±3.1) 2.7 2.872	2/24 1-2 (1.0)			1/20 1 (0.4)
<i>Amphipholis</i> sp.	15/24 2-5-22 (52.7±18.0) 15.8 3.572	17/24 2-4-6 (29.3±8.9) 17.4 2.890	5/20 1-2-10 (9.2±5.4) 3.1 6.956	13/20 2-3-9 (32.4±9.1) 62.3 2.593	10/20 2-4-14 (29.6±12.2) 9.2 4.017
<i>Amphipholis</i> sp. A	3/24 1-1-4 (2.0)	2/24 1-1 (0.7)		4/20 1-1-3 (2.4)	6/20 1-1-3 (4.4±2.0) 1.4 3.273
<i>Amphiodia repens</i>		1/24 1 (0.3)		1/20 3 (1.2)	1/20 2 (0.8)
<i>Amphiodia</i> sp. L				3/20 1-1-1 (1.2)	3/20 1-2 (1.2)
Ophiuroid sp. B	11/24 1-2-5 (22.7±12.1) 6.8 7.312	12/24 1-2-4 (12.7±4.5) 7.5 3.380	2/20 1-2 (1.2)		3/20 5-5-9 (7.6)
<i>Ophiozonoida</i> (?) sp.	6/24 1-2-7 (6.3±4.0) 1.9 9.544		2/20 1-1 (0.8)	1/20 1 (0.4)	

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Ophiothrix angulata</i>	20/24 5-10-15 (84.0±19.3) 25.2 2.126	15/24 1-3-7 (43.7±20.8) 25.9 6.077	9/20 1-2-10 (20.8±10.5) 7.1 4.477	3/20 1-1-2 (1.6)	6/20 2-4-7 (14.4±7.9) 4.5 6.413
ophiothricid sp.	1/24 2 (0.7)	2/24 1-1 (0.7)			
<i>Ophiacantha ophiactoides</i>	1/24 1 (0.3)		1/20 1 (0.4)		
<i>Axiognathus squamata</i>	1/24 43 (14.3)				
ECHINOIDEA					
<i>Eucidaris tribuloides</i>	2/24 1-1 (0.7)	2/24 1-1 (0.7)	+	1/20 1 (0.4)	+
<i>Tripneustes esculentus</i>				+	
<i>Lytechinus variegatus</i>	1/24 1 (0.3)	6/24 1-1-2 (3.3)	3/20 1-1-2 (1.6)	1/20 1 (0.4)	1/20 1 (0.4)
<i>Echinometra lucunter</i>	19/24 3-4-6 (29.7±4.8) 86.4 1.348	19/24 1-2-6 (19.3±5.0) 46.4 2.192	19/20 1-2-2 (6.0±1.7) 62.5 1.334	4/20 1-1-1 (1.6)	2/20 1-1 (0.8)
<i>Echinometra viridis</i>	4/24 1-1-1 (1.3)	5/24 1-1 (1.7)	1/20 1 (0.4)	2/20 1-1 (0.8)	1/20 3 (1.2)
<i>Diadema antillarum</i>	2/24 1-1 (0.7)	1/24 1 (0.3)	+	+	+
<i>Echinoneus cyclostomus</i>	3/24 1-1-2 (1.3)	13/24 2-5-5 (16.0±3.8) 38.4 1.851	3/20 1-1-2 (1.6)	6/20 1-2-4 (7.2±3.8) 56.2 5.621	1/20 1 (0.4)
<i>Brissus unicolor</i>	1/24 1 (0.3)	1/24 1 (0.3)		3/20 1-2-3 (2.4)	+

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
HOLOTHUROIDEA					
holothurian spp.	8/24 1-1-2 (15.0±11.9) -- 15.321	14/24 1-5-14 (34.7±11.3) -- 3.249	2/20 1-1 (0.8)	3/20 1-2-3 (2.4)	3/20 1-2-2 (2.0)
HEMICHORDATA					
hemichordate spp. (possibly 2 spp.)	2/24 1-4 (1.6)	1/24 1 (0.3)	1/20 1 (0.4)	4/20 2-4-4 (5.6)	6/20 1-2-3 (5.6±4.3)
POLYPLACOPHORA					
<i>Lepidochitona liozonis</i>	15/24 1-1-2 (9.3±0.3) 14.4 2.222	2/24 2-2 (1.3)	1/20 1 (0.4)	1/20 1 (0.4)	
<i>Acanthochitona hemphilli</i>	+	6/24 1-3-3 (4.0±0.2) 2.7 3.273	5/20 1-2-2 (3.2)	4/20 1-1-1 (1.6)	2/20 1-5 (2.4)
<i>Acanthochitona spiculosus</i>	4/24 1-1-1 (1.3)	4/24 1-1-1 (1.3)		1/20 1 (0.4)	
<i>Acanthochitona interfissa</i>	19/24 2-2-3 (23.3±0.8) 36.1 2.306	20/24 5-8-16 (79.3±2.2) 53.2 2.019	5/20 2-2-4 (8.0)		3/20 1-2-3 (2.4)
<i>Acanthochitona pygmaea</i>	5/24 2-2-2 (3.3)	18/24 1-2-3 (13.0±0.3) 8.7 1.101	4/20 1-1-3 (2.4)	2/20 1-1 (0.8)	3/20 1-1-2 (1.6)
<i>Choneplax lata</i>	11/24 1-2-3 (7.3±0.2) 11.3 1.662	19/24 2-3-5 (21.7±0.5) 14.5 1.431	7/20 2-6-7 (12.8±0.6) 26.9 3.065	3/20 1-1-2 (1.6)	4/20 1-2-3 (2.8)
<i>Calloplax janeirensis</i>	5/24 1-1-1 (1.7)				

	Coral line	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Ischnochiton</i>	12/24	14/24	8/20	1/20	3/20
(<i>Ischnoplax</i>)	1-2-3	1-3-4	2-4-6	1	1-1-1
<i>pectinatus</i>	(9.7±0.4)	(18.3±0.7)	(13.2±0.6)	(0.4)	(1.2)
	14.9	12.3	27.7		
	3.044	2.844	2.765		
<i>Ischnochiton</i>	3/24	3/24	2/20	3/20	2/20
(<i>Stenoplax</i>)	1-1-4	1-1-3	1-1	1-1-1	1-1
<i>purpurascens</i>	(2.0)	(1.7)	(0.8)	(1.2)	(0.8)
<i>Ischnochiton</i>	11/24	12/24	12/20	10/20	4/20
(<i>Ischnochiton</i>)	1-2-2	1-2-2	1-1-2	1-2-2	1-1-2
<i>papillosus</i>	(6.0±0.2)	(8.0±0.3)	(6.8±0.2)	(6.8±0.2)	(2.8)
	9.3	5.4	14.3	51.5	
	1.255	1.913	0.735	1.176	
<i>Chiton viridis</i>	2/24	1/24			
	1-1	1			
	(0.7)	(0.3)			
<i>Acanthopleura</i>					
<i>granulata</i>					+
GASTROPODA					
<i>Emarginula</i>			1/16		
<i>phrixodes</i>			1		
			(0.5)		
<i>Emarginula</i>	2/20				
<i>pumila</i>	1-1				
	(0.8)				
<i>Hemitoma</i>	+				
<i>octoradiata</i>					
<i>Hemitoma</i> sp.	1/20				
	1				
	(0.4)				
<i>Diodora minuta</i>	9/20	1/20			
	1-2-2	1			
	(7.6±2.9)	(0.4)			
	10.5				
	2.922				
<i>Diodora</i>	2/20				
<i>variegata</i>	1-1				
	(0.8)				
<i>Diodora</i>	3/20	1/20	2/16	1/16	
<i>dysoni</i>	1-1-1	1	1-1	2	
	(1.2)	(0.4)	(1.0)	(1.0)	

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Diodora</i>		3/20	1/16		2/16
<i>cayenensis</i>		1-1-1 (1.2)	1 (0.5)		1-1 (1.0)
<i>Fissurella</i>	3/20	5/20			
<i>barbadensis</i>	1-1-2 (1.6)	1-1-1 (2.0)			
<i>Fissurella</i>	4/20	2/20			
<i>angusta</i>	1-1-1 (1.6)	1-1 (0.8)			
<i>Acmaea</i>	10/20		1/16		
<i>antillarum</i>	1-1-3 (8.8±3.2) 12.2 2.682		1 (0.5)		
<i>Acmaea</i>				1/16	
<i>pustulata</i>				1 (0.5)	
<i>Acmaea</i> sp.		1/20 1 (0.4)			
<i>Cittarium pica</i>	+	+			
<i>Tegula fasciata</i>	1/20 1 (0.4)			1/16 1 (0.5)	
<i>Arene cruentata</i>	+				
<i>Arene</i>	1/20				
<i>tricarinata</i>	1 (0.4)				
<i>Astraea caelata</i>	+				
<i>Astraea phoebia</i>	1/20 4 (1.6)				
<i>Tricolia adamsi</i>	4/20 1-2-5 (3.6)	1/20 2 (0.8)			1/16 1 (0.5)
<i>Tricolia bella</i>		1/24 1 (0.3)	3/20 1-1-2 (1.6)		2/20 1-1 (0.8)

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Smaragdia viridis</i>				3/20 1-1-1 (1.2)	1/20 1 (0.4)
<i>Littorina lineolata</i>	1/24 3 (1.0)				
<i>Rissoina bryerea</i>		5/24 1-2-3 (3.7)			1/20 2 (0.8)
<i>Rissoina decussata</i>			1/20 1 (0.4)	1/20 1 (0.4)	
<i>Cyclostremiscus beauri</i>	1/24 1 (0.3)				
<i>Heliacus infundi- buliformis</i>	1/24 1 (0.3)	3/24 1-2-2 (1.7)	6/20 1-2-2 (4.4±1.7) 13.1 2.182		
<i>Heliacus cylindricus</i>	2/24 1-1 (0.7)	6/24 1-1-2 (3.3±1.4) 5.6 2.667	10/20 1-2-4 (10.4±3.1) 31.0 1.969	1/20 2 (0.8)	1/20 1 (0.4)
<i>Heliacus bisulcatus</i>	1/24 1 (0.3)				
<i>Modulus modulus</i>				3/16 1-1-2 (2.0)	2/16 1-2 (1.5)
<i>Cerithium eburneum</i>				2/16 2-3 (2.5)	4/16 1-2-3 (3.5)
<i>Cerithium variabile</i>					1/16 1 (0.5)
<i>Cerithium</i> sp. 1			2/16 1-5 (3.0)		

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Cerithium</i>					1/16
<i>litteratum</i>					3 (1.5)
<i>Bittium varium</i>					1/16 1 (0.5)
<i>Opalia crenata</i>			1/16 1 (0.5)		
<i>Opalia pumilo</i>			1/16 1 (0.5)		
<i>Epitonium</i>		2/20			
<i>candeanum</i>		1-1 (0.8)			
<i>Epitonium</i>	+				
<i>lamellosum</i>					
<i>Epitonium</i>		1/20			
<i>occidentale</i>		1 (0.4)			
<i>Epitonium</i> sp. 1	1/20 1 (0.4)		1/16 1 (0.5)		
<i>Balcis</i>				1/16	
<i>intermedia</i>				1 (0.5)	
<i>Balcis</i> sp. 1					1/16 1 (0.5)
<i>Cheila</i>			1/16		
<i>equestris</i>			1 (0.5)		
<i>Hipponix</i>	8/20	14/20		9/16	4/16
<i>antiquatus</i>	1-1-3 (6.8±3.0) 9.4 3.676	2-3-4 (22.8±6.6) 38.2 2.254		1-1-4 (9.0±3.0) 41.9 1.882	1-1-2 (2.0)
<i>Hipponix</i>		2/20			
<i>subrufus</i>		3-4 (2.8)			

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Crepidula plana</i>				1/16 1 (0.5)	
<i>Strombus raninus</i>				+	+
<i>Cypraea zebra</i>		+			
<i>Polinices lacteus</i>				4/16 1-2-2 (3.0)	4/16 1-1-2 (2.5)
<i>Cypraeacassis testiculus</i>			+		
<i>Charonia variegata</i>		+			+
<i>Cymatium nicabaricum</i>					+
<i>Cymatium pileare</i>					1/16 1 (0.5)
<i>Bursa cubaniana</i>		1/20 1 (0.4)	1/16 1 (0.5)		
<i>Drupa nodulosa</i>	15/20 1-2-4 (20.8±6.2) 28.7 2.368	5/20 1-1-1 (3.6)	2/16 1-2 (1.5)		1/16 1 (0.5)
<i>Risomurex muricoides</i>	4/20 1-2-2 (2.0)	1/20 1 (0.4)	1/16 1 (0.5)		
<i>Risomurex roseus</i>	1/20 1 (0.4)				
<i>Purpura patula</i>	+				
<i>Thais haemastoma</i>	1/20 1 (0.4)	2/20 1-1 (0.8)	1/16 1 (0.5)		
<i>Thais deltoidea</i>		3/20 1-1-3 (2.0)			
<i>Coralliophila aberrans</i>	3/20 1-1-1 (1.2)			1/16 1 (0.5)	

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Coralliophila caribaea</i>	1/20 1 (0.4)		4/16 1-1-1 (2.0)		
<i>Anachis catenata</i>	2/20 1-1 (0.8)				
<i>Anachis</i> sp. 1	1/20 1 (0.4)				1/20 1 (0.5)
<i>Anachis</i> sp. 2	1/20 1 (0.4)				
<i>Nitidella nitida</i>					1/16 1 (0.5)
<i>Nitidella</i> sp. 2	1/20 1 (0.4)	2/20 1-4 (2.0)			
<i>Psarostola monilifera</i>	2/20 2-3 (2.0)	1/20 1 (0.4)			
<i>Cantharus tinctus</i>	1/20 1 (0.4)				
<i>Bailya intricata</i>					1/16 1 (0.5)
<i>Fasciolaria tulipa</i>	+	+		+	
<i>Latirus carinifera</i>					1/16 1 (0.5)
<i>Leucozonia ocellata</i>	1/20 1 (0.4)				
<i>Vasum muricatum</i>				+	+
<i>Mitra</i> sp.			1/16 1 (0.5)		

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Hyalina avena</i>	5/20 1-1-1 (2.0)	4/20 1-2-5 (4.0)	5/16 1-1-4 (4.5)	1/16 1 (0.5)	6/16 1-1-3 (6.5)
<i>Hyalina albolineata</i>	1/20 1 (0.4)		2/16 1-1 (1.0)		1/16 1 (0.5)
<i>Hyalina tenuilabra</i>	2/20 1-2 (1.2)		1/20 1 (0.5)		
<i>Conus mus</i>	1/20 1 (0.4)	5/20 1-1-2 (3.2)			
<i>Crassispira</i> sp.			1/16 1 (0.5)		
<i>Mangelia fusca</i>				1/16 1 (0.5)	
<i>Daphnella lymneiformis</i>			1/16 1 (0.5)		
BIVALVIA					
<i>Arca imbricata</i>	15/20 1-1-3 (12.0±2.6) 9.0 1.241	9/20 2-2-3 (8.8±2.8) 3.0 2.164	6/16 1-3-3 (7.5±3.1) 5.0 2.589	2/16 1-3 (2.0)	7/16 1-2-4 (9.0±3.4) 4.5 3.032
<i>Barbatia</i> spp. (both <i>B. domingensis</i> and <i>B. tenera</i> , cf. Appendix C)	18/20 1-3-6 (27.2±5.9) 20.4 1.546	15/20 1-1-4 (12.8±3.1) 4.4 1.572	14/16 5-8-11 (65.5±12.9) 43.5 1.471	7/16 1-1-3 (10.5±6.0) 28.4 5.332	15/16 2-6-19 (88.5±27.7) 44.6 2.392
<i>Arcopsis adamsi</i>	6/20 1-1-1 (3.6±1.7) 2.7 3.332	6/20 1-2-3 (4.4±1.8) 1.5 2.544	6/16 1-4-7 (12.5±5.6) 8.3 3.520	3/16 2-3-10 (7.5)	4/16 6-11-14 (22.0)
<i>Modiolus americanus</i>	1/20 1 (0.4)			1/16 1 (0.5)	

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Brachidontes citrinus</i>	1/20 1 (0.4)				
<i>Brachidontes recurvus</i>	1/20 1 (0.4)				
<i>Lioberus castaneus</i>		1/20 1 (0.8)			1/16 1 (0.5)
<i>Lithophaga nigra</i>		2/20 1-1 (0.8)			1/16 1 (0.5)
<i>Lithophaga bisulcata</i>		3/20 1-1-2 (1.6)			5/16 1-1-1 (3.5)
<i>Gregariella coralliophaga</i>				1/16 1 (0.5)	4/16 1-1-1 (2.5)
<i>Isognomon bicolor</i>	11/20 2-3-11 (26.8±8.9) 20.0 2.812	18/20 3-12-30 (188.8±79.8) 65.6 4.360	4/16 1-2-8 (6.0)		6/16 2-6-11 (29.5±17.8) 14.9 16.266
<i>Isognomon radiatus</i>	18/20 3-7-12 (55.6±7.9) 41.6 1.248	10/20 1-1-2 (6.8±2.2) 2.4 1.910	5/16 1-2-2 (4.5)		4/16 1-1-9 (6.0)
<i>Pinctada radiata</i>					1/16 1 (0.5)
<i>Lima pellucida</i>	1/20 1 (0.4)	2/20 1-1 (0.8)			
<i>Coralliophaga coralliophaga</i>		10/20 1-2-4 (11.2±3.5)	2/16 1-2 (1.5)		2/16 1-1 (1.0)

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Diplodonta punctata</i>		7/20 1-1-1 (3.2±1.1) 1.1 0.714	7/16 1-1-2 (5.0±1.7) 3.3 1.600	1/16 2 (1.0)	3/16 1-2-3 (3.0)
<i>Lucina pensylvanica</i>					1/16 1 (0.5)
<i>Phacoides pectinatus</i>		1/20 1 (0.4)			
<i>Codakia orbicularis</i>	2/20 1-1 (0.8)	3/20 1-1-2 (1.6)	1/16 2 (1.0)	2/16 1-1 (1.0)	
<i>Codakia costata</i>				2/16 1-3 (2.0)	
<i>Codakia orbiculata</i>		1/20 1 (0.4)	1/16 1 (0.5)	1/16 1 (0.5)	
<i>Chama macerophylla</i>	1/20 1 (0.4)	1/20 1 (0.4)			
<i>Pseudochama arcinella</i>					+
<i>Erycina periscopiana</i>		1/20 1 (0.4)			
<i>Erycina emmonsi</i>	1/20 1 (0.4)				
<i>Tellina fausta</i>			1/16 1 (0.5)	1/16 1 (0.5)	
<i>Strigilla</i> sp.		1/20 1 (0.4)			
<i>Macoma tenta</i>	1/20 1 (0.4)				

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Sphenia antillensis</i>	2/20 1-1 (0.8)	4/20 1-1-2 (1.6)	2/16 1-1 (1.0)		1/16 1 (0.5)
<i>Corbula contracta</i>				1/16 1 (0.5)	2/16 1-1 (1.0)
<i>Gastrochaena hians</i>	4/20 1-2-3 (2.8)	2/20 1-1 (0.8)			
<i>Cumingia antillarum</i>	2/20 1-3 (1.6) 1.2 10.0	13/20 4-7-13 (41.6±11.4) 14.5 2.254	13/16 4-6-12 (45.0±10.8) 29.9 1.706	5/16 1-2-16 (8.4) 28.4 9.218	10/16 2-4-6 (30.0±12.5) 15.1 3.371
SIPUNCULA					
<i>Aspidosiphon broki</i>	16/24 1-4-15 (27.0±7.1) 15.5 2.066	16/24 1-6-31 (37.3±11.4) 10.1 2.930	9/20 1-10-29 (38.8±15.9) 14.5 1.611	11/20 1-4-15 (22.0±7.59) 11.0 1.190	11/20 1-3-14 (18.0±6.5) 2.7 3.111
<i>Aspidosiphon</i> spp. (probably 7 spp.)	3/24 1-3-10 (4.7)	2/24 3-6 (3.0)			3/20 1-1-6 (3.2)
<i>Dendrostomum</i> ? sp.				1/20 2 (0.8)	
<i>Golfingia</i> sp.		5/24 1-2-3 (3.0)		4/20 1-1-1 (1.6)	2/20 1-2 (1.2)
<i>Lithacrosiphon</i> spp. (probably 5 spp.)	17/24 1-3-11 (21.3±3.3) 12.2 2.095	16/24 1-8-28 (61.0±11.5) 16.5 1.695	13/20 1-2-14 (27.2±8.5) 10.2 1.039	4/20 1-2-3 (2.8)	11/20 1-2-5 (12.0±11.3) 1.8 17.724
<i>Paraspidosiphon fisheri</i>	18/24 1-3-9 (21.0±3.5) 11.9 1.290	17/24 1-7-35 (62.0±15.4) 16.7 2.296	17/20 2-10-32 (83.2±17.8) 31.2 1.781	16/20 1-12-53 (83.2±24.8) 41.6 1.041	18/20 3-13-25 (90.0±13.7) 1.8 1.353
<i>Paraspidosiphon speciosus</i> ?				2/20 1-1 (0.8)	

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Paraspidosiphon spinoso-scutatus</i>	5/24 1-1-4 (2.6)	10/24 1-1-5 (5.7±2.1)	9/20 1-2-7 (10.8±3.9)	12/20 1-3-13 (22.8±7.0)	16/20 1-5-16 (35.6±7.8)
		1.5 2.470	4.1 2.905	11.4 1.002	5.3 1.700
<i>Paraspidosiphon steenstrupi</i>	11/24 1-2-4 (8.3±2.3)	16/24 1-3-11 (22.0±5.2)	11/20 1-3-5 (11.2±2.7)	6/20 1-2-6 (6.0±2.8)	11/20 1-3-13 (16.8±5.5)
	4.8 1.840	5.9 1.963	4.2 1.481	3.0 1.676	2.5 2.694
<i>Paraspidosiphon</i> spp. (probably 7 spp.)	6/24 2-4-6 (8.7±3.6)	11/24 1-2-8 (10.3±3.2)	4/20 1-5-10 (8.0)	7/20 1-3-8 (12.4±5.3)	9/20 1-2-7 (10.0±3.5)
	2.5 4.209	2.8 2.529		6.2 1.591	1.5 2.667
<i>Phascolosoma antillarum</i>	18/24 1-2-10 (21.3±4.9)	23/24 1-5-12 (46.0±7.7)	15/20 1-5-10 (29.6±4.2)	10/20 1-3-45 (42.8±18.6)	19/20 2-32-134 (291.2±67.3)
	12.2 1.845	12.4 1.477	11.1 8.689	21.4 1.854	43.7 1.989
<i>Phascolosoma perlucens</i>	17/24 1-6-25 (38.0±12.9)	17/24 1-3-13 (26.6±7.8)	14/20 1-3-17 (27.6±8.1)	9/20 1-1-3 (6.4±2.6)	16/20 1-3-8 (133.2±94.6)
	21.6 2.589	7.2 2.692	10.4 2.361	3.2 1.200	20.0 10.547
<i>Phascolosoma varians</i>	11/24 1-3-7 (12.6±3.5)	20/24 2-5-14 (37.0±15.4)	10/20 1-3-9 (16.4±5.3)	1/20 2 (0.8)	10/20 1-2-3 (7.2±1.8)
	7.2 2.184	10.0 1.487	6.2 2.585		1.1 1.176
<i>Phascolosoma</i> spp. (probably 7 spp.)	8/24 1-2-4 (5.0±1.8)	7/24 1-2-8 (6.3±1.7)	6/20 1-4-6 (8.4±3.5)	7/20 1-1-7 (5.2±1.8)	11/20 1-1-4 (8.0±2.2)
	2.9 2.514	1.71 1.403	3.2 3.523	2.6 2.153	1.2 1.576
<i>Themiste</i> spp. (probably 3 spp.)	8/24 1-1-6 (4.6±2.0)	12/24 1-4-9 (18.3±4.6)	1/20 1 (0.4)	1/20 1 (0.4)	1/20 2 (0.8)
	2.7 4.219	4.9 2.225			
fragments in-determinable	5/24 1-2-2 (3.0)	11/24 1-3-8 (13.6±4.5)	1/20 9 (3.6)	3/20 1-1-1 (1.2)	6/20 1-2-5 (5.2±0.9)
		3.7 2.546			0.8 3.589

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<hr/>					
POLYCHAETES					
(Families presented					
in alphabetical					
order)					
Ampharetidae					
<i>Melinna</i> n. sp.				3/20	
				1-1-1	
				(1.2)	
Amphinomidae					
<i>Eurythoe</i>	17/24	16/24	16/20	5/20	14/20
<i>complanata</i>	1-2-7	1-2-41	1-3-16	1-1-2	1-3-27
	(16.3±3.6)	(37.3±15.1)	(27.6±7.0)	(2.8)	(39.6±13.6)
	0.6	0.6	2.0		2.7
	1.653	4.575	2.159		3.073
<i>Hermodice</i>	1/24				
<i>canunculata</i>	1				
	(0.3)				
Amphinomid				2/20	
sp. 1				1-1	
				(0.8)	
Amphinomid				1/20	
sp. 2				6	
				(2.4)	
Aphroditidae					
<i>Aphrodita</i>	4/24	5/24	5/20	1/20	1/20
n. sp.	1-1-3	1-1-2	1-1-16	1	1
	(2.0)	(2.3)	(8.0)	(0.4)	(0.4)
Arabellidae					
<i>Arabella</i>	10/24	18/24	10/20	12/20	9/20
<i>mutans</i>	1-3-14	1-8-22	1-4-12	1-2-12	1-5-13
	(11.3±4.9)	(45.6±9.5)	(16.8±5.3)	(19.6±5.7)	(18.8±6.5)
	0.4	0.8	1.3	2.9	1.3
	4.705	1.834	2.497	2.244	2.941
<i>Oenone fulgida</i>	1/24				
	1				
	(0.3)				
Capitellidae					
<i>Dasybranchus</i>	1/24			1/20	
<i>lumbricoides</i>	1			1	
	(0.3)			(0.4)	

	Coraline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Notomastus lineatus</i>	5/24 1-2-14 (7.0)	7/24 1-1-3 (3.0±1.2) 0.05 2.000	1/20 2 (0.8)	1/20 2 (0.8)	3/20 1-1-3 (2.0)
Chloraemidae					
<i>Pherusa inflata</i>	20/24 2-34-104 (236.6±41.8) 8.5 1.718	19/24 1-6-46 (85.6±20.6) 1.4 2.249	8/20 1-3-25 (20.0±10.5) 1.5 6.008	3/20 1-1-2 (1.6)	2/20 2-14 (6.4)
Cirratulidae					
<i>Cauleriella</i> sp. indet.		1/24 1 (0.3)			
<i>Chaetozone</i> sp. indet.	3/24 1-1-1 (1.0)	1/24 1 (0.3)			
<i>Cirratulus</i> ? <i>cirratulus</i>		1/24 1 (0.3)			
<i>Cirriformia</i> <i>luxuriosa</i>	3/24 1-3-4 (2.6)	1/24 1 (0.3)			
<i>Cirriformia</i> <i>punctata</i>	2/24 1-7 (2.6)	24/24 1-13-58 (96.3±29.3) 1.6 3.152	5/20 1-2-16 (9.2)	4/20 1-2-3 (2.8)	12/20 1-5-16 (27.6±7.6) 1.9 2.208
<i>Dodecaceria</i> <i>concharum</i>	2/24 1-2 (1.0)	4/24 1-3-4 (2.6)			
<i>Tharyx</i> sp. indet.	2/24 1-1 (0.6)	1/24 1 (0.3)			
Cirratulid sp. unknown				1/20 1 (0.4)	
Dorvilleidae					
<i>Dorvillea</i> <i>rubrovittata</i>		1/24 1 (0.3)			

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
Eunicidae					
<i>Eunice afra</i>	11/24 1-3-25 (36.3±11.5) 1.3 3.096	24/24 1-22-59 (189.3±29.8) 3.2 1.530	15/20 5-14-26 (76.8±13.9) 5.2 1.527	9/20 1-3-12 (13.6±6.2) 2.0 4.456	16/20 1-10-88 (108.4±35.3) 7.3 2.959
<i>Eunice antennata aedificatrix</i>	13/24 1-1-7 (10.6±2.8) 0.4 1.828	9/24 1-2-4 (5.6±1.8) 0.09 2.117	5/20 1-1-2 (2.4)	4/20 1-2-2 (2.8)	5/20 1-2-4 (4.0)
<i>Eunice aphroditois</i>	6/24 1-2-2 (3.3±1.3) 0.1 2.133	6/20 1-1-4 (3.3±1.5) 0.05 3.733	1/20 1 (0.4)		1/20 2 (0.8)
<i>Eunice (Nacidion) caribaea</i>	24/24 4-89-419 (929±149.5) 33.4 1.585	24/24 107-452-993 (3924.6±447.1) 65.9 1.295	20/20 2-41-304 (525.2±151.2) 39.4 2.575	16/20 1-13-74 (118.4±39.0) 17.8 3.010	20/20 4-51-144 (469.6±82.9) 31.6 1.576
<i>Eunice filamentosa</i>	12/24 2-5-26 (26.6±9.3) 0.9 3.546	13/24 1-5-43 (69.0±22.5) 0.2 3.337	6/20 1-3-7 (8.8±4.1) 0.7	6/20 1-4-12 (13.2±6.6) 1.9 5.378	7/20 1-4-5 (8.4±3.3) 0.6
<i>Eunice websteri</i>	3/24 2-2-4 (2.6)		3/20 1-1-2 (1.6)	2/20 1-1 (0.8)	2/20 1-4 (2.0)
<i>Eunice</i> sp. indet.	1/24 3 (1.0)	1/24 1 (0.3)			
<i>Marphysa</i> n. sp.	6/24 1-1-16 (7.0±5.3) 0.3 13.714	3/24 1-1-1 (1.0)		3/20 1-2-4 (2.8)	3/20 1-3-5 (3.6)
<i>Onuphis vermillionensis</i>		2/24 1-2 (1.0)	1/20 1 (0.4)	17/20 1-4-32 (58.4±16.4) 8.8 2.378	1/20 2 (0.8)

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Onuphis</i> sp.				1/20 1 (0.4)	
<i>Palola siciliensis</i>	21/24 1-4-57 (51.0±18.7) 1.8 3.973	20/24 1-6-20 (50.3±13.5) 0.8 2.500	8/20 1-6-13 (18.0±6.4) 1.4 3.070	5/20 1-1-3 (3.2)	5/20 1-1-4 (4.4)
<i>Palola</i> sp. indet.	1/24 3 (1.0)	2/24 2-4 (2.0)			1/20 1 (0.4)
Glyceridae					
<i>Glycera oxycephala</i>	3/24 1-1-4 (2.0)	1/24 1 (0.3)	1/20 1 (0.4)	5/20 1-1-2 (2.8)	
<i>Glycera tessellata</i>				2/20 1-1 (0.8)	1/20 1 (0.4)
<i>Glycera</i> sp.				1/20 1 (0.4)	
Goniadidae					
<i>Goniada acicula</i>	1/24 1 (0.3)				
Hesionidae					
<i>Hesione picta</i>					1/20 1 (0.4)
<i>Ophiodromus obscurus</i>		1/24 1 (0.3)			
Lumbrinereidae					
<i>Lumbrinereis inflata</i>	20/24 1-8-98 (108.0±37.0) 3.8 3.635	10/24 1-10-31 (42.6±14.9) 0.7 3.649			2/20 2-4 (2.4)
Lysaretidae					
<i>Lysaretid</i> sp. indet.	1/24 1 (0.3)				

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
Nereidae					
<i>Ceratonereis mirabilis</i>	18/24 1-8-45 69.6±20.0 2.5 2.791	23/24 1-12-48 121.0±23.1 2.0 1.774	20/20 1-16-70 178.4±36.3 13.4 1.748	17/20 4-18-68 218.4±38.9 32.7 1.570	14/20 1-15-62 118.4±32.3 7.8 2.358
<i>Neanthes</i> n. sp. 1	2/24 6-46 17.3			2/20 1-1 0.8	1/20 1 0.4
<i>Neanthes</i> sp. indet.		1/24 1 0.3			
<i>Nereis</i> <i>callaona</i>	14/24 1-3-25 33.6±11.8 1.2 3.630	9/24 1-2-6 7.3±2.6 0.1 2.909	8/20 1-3-28 16.4±11.2 1.2 9.658	6/20 1-2-4 5.6±2.4 0.8 3.296	1/20 3 1.2
<i>Nereis</i> n. sp. A	6/24 1-7-19 17.6±7.8 0.6 5.190	5/24 2-5-12 10.6			
<i>Nereis riseii</i>	1/24 1 0.3			2/20 1-1 0.8	1/20 1 0.4
<i>Perinereis</i> <i>elenacasoi</i>	21/24 2-9-23 67.0±11.3	23/24 1-9-106 100.3±42.5	15/20 1-7-17 36.4±10.3	14/20 1-3-20 30.4±9.4	16/20 1-5-148 102.8±62.6
<i>Perinereis</i> sp. indet. A	1/24 1 0.3				
<i>Perinereis</i> sp. indet. B				1/20 1 0.4	2/20 1-2 1.2
<i>Platynereis</i> <i>dumerilii</i>	15/24 2-7-102 86.3±36.6 3.1 5.048	14/24 1-4-22 29.0±9.6 0.5 3.297	4/20 1-1-4 2.8	5/20 1-1-2 2.4	3/20 1-1-4 2.4
<i>Platynereis</i> sp. indet.				1/20 4 1.6	

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Pseudonereis</i>	8/24	6/24	2/20	2/20	2/20
<i>gallapa gensis</i>	2-4-8 (11.0±3.8) 0.4 3.227	1-2-10 (7.3±3.6) 0.1 5.818	1-2 (1.2)	1-1 (0.8)	1-2 (1.2)
Oweniidae					
<i>Owenia collaris</i>				1/20 1 (0.4)	
Palmyridae					
<i>Bhawania</i>	7/24	4/24	1/20	1/20	
<i>goodei</i>	1-1-2 (3.0)	1-1-3 (2.3)	1 (0.4)	1 (0.4)	
Phyllodocidae					
<i>Anaitides</i>	1/24				
<i>erythrophylla</i>	1 (0.3)				
<i>Eulalia</i>	2/24	7/24	1/20	1/20	4/20
<i>myriacylum</i>	1-1 (0.6)	1-2-3 (4.0±1.4)	1 (0.4)	1 (0.4)	1-1-2 (2.0)
<i>Linopherus</i>				1/20	
<i>canariensis</i>				1 (0.4)	
<i>Sige orientalis</i>	3/24 1-1-3 (1.6)		2/20 1-1 (0.8)		1/20 1 (0.4)
Polynoidae					
<i>Halosydna</i>	10/24	21/24	1/20		
<i>leucohyba</i>	1-1-3 (4.6±1.4) 0.2 1.318	1-4-9 (28.3±3.8) 0.5 1.163	1 (0.4)		
<i>Halosydna</i> sp. 1	8/24 1-1-2 (2.6±1.0) 0.09 1.714				
<i>Harmothoe</i> sp. indet.		1/24 1 (0.3)			

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Lepidonotus humilis</i>	12/24 1-2-3 (7.3±1.6) 0.3 1.142	3/20 1-1-2 (1.6)	2/20 1-4 (2.0)	3/20 2-2-2 (2.4)	
Polynoid sp. unknown	1/24 1 (0.3)				
Sabellariidae					
<i>Phragmatopoma</i> sp. indet.	1/24 1 (0.3)				
<i>Sabellaria alcocki</i>	1/24 1 (0.3)				
<i>Sabellaria floridensis</i>	3/24 1-2-3 (2.0)	2/24 1-1 (0.6)	1/20 1 (0.4)		
sabellariid indet.	2/24 1-1 (0.6)				
Sabellidae					
<i>Chone</i> sp.		1/24 1 (0.3)			
<i>Demonax</i> sp.		3/24 2-3-3 (2.6)			
<i>Hypsiocomus torquatus</i>	16/24 1-5-17 (31.0±7.2) 1.1 2.002	15/24 1-2-20 (17.6±6.8) 0.3 4.049	3/20 1-1-2 (1.2)	2/20 2-2 (1.6)	1/20 1 (0.4)
<i>Megaloma vesiculosum</i>					2/20 1-1 (0.8)
<i>Potamilla fonticula</i>	3/24 1-3-4 (2.6)	4/24 3-15-52 (28.0)			

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Pseudopotamilla reniformis</i>	1/24 1 (0.3)				
<i>Sabella melanostigma</i>	5/24 1-1-11 (5.6)	8/24 1-2-3 (4.3±1.4) 0.07 1.846	1/20 1 (0.4)		1/20 1 (0.4)
<i>Sabella</i> sp. 17	1/24 1 (0.3)	1/24 17 (5.6)		2/20 1-1 (0.8)	
<i>Sabella</i> sp. 18		3/24 1-1-5 (2.3)	2/20 1-4 (2.0)	1/20 2 (0.8)	
Sigalionidae					
<i>Psammolyce spinosa</i>	3/24 1-1-3 (1.6)	8/24 1-3-5 (6.3±2.3) 0.1 2.807	8/20 1-2-5 (6.4±2.7) 0.5 3.416	7/20 1-3-5 (8.4±2.9) 1.3 2.571	1/20 2 (0.8)
Psammolyce-like			1/20 1 (0.4)		
Spionidae					
<i>Prionospio heterobranchia texana</i>				1/20 1 (0.4)	
Syllidae					
The statistics of the syllidae are based on 8 samples (samples no. 5 through 12). The relative abundance of syllids, however, are based on all 20 or 24 samples.					
<i>Autolytus</i> cf. <i>magnus</i>	8/8 7-21-50 (182±39) 4.1 1.284	5/8 1-22-45 (92)	2/8 1-4 (5)	4/8 2-4-8 (18)	4/8 1-11-37 (61)
<i>Autolytus</i> n. sp.		7/8 1-6-12 (40.0±12.5) 0.4 1.497	7/8 1-6-14 (42.0±12.2) 1.430		2/8 2-4 (6.0)

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Haplosyllis spongicola</i>	3/8 3-7-14 (24)	3/8 1-1-2 (4)			1/8 1 (1)
<i>Langerhansia cornuta</i>	8/8 1-12-41 (148.0±50.1) 10.4 1.757	2/8 2-13 (7.5)	4/8 12-15-49 (91)	5/20 2-9-21 (42)	3/8 1-2-4 (7)
<i>Langerhansia mexicana</i>		1/24 1 (0.3)			
<i>Odontosyllis</i> sp.	+				
<i>Opisthosyllis brunnea</i>	5/8 5-31-33 (126)	8/8 8-22-45 (168.0±34.3) 6.4 1.250	5/20 1-14-30 (62)	1/20 7 (7)	3/8 10-10-24 (44)
<i>Typosyllis aciculata</i>	+	+			
<i>Typosyllis prolifera</i>		+			
<i>Typosyllis variegata</i>	7/8 1-2-40 (80.0±39.5) 1.5 2.635	7/8 4-10-18 (80.0±18.0) 1.0 1.268	5/8 1-2-6 (14)		3/8 3-7-22 (32)
<i>Typosyllis</i> sp. A		+			1/8 1 (1.0)
Syllid, black stripes	+	+	+		
Syllid ?, black stripes - white bands					+
Syllid, brown dots		+			
Syllid, checkered	+	+			
Syllid, gray		+			
Syllid, leafy projections	+	+			
Syllid, maroon	+	+			

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
Syllid, with stripes					1/20 2 (0.8)
Syllid, sp. 4		+			
Syllid, sp. 10		+			
Syllid, sp. 13		2/8 2-2 (4)			
Syllid, sp. 26	+				
Syllid, sp. 36	1/8 7 (7)				
Syllid, sp. 37	1/8 3 (3)				
Syllid, sp. 38	+				
Syllid, sp. 39	+				
Syllid, sp. 41		1/8 2 (2)			
Terebellidae					
<i>Eupolytmia ?</i>	11/24	17/24	8/20	8/20	9/20
<i>nebulosa</i>	1-4-8 (15.3±4.1) 0.5 2.226	1-8-31 (62.0±13.9) 1.0 2.041	1-1-4 (5.6±2.0) 0.4 2.197	1-3-44 (30.0±18.2) 4.5 7.863	1-4-12 (17.2±6.3) 1.2 3.122
<i>Loimia medusa</i>	5/24 1-1-5 (3.0)	2/24 1-4 (2.0)	4/20 1-1-8 (4.4)	7/20 2-4-15 (18.0±10.8) 2.7 1.707	
<i>Pista fasciata</i>	2/24 1-1 (0.6)	4/24 1-1-2 (2.0)		1/20 1 (0.4)	
<i>Polycirrus</i> sp.	1/24 1 (0.3)	1/24 2 (0.6)			

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Streblosoma</i>	5/24	3/24	1/20	2/20	
<i>crassibranchia</i>	1-1-2 (2.3)	1-1-2 (1.3)	2 (0.8)	1-1 (4.8)	
<i>Thelepus</i>	1/24				
<i>setosus</i>	1 (0.3)				
PYCNOGONIDA					
<i>Anoplodactylus</i>	1/20	+			
<i>evelinae</i>	1 (0.4)				
<i>Anoplodactylus</i>		1/20			1/16
<i>batangense</i>		1 (0.4)			2 (1.0)
<i>Anoplodactylus</i>	6/20	8/20	2/16		4/16
spp.	1-2-3 (4.8)	1-1-3 (5.6)	2-2 (2.0)		1-1-2 (2.5)
<i>Achelia</i>	3/20	7/20	2/16	4/16	7/16
<i>sawayai</i>	1-1-2 (1.6)	1-2-2 (5.2)	1-1 (1.0)	1-1-1 (2.0)	2-2-2 (9.0)
<i>Ascorhynchus</i>	5/20	9/20	9/16	2/16	9/16
<i>latipes</i>	1-2-3 (4.4)	1-1-3 (6.4)	2-4-6 (17.5)	1-3 (2.0)	2-2-3 (14.5)
<i>Ascorhynchus</i>			3/16		1/16
<i>castellioides</i>			1-5-6 (6.0)		3 (1.5)
<i>Ammothella</i>	7/20	14/20	2/16		2/16
spp.	3-3-4 (9.2)	1-2-3 (10.8)	1-3 (2.0)		1-8 (4.5)
<i>Ammothella</i>					1/16
<i>appendiculata</i>					1 (0.5)
<i>Eurycyde</i>	1/20	1/20	3/16		3/16
<i>raphiaster</i>	1 (0.4)	1 (0.4)	1-1-2 (2.0)		1-2-2 (2.5)
<i>Eurycyde</i> sp.	6/20	2/20	2/16	1/16	3/16
	1-1-1 (2.4)	1-1 (0.8)	1-2 (1.5)	1 (0.5)	1-1-1 (1.5)
<i>Rhynchothorax</i>	2/20	2/20	3/16		
sp.	1-2 (1.2)	1-2 (1.2)	1-2-3 (3.0)		

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Tanystylum</i> sp.	1/20 1 (0.4)				
<i>Nymphopsis</i> <i>duodorsospinosa</i>		1/20 1 (0.4)	2/16 1-1 (1.0)		
<i>Pigrogromitus</i> <i>timsanus</i>		3/20 1-1-4 (2.4)	1/16 2 (1.0)		
<i>Callipallene</i> sp.					1/16 2 (1.0)
CRUSTACEA: STOMATOPODA					
<i>Gonodactylus</i> <i>oerstedii</i>	8/24 2-3-4 (7.7±0.3) 100.0 2.751	15/24 1-3-5 (14.0±0.4) 70.0 1.672	3/20 1-1-3 (2.0)	3/20 1-1-1 (1.2)	6/20 1-2-4 (4.8±0.3) 34.3 3.636
<i>Gonodactylus</i> <i>bredini</i>		5/24 1-1-2 (2.7)	1/20 1 (0.4)	10/20 1-2-2 (8.4±0.4) 61.8 2.286	9/20 1-1-3 (8.0±0.4) 57.1 2.526
<i>Gonodactylus</i> <i>austrinus</i>				5/20 1-1-1 (2.0)	
<i>Gonodactylus</i> sp. (unidentified juvenile)	6/24 2-2-4 (4.6±0.2) -- 3.956	6/24 1-1-2 (3.3±0.2) 16.7 3.733	1/20 1 (0.4)	3/20 1-2-2 (2.0)	3/20 1-1-1 (1.2)

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
CRUSTACEA: DECAPODA: NATANTIA					
Penaeidae					
<i>Trachypenaeus similis</i>	1/20 1 (0.4)			1/16 1 (0.5)	
<i>Sicyonia parri</i>					1/16 1 (0.5)
Palaemonidae					
<i>Periclimenes americanus</i>					2/16 1-2 (1.5)
Gnathophyllidae					
<i>Gnathophyllum americanum</i>	2/20 1-1 (0.8)				
Alpheidae					
<i>Alpheus armillatus</i>		6/20 1-2-2 (3.6±1.4) 11.5 1.667	7/16 1-3-7 (9.2±3.6) 36.5 2.563	7/16 1-1-3 (11.0±3.9) 45.0 1.778	12/16 1-3-10 (27.5±7.1) 42.3 1.789
<i>Alpheus bahamensis</i>		1/20 2 (0.8)			4/16 1-5-17 (9.0)
<i>Alpheus cristulifrons</i>	16/20 1-5-30 (48.0±9.4) 16.8 1.414	1/20 2 (0.8)			

	Coral line	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Alpheus formosus</i>	5/20 1-1-2 (2.4)				3/16 1-1-2 (2.0)
<i>Alpheus normanni</i>	2/20 1-2 (1.2)	5/20 1-1-2 (2.8)	1/16 1 (0.5)	2/16 2-2 (2.0)	2/16 1-1 (1.0)
<i>Alpheus nuttingi</i>	5/20 1-1-5 (4.3)	10/20 1-3-6 (13.2±3.8) 42.2 1.856			
<i>Alpheus paracrinitus</i>	11/20 1-4-5 (14.4±4.0) 1.5 1.809	3/20 1-2-3 (3.6)	11/16 1-2-8 (14.5±5.0) 32.2 2.167	1/16 2 (1.0)	8/16 1-2-3 (7.0±1.0) 10.8 1.670
<i>Alpheus peasei</i>	4/20 1-1-2 (2.8)				
<i>Alpheus schmitti</i>	3/20 1-3-3 (2.8)				
<i>Alpheus simus</i>					1/16 1 (0.5)
<i>Alpheus</i> sp.	1/20 1 (0.4)	2/20 1-1 (0.8)	1/16 1 (0.5)		
<i>Alpheus ridleyi</i>	1/20 1 (0.4)	1/20 1 (0.4)			
<i>Automate rectifrons</i>		1/20 1 (0.4)			

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Metalpheus</i> <i>rostratipes</i>	6/20 1-2-4 (4.8±1.0) 1.7 3.030				
<i>Salmonaeus</i> <i>ortmanni</i>	1/20 1 (0.4)	2/20 1-1 (0.8)	4/16 1-1-1 (2.0)	1/16 1 (0.5)	3/16 1-1-3 (2.5)
<i>Synalpheus</i> <i>anasimus</i>	2/20 1-1 (0.8)	1/20 1 (0.4)			
<i>Synalpheus</i> <i>fritzmuelleri</i>	20/20 2-10-36 (92.8±18.6) 32.5 1.519	3/20 1-1-2 (1.6)			2/16 1-1 (1.0)
<i>Synalpheus</i> <i>herricki</i>		1/20 1 (0.4)			
<i>Synalpheus</i> <i>minus</i>	16/20 1-6-15 (42.0±8.9) 14.7 1.512	1/20 1 (0.4)			
<i>Synalpheus</i> <i>pandionis</i>	4/20 1-1-1 (1.6)	1/20 1 (0.4)			
<i>Synalpheus</i> sp.		1/20 1 (0.4)			
<i>Synalpheus</i> <i>tenuispina</i>	3/20 2-2-5 (3.6)	1/16 1 (0.5)			
<i>Synalpheus</i> <i>townsendi</i>	14/20 1-4-11 (3.2±1.0) 9.6 1.005	1/20 1 (0.4)			
<i>Thunor</i> <i>rathbunae</i>	10/20 1-6-13 (18.7±6.4) 7.0 2.646				

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<hr/>					
Hippolytidae					
<i>Hippolyte curacaoensis</i>					1/16 6 (3.0)
<i>Lysmata intermedia</i>	1/20 1 (0.4)				
<i>Thor manningi</i>	1/20 1 (0.4)	2/20 1-1 (0.8)	1/16 2 (1.0)		1/16 2 (1.0)
Processidae					
<i>Ambidexter symmetricus</i>					1/16 3 (1.5)
<i>Processa bermudensis</i>				1/16 2 (1.0)	
<i>Processa fimbriata</i>				1/16 1 (0.5)	2/16 1-2 (1.5)
CRUSTACEA: DECAPODA: REPTANTIA					
Porcellanidae					
<i>Petrolisthes jugosus</i>	9/20 2-3-5 (12.4±4.0) 2.6 2.366	2/20 1-1 (0.8)			
<i>Petrolisthes galathinus</i>	2/20 1-2 (1.2)		1/16 2 (1.0)		2/16 1-1 (1.0)
<i>Petrolisthes armatus</i>	1/20 1 (0.4)			1/16 3 (1.5)	
<i>Petrolisthes sp.</i>	1/20 1 (0.4)				
<i>Pachycheles serratus</i>	17/20 5-7-11 (52.0±7.7) 11.0 1.276	1/20 1 (0.4)			

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Pachycheles chacei</i>	8/20 4-5-6 (16.8±5.2) 3.6 2.369				
<i>Pachycheles susanae</i>	12/20 1-3-4 (15.6±4.4) 3.3 2.078				
<i>Pachycheles cristobalensis</i>	3/20 1-1-2 (1.6)				
<i>Clastotoechus nodosus</i>		1/20 1 (0.4)			
<i>Megalobrachium roseum</i>	7/20 2-3-4 (8.8±3.2) 1.9 2.684				
<i>Megalobrachium poeyi</i>	5/20 1-1-2 (2.8±1.2) 0.6 1.905				
<i>Megalobrachium soriatum</i>	3/20 1-1-1 (1.2)				
Leucosiidae					
<i>Uhlias limbatus</i>	2/20 1-1 (0.8)		2/16 2-2 (2.0)		
Xanthidae					
<i>Paraliomera dispar</i>	20/20 6-21-40 (23.7±4.2) 40.3 1.556	2/20 1-9 (4.0)	2/16 1-1 (1.0)		
<i>Platypodia spectabilis</i>	5/20 1-1-1 (2.4±0.6) 0.5 1.333	1/20 1 (0.4)	7/16 1-2-2 (7.0±2.9) 15.4 1.758		

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Actaea setigera</i>	5/20 1-1-1 (2.0±1.3) 0.4 0.000	1/20 1 (0.4)			
<i>Leptodius floridanus</i>	1/20 2 (0.8)		1/16 1 (0.5)	8/16 1-2-4 (11.0±4.1) 27.5 2.494	6/16 1-2-4 (7.0±2.9) 8.9 2.637
<i>Xanthodius denticulatus</i>	4/20 1-1-2 (2.4)	2/20 1-2 (1.2)	1/16 1 (0.5)		
<i>Panopeus bermudensis</i>	1/20 1 (0.4)	4/20 1-1-1 (2.8)	5/16 1-1-1 (3.0±1.4) 6.6 2.133	4/16 1-1-2 (3.0)	10/16 1-2-4 (13.0±4.0) 16.5 1.871
<i>Panopeus</i> sp.	3/20 1-1-1 (1.2)	3/20 1-2-6 (3.6)	2/16 1-2 (1.5)	5/16 1-1-3 (3.5±0.2) 8.8 2.667	3/16 1-1-3 (2.5)
<i>Micropanope</i> sp.					2/16 1-1 (1.0)
<i>Pilumnus dasypodus</i>	10/20 2-2-3 (9.6±2.9) 2.0 1.594	2/20 1-3 (2.0)	3/16 1-1-1 (1.5)		2/16 1-1 (1.0)
<i>Pilumnus lacteus</i>	1/20 1 (0.4)				
<i>Pilumnus holosericus</i>	7/20 1-1-4 (7.2±3.2) 1.5 3.922	1/20 1 (0.4)	1/16 1 (0.5)		
<i>Pilumnus reticulatus</i>	3/20 1-1-3 (2.0)				1/16 1 (0.5)

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Pilumnus</i> sp.	1/20 1 (0.4)				1/16 1 (0.5)
<i>Eriphia gonagra</i>	2/20 1-2 (1.2)	1/20 1 (0.4)			1/16 1 (0.5)
<i>Domecia acanthophora</i>	3/20 1-1-1 (1.2)				1/16 1 (0.5)
Xanthid sp. F		2/20 1-1 (0.8)		1/16 1 (0.5)	
Pinnotheridae Pinnotherid sp.		1/20 1 (0.4)			
Grapsidae					
<i>Pachygrapsus transversus</i>	5/20 1-3-9 (9.2±6.2) 1.9 7.194	16/20 3-5-16 (54.8±12.5) 35.9 1.853	6/16 1-2-4 (7.0±2.9) 15.4 2.637	1/16 1 (0.5)	9/16 1-1-4 (13.0±6.1) 16.5 3.889
<i>Pachygrapsus marmoratus</i>	1/20 1 (0.4)				
Majidae					
<i>Acanthonyx petiverii</i>		2/20 1-1 (0.8)			
<i>Epialtus</i> sp.		1/20 1 (0.4)	1/16 2 (1.0)		
<i>Thoe puella</i>	3/20 1-1-1 (1.2)				
<i>Pitho aculeata</i>				2/16 1-1 (1.0)	1/16 2 (1.0)
<i>Mithrax (Mithrax) spinossissimus</i>	+				

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Mithrax (Mithrax)</i> <i>acuticornis</i>				1/16 1 (0.5)	
<i>Mithrax (Mithrax)</i> sp.	4/20 1-1-1 (1.6)	2/20 1-2 (1.2)		1/16 1 (0.5)	
<i>Mithrax</i> (<i>Mithraculus</i>) <i>coryphe</i>	19/20 4-10-21 (119.2±28.5) 25.3 2.025	17/20 1-4-9 (40.4±10.9) 26.4 2.198	5/16 3-4-6 (12.5±6.2) 27.5 4.213	1/16 1 (0.5)	3/16 1-1-2 (2.0)
<i>Macrocoeloma</i> <i>subparallelum</i>	2/20 1-1 (0.8)	2/20 1-2 (1.2)		1/16 1 (0.5)	
<i>Microphrys</i> <i>bicornutus</i>	5/20 1-1-2 (2.8±1.2) 0.6 1.905	17/20 1-4-9 (37.6±8.3) 24.6 1.739	5/16 1-1-2 (6.5±4.0) 14.3 5.949	11/16 1-2-5 (17.5±4.5) 43.8 1.587	14/16 2-3-10 (36.0±9.1) 45.6 1.753
Majid sp. F	1/20 2 (0.8)	1/20 1 (0.4)			
Parthenopidae <i>Heterocrypta</i> <i>macrobrachia</i>				+	

APPENDIX C

Occurrence of two species of *Barbatia* in 0.06 m² quadrats on the intertidal reef flat of Galeta. The survey presented in Appendix B was made before it was realized that some of the *B. dominicensis* were actually *B. tenera*. The three statistics are as follows, from top to bottom in each unit:

1. Frequency (0.06 m² samples): no. of samples in which species were present/total no. of samples sorted for these species.
2. Abundance (0.06 m² samples): median plus quartiles of abundance counts.
3. Abundance (calculated mean and standard error per 1 m²).

	Coralline	Laurencia	Zoanthus	Thalassia	Acanthophora
<i>Barbatia dominicensis</i>	15/18 1-3-4 (41.8±9.8)	12/24 1-2-3 (16.0±4.5)	12/16 1-2-3 (26.0±5.2)	1/16 1 (1.0)	9/16 1-1-3 (16.0±4.6)
<i>Barbatia tenera</i>	7/18 1-1-2 (8.9±3.2)	4/24 1-1-3 (4.0)	7/16 1-1-2 (10.0±3.2)	1/16 1 (1.0)	1/16 1 (1.0)

APPENDIX D

Catalog of mollusks from the high intertidal "splash" zone at the Galeta marine laboratory. The "splash" zone consists of a pile of rubble along the base of the wall of the laboratory building next to the Acanthophora zone. The descriptive statistics are the same as explained for Appendix B.

<i>Nerita fulgurans</i>	19/40 1-5-16 (82.0±25.5) 12.3 4.587
<i>Nerita versicolor</i>	14/40 1-4-7 (31.2±11.5) 4.7 5.834
<i>Nerita tessellata</i>	15/40 1-3-3 (19.6±6.6) 2.9 4.694
<i>Nerita peloronta</i>	2/40 1-3 (1.6)
<i>Littorina ziczac</i>	16/40 1-2-10 (36.8±13.5) 5.4 5.905
<i>Littorina lineolata</i>	19/40 7-11-48 (181.2±54.2) 27.1 4.407
<i>Littorina tessellata</i>	+
<i>Littorina meleagris</i>	4/40 1-1-6 (6.0)
<i>Nodilittorina tuberculata</i>	4/40 1-2-2 (2.4)
<i>Tectarius muricatus</i>	+

<i>Batillaria minima</i>	9/40 1-2-3 (14.0±8.5) 2.1 15.832
<i>Cerithium variable</i>	1/40 1 (0.4)
<i>Planaxis lineatus</i>	8/40 8-18-36 (286.8±235.4) 42.9 27.261
<i>Planaxis nucleus</i>	4/40 1-1-1 (2.0)
<i>Drupa nodulosa</i>	3/40 1-1-1 (1.2)
<i>Thais haemastoma</i>	4/40 1-1-2 (2.4)
<i>Isognomon radiatus</i>	1/40 4 (1.6)

APPENDIX E

Catalog of species found along the transect line on the intertidal andesite rock beach at Paitilla on the Pacific coast of Panama in Panama City. Calculations are based on eight 0.125 m² samples in the Abietinaria Zone, two 0.06 m² samples in the Chthamalus Zone and twelve 0.125 m² samples in the Tetracrita Zone. Abundances of gastropods were estimated from twelve 0.125 m² quadrats in the Tetracrita Zone, four 0.125 m² quadrats in the Abietinaria and Chthamalus Zones, ten 1 m² quadrats in the Abietinaria and Littorina Zones and one hundred twenty 1 cm² quadrats in the Chthamalus Zone. Species observed in the zones or samples but not counted are indicated by "+". The descriptive statistics are as follows, from top to bottom in each unit:

1. Frequency: no. of samples in which the species were present/total no. samples sorted for this species.
2. Abundance (1 m² calculated).
3. Relative abundance: per cent of class within the zone numerically represented by the species.

The algae were identified by Joyce Redemske Young.

	Abietinaria	Chthamalus	Tetracrita	Littorina
<hr/>				
CHLOROPHYTA				
<i>Bryopsis galapagensis</i>	+			
<i>Caulerpa racemosa</i> V. <i>occidentalis</i>	+			
<i>Chaetomorpha antennina</i>			+	
<i>Chaetomorpha</i> sp.		+	+	
<i>Cladophora</i> sp.	+	+	+	
<i>Codium santamariae</i>	+			
<i>Enteromorpha flexuosa</i>			+	
<i>Ulva lactuca</i>	+	+	+	
<i>Cladophoropsis robusta</i>	+		+	
PHAEOPHYTA				
<i>Dictyota conerescens</i>	+			
<i>Padina</i> sp.	+			
<i>Sphacelaria</i> sp.	+			

	Abietinaria	Chthamalus	Tetraclita	Littorina
RHODOPHYTA				
<i>Amphiroa polymorpha</i>	+			
<i>Antithamnion occidentale</i>	+			
<i>Bostrychia radicans</i>		+		
<i>Bostrychocladia tenuissima</i>	+			
<i>Caloglossa leprieurii</i>	+	+	+	
<i>Centroceras clavulatum</i>	+		+	
<i>Ceramium byssoideum</i>	+			
<i>Ceramium fastigiatum</i>	+		+	
<i>Ceramium personatum</i>	+			
Crustose coralline, multipored	+			
Crustose coralline, one pore level	+	+		
Crustose coralline, one pore raised	+		+	
<i>Fosiella</i> sp.	+			
<i>Gelidiella</i> sp.	+	+	+	
<i>Gracilaria brevis</i>	+			
<i>Gymnogongrus crustiforme</i>			+	
<i>Herposiphonia secunda</i>	+			
<i>Herposiphonia tenella</i>	+			
<i>Hildenbrandia prototypus</i>	+	+	+	
<i>Hypnea cervicornis</i>	+			
<i>Jania adherens</i>	+			
<i>Laurencia</i> sp.	+			
<i>Peyssonnelia rubra</i>	+		+	
<i>Polysiphonia homoia</i>			+	
<i>Pterocladia musciformis</i>	+	+	+	
<i>Pterocladia</i> sp.	+	+	+	
<i>Rhodomenia palmetta</i>	+			

	Abietinaria	Chthamalus	Tetracrita	Littorina
<hr/>				
GASTROPODA				
<i>Fissurella microtrema</i>			1/12 0.6 0.2	
<i>Fissurella rugosa</i>			+	
<i>Fissurella virescens</i>	+			
<i>Notoacmea filosa</i>	+		1/12 0.6 0.2	
<i>Patelloida semirubida</i>			2/12 1.8 0.6	
<i>Tegula panamensis</i>		+		
<i>Tricolia phasianella</i>			2/12 4.2 1.3	
<i>Nerita scabricosta</i>	+	+		
<i>Nerita funiculata</i>	+	+	5/12 9.6 3.0	
<i>Littorina aspera</i>				+
<i>Littorina dubiosa</i>		+		
<i>Aorotrema</i> sp.		+		
<i>Cyclostremiscus panamensis</i>		+		
<i>Fartulum</i> sp.		+		
<i>Caecum</i> spp.	+	+		
<i>Modulus disculus</i>		+	+	
<i>Tripsyche tulipa</i>			+	
<i>Cerithium stercusmuscarum</i>	+			
<i>Cerithium gemmatum</i>		+		
<i>Epitonium nitidisca</i>		+		
<i>Hipponix grayanus</i>	+	+		
<i>Hipponix panamensis</i>	+		10/12 26.0 8.3	
<i>Hipponix pilosus</i>	+			

	Abietinaria	Chthamalus	Tetraclita	Littorina
<i>Fossarus atratus</i>		+	3/12 4.2 1.3	
<i>Fossarus megasoma</i>		+	1/12 0.6 0.2	
<i>Crepidula aculeata</i>	+		1/12 0.6 0.2	
<i>Crepidula incurva</i>	+	+		
<i>Crepidula lessonii</i>	+		1/12 0.6 0.2	
<i>Crepidula marginalis</i>	+			
<i>Crepidula onyx</i>	+			
<i>Crepidula striolata</i>	+		9/12 11.4 3.6	
<i>Cypraea arabicula</i>	+			
<i>Cypraea cervinetta</i>	+			
<i>Cymatium gibbosum</i>	+			
<i>Muricanthus radix</i>	+			
<i>Muricopsis zeteki</i>	+			
<i>Aspella indentata</i>	+			
<i>Eupleura nitida</i>	+			
<i>Coralliophila squamosa</i>	+			
<i>Thais triangularis</i>	+			
<i>Thais biserialis</i>	+			
<i>Thais melones</i>	+	+	3/12 20.4 6.5	
<i>Acanthina brevidentata</i>	+	+	9/12 22.8 7.3	
<i>Acanthina muricata</i>	+			
<i>Morula lugubris</i>	+			

	Abietinaria	Chthamalus	Tetracita	Littorina
<i>Anachis lyrata</i>			2/12 1.2 0.4	
<i>Anachis boivini</i>		+	2/12 6.0 1.9	
<i>Anachis fluctuata</i>	+	+		
<i>Anachis fulva</i>		+		
<i>Anachis rugosa</i>			3/12 27.0 8.6	
<i>Anachis varia</i>		+		
<i>Anachis diminuta</i>		+		
<i>Nassarius exilis</i>	+			
<i>Opeatostoma pseudodon</i>	+			
<i>Mitra lens</i>	+			
<i>Conus purpurascens</i>	+			
<i>Conus fergusonii</i>	+			
<i>Crassispira discors</i>	+			
<i>Onchidella</i> (?binneyi)			7/12 21.0 6.7	
<i>Onchidella</i> (?hildae)			10/12 70.8 22.7	
<i>Siphonaria maura</i>	+		9/12 88.8 28.5	
BIVALVIA				
<i>Arca mutabilis</i>			1/12 0.6 0.02	
<i>Brachidontes puntarenensis</i>			3/12 6.6 0.3	
<i>Brachidontes semilaevis</i>		+	10/12 830.4 37.3	

	Abietinaria	Chthamalus	Tetraclita	Littorina
<i>Lithophaga aristata</i>		+	12/12 236.4 10.6	
<i>Isognomon recognitus</i>	+		12/12 86.4 3.8	
<i>Ostrea conchaphila</i>			2/12 1.2 0.05	
<i>Ostrea iridescens</i>			4/12 7.8 0.4	
<i>Ostrea palmula</i>			2/12 4.6 0.2	
<i>Cardita radiata</i>			6/12 7.8 0.3	
<i>Lasaea rubra</i>			5/12 7.8 0.4	
<i>Chama echinata</i>	+			
<i>Cumingia lamellosa</i>			1/12 0.6 0.03	
<i>Sphenia fragilis</i>	+		12/12 984.6 44.3	
AMPHINEURA				
amphineuran spp.	+		11/12 14.4	
BRACHIOPODA				
<i>Discinisca strigata</i>	+		1/12 2.4	
POLYCHAETA				
(Families presented in alphabetical order)				
Arabellidae				
<i>Arabella mutans</i>	4/8 28 3.4			

	Abietinaria	Chthamalus	Tetracrita	Littorina
<i>Arabella</i> sp. indet.	1/8 1 0.1			
Chloraemidae				
<i>Pherusa inflata</i>	4/8 34 4.0			
<i>Piromis americana</i>	2/8 4 0.5			
Cirratulidae				
<i>Dodecaceria concharum</i>	2/8 2 0.2			
<i>Cirriformia luxuriosa</i>	4/8 37 4.4		4/12 9.0 0.8	
<i>Cirriformia tentaculata</i>	1/8 1 0.1			
<i>Tharyx</i> sp.	2/8 2 0.2		3/12 3.0 0.3	
Cirratulid sp. indet.	1/8 1 0.1		1/12 0.6 0.05	
Dorvilleidae				
<i>Dorvillea cerasina</i>	2/8 2 0.2			
Eunicidae				
<i>Eunice</i> sp. indet.	1/8 1 0.1			
<i>Lysidice ninetta</i>	6/8 42 5.0		10/12 14.4 1.3	
<i>Palola siciliensis</i>	4/8 27 3.2		1/12 0.6 0.1	

	Abietinaria	Chthamalus	Tetraclita	Littorina
<i>Palola</i> sp. indet.	1/8 1 0.1			
Hesionidae				
<i>Ophiodromus pugettensis</i>	1/8 1 0.1			
Lumbrineridae				
<i>Lumbrinereis inflata</i>	3/8 24 2.8			
Nereidae				
<i>Eurinereis</i> n. sp.	2/8 2 0.2			
<i>Neanthes pseudonoodti</i>		1/2 32 33.2	2/12 10.8 0.9	
<i>Nereis callaona</i>	8/8 56 6.7	+	9/12 126.6 11.4	
<i>Perinereis elenacaso</i>	2/8 50 6.0		2/12 66.0 5.9	
<i>Perinereis</i> sp. indet.	1/8 1 0.1			
<i>Platynereis dumerilii</i>	1/8 1 0.1		2/12 16.8 1.5	
<i>Pseudonereis gallapagensis</i>	5/8 15 1.8	1/2 16 16.6	11/12 223.2 20.0	
nereid indet.		+	4/8 5.4 0.5	
Palmyridae				
<i>Bhawania goodei</i>	2/8 2 0.2		2/12 1.2 0.9	

	Abietinaria	Chthamalus	Tetraclita	Littorina
<i>Bhawania riveti</i>	4/8 10 1.2		2/12 4.2 0.4	
Phyllodocidae				
<i>Anaitides panamensis</i>			4/12 8.4 0.8	
<i>Anaitides</i> sp.	1/8 1 0.1			
<i>Eteone</i> sp. indet.	1/8 3 0.4			
<i>Eulalia myriacylum</i>	2/8 2 0.2			
<i>Eulalia</i> cf. <i>viridis</i>	2/8 8 0.9			
<i>Eumida bifoliata</i>	1/8 1 0.1			
<i>Notophyllum</i> sp. indet.	1/8 2 0.2		1/12 0.6 0.05	
Phyllodocid sp. indet.	2/8 13 1.5		1/12 0.6 0.05	
Polynoidae				
<i>Lepidasthenia gigas</i>	1/8 1 0.1			
<i>Lepidonotus crosslandi</i>	2/8 6 0.7		6/12 6.6 0.6	
<i>Lepidonotus nesophilus</i>	2/8 24 2.8			
<i>Lepidonotus</i> (?) <i>pomarae</i>	1/8 1 0.1			

	Abietinaria	Chthamalus	Tetraclita	Littorina
polynoid indet.	1/8 4 0.5			
Sabellariidae				
<i>Phragmatopoma</i> sp. indet.	2/8 2 0.2			
<i>Sabellaria alcocki</i>	2/8 29 3.5		1/12 1.2 0.1	
<i>Sabellaria floridensis</i>	1/8 5 0.6			
<i>Sabellaria moorei</i>			2/12 1.8 0.1	
<i>Sabellaria spinulosa</i>	1/8 28 3.4			
Sabellidae				
<i>Hypsicomus torquatus</i>	4/8 11 1.3			
<i>Pseudopotamilla</i> ? <i>brevibranchiata</i>	3/8 3 0.4		1/12 0.6 0.05	
<i>Sabella melanostigma</i>	1/8 1 0.1			
<i>Sabella</i> sp.	1/8 2 0.2			
Serpulidae				
Serpulid sp. 1	5/8 56 6.7		11/12 258.0 23.2	
Serpulid sp. 2	1/8 1 0.1			
Serpulid sp. 3	1/8 1 0.1			

	Hydractinia	Chthamalus	Tetractita	Littorina
Serpulid sp. 4	3/8 12 1.4			
Serpulid sp. 5	1/8 13 1.5			
Serpulid sp. 6	1/8 1 0.1			
Serpulid sp. 7	4/8 93 11.2		5/12 9.0 0.8	
Serpulid sp. 8	1/8 1 0.1			
Serpulid sp. 9	1/8 4 0.5		7/12 13.8 1.2	
Serpulid sp. 11			2/12 1.2 0.1	
Spionidae				
<i>Boccardia proboscidea</i>	2/8 8 0.9	1/2 48 16.3	5/12 58.8 5.3	
<i>Boccardia tricuspa</i>			9/12 24.6 2.2	
Syllidae				
<i>Autolytus</i> cf. <i>magnus</i>			2/12 18.0 1.6	
<i>Haplosyllis spongicola</i>			2/16 5.4 0.5	
<i>Odontosyllis</i> sp. indet.	1/8 1 0.1		1/12 1 0.1	
<i>Opisthosyllis brunnea</i>	1/8 21 2.5		12/12 42.0 3.8	

	Abietinaria	Chthamalus	Tetracrita	Littorina
<i>Opisthosyllis</i> sp. indet.			2/12 2.4 0.2	
<i>Syllis gracilis</i>	5/8 18 2.1		8/12 88.8 7.9	
<i>Typosyllis aciculata</i>	1/8 1 0.1		3/12 7.8 0.7	
<i>Typosyllis variegata</i>	1/8 8 0.9		1/12 1 0.1	
syllid epitoke indet.	1/8 8 0.9		1/12 1 0.1	
Syllid sp. 9	1/8 1 0.1		2/2 4.8 0.4	
Terebellidae				
<i>Eupolymnia</i> (?) <i>nebulosa</i>	2/8			
<i>Loimia medusa</i>	1/8			
<i>Pista brevibranchiata</i>	1/8			
terebellid indet.	2/8		1/12 0.6 0.05	
PYCNOGONIDA				
<i>Ammonothea</i> sp. 1 & 2	5/8 36 9.4			
<i>Nymphopsis</i> <i>duodorsospinosa</i>	5/8 29 7.5			
<i>Tanystylum intermedium</i>	5/8 35 9.1			
<i>Tanystylum</i> sp. 1	5/8 12 0.3			
<i>Tanystylum</i> sp. 2	5/8 109 28.3			

	Abietinaria	Chthamalus	Tetraclita	Littorina
<i>Pigromitus timsanus</i>			1/12 0.6 50.0	
<i>Anoplodactylus erectus</i>	1/8 3 0.8			
<i>Anoplodactylus evelinae</i>	5/8 59 12.7			
<i>Anoplodactylus portus</i>	4/8 18 4.7			
<i>Anoplodactylus pygmaeus</i>	3/8 3 0.8			
<i>Anoplodactylus viridintestinalis</i>	5/8 65 16.9		1/12 0.6 50.0	
<i>Anoplodactylus</i> sp.	2/8 4 1.0			
<i>Pycnogonum cessaci</i>	3/8 14 3.6			
CRUSTACEA: CIRRIPEDIA				
<i>Balanus amphitrite</i>			+	
<i>Balanus inexpectatus</i>			+	
<i>Balanus tintinnabulum</i>			+	
<i>Chthamalus panamensis</i>		+		
<i>Tetraclita stalactifera panamensis</i>			12/12 318.6 44.6	
CRUSTACEA: STOMATOPODA				
stomatopods (number of species unknown)	2/8 4 0.2			
CRUSTACEA: TANAIDACEA				
tanaids (number of species unknown)	2/8 4 0.2		4/12 16.2 2.3	

	Abietinaria	Chthamalus	Tetraclita	Littorina
CRUSTACEA: ISOPODA				
<i>Alcirona insularis</i>	3/8 28 1.4			
<i>Dynamenella</i> aff. <i>acutitelson</i>	4/8 213 10.6		2/12 34.2 4.7	
<i>Dynamenella josephi</i>		1/2 192 65.2		
<i>Dynamenella setosa</i>	1/8 1 0.05		3/12 30.6 4.2	
<i>Dynamenella</i> n. sp. A	4/8 198 9.9			
<i>Dynamenella</i> sp. 1			7/12 49.2 6.8	
<i>Dynamenella</i> sp. 2	1/8 1 0.05		3/12 4.2 0.6	
<i>Excorallana</i> aff. <i>tricornis</i>	4/8 53 2.6			
<i>Jaeropsis rathbunae</i>	3/8 6 0.3			
<i>Mesanthura</i> (?)			2/12 7.2 1.0	
<i>Paracerceis</i> sp. 1	4/8 9 0.4			
Sphaeromatid sp. 1			1/12 0.6 0.08	
sphaeromatid juvenile	1/8 1 0.05			

	Abietinaria	Chthamalus	Tetraclita	Littorina
<hr/>				
CRUSTACEA: DECAPODA: NATANTIA				
<i>Gnathophyllum panamense</i>	1/8 1 0.05			
<i>Synalpheus</i> sp.			1/8 1 0.05	
<i>Thor</i> sp.	1/8 1 0.05			
other shrimps (species unknown)	2/8 2 0.1		3/12 12.6	
CRUSTACEA: DECAPODA: REPTANTIA				
Diogenidae				
<i>Calcinus obscurus</i>			1/12 0.6	
<i>Clibanarius albidigitus</i>			1/12 0.6	
Porcellanidae				
<i>Neopisosoma mexicanum</i>			1/12 1.8	
<i>Pachycheles calculosus</i>			1/12 1.2	
Paguridae				
pagurid (juvenile)	1/8 3 0.2			
Grapsidae				
<i>Pachygrapsus transversus</i>	5/8 47 2.3		9/12 25.2	
Majidae				
<i>Eupleurodon trifurcatus</i>	2/8 2 0.1			
<i>Inachoides laevis</i>	2/8 6 0.3			
<i>Pelia pacifica</i>	4/8 41 2.0			

	Abietinaria	Chthamalus	Tetraclita	Littorina
Portunidae				
<i>Portunus</i> sp.	1/8 1 0.05			
Xanthidae				
<i>Eriphia squamata</i>	1/8 1 0.05		3/8 2.4	
<i>Menippe obtusa</i>	1/8 2 0.1			
<i>Panopeus bermudensis</i>	4/8 6 0.3		4/12 8.4	
<i>Platypodia</i> (?) sp.	1/8 3 0.2		1/12 0.6	
<i>Pilumnus reticulatus</i>	4/8 4 0.2			
<i>Xanthodius stimpsoni</i>	4/8 19 0.9			
xanthid indet.	3/8 4 0.2		2/12 3.6	

APPENDIX F

A catalog of macroscopic species found in ten 0.125 m² quadrat samples in the mangrove community adjacent to the Galeta laboratory. A "+" indicates presence; "++" indicates great abundance. Joyce Redemske Young provided the data for the algae.

the data for the algae.

TAXA	Quadrat Number										Ave/m ²
	1	2	3	4	5	6	7	8	9	10	
CYANOPHYTA											
Filamentous blue-green						++			++		
Large bulbous blue-green				+							
CHLOROPHYTA											
<i>Caulerpa fastigiata</i>		++					+				
<i>Chaetomorpha brachygona</i>	+	+			+						
<i>Chaetomorpha clavata</i>									+		
Chaetophoraceae- - appressed green coalesced filaments						+					
<i>Cladophora</i> sp.									+		
<i>Cladophoropsis membranacea</i>	++	+		+	+		+	++	+	++	
<i>Halimeda opuntia</i>											+
RHODOPHYTA											
<i>Bostrychia binderi</i>		++		+	++		++	++		++	
<i>Caloglossa leprieurii</i>		+			+		+	+		+	
<i>Catenella repens</i>		++		+	++	+	++	++		++	
<i>Centroceras clavulatum</i>		+									
crustose red coralline					+		+		+		
creeping gelidiale							+		+		
<i>Laurencia papillosa</i>		+				+	+		+	+	
<i>Murrayella pericladus</i>		+			+		+				
<i>Peyssonnelia amorea</i>						+					

TAXA	Quadrat Number										Ave/m ²
	1	2	3	4	5	6	7	8	9	10	
<i>Polysiphonia howei</i>							++				
<i>Spyridia filamentosa</i>					+						
PORIFERA											
Class Demospongia											
<i>Geodia</i> sp.		+									
Porifera sp. 1 M					+						
Porifera sp. 2 M						+					
COELENTERATA											
Class Anthozoa											
<i>Anthopleura krebsi</i>	3		3								4.8
<i>Zoanthus sociatus</i>						275		21	945		992.8
SIPUNCULA											
<i>Golfingia</i> sp. 1					7						5.6
<i>Golfingia</i> ? sp. 2				7							5.6
<i>Golfingia</i> ? sp. 3										1	0.8
<i>Golfingia</i> ? sp. 4										1	0.8
<i>Lithacrosiphon</i> sp. 3										1	0.8
<i>Paraspidosiphon fisheri</i>									2		1.6
<i>Paraspidosiphon spinoso-scutatus</i>				2	2		1		9		12.0
<i>Paraspidosiphon steenstrupi</i>						2			3		4.0
<i>Paraspidosiphon</i> sp. 4					2				4		4.8
<i>Phascolosoma antillarum</i>					2						1.6
<i>Phascolosoma perlucens</i>				1	5	6			226		190.4
<i>Phascolosoma</i> sp. 3									3		2.4
<i>Phascolosoma</i> sp. 4						6			1		5.6
ANNELIDA											
Class Polychaeta											
Family Amphinomidae											
<i>Eurythoe complanata</i>					4		1	2			5.6
Amphinomid sp. 1									2		1.6
Family Arabellidae											
<i>Arabella mutans</i>				2	1	6			14		18.4

TAXA	Quadrat Number										Ave/m ²
	1	2	3	4	5	6	7	8	9	10	
Family Capitellidae											
<i>Notomastus lineatus</i>						8			3		8.8
Family Glyceridae											
<i>Glycera oxycephala</i>									1		0.8
Family Leodicidae											
<i>Eunice afra</i>									8		6.4
<i>Eunice aphroditois</i>											
<i>Eunice caribaea</i>		1			1	1			6		7.2
Family Nereidae											
<i>Nereis callaona</i>			3								2.4
<i>Perinereis elenacasoii</i>						4			99		82.4
<i>Platynereis dumerilii</i>		1									0.8
<i>Pseudonereis gallapagensis</i>				1			2				2.4
Family Phyllodocidae											
<i>Eulalia myriacyclum</i>								1			0.8
Family Sabellidae											
<i>Hypsiocomus torquatus</i>					1						0.8
Family Syllidae											
<i>Autolytus magnus</i>						1			1		1.6
<i>Langerhansia cornuta</i>						1					0.8
<i>Opisthosyllis brunnea</i>						1					0.8
Family Serpulidae											
Serpulid sp. 1					1						0.8
Serpulid sp. 2						2					1.6
<i>Spirorbis</i> sp.	++	++		++	++						
Family Terebellidae											
<i>Eupolymnia ? nebulosa</i>						2					1.6
<i>Loimia medusa</i>								1			0.8
ARTHROPODA											
Class Crustacea											
Order Decapoda											
Suborder Natantia											
Natantia sp. 1								1		1	1.6
Pasiphaeid sp. 1								2		2	2.4

TAXA	Quadrat Number										Ave/m ²
	1	2	3	4	5	6	7	8	9	10	
<i>Alpheus</i> sp.			1								0.8
<i>Alpheus viridari</i>								1			0.8
<i>Alpheus armillatus</i>			1	1	3			1			4.8
<i>Ambidexter symmetricus</i>									1		0.8
Suborder Reptantia											
<i>Upogebia</i> sp.								2			1.6
<i>Clibanarius</i> sp.	10	8			131	6	9	8	17	4	153.6
<i>Panopeus</i> sp. 1	5	2		1	1			1			8.0
<i>Panopeus</i> sp. 2	3					1				1	4.0
<i>Panopeus</i> sp. 3										1	0.8
<i>Pachygrapsus</i> sp. 1	1		1		2				2		4.8
<i>Microphrys bicornutus</i>	1		1	1							2.4
<i>Uca</i> sp. 1							1	1		1	2.4
MOLLUSCA											
Class Gastropoda											
<i>Batillaria minima</i>	820	79		324	147		49	17	25	227	1350.4
<i>Neritina virgines</i>							1	2	27	41	60.0
<i>Nassarius vibex</i>	3	1					1				4.0
<i>Planaxis nucleus</i>		1									0.8
<i>Planaxis lineatus</i>					1						0.8
<i>Tricolia bella</i>										1	0.8
Gastropod sp.							1		6		5.6
Cerithiid sp.									2	1	2.4
<i>Bailya intricata</i>									4		3.2
<i>Cerithium</i> sp.									3		2.4
<i>Hyalina avena</i>									2		1.6
<i>Rissoina decussata</i>									2		1.6
<i>Cantharus auritulus</i>									1		0.8

TAXA	Quadrat Number										Ave/m ²
	1	2	3	4	5	6	7	8	9	10	
<i>Cerithiopsis emersoni</i>									1		0.8
<i>Heliacus infundibulus</i>									1		0.8
<i>Anachis crassilabris</i>										1	0.8
Class Bivalvia											
<i>Phacoides pectinatus</i>	5	11		4	4		3	2		11	32.0
<i>Isognomon bicolor</i>		1			1						1.6
<i>Codakia orbicularis</i>	3	1			2		1	1		9	13.6
<i>Codakia orbiculata</i>		1									0.8
<i>Arcopsis adamsi</i>					8				11		15.2
<i>Cyathodonta semirugosa</i>				1		2			6	2	8.8
<i>Brachidontes exustus</i>								3			2.4
<i>Lithophaga nigra</i>									4		3.2
<i>Lithophaga bisulcata</i>									3		2.4
<i>Pinctada radiata</i>										2	1.6
<i>Diplodonta punctata</i>										1	0.8
ECHINODERMATA											
Class Ophiuroidea											
<i>Ophiolepis paucispina</i>					1						0.8
Ophiuroid sp.					1						0.8

APPENDIX G

Names and present addresses of the authors of each section are given below. Questions, requests for further details or for general information would be most efficiently addressed directly to the person responsible for the specific section. It is suggested that specific taxonomic questions be referred to the authority on the subject cited in the Acknowledgments section.

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SECTION XVI

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16. ABSTRACT <p>Baseline surveys were conducted on both the Caribbean and Pacific coasts of Panama. The structure of macroinvertebrate communities along the Caribbean transect are presented from data collected for over 500 identified species in 108 samples including a total of over 50,000 specimens. Recruitment to benthic communities was investigated with settling plates. The Caribbean was found to be seasonal in species occurrence while the Pacific was seasonal in productivity.</p> <p>The effects of oil pollution on tropical intertidal marine communities were tested by precisely controlled experiments utilizing tarry Bunker C and volatile marine diesel oils. Field experiments were performed on a Caribbean intertidal reef flat community, a Pacific rocky shore community, settling plates in both oceans, mangrove trees sprayed with oil on the leaves and/or stilt roots and on coral growth. Bunker C oil had a greater detrimental effect than did marine diesel oil on coral growth. Marine diesel oil had a greater detrimental effect than did Bunker C oil on fouling communities of settling plates. When comparing experimentals with controls, growth rates were used as an indicator of the presence of unobserved physiological stress or damage and a quantitative index of the cost of repair. Susceptibility to oil pollution varied significantly with location and time of year so that very precise controls were required in the experiments.</p>		
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