Bulletin of the Biological Society of Washington
No. 2

THE PANAMIC BIOTA:

SOME OBSERVATIONS PRIOR TO A SEA-LEVEL CANAL

A Symposium Sponsored by
The Biological Society of Washington
The Conservation Foundation
The National Museum of Natural History
The Smithsonian Institution

MEREDITH L. JONES, *Editor*

September 28, 1972

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FOREWORD

The Biological Society of Washington is pleased to present the papers in this volume as a contribution toward the dissemination of fundamental knowledge of a controversial topic. The Society, as well as the other sponsoring groups and the Editor, must disclaim responsibility for the statements included herein. Each author is responsible for the content of his own paper.

As Editor, I have been confronted, as all editors are, with as many individual writing styles as there are contributors and as many formats as there are disciplines. I have tried to edit with as light a hand and as pale a blue pencil as I felt possible. This was done in the interests of preserving individual style, discipline format, and the passions of the moment of the several authors who have shown their sincere and profound feelings concerning the sea-level canal.

It should be noted that the term "Panamic", as used in the following papers, refers to the Panamanian region, in general, and not to the zoogeographic Panamic Province, unless otherwise indicated.

As Convenor and Editor of the Symposium I am most grateful to the Conservation Foundation, Washington, D. C., and especially to Mr. John P. Milton, for defraying publication costs, to the National Museum of Natural History, Smithsonian Institution, for providing funds for the travel and expenses of the participants from beyond the Washington area, and to the Council of the Biological Society of Washington for permission to resurrect the Society's Bulletin series for the Symposium and for permission to seek travel and publication funds for the Symposium, as I could find them. Finally, I would thank Teresa Smith, Division of Worms, National Museum of Natural History, Smithsonian Institution, for cheerfully and competently putting up with the inherent grouchiness and perpetual demands for retyping which characterize an editor.

MEREDITH L. JONES

INTRODUCTION

By Meredith L. JONES
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Past President (1970), the Biological Society of Washington

As a point of departure for this Symposium, it might be well to restate a few fundamental facts concerning Central America and the Panamanian isthmus.

1. Until the opening of the present canal in 1914, the Central American land mass constituted a barrier to the organisms of the Pacific and the Caribbean, and a land bridge for terrestrial organisms.
2. The marine species had been separated, and the terrestrial species had been linked, for from one to five million years; in the case of the marine faunas and floras, there were classical textbook opportunities for the formation of geminate species through independent evolution.
3. With the building of the present canal, a fresh water barrier was formed with respect to the terrestrial forms, and a barrier, only slightly less formidable than the previous one, was established for the marine forms.
4. Presently, the building of a new canal, a sea-level canal, has been proposed.

A number of rather basic questions are suggested by these facts:

1. In the case of geminate species, how far have they diverged? What are their morphological, their physiological, and their biochemical differences—in short, what are the genetic differences between species pairs?
2. How do the present faunas and floras, the marine, the terrestrial, and those of the northern and southern fresh water habitats, differ?

3. How much faunal and floral mixing of marine species has taken place? Is this due to shipping, as fouling organisms or as ballast-water survivors? Or is it due to normal dispersion?

4. What might be the effect of a sea-level canal on the Panamic biota—both as a continuum of salt water from ocean to ocean and as a salt water barrier to terrestrial and fresh water forms?

All of these, as well as the many more which undoubtedly come to mind, are interesting, intriguing, and important, insofar as distributional, ecological, physiological, and evolutionary studies are concerned.

However, the answers to all of these questions, and the foundation for all of these and other studies, no matter how far removed, ultimately devolve from one basic premise: To evaluate differences, to justify comparisons, to analyze observations, one must have a valid point of departure. In order to compare floras and faunas, one must know what species are present. In order to study similarities and differences between geminate species, one must recognize their existence. In order to assess the role of ships in the dispersal of species, one must know the fouling organisms on the ships' hulls, as well as the potential fouling organisms of both sides of the isthmus, and one must know what organisms, if any, can survive a ballast-water environment. In order to hypothesize concerning the effects of a sea-level canal on the Panamic biota, even assuming that the hydrologic and hydrographic parameters are unequivocally known, the faunas and floras of both oceans, as well as the northern and southern terrestrial and fresh water floras and faunas, *must* be known.

In short, we can not say what differences exist now, we can not access the independent evolution of geminate species, we can not comment on the amount of mixing between areas, we can not evaluate the effect of shipping, and we can not theorize about the effects of a sea-level canal, unless we have a basic knowledge of the organisms.

As a first step toward this end, we are convened here to summarize the present knowledge of the Panamic biota.

The importance of base line collections and observations, such as are called for here, long have been recognized, whether it was by Verrill in New England, by Wyville Thompson on the CHALLENGER, or by Agassiz on the BLAKE and ALBATROSS, to name but a few of the pioneers. There is such a man with us today; one who worked on then-recently-collected ALBATROSS material in the early 1900's and was senior biologist on a cruise to the Antarctic forty years later—a man dedicated to base line collecting, to the working up of such collections, and to the zoogeographic analysis of the data—a man to whom we pay tribute today, albeit inadequately relative to the leadership he has shown, the inspiration he has given, and the contributions he has made to marine biology and marine biologists. Our next speaker will speak in detail of the contributions of Waldo Lasalle Schmitt.

A TRIBUTE TO WALDO LASALLE SCHMITT

By GEORGE A. LLANO
Acting Chief Scientist, Office of Polar Programs
National Science Foundation, Washington, D. C.

There are many present here who have known Waldo L. Schmitt longer than I; or who, during his fifty years of service with the Smithsonian Institution, have been professionally more closely associated with him. As a matter of record I have come to know Waldo best since 1959, after he retired; and, as a consequence, I can best address myself to those quiet years which, theoretically, come with retirement.

I am most appreciative of being given the opportunity of rendering this small tribute to one who, by his name and through his works, has identified himself with this Institution and who, as a civil servant, has served his government in full measure.

This symposium on the Panamic Biota reminds me that Waldo's first visit to Panama came when he was but half his present age. The opportunity, made possible by the Walter Rathbone Bacon Traveling Scholarship, enabled him in 1926 to reconnoiter the crustacean fauna of South America. This trip of almost a year took him down the coast of Ecuador, Peru and Chile by way of Juan Fernandez to the Straits of Magellan, and then north to Montevideo and east to Las Islas Malvinas, the Falklands. In the Falklands, he met the captain of the FLEURUS, the yearly mail and supply ship to the Norwegian whaling fleet, who gave him passage south of the Antarctic Convergence. Waldo has related that one of his unforgettable recollections of this first visit to Antarctic waters is the memory of 11 whalers flensing their catches in the old-fashioned way, in the waters of Port Foster, Deception Island.

DR. WALDO LASALLE SCHMITT (photograph by Robert G. Tuck, Jr., August 1967)

On my return from Antarctica in 1959, at the close of the International Geophysical Year, I, too, stopped in Montevideo. In the mail received by our ship, the ARNEB, was an invitation to join the staff of the Committee on Polar Research of the National Academy of Sciences. The selection of members for the Panel on Biological and Medical Sciences was one of the Panel's first tasks; and the need for guidance in oceanography and marine biology was one of the most pressing. In turning to Waldo Schmitt, the Panel benefitted, not only from his preeminence as a marine zoologist and his wide acquaintance with specialists in the life sciences, but from his spontaneous enthusiasm and many ideas for the initiation and furtherance, not only of studies in his area of knowledge, but in all fields of science.

Waldo joined the Panel on Biological and Medical Sciences in 1960 and served as the oceanographic and marine biological advisor on the Panel and to the Committee on Polar Research of the Academy until 1966. In 1961, when the National Science Foundation decided to establish a station in the Antarctic Peninsula, with the thought of a site that would best serve the needs of marine biological studies, I asked Waldo to accompany the site survey team as biologist. Thus, in 1962, he left Washington for Antarctica, by way of New Zealand. Unforeseen delays gave him the opportunity of visiting the McMurdo Station on the Ross Sea and to observe the scientific activities at this far south Antarctic station. On his return to New Zealand, he boarded the icebreaker STATEN ISLAND at Wellington which, under the command of Captain Price Lewis, Jr., in January steamed across the South Pacific to the base of the Antarctic Peninsula. In all, he inspected some 20 possible sites along the Peninsula from Marguerite Bay, north through the Bellingshausen Sea, along the Drake Passage and into the Weddell Sea as far south as the Robinson Ice Shelf. While cruising through Bransfield Strait, Waldo again was enabled to visit Whalers Bay, Deception Island, where he made collections forty-five years earlier. 1963 was an open ice year, most favorable to the cruise and for collecting inshore and offshore. Unequipped for field work, Waldo induced the STATEN ISLAND's engineering department to improvise dredging and other overside collecting gear, as well as a Berlese rig for securing the insects and other organisms infesting the Antarctic moss and the lichen cover of exposed rocky areas. The cook most helpfully set aside no end of emptied glass jars, bottles, and sizable tins for preserving marine invertebrates, algae, and the stomach contents of seals. Of the several hundred fish taken in traps, constructed for the purpose in New Zealand, together with a few that were handlined, some 85 to 90 fish were frozen for convenient transport back to Washington. From Sick Bay, he scrounged all of the formaldehyde and ethyl alcohol the Medical Officer would release. Whenever and wherever the opportunity permitted, all manner of collections were made, botanical and zoological. At the conclusion of the STATEN ISLAND cruise, he brought back some 29,000 specimens. Though largely a general collection, it was particularly rich in specimens of polychaetes, ascidians, and mollusks. I have Captain Lewis's word that Waldo set a strenuous pace, and that he never missed an opportunity to go ashore to collect or to haul traps and lines, as the occasion demanded.

With the development of the *Antarctic Research Series* under the American Geophysical Union, I again called upon Waldo who agreed in 1962 to serve on the Board of Editors as the marine biology-oceanography editor. As a member of the Board of Editors, his standards for quality and preciseness in writing, for observance of style and accuracy and for authors' instructions for the preparation of manuscripts, contributed much to the overall success of the Series and to its establishment as a highly regarded journal.

Waldo suggested the title of the Series, the *Antarctic Research Series* and was instrumental in the development of the monographic volumes, which, so far, have served systematic biology well, with Hartman's publications on polychaetes, Kott's work on ascidians, and Newman and Ross' recent report on the Cirripedia. He has also urged the publication of handbooks, the first of which will be a *Handbook of Antarctic Birds.*

On several occasions Waldo has taken part in conferences at Skyland where the National Science Foundation annually brings together field participants in upper atmosphere, earth, and biological research to orient them in the overall objectives of the national Antarctic research program. His talks have encouraged, inspired and given emphasis to the needs of biological research in Antarctica. He has served as a member of the advisory board of the Antarctican Society and through his ideas and enthusiasm actively sustained the Society in its organization and growth.

Waldo is the recipient of the Antarctic Medal, conferred by Congress and presented by the National Science Foundation to those participating in U. S. Antarctic expeditions. Further, in recognition of his contribution to the U. S. Antarctic Research program, the Board of Geographic Names has named a 30-mile, ice-covered series of outcrops, west of the Weddell Sea at the base of the Antarctic Peninsula (74°, 50' S., 64°, 05' W.), Schmitt Mesa.

His door has always been open to those who sought his help or advice. His friendship is genuine and as freely given to a President, as to you and me—you may recall that he was a companion of Franklin D. Roosevelt on his fishing trip to Clipperton, Cocos, and the Galapagos Islands.

Above all he has shown a special talent in attracting and encouraging young people in systematic zoology.

One of Waldo's characteristics is impatience with anything less than the very best efforts. In all his dealings with his colleagues as a friendly critic, he strives for excellence. Indeed, he tries to live by these principles. Nothing better records this than the recent announcement that his study of the "Marine Decapod Crustacea of California," printed in 1921 by the University of California Press, is being reissued in this year as part of a series of the Crustacea of America. This large report, submitted as a Master's thesis to the University of California in 1916, is in itself proof that Waldo Schmitt has from the first, practiced what he preached.

RESPONSE

By WALDO L. SCHMITT

Zoologist Emeritus, National Museum of Natural History
Smithsonian Institution, Washington, D. C.

Dr. Llano, I thank you for "them kind words." As to the relevance of the honor being paid me on this very flattering occasion, I must confess to having made some contribution to our knowledge of the flora and fauna of the Isthmus, by way of specimens gathered in the Canal Zone, on Barro Colorado Island, and the Pacific shores of Costa Rica, Panama and Colombia, as well as in the San Blas country fronting the Gulf of Darien. Moreover, I also identified the marine and freshwater shrimps that Dr. Samuel F. Hildebrand collected in 1935-1937 while looking into "The Panama Canal as a Passageway for Fishes." I thank you one and all!

BACKGROUND FOR A NEW, SEA-LEVEL, PANAMA CANAL

By DAVID CHALLINOR
Smithsonian Institution, Washington, D. C.

The history of the Panama Canal is inexorably connected with international politics. The Spaniards of the 16th century, realizing the geographic significance of the isthmus, planned a canal, and we know from early records that in the 17th century fairly large ships were actually moved across the isthmus on rollers.

Not until the end of the 19th century was serious construction started in what was then the Colombian province of Panama. The efforts of de Lesseps to repeat his engineering triumph at Suez were defeated by the failure to protect the laborers from yellow fever. The American success, therefore, can be attributed largely to General Leonard Wood and his colleagues' successful discovery of the yellow fever vector. Once known, appropriate control measures could be taken and Colonel George W. Goethals and his engineers were able to complete their task.

Initially, there was considerable discussion as to what sort of canal was to be constructed; whether a sea-level or a high-level lake and lock type. The latter was approved by Congress in 1906, although a majority of an international board of consulting engineers had recommended a sea-level canal. With that important decision resolved, construction started and the canal was opened in August, 1914.

At that time, the locks were considered oversized (1000' x 110'), but this foresight was well-justified, as it was not until just before World War II, that concern was felt that larger locks and an extra set were necessary for purposes of defense.

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In 1939, Congress, therefore, authorized the construction of a third set of locks (1200' x 140'>< 50'). Construction was soon begun, but shortly after our entry into the war, other priorities intervened and work was abandoned in May, 1942, after spending about 75 million dollars. These excavated locks still lie unfinished at the Pacific end of the canal.

Interest in improving the canal to meet ever-increasing traffic never waned however, and with the control of nuclear energy during World War II, it was logical to start thinking of ways of putting this new source of energy to peacetime use. If this could be done in some spectacular fashion it might capture the public fancy.

The number of annual transits possible through the existing canal is limited by the amount of water that can be stored in the high-level lake system. The maximum number is estimated at 26,800 and in 1970 there were already 15,500. The projections also indicate that, at roughly the present rate of increase, the canal should reach its maximum ship transit capacity by about the end of this century. Therefore, the possibility of using nuclear devices to dig a new sea-level canal was among the factors which evidently prompted President Johnson to appoint the Atlantic-Pacific Interoceanic Canal Study Commission in April 1965.

When the Commission finished its report in December 1970, they had spent about 22 million dollars, 17.5 of which was devoted to evaluating nuclear routes and only about 3 million to conventional ones. The Commission concluded that the techniques of nuclear excavation had not yet been developed to a sufficiently safe level to be considered at this time. Given all the circumstances, Route 10 across the isthmus, to be dug conventionally about ten miles west of the present canal, was deemed the best site for a sea-level canal.

Ever in the background of the engineering plans to construct another canal are political considerations and, at this point in history, they seem to be the paramount factor in determining the likelihood of any canal ever being built. The actual incidents of the past often become distorted with time, and, just as the role of the French in our own Revolution has tended to be de-emphasized with time, so has the role of the United States in the Panamanian Revolution of 1903 become clouded almost four generations later. Most Panamanians today probably consider that the Hay-Bunau-Varilla Treaty took unfair advantage of their new country and feel that they were unfairly deprived of their birthright. All legal counter arguments are to no avail when a peoples' nationalistic emotions are aroused.

The current strong feelings of nationalism on both sides was reflected in the efforts to draft a new set of treaties in 1964-7 to replace the original one of 1903. The terms of the latter were slightly modified in 1936 by the Hull-Alfaro Treaty, by which the United States relinquished its right of eminent domain for canal purposes within the Republic of Panama, and we further agreed to raise our annuity to Panama from $250,000 to $430,000. In 1955, the Eisenhower (Milton)—Rem& Treaty raised the annuity once more, to $1,930,000. However, it was not until 1964, following severe local riots, that President Johnson appointed a negotiating team under Ambassador Robert B. Anderson to draft a new treaty. The United States and Panamanian diplomats met for three years and, after a great deal of hard work, presented drafts of three new treaties dealing with the canal. Considering the enormous political pressures in both countries, the compromises reached were probably the best that could be achieved.

The first proposal dealt with the operation of the present canal and, in effect, abrogated the 1903 treaty by recognizing Panamanian sovereignty and by giving joint jurisdiction over the present Canal Zone. It established a new operating authority for the Canal consisting of five Americans and four Panamanians, and it also increased the royalty payments to Panama from 17 cents to 22 cents per long ton of cargo. Finally, Panama would take possession of the canal in 1999 if no new one were built. If such a canal were built, then Panama would take title to the existing one shortly after the new canal was opened, but no later than 2099, in any case.

The second proposed treaty gave the United States a 20-year option (from the time of ratification) to build a sea-level canal in Panama in 15 years. The United States would have the controlling authority over the new canal for 60 years after it opened or until 2067, whichever was earlier. The financing, location and construction methods would all have to be agreed on after the United States exercised its option.

The third treaty would have allowed the United States to maintain its military bases for five years beyond the end of the proposed treaty for the continued operation of the present canal.

Needless to say, the idea of a Panamanian minority in the proposed operating authority described in the first treaty was politically unacceptable in Panama and, in 1970, the provisional junta rejected the entire draft package. Such a showdown never developed in the United States, but at best, there would have been strong opposition in the Senate to relinquishing our "sovereignty" over the Zone. The question of exactly what the language of the treaty meant with respect to sovereignty has been the source of endless discussion. The actual wording of the treaty grants to the United States all the rights, power and authority within the Zone

> ". . . which the United States would possess and exercise *if it were the sovereign* of the territory within which said lands and waters are located to the entire exclusion of the exercise by the Republic of Panama of any such sovereign rights, power or authority . . ." (italics mine).

Arguments over the interpretation of the italicized words above began during the administrations of Theodore Roosevelt and William Howard Taft, and have continued intermittently ever since. It seems relatively clear that the question of sovereignty in all its aspects is of paramount concern to Panama and that this issue will have to be resolved before any new canal is constructed. In fact, there seems to be some doubt whether a new sea-level canal can be built even within the boundaries of existing Canal Zone without a new treaty. It has been argued that the Treaty of 1903 only covers the construction, maintenance, operation, etc., of *the existing canal.* Thus, the question of sovereignty will have to be faced and resolved before any realistic agreement on new construction can be reached between the two countries. The major hurdle for a new canal may, therefore, be a political one rather than either technological or financial.

One aspect of the construction of a new sea-level canal that many scientists felt did not receive sufficient priority in the research plans of the Commission was the biological consequences of joining two oceans. The Smithsonian Institution, which had operated biological research facilities in Panama for 25 years, first sought to bring this matter to the attention of the Commission in April, 1966. At this time, only very limited biological research was being done by the Battelle Memorial Institute, which was under contract to the Commission, and much of this was oriented toward studying the consequences of the release of radioactive particles from nuclear detonations. The Smithsonian, however, felt that more emphasis should be given to baseline studies which should start as soon as possible. Such monitoring would determine natural fluctuations in populations, especially of marine organisms. In this way any sudden decline or increase in a population of marine organisms near the entrance of a new sea-level canal could be attributed to purely natural causes if similar phenomena had been observed before construction.

In any case, environmental concerns were finally voiced sufficiently so that the National Academy of Sciences was asked by the Commission in February 1969 to examine the ecological issues implicit in the construction of a sea-level canal through Panama. Special reference was to be given the marine environment. The committee assumed that a sea-level canal would be dug conventionally and recommended a research program to be carried out before, during, and after construction. The committee also recommended possible ways of minimizing potential damage to the environment as a result of construction.

Perhaps the brightest side of the picture is the growing awareness on the part of the authorities in both the United States and Panama that environmental considerations must be made part of any plan for a new canal.

The economic aspects do not yet seem to be quite clear. For example, it may be more practical and cheaper to move bulk cargoes across the isthmus by pipeline and conveyor belt than to pay tolls for a super-tanker. Militarily, the plea has been made that our largest aircraft carriers cannot fit through the existing canal; countering this argument is the accumulating evidence of the vulnerability of ships this size and the possibility of their early obsolescence.

Finally, there are the political considerations, which still seem to be the most difficult of all, both for the future of the existing canal, as well as for plans for a new one. Achieving a successful political agreement would have beneficial consequences that would reach far beyond Panama and would affect the United States relations with almost every Latin American nation.

OBSERVATIONS ON THE ECOLOGY OF THE CARIBBEAN AND PACIFIC COASTS OF PANAMA

BY PETER W. GLYNN
Smithsonian Tropical Research Institute
Balboa, Canal Zone

Compared with studies of the hydrography and plankton of the oceanic province and of the waters over continental shelves, relatively little effort has been directed to the near-shore and littoral environments of Panama. The biological oceanography of the Gulf of Panama and the Panama Bight is summarized in Smayda (1966) and Forsbergh (1969); Blackburn (1966) provides a more general review of our knowledge for the entire eastern Pacific basin. Hubbs and Roden (1964) and Collier (1964) also give useful summaries which serve to illustrate the contrasting nature of the marine environments of the eastern Pacific and Caribbean regions of Central America.

Information on inshore areas was obtained by the early exploratory expeditions, *e.g.,* the ALBATROSS, the S. Y. ST. GEORGE, by Galts off (1950), and more recently by the Allan Hancock Foundation, the University of Panama, the Puerto Rico Nuclear Center, the University of Miami, Stanford University's TE VEGA Cruise 18, and the eastern Pacific Expedition of the R/V ALPHA HELIX, Scripps Institution of Oceanography. Most of our knowledge of the littoral marine communities of Panama is based on the results of these efforts and on studies recently initiated by the Smithsonian Tropical Research Institute. Despite these contributions, it is clear that Panama, like most other regions in the low latitudes, is in need of a more thorough biological inventory and greater emphasis on ecologically oriented studies designed to evaluate seasonal variations and longer term annual trends. Information of this nature is needed in order to develop a rational approach toward evaluating the consequences of the possible commingling of the biotas of Central America.

In this paper I hope to provide a brief overview of (a) some of the major differences in the physical environments on either side of the Isthmus of Panama and (b) some of the evident differences which exist in the biotic communities and how work in progress is modifying our understanding of these. It will not always be obvious to what extent certain physical factors are important to marine life—these are mentioned mainly to identify some of the parameters thought likely to have an important influence. The coastal areas known best to me will receive greatest attention. These include, on the Pacific side, the Gulf of Panama and southwestern Panama (the mainland and island groups west of the Azuero Peninsula) and, on Atlantic shores, the coastline, islands, and coral reefs from the Chagres River mouth to Narganá (Rio Diablo Village), San Blas.

THE LITTORAL ENVIRONMENTS: SOME CONTRASTING PHYSICAL CHARACTERISTICS

Both sides of the Isthmus of Panama are subject to pronounced seasonal changes in climate which have their origin in the relative position of the ITCZ (Intertropical Convergence Zone). Although quite variable in timing and duration from year to year, the rainy season often begins in May and increases in intensity through October or November. The dry season, a result of the southward migration of the ITCZ, is characterized by winds of high velocity (the Trade Winds) which often persist from January through April. While the annual climatic regimes are similar, Caribbean shores are buffeted by strong winds, receive greater rainfall and are subject to greater seasonal variations in cloud cover (Fig. 1).

One of the most obvious hydrographic effects evident during the dry season is the initiation of upwelling in the Gulf of Panama, a result of the offshore displacement of surface water by northerly winds. At such times the sea surface temperature may vary from 27°C to as low as 15°C in a 24-hour period in certain parts of the Gulf (Fig. 2). This upwelling brings about

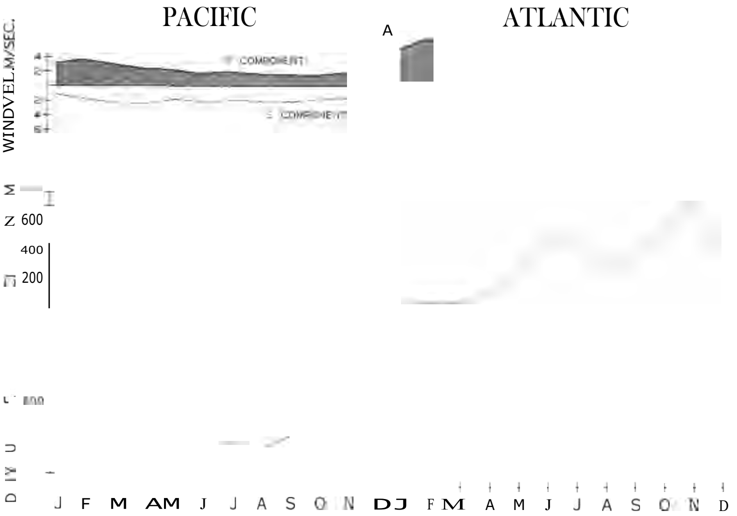

FIG. 1. Seasonal variations in wind velocity (A), precipitation (B) and mean daily sunshine (C) at the Pacific (Balboa) and Atlantic (Cristóbal) entrances of the Panama Canal, 1967 (Panama Canal Co., 1967). Wind data represent mean velocities of winds with northerly and southerly components.

an enrichment of nutrients at the surface which leads to increased phytoplankton production. These changes are visibly evident at higher trophic levels with an influx of anchovies, numerous schools of predatory carangids and scombrids, and large flocks of sea birds, such as pelicans and cormorants.

In contrast, the water column over the Atlantic shelf remains stratified throughout the dry season, though there is evidence that the high seas buffeting the coast have a direct influence on some shore species. Motile animals inhabiting the shallow reef zones, such as gastropods, amphineurans, and echinoids, often become dislodged during the sudden onset of high seas. Further, exceptionally strong surf can uproot gorgonians and topple large branching corals. Turbidity and suspended sediment load also increase with the high seas generated by strong onshore winds.

Dry season vertical temperature profiles over the shelf in the Gulf of Panama often show a well-developed thermocline

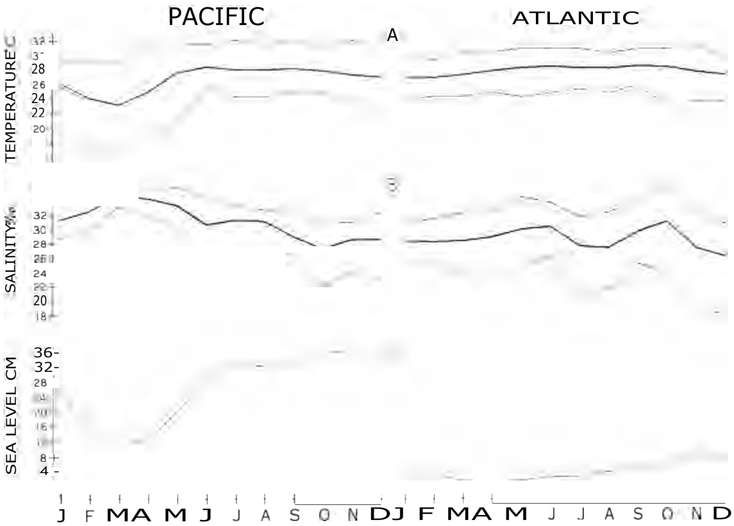

FIG. 2. Seasonal variations in sea surface temperature (A), salinity (B) and sea level (C) at the Pacific and Atlantic entrances of the Panama Canal. Temperature records from Balboa (Pacific), 1907-1967 and Cristóbal (Atlantic), 1908-1967 (Panama Canal Co., 1967). Salinity records from Naos Island (Pacific), 1965-1967, courtesy United States Coast & Geodetic Survey, and Cristóbal, 1949-1954 (United States Coast & Geodetic Survey, 1960). Monthly mean and extreme values are indicated by heavy and light traces, respectively. Mean sea level above precise level datum, records from Balboa and Cristóbal, 1935-1953 (Panama Canal Co., 1967).

present at from 2 to 5 m depth (Lowman, et al., 1970; Anderson, et al., 1969). The mixed layer depth is 5 m or less in the Panama Bight during upwelling (Forsbergh, 1969). No discontinuity layer has been found off Cristóbal at shallow depth (to 12 m) during the dry season. Although a slight discontinuity layer near 25 m was detected on the Caribbean shelf of eastern Panama during the dry season, the temperature remained above 25°C at 50 m (Lowman, et al., 1970). The distribution of sea surface temperatures indicates that the inshore waters of Panama, west of the Azuero Peninsula (ca. 81°W and beyond), are not subject to the low thermal conditions which prevail in the Panama Bight (Galtsoff, 1950; Renner, 1963; Hubbs and Roden, 1964; and unpublished data). This

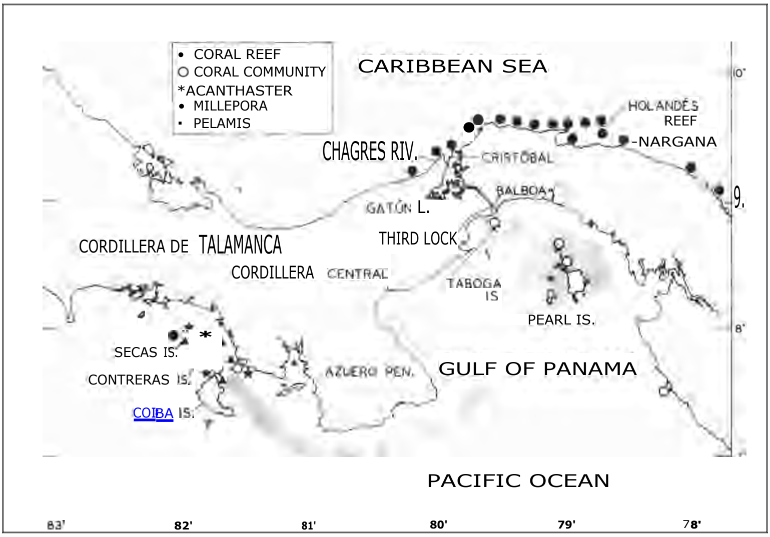

FIG. 3. Preliminary distributional data on hermatypic corals (accretionary coral reefs and coral communities), *Acanthaster ellisii*, *Millepora* spp., and *Pelamis platurus* along the Caribbean and Pacific coasts of Panama. Information on *Pelamis* was provided by Ira Rubinoff and the distribution of coral reefs east of Narganá by Robert H. Stewart.

southwestern sector of Panama is in the lee of high mountain ranges, the Cordillera Central and Cordillera de Talamanca (Fig. 3).

The influence of the large quantity of river runoff is reflected in the surface salinity records. Minimum values approach 18‰ to 22‰ in the wet season near the Atlantic and Pacific canal entrances, respectively. Nearer the canal locks the salinity declines abruptly in all seasons due to the freshwater outflow of Gatún Lake. Unfortunately, few salinity data are available over the Caribbean shelf. Abundant reef corals and other stenohaline marine groups present along this coast would indicate that high salinity conditions generally prevail near shore. Coral communities occur at some nearshore localities in the Gulf of Panama, e. g., Taboga and Taboguilla Islands and the Pearl Islands, indicating a fairly abrupt gradient of normalization of this parameter along Pacific shores. However, the permanent salinity front extending along the Colombian coast (Forsbergh, 1969) probably has a marked effect on the biota in this area.

The tides in the Gulf of Panama are semi-diurnal, of large amplitude (maximum diurnal range ca. 6 m) and highly predictable. The Caribbean tides of Panama are both semi-diurnal and diurnal (mixed), of slight amplitude (< 0.5 m) and much less predictable. The latter are greatly influenced by local meteorologic conditions, e. g., onshore winds during the dry season can produce abnormally high water levels. Another important feature of the tidal regime in many Caribbean areas is the abrupt seasonal shift in the timing of low water, often accompanied by a change to a diurnal cycle. This results in sudden and prolonged periods of exposure during mid-day hours, which can lead to heavy mortalities of the intertidal biota in Puerto Rico, as well as in Panama (Glynn, 1968a). The sea level is significantly lower on the Pacific side during the dry season, but only slightly so on the north coast (Fig. 2).

Drift lines and slicks are commonly present in the eastern Pacific basin, presumably formed by strong convergent currents. Generally, these occur offshore, but occasionally do move into the littoral zone.

CONTRASTING PROPERTIES OF TRANSISTHMIAN LITTORAL COMMUNITIES

Corals, Coral Reefs and Associated Biota

Presently, 20 hermatypic scleractinian corals are known to occur in the Recent fauna of the American Pacific coast (Durham, 1962). Fourteen of these have been found at single collecting localities in southwestern Panama. In contrast, 49 hermatypic corals are now known from the Caribbean reefs of Panama (as of July, 1971; Glynn, in press). While it is possible that one or two species are common to both regions, all available evidence indicates distinctive differences at the generic level, with the eastern Pacific fauna showing a close relationship to the Indo-Pacific region (Durham and Barnard, 1952; Durham and Allison, 1960).

Crossland (1927) was impressed with the development of coral reefs on the Caribbean shores of Panama and their apparent absence in the eastern Pacific basin. Our experience in the Gulf of Panama essentially confirms the broad differences in reef distributions noted by Crossland. However, outside the Gulf, especially along the southwestern coast of Panama, we have found several accretionary coral reefs and significant sedimentary deposits of bioclastic reef materials. Thus far, the best developed fringing and patch reefs have been found at the Contreras and Secas island groups (Fig. 3). The majority of these, with a minimum framework height of 3 m, are formed predominantly of Pocillopora spp., and appear to be undergoing vigorous accretion in protected coves, as well as on the seaward sides of these islands. Generally, the reefs are subtidal; the shallow-most sections are exposed only at extreme low water. Several other hermatypic corals, e. g., Pavona spp. and Porites spp., also contribute substantially to the construction of the reefs, especially at somewhat greater depths. In the areas investigated, which are largely characterized by abundant shelf sediments, coral reefs occur no deeper than 10 m. Firm substrata at deeper levels have not yet been adequately explored, so that it is now difficult to decide whether this firmness or other factors (e. g., light penetration, sedimentation, thermal conditions) are instrumental in confining coral growth to shallow depths.

The upper sections of Caribbean reefs are often exposed at low water and emergent fossil structures are rather common in certain areas. The Holandés Reef in San Blas contains an emergent algal ridge along the seaward front, formed by actively accreting crustose coralline algae and vermetid gastropods. This type of structure is now being described for the first time in the Caribbean Sea (Glynn, in press). Calcareous beach sands and shelf sediments derived from coral reef environments are considerably more widespread on the Caribbean side of Panama. Conditions also favor abundant coral growth to relatively great depths—in San Blas dense populations of Agaricia extend to 45 m depth.

At least three species of the hydrocoral Millepora are important hermatypic elements of coral reefs in the Caribbean Sea; until recently, this genus was presumed to be absent from the eastern Pacific. The eastern-most range extension of

Millepora in the Pacific Ocean was considered to be in the Tuamotu Archipelago. Within the last year Millepora intricata Milne Edwards and M. platyphylla Hemprich and Ehrenberg, both widely distributed species in the Indian Ocean and western Pacific (Boschma, 1948), and a new, possibly endemic, robust species of Millepora, have been found associated with reef corals in the Contreras-Secas and Coiba sector of southwestern Panama (Fig. 3).

The Crown-of-Thorns starfish Acanthaster, long known from the eastern Pacific region (Madsen, 1955; Caso, 1962), has been found recently to be an important predator of corals in southwestern Panama. Population densities of 2.2 to 2.5 individuals/100m were observed in certain localities (Smithsonian Institution, 1970). Preliminary comparative study of the saponins (Stallard, 1970) indicates a possible specific difference between the eastern and western Pacific forms [A. *ellisii* (Gray) and A. planci (L.)], but, morphologically, the two are not readily distinguishable. The feeding habits of A. ellisii appear to differ from those of A. planci in the western Pacific (Chesher, 1969). For example, eastern Pacific populations commonly prey upon Millepora in Panama (even though scleractinian corals are available) and forage actively during the day and night in Panama, as well as in the Gulf of California (Dana and Wolfson, 1970; unpublished data). The Panama populations may also differ in their feeding behavior from those in the Gulf of California. Small encrusting Porites colonies are eaten preferentially by Acanthaster in the Gulf (Dana and Wolfson, 1970; Eric G. Barham, personal communication); in Panama Acanthaster concentrates more on ramose Pocillopora and large massive Pavona and Porites colonies. Hymenocera, the reputed caridean predator of Acanthaster (Wickler and Seibt, 1970), was observed on the asteroid on one occasion. No signs of feeding were evident; indeed, the shrimp moved among the aboral spines and eventually under Acanthaster upon repeated molestation. Although Acanthaster is presently consuming significant quantities of coral in southwestern Panama, there is no clear evidence that this destruction has resulted from local, man-induced disturbances. Present collecting records suggest that Acanthaster may be confined to areas outside of the Gulf of Panama.[1]

Several Indo-Pacific fishes, including new records for the eastern Pacific region, have been collected recently from southwestern Panama (Rosenblatt, et al., in press). All of these fishes, members of the families Holocentridae, Zanclidae, Acanthuridae, and Muraenidae, are generally associated with coral reefs. Thus, it seems reasonable to assume that the occurrence of these groups in southwestern Panama is due, in large part, to the abundant coral growth present in this area.

Observations on coral predation by fishes on the Atlantic and Pacific sides of Panama indicate markedly different degrees of utilization of this food resource. All of the common Pacific hydrozoan and scleractinian hermatypes are heavily predated by fishes. Scarids rasp massive Porites and Pavona, balistids break off large sections of these corals in search of Lithophaga, and tetraodontids bite off the terminal branches of Pocillopora. Several species of Atlantic corals are also attacked by fishes (e. g., scarids rasp Siderastraea), but not nearly to the extent observed on Pacific shores.

Similarly, experimental exposure of the under-rock fauna in comparable situations in the eastern Pacific and Caribbean demonstrates that the encrusting fauna, particularly sponges, are under a more stringent grazing pressure by fishes in the eastern tropical Pacific (Charles Birkeland, personal communication). The conclusions of Bakus (1969) and Randall and Hartman (1968), who argued, respectively, for and against fish predation as an important factor in limiting sponge growth, rather than conflicting with each other, could be intepreted as corroborating this difference. The three species of *Holacanthus* in the Caribbean appear to be sponge specialists (Randall and Hartman, 1968) while the single eastern Pacific species, H. passer Valenciennes, appears quite generalized in diet. That the food specialists are not able to influence the distribution of their prey implies that these predators are limited by factors other than the abundance of food. Because fishes are so quick to exploit the general encrusting biota of overturned rocks in the eastern Pacific, and appear so much

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Editor's note: See footnote 3 of R. H. Chesher's paper, this symposium, p. 156.

less selective in their diets, this could imply that food is generally less available. These observations may help explain some striking differences in the predominance of sponges in the two communities and indicate that the functional role of similar species in different communities cannot always be inferred from taxonomic affinities.

An evident difference in the character of the benthic flora adjacent to coral reefs is the general absence of spermatophytes on the Pacific side and their widespread occurrence in the Caribbean. While Diplanthera and Halophila have been observed to form dense populations in certain areas, as at Punta Naranja and Jicarón (Dawson and Beaudette, 1959), extensive surveys of coral communities in the Gulf of Panama and around coral reefs in southwestern Panama have failed to reveal any significant sea grass beds. Algal nodules often dominate bottom areas near coral reefs and at greater depths (10 m).

Several species of marine spermatophytes are present in the littoral and sublittoral zones of the Caribbean. In Panama, the Hydrocharitales are represented by Thalassia testudinum Konig, which forms continuous large patches from the lower intertidal zone to depths of about 10 m, and by Halophila *baillonis* Ascherson, present at greater depths or in shaded shallow situations, as under a mangrove canopy. The Naiadales are represented by Cymodocea *manatorum* Ascherson, often found with Thalassia, by Diplanthera wrightii (Ascherson) Ascherson, common in the intertidal zone, and by Ruppia maritima Linnaeus, present in coastal lagoons of variable hydrographic character. While nullipore-carpeted bottoms have been reported in the Caribbean (Zaneveld, 1958), these have not yet been observed in Panama.

Rocky Intertidal Communities

Differences in the patterns of zonation and the character of the respective species groups at different levels are evident on the stable intertidal surfaces of opposite coasts. Along Pacific shores, the high and mid-tidal levels are often densely populated with sessile cirripeds and oysters, which provide a variety of microhabitats for a rich microbiota (Glynn, 1968b). Sessile shelled species are absent or at low density at comparable levels of exposure on Atlantic shores. At lower levels of the intertidal zone, a variety of macroscopic fleshy algae are present in the Caribbean; in the Pacific the lower tidal levels are populated with minute filamentous algae and, frequently, dense growths of bryozoans and hydroids.

Current study of the annual patterns of reproduction and recruitment in selected invertebrate herbivore species indicates a strong correlation in the periodicity of these events and the timing and intensity of upwelling. For example, Chiton stokesii Broderip and Echinometra vanbrunti (Agassiz) show a gonadal buildup during the dry season, breed when the water warms, and undergo heaviest recruitment in August and September, before the succeeding upwelling season.

Numerous other biological events are correlated with upwelling, e. g., mass fish kills, migrations of Panulirus gracilis Streets into the intertidal zone, and red waterblooms caused by a variety of plankters, including holotrichous ciliates (*Mesodinium*) and dinoflagellates such as *Exuviaella compressa* Ostenfeld, *Prorocentrum* micans Ehrenberg and Peridinium *pellucidum* (Bergh) Schütt. The inshore movement of drift lines, under the influence of local wind conditions and surface currents, allows certain neritic species, such as the sea snake Pelamis platurus (Linnaeus), to approach the coastline.

Sandy Beach *Communities*

Conditions suitable for the establishment of an abundant sand beach fauna appear to be more restricted on Caribbean as compared with Pacific shores. This may be related to the prevalence of coarse bioclastic sediments and the transformation of Atlantic beaches to typical high energy environments in the dry season. Where fine sediments are present, as the calcareous deposits along protected coastlines or terrigenous deposits near river mouths, an abundant fauna can be found.

A recent comparative study of the macroscopic infauna of isthmian sand beach environments demonstrated significant differences in certain community characteristics (Dexter, in press). A Pacific beach contained approximately three times as many species (41), six times the density of individuals ($1434/m^2$) and nine times the biomass ($9.13\ gm/m^2$) of an

Atlantic beach community. On the other hand, the Atlantic beach showed a more equitable distribution of species. The faunas show strong taxonomic affinities—several congeneric species are represented and possibly two of conspecific rank are found on either side of the Isthmus. Genera confined to either the Atlantic or Pacific sides represented only 10% and 7% of these faunas, respectively.

Subsequent sampling at the Atlantic study site in the dry season indicates significantly lower population densities than observed in the wet season (Birkeland, *et al.,* 1970). As noted earlier, wave action and sediment transport are much greater at such times.

Mangrove Shores

Where the tidal range is great in the Gulf of Panama, mangroves bordering the shoreline are exposed for several hours at low water. As a result, the occurrence of abundant epibenthic populations associated with the prop roots of *Rhizophora* is very limited. Large areas of the prop roots of red mangroves in the Caribbean, however, are often submerged continuously; these frequently contain lush growths of algae, sponges, cirripeds, oysters, bryozoans, tunicates, and a variety of smaller associated animal species.

The unique environmental setting provided by the Third Lock Lagoon (near the Miraflores Locks on the Pacific side) is mentioned here because it appears to have offered a refuge for the colonization of certain Atlantic fishes which have presumably migrated through the Canal. The hydrographic character of this lagoon is favorable for the growth of the mangrove oyster, *Ostrea palmula* Carpenter, which provides habitat niches generally unavailable in neighboring Pacific waters (Bozniak, *et al.,* 1969). Evidence of a distributional nature indicates that an Atlantic gobiid (Rubinoff and Rubinoff, 1968) and a blenniid (Dawson, 1970) have successfully colonized the Third Lock Lagoon since its completion approximately 28 years ago. A second Atlantic blenniid was discovered more recently (John E. McCosker, personal communication), offering further substantiation of the notion that this special environment is providing the requisite ecologic conditions for the establishment of certain Atlantic species on Pacific shores.

Fouling Communities

Fouling species would be expected to assume a particularly effective role in transisthmian migrations; colonization by this means has been considered important by many workers. Data on the distributions of two groups in Panama, namely bryozoans and isopods, indicate that successful colonizations may not be so extensive as commonly assumed. Powell (1971) has shown that three of the ten bryozoans belonging to the fouling community near Balboa are conspecific with Atlantic populations. Among the Isopoda and Tanaidacea inhabiting buoys, only one species from a sample of 29—the pantropical species, Sphaeroma walkeri Stebbing—was found in both the Atlantic and Pacific Oceans (Miller, 1968). A continuing survey of the sphaeromatid faunas in the waters of the Panama Canal and adjacent coastal areas has, thus far, revealed only a single species, out of 12 associated with fouling communities, with an amphi-American distribution. Of these species, four were described as recently as 1968 and six are still unnamed; only two were known earlier.

While much discussion has centered around the extent of migrations of fouling organisms through the Canal (e. g., Menzies, 1968), no attempt has yet been made to survey the species populations inhabiting ship bottoms before and after transit. Information on the tolerances of the various fouling groups would provide a good basis for further studies to determine reproductive success and the ability to compete with established species. Perhaps this last aspect is the reason why the movement of sessile and sedentary organisms on the hulls of ships and barges has not figured as prominently as expected in the migration of species through the Suez Canal (Thorson, 1968).

CONCLUDING REMARKS

Several important considerations emerge from this brief treatment. Obvious environmental differences exist in the inshore littoral habitats across the Isthmus of Panama. The thermal climate is more variable along eastern Pacific shores, especially in regions of upwelling, such as the Gulf of Panama. The irregular nature of Caribbean tides and ever-changing state of the sea result in rigorous physical perturbations, not generally felt in the Gulf of Panama. Clearly, attempts to compare the severity of environmental conditions in these two regions must take into account all relevant factors.

The relatively stable marine climate in southwestern Panama is characterized by the presence of rich stenothermal biotic communities. Structural coral reefs are present in this area, as well as several recently discovered animal species that represent integral components of this community (e. g., hermatypic elements and important coral predators). Many of these species, known previously from the Indo-Pacific region, have been found for the first time along eastern Pacific shores. It would appear that a greater number of central Pacific species have successfully crossed the eastern Pacific barrier than formerly supposed (Briggs, 1961, 1967; Rosenblatt, 1963). It is possible that long distance larval transport may not be so important for some groups as the availability of preferable habitats necessary for successful colonization. Thus, when considering questions of how amphi-American faunas may interact if allowed to fuse, it will be necessary to frame these problems in the context of an Indo-Pacific component, as well. Possibly the situation would have been even more serious if the present canal, and the preferred sites for construction of a sea-level canal, had not been located across such dissimilar marine environments. However, it must be cautioned that there still exists a very broad potential spectrum of possible modes of interaction.

The few examples considered in this paper clearly indicate that our knowledge of the biota and general ecology of the Panamic region is very limited. This is most unfortunate in the light of present attempts to predict, in a scientifically rigorous manner, some of the potential biological problems posed by a sea-level canal. An additional critical area of study is that of determining the interactions of alien predator-prey, parasite-host and potential competitive species groups. An example of the importance of this approach was recently demonstrated by Rubinoff and Kropach (1970) who showed that closely related amphi-American fish predators elicit very different feeding reactions to *Pelamis.*

ACKNOWLEDGMENTS

I am grateful to Charles Birkeland and Ira Rubinoff, Smithsonian Tropical Research Institute, H. Boschma, Rijksmuseum van Natuurlijke Historie, Leiden, Maureen E. Downey and David L. Pawson, National Museum of Natural History, Smithsonian Institution, J. Wyatt Durham, University of California, Berkeley, John E. McCosker, Scripps Institution of Oceanography, and Robert H. Stewart, Panama Canal Company, and others, who have provided much of the information upon which this paper was based. My own observations have been made possible through support by the Smithsonian Research Foundation.

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NOTE ADDED IN PROOF

A recent monograph on sea grasses by den Hartog (1970) has resulted in the following alterations of nomenclature: Syringodium filiforme Kütz. [= Cymodocea manatorum Ascherson] and Halodule wrightii Ascherson [= Diplanthera wrightii (Ascherson) Ascherson]; the junior synonyms were used in this paper. Reference: Hartog, C. den, 1970. The Sea-Grasses of the World. North Holland Publ. Co., Amsterdam, 275 pp.

PHYSICAL CHARACTERISTICS OF THE PROPOSED SEA-LEVEL ISTHMIAN CANAL

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It is the purpose of this paper to outline the physical characteristics of the sea-level canal recommended by the Canal Study Commission and to present qualitative estimates of the amount of water that might be transferred between oceans.

The five routes investigated are shown in Figure 1. Routes 8, 17, and 25 were considered only for nuclear excavation and have had to be eliminated from further consideration, for the forseeable future, inasmuch as the feasibility of nuclear excavation has not been established as yet.

Routes 10 and 14 are about 40 miles in length, not counting the off-shore approach channels. These two routes for conventional excavation are the only suitable ones for sea-level canal construction, unless there are unforeseen technical and political breakthroughs in the further development of nuclear excavation technology. The Commission found Route 10 the better choice, primarily because it would not involve destruction of the existing canal, as would construction on Route 14.

Figure 2 shows the Pacific tidal pattern in the vicinity of Routes 10 and 14 and it should be noted that the maximum range is about 20 feet. Figure 3 shows the tides on the Caribbean side for the same 7 days; the maximum range is seen to be only two feet.

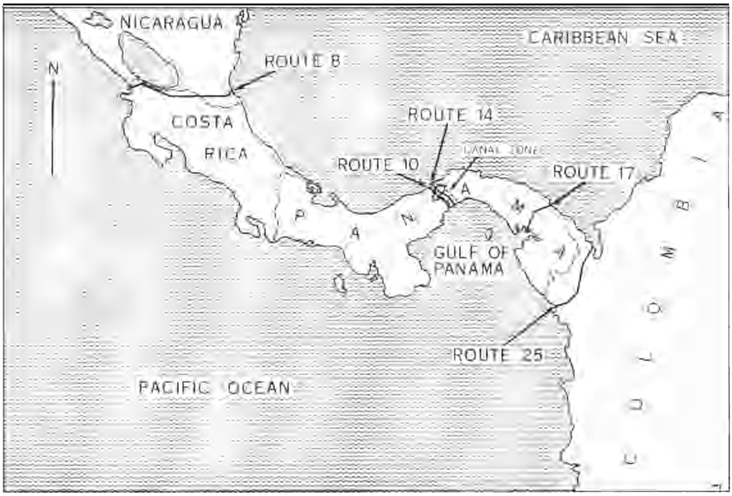

FIG. 1. The Isthmian region, showing sea-level canal routes studied. Routes 8, 17, and 25 were considered to be possible only for nuclear excavation and have now been discarded. Routes 10 and 14 were considered possible by conventional excavation methods.

The mean sea levels on the two sides of the isthmus vary only slightly. There are some changes during the year, but the Pacific mean sea level averages about a foot higher than that of the Atlantic in the vicinity of the Canal Zone. Figure 4 shows the percentage of time that various differences in ele-

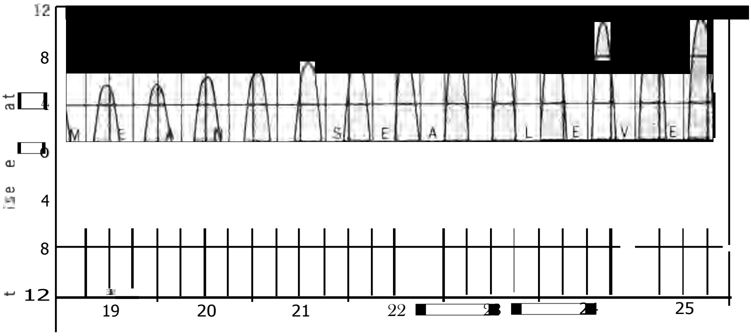

FIG. 2. Tidal pattern at Balboa (Pacific) through a seven-day period (19-25 September 1957).

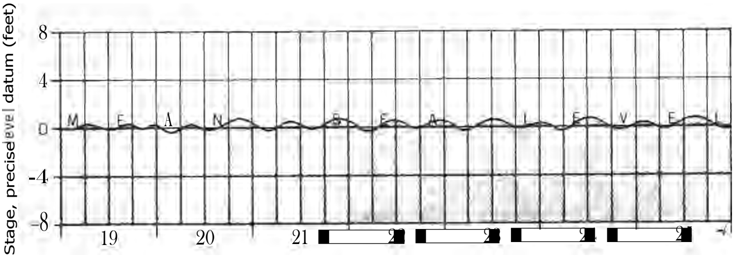

FIG. 3. Tidal pattern at Cristóbal (Atlantic) through the same seven-day period as Figure 2.

vations exist between the oceans as the tides go through two full cycles each lunar day (about 25 hours). Note that the differences in elevation range from zero to five feet 90 percent of the time and from five feet to the ten feet maximum only 10 percent of the time.

Model tests and computations indicate that maximum currents can be expected at the Atlantic end of a sea-level canal where the cross-section of the navigational channel at low water would be minimum. Table 1 shows the calculated maximum currents for a channel 600 feet wide and 60 feet deep. Bear in mind that the maximum currents would be of short duration. Figure 5 shows the percentage of time that various current speeds from zero to the maximum would be equalled or exceeded; it should be borne in mind that the currents would reverse direction every six hours. The average speed and duration of water movement toward the Atlantic would be slightly greater than those toward the Pacific because of the difference between mean sea-levels mentioned above. On the rising Pacific tide the entire contents of the canal channel

Table 1. Calculated maximum tidal currents at the Atlantic end of a sea-level canal (in knots) for three Pacific tidal ranges.

	Direction of flow	
Range of Pacific tide	To Pacific	To Atlantic
Extreme (range, 21.1 feet)	3.6	5.1
Intermediate (range, 16.2 feet)	3.3	4.3
Mean (range, 12.7 feet)	2.5	3.7

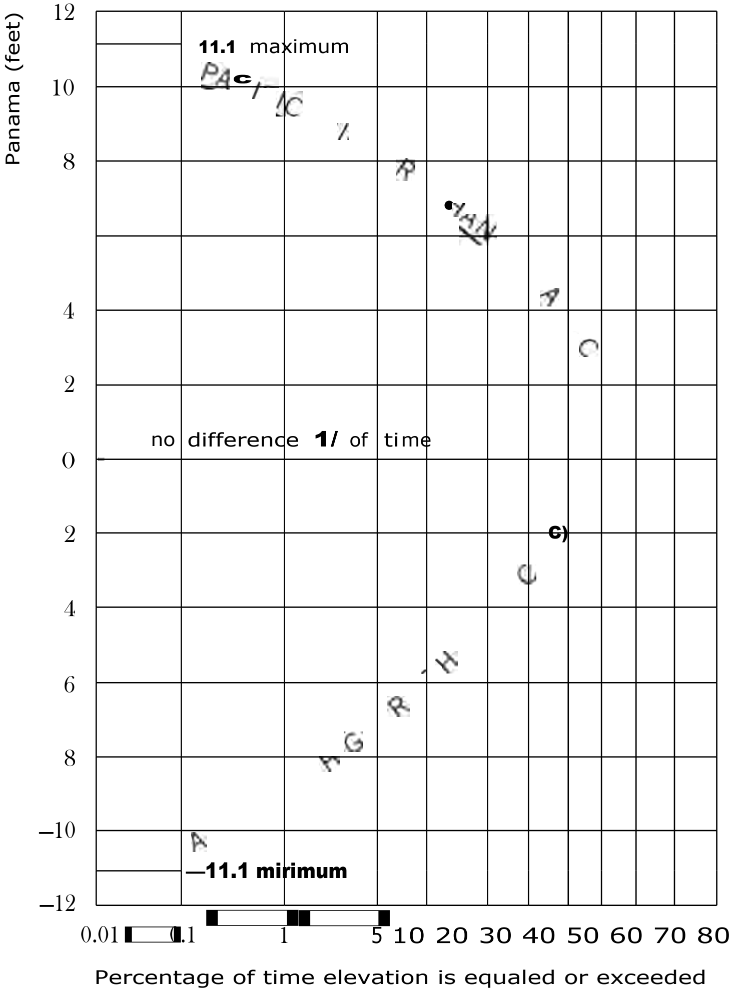

FIG. 4. Differences in water-surface elevation (in feet) between the Atlantic and Pacific Oceans at Panama, based on a four-year record (1957-1961). Curves indicate the percentage of time that each body of water is as high or higher than the other. Abscissa is based on a probability scale.

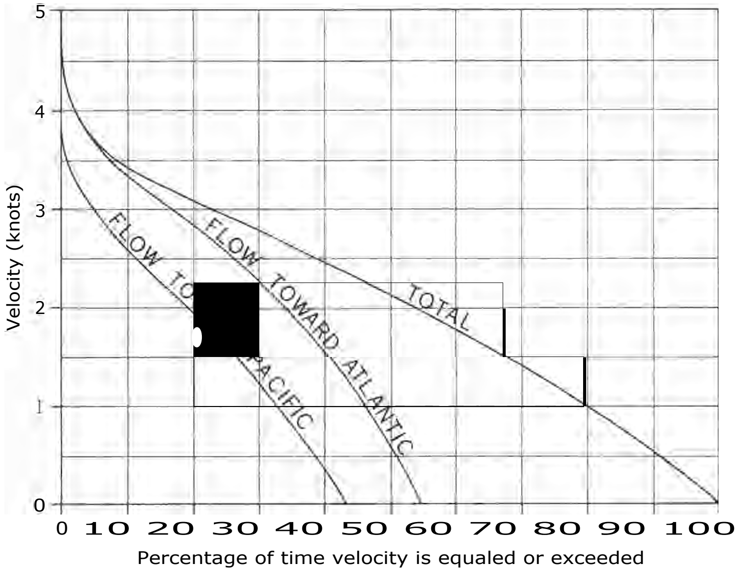

FIG. 5. Calculated tidal velocity duration curves of a sea-level canal, 2.5 miles from the Atlantic end, based on a channel 600 feet wide, 60 feet deep, 35 miles long, with 1:1 slopes, and a roughness coefficient of 0.025.

would move northward for a little more than six hours, at an average speed of about 2 knots. The movement would then reverse, to the south, with the falling tide, for somewhat less than six hours, at a slightly lower average speed. Thus, the northward movement for a peak Pacific tide would be about 14 miles during the rising tide and the return movement, on the falling tide, would be a little less. The average daily movements throughout the year would be considerably less. The net northward movement would result in the discharge into the Caribbean of from 39,000 to 50,000 acre-feet of water per tide cycle from the mean to extreme ranges of Pacific tides. This means a maximum transport of about 100,000 acre-feet of Pacific water to the Caribbean through a canal 600 feet wide and 60 feet deep in any one day, with the average about 78 percent of that. A channel of larger cross-section would transport proportionately more water.

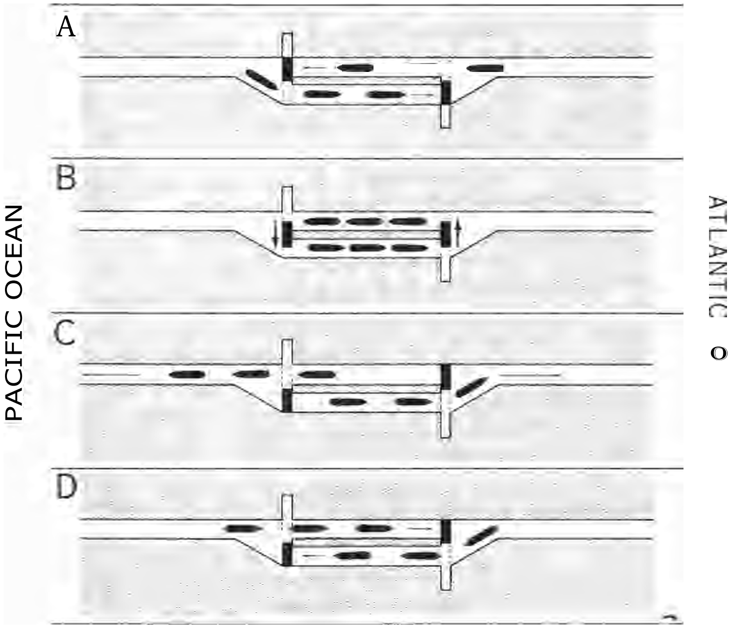

FIG. 6. Sequence of operation of tidal check structures and ship movement. A. Pacific at high tide; high differential head; gates are closed; ships move into bypass. B. Pacific at mean tide, low differential head; gates are shifted to other lane; ships remain in bypass. C. Pacific at low tide, high differential head; gates are closed, ships leave bypass. D. Pacific at low tide, high differential head; gates are closed; new ships move into bypass.

The average water temperatures vary about 2.2° F between the Bay of Panama and the Caribbean at Cristóbal. The extreme variation is about 7° F. The back and forth movements through the canal would greatly reduce temperature differences, and the Pacific water would enter the Caribbean at essentially the same temperature as the water already there.

The net northward movement of water in the canal channel each tidal cycle would be such that the water mass would be comprised almost entirely of Pacific water at a high Pacific tide and Caribbean water would be allowed to move southward only about one-third the canal's length during a low

Pacific tide. However, the oscillating tidal currents and accompanying turbulence could diffuse Caribbean water throughout the length of the channel and some small amounts could reach the Pacific with the southward currents.

Thus far, I have spoken only of an unobstructed sea-level canal channel. The tidal currents in such a canal would present some hazards to navigation, particularly to large ships with poor handling characteristics. The Commission has recommended construction of tidal regulating structures to reduce or eliminate tidal currents. Figure 6 shows the configuration of a conventionally excavated canal with center passing lanes and simple tidal gates. Convoys would enter simultaneously from each end while the gates are closed, and would be timed to reach the gates at zero tide (Fig. 6A). The gates would then be shifted to the opposite channel (Fig 6B), the convoys would continue on (Fig. 6C), and the sequence would be repeated (Fig. 6D). This arrangement would result in there being little or no transfer of water between the oceans when the gates are in use. Further, the slack water between the gates could lend itself to manipulation to make it a more effective faunal barrier. Its salinity could be greatly reduced by introduction of fresh water from stream flows in the area and from stored fresh water in Gatún Lake. Possibly, its temperature could be raised by waste heat from a nuclear power plant. In any event, the tidal gates would make possible a reasonably effective barrier to the transfer of marine life, if such is found necessary. There is a wide divergence of opinion in the scientific community as to the need for such a barrier, but almost everyone agrees that further studies are needed. The Commission has recommended that such studies be made if the decision is made to build a sea-level canal. From an operating point of view it would be desirable that the gates be used only in the seasons of peak tides and then only for the transits of convoys of very large ships. Most ships are expected to be able to navigate a sea-level canal safely without regulation of tidal currents.

A sea-level canal on Route 10 would result in very little change in fresh water flows into the Pacific or the Caribbean, e. g., the Trinidad River flow would enter the Caribbean a few miles further west of where it now flows out with the waters of the Chagres.

A sea-level canal would transport some sedimentary material. Fortunately, most of Routes 10 and 14 are in hard materials that would not scour or erode excessively. The oscillating movements of the tidal currents would tend to retain much of the sediment in the canal channel and the channel would require considerable maintenance dredging. Dredged spoil would be used for nearby land fill to the maximum extent as is the practice for the present canal, which must be dredged more or less continuously.

I hope this brief summary will give you an understanding of the physical effects on the ocean environment that might be caused by a conventionally constructed sea-level canal. The Commission did not ignore the potential ecological problems in its investigation, but was not able to carry out extensive investigations in this area. At the outset of its investigation the Commission had only three years and quite limited funds for the accomplishment of its studies. We were advised by the Smithsonian Institution and others that the question of whether a sea-level canal would pose any threat to marine life simply could not be answered in the time available. In fact, we were advised that it really could not be answered at all, because it is impossible to reproduce in the laboratory the conditions that would be created by a sea-level canal. When the Commission's study was extended to five years and its funds increased, it did attempt to obtain such answers as were possible in the time available. The Battelle Memorial Institute had already acquired a great amount of biological data, based on the isthmus and adjoining oceans, in the course of its radiological studies of the food chains on land and sea. The Commission extended Battelle's study to cover the potential exchange of marine life through a sea-level canal, to give us the Institute's best judgment as to any identifiable threat to marine life, with special attention to commercial and sport fishes. Battelle found no clear threat to such fishes and was generally sanguine about the total ecological threat, while acknowledging that available data are inadequate for a comprehensive evaluation. Dr.

Gilbert Voss of the University of Miami, who follows me, will report on this study.

The other part of our effort in this field was through the National Academy of Sciences (NAS). Should a decision be made tomorrow to build a sea-level canal, it would be 12 to 15 years before it could be opened. We asked the National Academy to assume that such a canal would be built and to advise us as to what studies should be undertaken before, during, and after its construction. The NAS recommendations for long term studies were made a part of the Commission's report. Dr. William A. Newman, who served on the NAS committee that developed the study recommendations, is scheduled to speak to you about them tonight.

In closing let me ask only that the threats of the sea-level canal be evaluated in proper perspective. I, as a layman, have been greatly concerned over the willingness of some scientists to make alarmist statements about the potential threats, without obtaining available facts. Many have speculated in writing about the flows between the oceans, with the firm, but erroneous, conviction that one is ten feet or more higher than the other in the Isthmian area. Some articles have been written in ignorance of the limitations on northward flows through an unrestricted sea-level channel and the impossibility of significant southward flows. Tidal gates, of course, could nearly eliminate all flows. Few writers on the subject appear to be aware of the rather extensive transfers of biota between the oceans through the present canal. Barnacles and other clinging creatures ride through on ships. Swimming and drifting biota that thrive in both fresh and salt water can readily make their way through the locks and eventually reach the opposite ocean. Salt water ballast is taken on in one ocean and discharged in the other by dozens of ships daily, transporting with it all the small forms of life that would be found in random samples of the upper 40 feet of both oceans. Thus, we are not faced with completely new exposures of all the biota of the two oceans to each other, but, instead, we face the possibility of a vastly larger transport of the forms that already pass through the canal and of the opening of a passage previously denied to the remainder.

EXCHANGE OF WATER THROUGH THE PROPOSED SEA-LEVEL CANAL AT PANAMA

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1. Introduction

The objective of the study was to determine the magnitudes and directions of tidal currents, for several proposed routes and canal cross-sections, of a sea-level canal across the Isthmus of Panama. The magnitudes and directions of the tidal currents determine the net exchange of water between the two oceans. In addition, the tidal currents are of interest in assessing potential navigational problems for ships transiting the canal. The tidal currents are influenced by the following factors:

i. The canal route, which determines the total length of the canal.
ii. The canal geometry, primarily the depth and cross-sectional area.
iii. The characteristics of the ocean tides at either end of the canal.
iv. The roughness of the boundaries of the canal cross-section.
v. The fresh water inflow into the canal.

During the course of investigations carried out intermittently between January 1967 and May 1970, tidal computations were made for a total of 88 cases representing variations in the parameters listed above. The detailed results are available (Harleman, 1967; 1968; 1969; and 1970). A brief summary of the mathematical model and results for a few typical cases are given below.

2. *Mathematical Model*

The mathematical model for the tidal calculations was developed by Harleman and Lee (1969) as part of a general study of techniques for tidal calculations in estuaries and sea-level canals. The two basic equations are the continuity equation and the momentum equation. A one-dimensional formulation was adopted in which tidal elevations, velocities, and discharges are functions of longitudinal position "x," measured along the axis of the canal, and time "t."

The continuity equation is given by

$$\frac{\partial Q}{\partial x} + b\frac{\partial \eta}{\partial t} - q = 0 \qquad (1)$$

where

Q = instantaneous tidal discharge, (ft^3/sec)
b = instantaneous water surface width, (ft)
= instantaneous water surface elevation above horizontal datum (P.L.D.), (ft)
q = lateral inflow of fresh water, (ft"/sec-ft).

The momentum equation is given by

$$\frac{\partial Q}{\partial t} + \frac{Q}{A}\left[\frac{(b+b_0)}{2}\frac{\partial \eta}{\partial t} - \frac{\partial Q}{\partial x}\right] + gA\frac{\partial \eta}{\partial x} + \frac{gQ|Q|}{AC^2R} = 0 \qquad (2)$$

for the trapezoidal cross-section shown in Figure 1, where

A = cross-sectional area — $\frac{(b + b_0)(d + \eta)}{2}$, (ft^2)

$h = d + \eta + z_0$

$C = \frac{1.49}{n} R^{1/6}$

n = canal roughness coefficient
R = hydraulic radius, cross-sectional area divided by wetted perimeter of the canal section

In Equations (1) and (2), the dependent variables or unknown quantities are "η," the tidal elevation and "Q," the tidal discharge which are functions of "x" and "t." All other quantities are functions of the geometry and roughness of the canal. The tidal velocity at any "x" and "t" may be obtained by dividing the tidal discharge by the instantaneous cross-sectional area.

The complete mathematical statement requires the specification of two boundary conditions and an initial condition for the solution of Equations (1) and (2). The boundary conditions are the known ocean tidal amplitudes and phase at both ends of the canal. The initial condition requires that the water surface elevations and discharges be known throughout the canal at one instant of time. These are not known, a priori, however the difficulty can be overcome by an iterative technique as discussed below.

Equations (1) and (2) are written in finite difference form using central differences and the calculations are performed on a digital computer by means of an explicit scheme. The choice of Δx and Δt for the finite difference calculations are governed by stability criteria and by computer storage capacity. A property of the partial differential equations of the type of Equations (1) and (2) is that the effect of assumed initial conditions on the solution diminishes rapidly. Thus, it may be assumed initially that at time $t = 0$, there is no tidal flow ($Q = 0$) and that a horizontal water surface exists throughout the canal ($\eta = 0$). A quasi-steady state solution is obtained (after about five tidal cycles) which is independent of the initial assumptions.

3. *Results* of Numerical Calculations

The following results are presented for one of the sea-level canals considered in the study. The length of the canal is 35 miles and the cross-section is as shown in Figure 1 with $b_o =$ 600 feet and $ss = 1$. The depth below the principal level datum (P.L.D.) is 60 feet at the Atlantic end and 70 feet at the Pacific end. Figure 2 shows a typical 14-period tidal record at the Atlantic and Pacific ends of the canal. The mean range of tide during this period is about 12.7 feet at the Pacific end

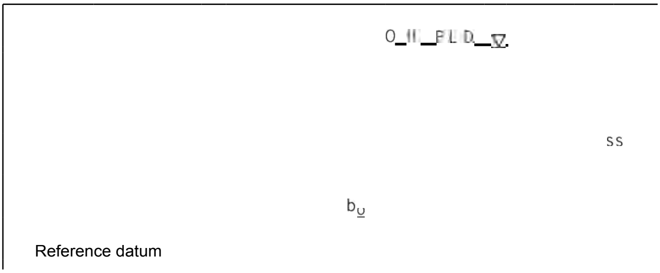

FIG. 1. Transverse cross-section of the sea-level canal.

and 1 foot at the Atlantic end. The calculations shown are for the mean tidal range and a value of $n = 0.025$ was used for the canal roughness coefficient.

The magnitudes and directions of the tidal currents along the canal at various instants of time during the tidal period are shown in Figure 3. Figure 4 shows the temporal variation of tidal current near both ends of the canal during one tidal period.

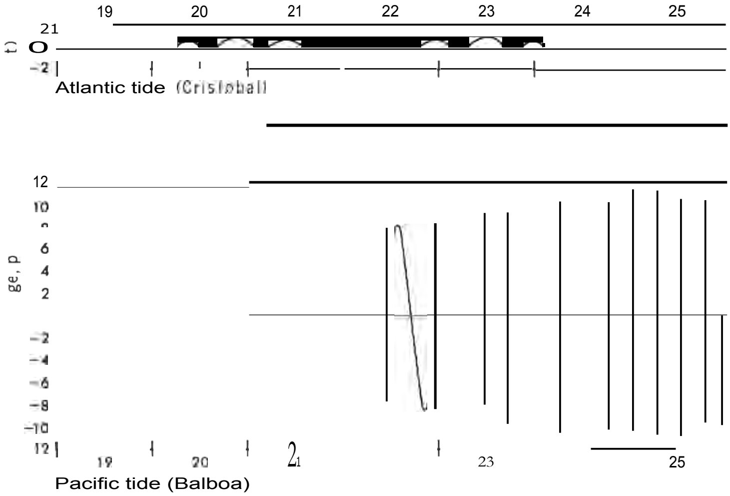

FIG. 2. Tidal records at Atlantic and Pacific ends of the canal for a one-week interval (19-25 September, 1957).

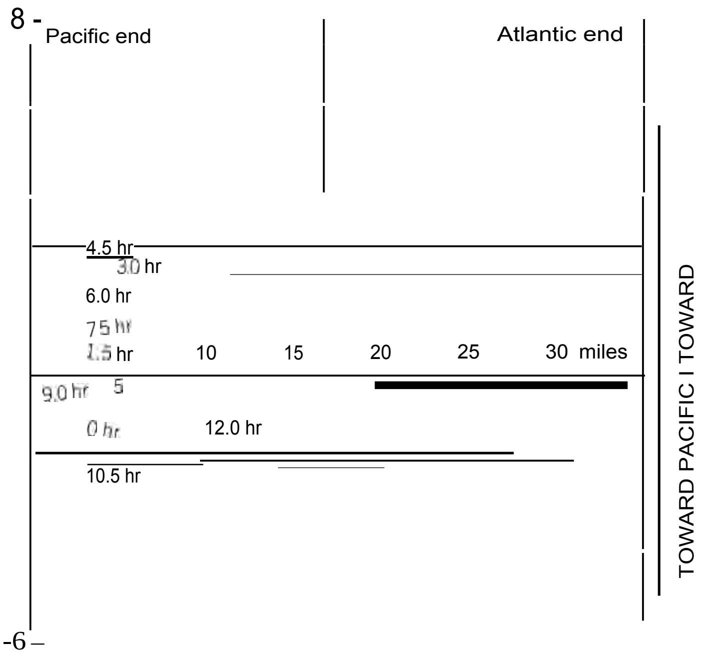

FIG. 3. Time and spatial variation of the tidal current along the sea-level canal.

4. *Exchange of Water Through the Canal*

For biological and other reasons, it may be important to determine the net transport of sea water through the canal. The computer program was modified to include the computation of the net water transport over one tidal cycle. For the canal conditions described above, the calculations indicate an average net flow of approximately 40,000 cubic feet per second from the Pacific to the Atlantic. Similar evaluations for other canal cross-sections show that the net water transport varies linearly with the cross-sectional area. For the case considered, the mean cross-sectional area is 45,000 ft^2. Therefore, the mean velocity of passage through the canal is about 0.9 ft/sec.

Under the above conditions, organisms entering the canal at the Pacific end would take approximately two and one-

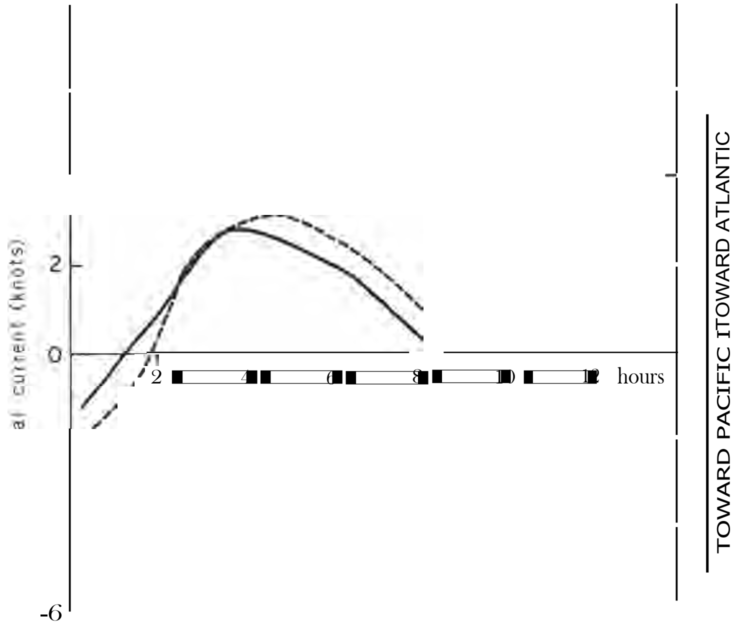

FIG. 4. Time variation of tidal current near the Atlantic and Pacific ends of the sea-level canal; solid line, velocity at 2.5 miles from Pacific end; dashed line, velocity at 2.5 miles from Atlantic end.

half days to transit the canal. These calculations are for a sea level canal without tidal gates or other obstructions. If such gates were used, they would materially reduce the net inter-ocean flow. In addition, no fresh water inflow to the canal has been considered since this quantity depends on the precise location of the canal route. For the present canal, fresh water inflows from four major rivers are of the same order of magnitude as the net flow of sea water calculated above.

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BIOLOGICAL RESULTS OF THE UNIVERSITY OF MIAMI DEEP-SEA EXPEDITIONS. 93. COMMENTS CONCERNING THE UNIVERSITY OF MIAMI'S MARINE BIOLOGICAL SURVEY RELATED TO THE PANAMANIAN SEA-LEVEL CANAL'

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In 1964, with my colleagues C. Richard Robins, and Frederick M. Bayer, I began a study of the zoogeography of the tropical Atlantic with the objective of describing the major patterns of distribution of the macrofauna of the region, the affinities and differences of the faunas and the communities or natural assemblages found therein. Cruises in 1964 and 1965 were made along the West African coast from Monrovia to the Congo Rise, and it was planned to spend the summer of 1966 along the Brazilian coast from Recife to French Guiana.

Two events conspired to change the direction of our work: international problems concerning clearance for working in Brazil's coastal waters and the announcement in the press of plans for the construction of a sea-level canal across the Isthmus of Panama, with the concomitant need for information concerning the biological oceanography of the region. We discussed these matters at length and finally decided in the fall of 1965 that our summer cruise in 1966 would be

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Contribution No. 1524 from the University of Miami, Rosenstiel School of Marine and Atmospheric Science. This paper is one of a series resulting from the National Geographic Society-University of Miami Deep-Sea Biology Program. The work was supported in part by National Science Foundation grants GB-1204 and GB-5776 for ship support and a grant from the Atlantic-Pacific Interoceanic Canal Study Commission (the Commission) through the Atomic Energy Commission (AEC) and the Battelle Memorial Institute (Battelle).

made in the Caribbean from the mouth of the Panama Canal to Cartagena, Colombia.

At about the same time we held discussions in Miami with representatives of the Battelle Memorial Institute concerning possible participation in the Commission's feasibility studies. As a result, my colleagues and I prepared a comprehensive proposal to study the biological, physical and geological oceanography of the Caribbean area involved. A meeting was held in early 1966 at Columbus, Ohio, with numerous scientists from various institutions interested in the problems, including biologists from Scripps Institution of Oceanography, who also had submitted a proposal for comprehensive research.

At the end of this meeting, my colleagues and I prepared a report on the marine biological problems of the area and emphasized in the strongest terms the need for thorough comprehensive marine studies before any work was begun on a new canal, warning of the possibility of drastic changes to the faunas and the environment due to possible interchange of faunas, radiological hazards, siltation and other factors. The Scripps biologists presumably did the same. The ultimate effect of this report and its distribution are unknown to us. Both the University of Miami and the Scripps proposals were rejected as too costly.

With funds from the National Science Foundation and the National Geographic Society, the 1966 cruise was conducted from Escudo de Veraguas, Panama, to off Cartagena, Colombia, in a carefully laid out series of transects. Approximately 135 stations were occupied, utilizing a wide variety of types of gear, but standardized as to use and treatment of the catch (Anonymous, 1967; Voss, 1968a).

As a result of our years of study of the Caribbean fauna and involvement in ongoing problems of tropical zoogeography and ecology, the Commission, through the Battelle Memorial Institute, invited us to undertake a six-month's literature study of the marine ecology, faunal records and fisheries of the Panamic region, based upon published and unpublished data in pertinent files throughout the United States. A similar invitation was made to Scripps but was rejected. Dr. Schaeffer reportedly refused to have anything to do with the Panama Canal problem thereafter.

We accepted the contract, and members of our staff visited Scripps Institution of Oceanography, University of Southern California, University of California at Los Angeles, the Los Angeles County Museum and the California Academy of Sciences on the Pacific coast, the then Bureau of Commercial Fisheries laboratory at Pascagoula, the Smithsonian Institution, the National Oceanographic Data Center and Harvard University on the Atlantic coast. On the basis of the accumulated records, our intensive literature survey, and our own preliminary studies in the Caribbean sector we prepared a 143-page report on the present knowledge of the marine resources and ecology of the area, including an extensive bibliography, the first compiled for the region (Voss, Bayer and Robins, 1967). The report stressed the fact that our knowledge of the area is fragmentary at best, as no true ecological studies have ever been undertaken in the area, and reiterated the need for comprehensive studies.

In 1967, another meeting was held at Columbus; again we stressed the need for comprehensive marine work and again we prepared a report on the need for marine biological research.

In the summer of 1967, in an attempt to obtain at least some of the data required, we made another cruise with the R/V JOHN ELLIOTT PILLSBURY, this time in the Gulf of Panama where a series of about 185 stations were occupied at ten-mile intervals throughout the Gulf (Voss, 1968b). When we returned to Miami I attempted to find funds to work up this material but none could be obtained.

In 1968, we began preparing a proposal for ecological and faunistic studies of inshore waters of the Caribbean and Pacific sides of the Isthmus involving the cooperation of staff and students from Jamaica, the University of Panama, Scripps Institution of Oceanography, the Smithsonian Institution and the University of Cartagena. Before this was completed, the Commission announced that no further field work would be conducted in Panama and work on the proposal was stopped.

At this time the situation was grave concerning the knowledge of the marine biology of Panama in relation to the proposed canal. No field work dealing with the marine faunas and their ecology had been funded by the Commission. The sole work in the marine waters was a study of specific activity conducted by Dr. Frank Lowman of the Puerto Rico Nuclear Center. This work was ecological in only the vaguest terms, as the hydrographic data are not usable for ecological studies and the specimens examined isotopically were often unidentified, erroneously identified or lumped in broad categories. The residual collections were requested by Dr. I. E. Wallen, stored at the Smithsonian Oceanographic Sorting Center and, subsequently, examined by us.

In 1969, a meeting was announced to be held at Columbus in conjunction with the meetings of the American Institute of Biological Sciences, at which the feasibility studies would be reviewed. Against the advice of my colleagues I decided to attend. No review was made of the marine research. Dr. I. E. Wallen proposed a program of intensive collecting under the auspices of the Smithsonian Institution. No other voice was raised by the "concerned" biological community at this or any other meeting during the course of the canal studies.

Finally, at an evening meeting, I made a strong plea that if original marine field work was not to be supported, the least that could be done would be to support the analysis of the data obtained by the R/V JOHN ELLIOTT PILLSBURY. This would at least be a starting point for the study of the marine areas. One of the Commissioners was present and interested, and the next day I was invited to prepare a proposal for the study.

On my return to Miami, we prepared a proposal for the analysis of our material, a study of the relationships of the two faunas, and our conclusions as to the possible results of mixing the faunas. This was submitted to Battelle which, as required, forwarded it to AEC, Nevada, for consideration. After about two months we were informed that it had been approved but reduced to one half of the amount requested. Finally, after more negotiations, approval was obtained from AEC for the full amount. It was further required that the final report be in the hands of Battelle one year from the date of acceptance.

Through the efforts of many friends among the systematists of this country and abroad, a total of 33 specialists representing six countries and 12 institutions, aided by funds specially requested for this purpose, the identifications of all specimens of the major groups, 1878 species in all, were obtained, their numbers listed and greatest and least sizes recorded. This was accomplished in 6 months. These data were then entered on IBM punch cards along with all pertinent station data.

These data were then analyzed using the recurrent-group analysis as described by Fager (1957) and utilized by Longhurst (1969) in his studies of the benthic fish fauna of the Gulf of Guinea. This resulted in the grouping of eight invertebrate and eight fish communities or associations of the Caribbean shelf area and nine invertebrate and four fish communities or associations in the Gulf of Panama. Similar analyses were done on the faunas of the slope, deep-sea bottom and mid-waters.

With these data and knowing the feeding habits or preferences of many of the animals involved, it was possible to construct a theoretical food web for the various associations. These associations were also correlated with bottom preferences both as to substrate type and depth.

While these studies were being conducted, an intensive research program was initiated to determine, where possible, the number of species in all groups considered within the West Indian and Panamic faunal provinces and the percentage of cosmopolitan and closely related analogous, twin, geminate or identical species. In all possible cases these figures were checked by recognized specialists in their fields, among them Bayer and Olsson in mollusks and coelenterates, Manning and Holthuis in crustaceans, Deichmann, Thomas and Chesher in echinoderms, Robins and Eschmeyer in fishes, and numerous others.

On the basis of these lists it was possible to evaluate the percentage of relationship between the various groups on both sides of the isthmus. This, together with a review of the historical geology of the area, also yielded information on the rate of speciation among the various groups existing at the present time.

We also searched the literature and our own files for any and all data referring to past and present migrations through the existing canal, searched the literature on means of dispersal, and discussed the problem with numerous knowledgable biological oceanographers. In addition we discussed with Israeli scientists at length, in person, the matter of migration through the Suez Canal and received a detailed personally written report on this aspect from Dr. Por and his associates, after his return to Israel. The possible effects of species migrations and resulting competition on the fisheries of the Caribbean and Gulf of Panama were also discussed with fisheries biologists.

On the basis of these investigations, we prepared a detailed report to the Canal Commission amounting to 480 pages (Bayer, Voss and Robins, 1970). It set forth the geologic history of the isthmian region, insofar as it pertained to the present faunal composition and distribution, and a description of the present Caribbean and Panamic faunas, their origins and possible numbers, and their estimated degree of relationship or affinity. On the basis of our own shipboard work we described the faunas of the shelf areas beyond the ten-meter curve, the slope, sea floor and mid-waters, enumerated the communities and their structure and pointed out those which were similar on the two sides. We also gave our findings concerning the relative productivity of the two areas.

On the basis of these findings we then presented our major conclusion: there does not appear to be a valid biological reason for opposing the construction of a sea-level canal by conventional means. If certain safeguards are built in, there is no reason to believe that mass migrations will occur nor that faunal catastrophes will take place, since about 50 percent of the species are similar or, in some groups, even identical, on the two sides, the analogous species often representing dominant species within comparable communities. We believe that there will be only a small faunal exchange, probably involving those groups most recently separated, and that most of the exchange will be from the Pacific to the Atlantic.

In order to reduce the percentage of successful migrations and colonizations, the canal route should be chosen with the view of connecting the most divergent ecological areas, thereby minimizing the possibility of survival of migrants. The entire set of recommendations and predictions is too voluminous to give in full here but are now publicly available. We concluded by saying "Despite our optimism concerning the biological effects of the construction of a sea-level canal, our knowledge of the fauna and flora of the isthmian region and the biology of its component species is extremely fragmentary, and many possible hazards may exist of which we are now unaware. As a result, we strongly urge that some type of effective barrier be built into the canal that would prevent invasion of potentially dangerous species" (Bayer, *et al.,* 1970, p. 88). We suggested a combined low salinity-thermal barrier.

We then made some detailed recommendations for further studies, reiterating the need for detailed ecological studies, the compilation of species inventories for evolutionary studies, physiological investigations, depth limitations for future surveys, genetic studies, life history studies, and ways and means of management and funding.

During the latter part of the compilation of data and writing of the report, the National Academy of Science was requested by the Commission to establish a committee to consider and report upon the need for and kinds of research that should be done if a canal were constructed. The Academy requested nominations for membership to the committee from various institutions including the National Science Foundation and the Smithsonian Institution. The names of Bayer, Robins and me were submitted by at least two different institutions. When the committee was finally constituted it contained not a single person widely conversant with the Caribbean and Eastern Pacific faunas and their zoogeographic affinities.

Information from our extensive studies was freely offered to the committee; it was never requested. No member of our group was even asked to meet with the committee or to serve on any of the subcommittees. In the report by the National Academy of Sciences no reference is made to our research. In the appendix reporting upon the sea-level canal meeting at

Boston, during which I gave our full predictions and recommendations, they are summarized in four short innocuous sentences. In the lists of laboratories and research facilities around the Caribbean, the Rosenstiel School of Marine and Atmospheric Science is relegated to a brief section on "Ancillary Resources" and listed by name only, despite the fact that practically 100% of the research of the School is conducted in the Caribbean and upon the West Indian fauna and flora. Such omissions seem to reflect bias, to say the least.

A number of reputable scientists have made "scare" statements and dire predictions regarding the possible effect of the construction of an interoceanic sea-level canal across the isthmus of Panama. Two of the most outspoken alarmists have had no personal experience in the areas and have not engaged in research relating to the problem. One has predicted the almost complete extinction of the Pacific fauna and serious disturbances in the Caribbean.

The chairman of the National Academy of Sciences committee has been widely quoted in the press and in popular and scientific magazines concerning his prediction that central Pacific sharks, which had alarmed him during one of his trips, would pass through such a canal and invade the Caribbean, threatening the tourist industry. Fortunately, this statement has no factual basis since most of these shark species have, in several million years, been unable to cross the Eastern Pacific Basin and do not occur in the eastern Pacific. Those sharks that now inhabit the Gulf of Panama also occur naturally in the Caribbean. Such statements can only be considered as alarmist in nature with no foundation in facts.

We have been strongly criticized by certain persons concerning our report, which they have not read. There *are* dangers inherent in the construction of such a canal and we have pointed these out. We have also urged wide-ranging studies with special emphasis upon the intertidal and shallow-water zones. Investigations have been initiated in Panamanian waters by staff members of the Smithsonian Institution, the University of Panama, and Caribbean laboratories, distant, but still concerned about possible effects in their areas. However, all of this is only a beginning and, if biology is going to benefit from this gigantic faunal experiment, sufficient funds must be made available by Congress to support them, and the biological community must close ranks and work toward common goals.

In summary, the research conducted at Miami has resulted in the following contributions:

1. The only general survey of the ecology of the two coasts and a detailed bibliography useful to anyone working in the area.
2. The only major faunal survey of the shelf, slope, deep-sea and mid-water faunas of the isthmian region.
3. The largest collections of isthmian marine life so far obtained.
4. A working computer retrieval system holding all of our isthmian data.
5. A detailed modern analysis of the relationships of the Caribbean and Panamic faunas.
6. Continuing studies of the two faunas.

We do not pretend that we have more than scratched the surface of the problems related to the isthmian faunas. But, if many of the people who have criticized our results had done as much in their respective fields, we would be a lot further along the road to solving the problems we are discussing today.

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MUSEUMS AS ENVIRONMENTAL DATA BANKS: CURATORIAL PROBLEMS POSED BY AN EXTENSIVE BIOLOGICAL SURVEY

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Before launching into a review of present and potential problems of biological surveys, I should like to put natural history museums, generally, and especially the systematic biology practiced there, into perspective with the ecoconcerns we all share to some degree.

Natural history museums, large and small, have always been the keepers of the baseline documentation for what the environment was like in historical times, just as surely as their anthropological artifacts are the documentation for the evaluation of cultures, man's adaptation to environmental stresses. But these collections are valueless without the researches of systematic biologists who describe and interpret the living or formerly living components of environments. The syntheses of systematics provide the constantly recurring theme of the symphony of biology, whether it is directed toward biochemistry, cytogenetics, or the attack on current ecoproblems. A quotation from a just-released report ("The Systematic Biology Collections of the United States: An Essential Resource") puts it this way:

> "Systematic biology has experienced at least four recognizable phases thus far: descriptive (pioneer exploration and the making of biotic inventories), biogeographic (geographic distribution of organisms), systematic (the nature of species and other units of classification), and biosystematic (the dynamic nature of populations of organisms). Now, a fifth phase is upon us, the ecosystematic, in which all aspects of the environment—non-

> living and living (including human)—are taken into account. It is important to note that the successive phases in this evolution have not replaced earlier phases; they have merely broadened the horizon. All five phases are operative today because our knowledge of organisms is very uneven. We have still to explore for the first time vast areas in tropical South America. In Europe and eastern North America, where the catalogs of plants and animals have long been well-known, the basis of study is increasingly an intensive analysis of organism-environment relationships. At any level of study, the systematic collections are the fundamental resource for basic evidence."

The report (which we can call the "Steere Report" after the chairman of the committee which wrote it) goes on to point out that no single physical arrangement of collections serves all needs equally well and that the present arrangement of most large collections is related closely to descriptive activities. While the sequence of collections often reflects ideas of evolutionary relationships, there has been in the past several decades very little rearrangement resulting from improved knowledge of evolutionary pathways, largely because of the enormous labor of a re-ordering. Of course, with the availability of computer applications in museums, the physical arrangement will be progressively less important, but I will return to computers later.

The Steere Report, speaking of ecosystematics, remarks:

> "The ecosystem phase has only just begun to affect systematic collections. Inherent in the evolution of ecosystem science will be a strengthening of the traditional alliance between systematists and ecologists. An ecosystematist will be mainly concerned with the distribution of organisms as they correlate with environmental factors, such as pollutants. He will want to study the inter-relationships and the coevolution of plants and animals—man included. He will need much more flexible access to data already present in systematic collections but as yet beyond retrieval, data that will become accessible with increased use of computerized data banks."

But I will speak repeatedly of computer applications in museums.

Now, I would like to turn specifically to the subject assigned me, but rather than try to provide a blueprint for collection management of the documentary specimens from an extensive biological survey, I want to pose some of the important questions and express a few of my early thoughts about them.

1. *In such a survey, what do you collect? Who does the collecting? How much do you collect for an "adequate sample"? How much do you keep?*

In using the second-person plural "you" in this context, I am thinking of curators and administrators of museums, for the field study and collection of specimens, as well as their characterization, have been done by natural history types, mostly in museums. This will probably continue to be true even in spite of our attempts to teach non-taxonomists how to collect proper documentary materials. *What* we collect surely must be carefully planned because the survey effort could become hopelessly bogged down in the kind of collecting that specialists do for the in-depth study of population problems. But *how much* do you collect and, perhaps more important, *what do you keep?* This symposium is designed to help identify those biotic groups that are reasonably well-known and can receive less attention than groups which are relatively unknown. Naturally, a specialist in any group is going to want as wide a range of specimens as possible to study variation and distribution, but perhaps all of the specimens need not be retained by his institution and can be dispersed to other collection centers when his studies are completed. I believe these are critical questions which if unanswered beforehand may limit all of us to one great survey effort and then neither space or other resources will be available to mount a second one anywhere!

2. *Are current preservation techniques adequate for future needs?*

To answer this we have to consider what future needs may be. I will only mention a few present examples of unanticipated requirements.

It was coincidental, but most fortunate, that museums had preserved eggs of birds because it was only by measuring shell thickness of eggs in pre- and post-pesticide eras that biologists were able to explain the decrease in populations of some bird species. From this example we systematic biologists, museum curators, should certainly be planning for preservation of many materials not now collected, by techniques presently neglected or unknown. Since radioactivity, heavy metals, and other pollutants are known to accumulate in some kinds of organisms, should we not be making certain that preserving solutions, for example, will prolong the usefulness of collections for biochemical, as well as for morphological, taxonomic use? That biochemical purposes may in fact serve our own taxonomic interests does not need emphasizing, since refined serology and chemotaxonomy generally have become a part of the systematist's repertoire of techniques. Are there some liquid preservatives we should be considering? How about freeze-drying whole specimens, or some organs, or tissues? We need to be able to store collections for long periods without significant structural or chemical changes and neither of these conditions are met now. For example, flowering plant collections are most easily preserved by drying them quickly over artificial heat and, if properly protected from damage, they are as good 200 years later for *morphological* purposes as they were fresh. There is now reason to consider other techniques, but little experimentation of which I am aware. In the area of microbial organisms there has been much greater progress in these matters, for a culture may be kept in viable condition for years at extremely low temperatures and then, as it reaches room temperature, become active again. Does this offer possibilities for more complex organisms?

3. *What kind of data do you collect and how do you record them?*

Now, we all know that marine biologists and terrestrial biologists collect different kinds of data, even for the same major group of organisms. The principal point I would like to emphasize in this connection is that we need to broaden our thinking about what classes of data we do record. Geography, date, collector, sometimes color notes, even more rarely, associated organisms, will not be enough to satisfy future research needs. We should develop an increased awareness of both the biotic and abiotic factors related to the organisms we collect and attempt to record more about those which seem to have other than chance correlation with the organisms. Many biologists who conduct field studies perhaps will resist this recommendation because they will see data-collection, at this level of completeness, as taking too much time and effort away from the number of population samples obtained. That is, if one has the choice of collecting 75 species or 100 species, the number depending on the completenesss of the data, which is the best course? Fortunately, we really need not answer that question in that form: Our mammalogists are preparing to test the field application of a data-gathering technique that is not expected to reduce time for other field activities significantly. The man in the field is outfitted with a stack of 40-column IBM cards and a special hand punch. Either at the actual collecting point or later in the day, a wide range of field information can be recorded by punching appropriate points in the cards rather than making handwritten notes. When the collector returns to his laboratory or museum, the cards are used to generate labels for the specimens, to list collections for a field book or station record, and as an important means of introducing new information into the inter-museum data network many of us anticipate. It should be clear that it will be in those groups of organisms with specialists willing to plan and experiment with new techniques that the greatest advancements in scientific understanding will come, soonest. The alternative is depressingly apparent to me: Cling to traditional methods and the same level of understanding *may* be achieved (though I doubt that), *if* there are enough generations beyond our own that care and if we somehow succeed in preserving adequate representations of the earth's biota.

4. *Who owns the collections from a multi-institutional, bi-national biological survey?*

I pose the question in these terms because it is the sea-level canal in the Panama area we are thinking about today, and also because it is in developing areas where much of the natural conditions persist that make large-scale surveys worth a major effort.

Ownership of the fruits of such inventories is a very delicate question that will not go away just because we ignore or refuse to ask it. Categorical rules are impossible, but the "Guidelines for Biological Field Studies" have been published in the past year that will (1) ensure the care of the collections in perpetuity, (2) recognize the needs of the developing area, and (3) promote preservation or conservation of natural resources for both practical and aesthetic purposes.

About 35 systematic collection centers have agreed to inform each other of proposed field expeditions in the other's territory, to assist in reciprocal training of students, never to collect for commercial purposes, to cooperate scientifically with each other in joint research efforts, to "share with scientists of the host country the results of the cooperative field studies by division of collections" and to "deposit types in accordance with the International Codes of Botanical and Zoological Nomenclature." These last two portions quoted are all that the framers of the "Guidelines" were able to say about who owns collections that is generally applicable and sufficiently flexible for negotiation.

I think there is no problem about non-type collections—a set as complete as scientifically possible should certainly be made available to the most appropriate museum or other institution in the area of origin of the collections. For the sake of science, reasonable care of these specimens should be assured and the decision concerning place of deposit should not be made on other than scientific grounds. Where truly adequate conditions for long-term preservation of collections do not exist in one of the partner countries, it is possible to maintain a set of the resulting specimens elsewhere, pending the development of adequate preservation facilities. In fact, the development of such facilities in a country may be hastened by the demonstration that they are needed for housing the materials from a biological survey of its own natural resources by its own scientists in concert with colleagues from elsewhere.

5. How do the collection centers obtain new space for curating the results of *biosurveys?*

The greatest problem for such surveys that we all face is SPACE, which I put in capitals because it is so important. The natural history museums of this country certainly are not in any position to take in vast numbers of additional specimens, and yet they must continue to grow by the addition of collections from just such surveys. The report on the nation's systematic collections which I mentioned earlier, the Steere Report, estimates a need for 40% new space (from 3.5 million square feet to five million) by the country's systematic centers. It requests nearly 60 million dollars just for new space, for renovation/rehabilitation of existing structures, and for new specimen cases. I am not confident that this volume of need will be met in one action or even stepwise over the next ten years as the report requests. It is slight solace to observe that some of the equipment may be obtained as a part of the cost of doing particular projects, but the floor space to set storage cases is still another matter. The report concludes:

> "If the national needs of science are to be met, the Federal Government must ... continue support of facilities for this research [systematic biology] ... and inaugurate a wholly new program of support for curatorial activities in museums of systematic biology."

It goes on to propose that a panel of qualified scientists and administrators be appointed by the National Science Foundation to review the "unique qualities, capabilities, and needs" of such institutions. To make the Federal support requested most effective, representatives of the museums involved would develop means for increasing cooperation among systematic collection centers to eliminate overlap and duplication.

6. *Who will do the routine identifications and taxonomic research required for large biosurveys?*

About two or three years ago the National Institutes of Health asked the National Academy to study the question of how it and other applied organizations could obtain identifications and other systematic services in a timely way. The Academy committee, chaired by Charles Michener, broadened its charge to "Systematics in Support of Biological Research." The principal concern of the report is the need for additional personnel in systematic biology to curate the collections, to assist in planning major programs, and, especially, to provide the systematic information required, particularly by environmental programs.

The Steere Report also emphasizes the inadequate staffing of all systematics centers. It is estimated that to do a decent job, the principal centers require at least 100 new professional researchers and more than 200 supporting staff. The "crunch" in general, broadscale, biological surveys, as in all environmental undertakings, is well-put by the Steere Report:

> . . . environmental research and its application to such problems as the varied facets of pollution have made demands in crescendo for expansion of the supporting base of systematic biology. To meet a potentially critical situation, the systematic institutions must develop means to provide general information and identification services not now available. Identifications are essential to practical environmental work, such as pollution studies, agriculture, and epidemiology, because names unlock the information-storage and retrieval system ... identification is essential as the nucleus around which significant information can accumulate for future use ...."

At the present time, personnel is still one of the most serious of all the problems facing those who would mount large, intensive biological surveys. There simply are never enough systematic biologists, and their support is so minimal that the job ahead cannot be done without some very major changes either in their numbers or in the ways they are used. As the needs for identifications have mushroomed, today's professional tends to guard his time more carefully so that his efforts are worthy of his training and experience. New systematists coming along are "turned off" by the repetitive, often tedious aspects of routine identification service, so the situation worsens.

The Michener Report proposes an American Institute of Applied Systematics which would consist of an administrative center and a number of "service centers," the number limited only by the needs of the scientific community and the support that can be generated. These service centers would be located at the sites of major systematics activities, to be complementary rather than competitive. Three kinds of personnel would staff the centers:

1. Technicians, who would do the repetitive chores such as preliminary sorting, specimen preservation, etc.

2. Taxonomic Specialists, whose primary assignment would be to produce identifications, but who might spend part-time at research needed for the identification function; and they would supervise the technicians.
3. Research Scientists, who would do the research on which the applications are based; many would have joint appointments at universities where the service centers would be located so that they could direct the work of graduate students in systematic biology, thereby assuring a continuing cadre of systematists.

Such an organizational structure with even modest support might well expand the numbers of systematic biologists and their supportive staffs. Moreover, because the centers would be on university campuses, more economical space might be available, there should be a continuing supply of the personnel required and, above all, the relevance of systematics to other areas of learning would be demonstrated.

The encouragement and development of training programs in the university- and museum-based service centers would be but one of the functions of the Secretariat of the American Institute of Applied Systematics. In addition, it would act as a clearinghouse of information about what and where systematics expertise would be available and, in general, be the coordinator of systematic biology so that the input required for solving the kinds of problems we now face always would be available.

I want to conclude with what I see as the one development that will permit intensive biological surveys without diverting all taxonomic talent and still result in a body of data that may be applied profitably to a range of real problems. I refer to the developing computer-based data-processing capabilities in museums. Even with armies of technicians, the quantity of data we are considering cannot be handled by conventional means. The strategy of the moment in the National Museum of Natural History is to capture all the information possible about newly received collections. In addition, as a particular group of organisms comes under study, the data on the holdings of this group in the major museums will be entered in the system. These data bases would become a very important part of the total resources for solving problems. In the environmental area, they constitute the baseline from which change can be detected, assessed, and evaluated. I am confident that computer applications represent a very significant tool in solving curatorial problems associated with intensive biological surveys.

I may not have referred adequately to all these problems, and some of you may remember that it was a National Academy report, with which Waldo Schmitt had a great deal to do, that called attention to many of these same questions 15 years ago. The time has already passed when we can consider such things at leisure. It is time we move out, while there are yet biotas worth surveying.

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A REVIEW OF THE MARINE PLANTS OF PANAMA

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This review is intended to summarize the current state of knowledge regarding plants that grow along the Atlantic and Pacific coasts of Panama. It may seem remarkable that little is recorded about the marine plants of an area that serves as crossroads between two oceans and two continents, but in fact, the species composition, ecology, distribution, and other aspects of the biology of the marine algae and sea-grasses of Panama are virtually unknown.

Only 62 years have passed since Marshall A. Howe published the first remarks on the marine plants of the area, based on a brief expedition sponsored by the New York Botanical Garden (Howe, 1910). In 1918, he published a short paper on coralline algae from Panama.

Mme. P. Lemoine, in 1929, reported 14 species of corallines collected in 1927 by Dr. Cyril Crossland from the Gulf of Panama.

Forty-nine species of algae collected along the Atlantic coast by C. W. Dodge in 1925 in the Bocas del Toro area (Careening Cay, Nancy Cay, Provision Island, and Columbus Island) were noted by Taylor (1929). A small collection made at Cristóbal in 1939 by Mrs. George Artamanoff was included in Taylor's report (1941) of marine algae in the Arthur Schott Herbarium. In 1942, Taylor reported on the marine algae collected in the Caribbean during the 1939 Allan Hancock Expedition, including 67 species from Caledonia Harbor.

Marine plants obtained from the Pacific coast of Panama during cruises of the VELERO III in 1934 and 1939 were listed by Taylor in 1945. Localities included Islas Secas, Chiriquí Province; Isla Jicarita, Veraguas Province; Bahía Honda, and in the Gulf of Panama, Isla Taboga and the shoreline at Balboa and San Francisco. Altogether, only 24 species were noted.

In 1959 during a Pacific cruise of the STELLA POLARIS, E. Y. Dawson collected at Isla del Rey in the Perlas Islands, Punta Naranja on the mainland, Isla Jicarón, and Isla Brincanco in the Islas Contreras. For the first time, SCUBA was used for observations and collections of marine plants in Panama, and, thus, Dawson was able to make some significant ecological notes on subtidal circumstances, as well as obtaining many new records of marine algae and sea-grasses (Dawson, 1960; Dawson and Beaudette, 1959). C. den Hartog (1960) described sea-grasses obtained by Dawson as two new species, *Diplanthera beaudettii* and *D. dawsoni,* but later (1970) treated both as *Halodule beaudettii,* and indicated that the species had wide distribution in the Caribbean Sea and the Gulf of Mexico.

My first-hand knowledge of the marine flora of Panama is based on several visits from 1965 to 1971. Using dredges, SCUBA and shore-collecting techniques, I sampled marine plants in the vicinity of Holandés Cay and Duarte Cay in the San Blas area of Atlantic Panama in September, 1965, during cruise 10 of the R/V ANTON BRUUN. I returned to Panama in November, 1965, for shore work at Colon on the Atlantic arid Balboa on the Pacific coast. Once again, aboard the R/V ANTON BRUUN, cruise 19, I returned to the Pacific coast in October, 1966, went through the canal to the Atlantic, and made further collections near both ends of the canal.

In December, 1966, a trip to Isla Taboguilla in the Bay of Panama and to the Perlas Islands was arranged through the Smithsonian Tropical Research Institute. Subtidal and shore collections were made at Isla Saboga, Isla Chapera, Isla Señora, Isla Señorita, and Isla Pedro Gonzales. Samples were taken by diving at several locations on the Atlantic coast in the vicinity of Galeta, near Colón.

During April, 1967, additional collections and observations were made in the Bay of Panama at Isla Taboga, Isla Taboguilla, Isla Valladolíd, and along the shore at Paitilla Point.

Stations in the Perlas Islands included Isla Bartolomé, Isla Chapera, and Isla Contadora. On the Atlantic coasts, collections were made at several sites in the vicinity of Colon. Observations, but no collections, were made during a brief visit to Panama in September, 1968, and in June and July, 1971, I revisited diving stations at Galeta, Isla Taboga, Isla Taboguilla, and in the Perlas Islands, at Isla Chapera, Isla Saboga, and Isla Señorita; again the trip was arranged by the Smithsonian Tropical Research Institute.

In addition, I gathered a small collection of algae growing in depths to six meters along the sides of the Third Locks, a slightly brackish artificial lake described by Bozniak, *et al.*, 1969.

Systematic treatment of my Pacific collections, including more than 30 new records, is in preparation and will be reported separately. Most of the Atlantic material that I have collected has been made available to Joyce Redemske Young, currently in her third year of a floristic and ecological study of the algae of Atlantic Panama, with special reference to Galeta.

DESCRIPTION OF THE FLORA AND THE ENVIRONMENT

Panama has more than 1,500 km of mainland coastline and extensive island shores, but only a few places in this vast expanse have been looked at with marine plants in mind. Especially lacking are observations in subtidal areas where most marine plants live. Benthic algae occur from the upper limits of high water to more than 200 m depth, but the greatest development is normally found in depths less than 30 m.

Peter Glynn, earlier in this symposium, has given an excellent general analysis of ecological conditions on both sides of the isthmus. Specific physical data correlated with the biology of marine plants is lacking, however, except for recent studies at Galeta by Joyce Redemske Young. Factors known to influence algal distribution include kind of substrate, light, salinity, available oxygen, nutrients, water movement, tidal

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[1] Based on personal observation since 1953 including dredging, diving, and submarine viewing at more than a thousand sites in the Indian, Atlantic, and Pacific Oceans.

amplitude, presence of herbivores, and, perhaps most significant, temperature (Dawson, 1960). Setchell (1935) studied the effect of temperature on the distribution of marine algae and distinguished regions based on the average water temperature during summer months. Atlantic Panama is clearly tropical in shallow water by Setchell's definition, with temperatures usually within the 25-30°C range. Summer temperatures of shallow water along Pacific Panama are within the tropical range, but, during periods of upwelling, may fall below 20°C.

The Atlantic coast is quite different, ecologically, from the Pacific. The water of the Atlantic, in general, is clear, with relatively little tidal or temperature amplitude. Terrain includes rock, sand, and mangrove shores, with conspicuous development of fringing coral reefs and associated biota. Seagrass beds are well-developed in shallow water, with *Thalassia testudinum* and *Halodule wrightii* occurring intertidally to about 10 m depth and *Syringodium filiforme* and *Halophila baillonis,* subtidally.

There appears to be little variation in the abundance and diversity of marine plants throughout the year along the Atlantic side of Panama, except in response to mid-day low tides that may result in desiccation and death of many intertidal plants. There may be patterns correlated with seasonal variations in rainfall, light, slight temperature changes, or other environmental factors, but what actually happens has yet to be documented. Environmental change is slight compared to the marked seasonal events evident in Pacific waters.

Howe (1910) described Point Toro, near Colon, as follows: ... the reef has a fairly well-developed algal flora in striking contrast to that of the Bay of Panama, with its heavy tides, less than 50 miles to the southward."

Near Colón, I have observed algae in abundance in intertidal areas. In addition to the expected assortment of encrusting and upright coralline red algae, there are, in places, dense stands of *Acanthophora, Chondria, Gelidium, Gelidiella, Laurencia, Cladophoropsis, Anadyomene, Caulerpa, Halimeda, Lobophora,* and many others. In shallow sandy areas, siphonous green algae, *Avrainvillea, Caulerpa, Halimeda, Penicillus,* Udotea, as well as Dictyota, and sea-grasses, Thalassia, *Halodule*, and Syringodium, are common. Subtidally, diversity increases, often including most of the assortment found intertidally, as well as Halymenia, Botryocladia, Bryothamnion, Gracilaria, Eucheuma, Sargassum, Padina, Halimeda, and many others.

Joyce Redemske Young has, thus far, catalogued nearly 200 species of marine plants from Atlantic Panama, mostly gathered near Galeta. It is likely that more than 300 species will eventually be found along Panama's northern shore.

The first botanist who commented on the marine plants of Pacific Panama was Marshall A. Howe, a keen observer and excellent phycologist, who, with his wife, spent a part of December, 1909, and January, 1910, in Panama. Howe was given permission to stay for a week at a sanitarium for convalescents located on Taboga Island in the Bay of Panama and to explore for algae. He observed (Howe, 1910) : "The sanitarium is located near the rocky shore, and, altogether, our surrounding seemed ideal for successful work with the marine flora—except for the one unhappy fact which gradually became apparent, that a marine flora, in the ordinary sense, was in that region, almost non-existent. The vertical rise and fall of the tide on this and the adjacent islands appeared to be, while we were there, from twelve to fifteen feet, but at the ebb of the tide the pools, and the rocks and the stones, both above and below the low-water line, were seen to be nearly destitute of plant life—at least, of conspicuous species. And not a fragment of an alga or any marine seed plant was found washed shore at any point on the part of the Bay of Panama that was examined. There were a few closely encrusting species of Ralfsia, Hildenbrandia, Squamariaceae, Corallinaceae, and Cyanophyceae, and certain minute filamentous and unicellular forms representing various groups of algae."

Howe suggested that the wide range of tides, coupled with the scorching effects of the tropical sun, might be unfavorable to any luxuriant growth of marine plants. Dawson (1966) remarked that a large tidal amplitude may control the occurrence of whole formations of plants (and animals) upon which much of the diversity of the flora may depend. Intense insolation and desiccation, as well as exposure to rain during periods of low water, may inhibit algal growth. However, Dawson and Beaudette (1959) and Joyce Redemske Young (personal communication) have observed abundant intertidal plants at Isla Jicarón, comparable in aspect to Atlantic reefs near Galeta.

It is quite likely that heavy grazing by herbivorous fishes, notably parrotfishes, surgeon fishes, blennies, and gobies, as well as by herbivorous invertebrates such as the urchin, Diadema, is in part responsible for the reduced aspect of marine plants present. Randall (1961, 1965), Hiatt and Strasburg (1960), and Earle (in press) have demonstrated the dramatic increase in plant growth in certain tropical areas where herbivorous animals have been excluded. No studies of this sort have been made along the Pacific coast of Central America, but circumstances there, including an abundance of herbivorous fishes and urchins, strongly suggest that if grazers were excluded, an increase in plant growth could be expected.

Whatever the causes, the general aspect of the flora of Pacific Panama in shallow water is just as Howe described it—poor. The diversity may not be as restricted as has been reported, however, if year-round observations are made and seasonal behavior taken into account. Elsewhere, where seasonal periods of cold water alternate with seasonal warm water, a seasonal flora may develop. For example, in North Carolina, numerous species are present during fall and winter that disappear as water warms in the spring. Other species develop during the spring and summer. More than 300 species of marine plants have been recorded from the area (Hoyt, 1920; Blomquist and Humm, 1946; Williams, 1949a and b) but probably less than half of the species can be found at any given time.

Dawson, who visted Panama during March–April and measured water temperatures from 20°C near the entrance to the canal to 23°C at the Perlas Islands, commented that the algae were in exceptionally poor development and proposed marked seasonality as a possible explanation. He found young Padina and *Sargassum* plants, an indication that a period of increased growth would follow.

In April, 1967, at Taboga and Taboguilla Islands in the Gulf of Panama, and at several stations among the Perlas Islands, I observed sparse to luxuriant stands of *Sargassum* and *Padina* at a time when there was moderate upwelling. Water temperatures ranged from 18.5°C to 25.6°C, and the surface water from the Perlas Islands shoreward was thick with flocculent masses of diatoms, salps, and other planktonic organisms. Several of the same sites were revisited in July, 1971, when the water temperature was 27°-28°C. No plankton blooms were apparent, no trace of *Sargassum* was found, and only a few tattered fronds of *Padina* were located. Plants seen were mostly small, a diverse microflora of filamentous, encrusting, and fleshy species.

Algal forests in miniature have been observed elsewhere in Pacific Panama. Dawson and Beaudette, who explored the shore and subtidal areas at Isla del Rey, noted a rich growth of short, tufted algae in exposed areas, and, in 5 m depth, observed that a "uniform, monotonous turf of small red algae covered everything" (Dawson and Beaudette, 1959).

Another explanation for the apparent scarcity of marine plants along Pacific Panama is that most observations are made from the shore or in the intertidal zone, merely the rim of the area where algal vegetation is likely to occur. For a floral survey to be valid, it is essential that observations be made underwater. Dredges and trawls are useful in deep water, but most of the region between shore and the seaward limit of attached vegetation is best evaluated by direct observation. Because dredges are quickly lost on rocky substrates, such areas can be sampled effectively only by diving. A situation analogous to Panama occurs in the northern Gulf of Mexico, which was evaluated from shore and judged to be depauperate with regard to marine plants (Taylor, 1954). Subsequent subtidal work revealed an extensive and diverse flora (Humm, 1963; Humm and Caylor, 1957; Humm and Hildebrand, 1962; Humm and S. E. Taylor, 1961; Earle, 1969).

Regarding Pacific Panama, I concur with W. R. Taylor (1945) who remarked, ".. . more detailed studies of Panama

(Pacific) are called for, because the apparent poverty of the marine algal vegetation there is probably a misconception, and the study of coves and rocky points will probably show a rich flora, as has been noted on the Atlantic side, where, in the accessible spots near the Canal it is poor, but rich only a few miles each side." Preliminary work by Dawson, *et al.*, indicates that this prediction is true. At Punta Naranja, and near Isla Jicarón, Dawson discovered extensive beds of sea-grasses (Dawson and Beaudette, 1959; den Hartog, 1960). In 2 to 10 m depths at Isla Brincanco, algal growth in fair quantity was observed, including mats of *Spyridia* and *Dictyota* of considerable extent, although the intertidal reef above proved to be poor for algae.

I observed only encrusting and fine filamentous species in intertidal areas at Isla Taboga on April 7, 1967, but along the same shore in 3 to 24 m depth, rocks were covered with algae: *Sargassum* in scattered and dense patches 4 to 15 cm high; *Enteromorpha* in well-lighted locations; *Padina* on level and sloping surfaces; *Nemalion* on nearly every small pebble in 10-15 m depth; occasional clumps of *Codium,* and abundant masses of *Colpomenia.* Several minute *Acetabularia pusilla,* a distinctly tropical species, were obtained. Well-developed assortments of algae are not found in every subtidal location explored, but certainly, in general, more abundance and diversity is found below water than in the intertidal above.

FLORAL RELATIONSHIPS

It is premature to analyze affinities of the marine flora of either coast of Panama, or to compare, meaningfully, one with the other. It is probably significant, however, that nearly all of the genera of marine plants reported from Pacific Panama also occur in the Atlantic. Only *Cruoriella* and *Mesophyllum* appear to be unique to the Pacific coast, although the list will surely grow as exploration continues. The following genera have been found in Atlantic Panama that have not yet been discovered in Pacific Panama, nor along the eastern Pacific mainland: Rhodophyta—Amansia, *Contarina, Euchema, Meristotheca, Octodes;* Chlorophyta—Anadyomene, *Penicillus,* Rhipocephalus, Syphonoclathrus, Udotea, Valonia; Phaeophyta —Cladosiphon, *Turbinaria*; Spermatophyta—Syringodium. Halimeda (Chlorophyta), Dictyopteris and Spatoglossum (Phaeophyta) have not been found in Pacific Panama, but Halimeda is reported for Pacific Costa Rica by Dawson and Beaudette (1959), and I have collected the other two genera near Salinas, Ecuador.

On the species level, nearly all recorded to date are specific to one coast or the other. Only the following Panamanian algal species have been found in both the Atlantic and Pacific oceans: Chlorophyta—*Caulerpa* microphysa,[2] Caulerpa peltata,[2] Caulerpa racemosa,[3] Caulerpa sertularioides,[2] *Cladophoropsis* membranacea[3]; Phaeophyta—*Colpomenia* sinuosa,[3] Lobophora variegate; Rhodophyta—Acanthophora spicifera,[3] Centroceras *clavulatum*, Her posiphonia secunda,[4] Hildenbrandia prototypus,[3] Polysiphonia howei,[5] Spyridia filamentosa,[4] Wrangelia argus,[4] Wurdemannia miniata[5]; Cyanophyta-Microcoleus lyngbyaceus,[4] Schizothrix mexicana.[4] The species that are common to both oceans are, in general, widely distributed, most occurring in warm seas throughout the world.

Sea-grasses on the Atlantic coast of Panama include *Thalassia* testudinum, Halodule wrightii, Halo phila baillonis, and Syringodium filiforme. According to den Hartog (1970), *Halodule* beaudettii is widespread in the Caribbean, but has not been reported from Atlantic Panama. It is locally abundant on the Pacific coast, however, sometimes mixed with Halo phila baillonis (den Hartog, 1960). Another species, Halodule ciliaris, is known only from the original collection by Mortensen in 1916 from Taboga in the Gulf of Panama (den Hartog, 1960; 1964; 1970). There are doubtful Pacific coast records of Thalassia testudinum and Halodule wrightii noted by Setchell (1935) and den Hartog (1960).

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[2] Collected by S. A. Earle from the Atlantic near Colon and from the Pacific in the P[illegible] Islands.

[3] Previously recorded from Atlantic Panama; on the Pacific coast, collected by S. A. Earle at several stations among the P[illegible] Islands. Colpomenia sinuosa and Caulerpa racemosa were also found in [illegible] along the mainland shore, near Balboa.

[4] Previously reported from Atlantic and Pacific Panama (Taylor, 1929, 1941, 1942, 1945; D[illegible] and Daily, 1954; Dawson, 1960; D[illegible], 1968).

Recorded from Pacific Panama; known from various parts of the Caribbean and collected by S. A. Earle on the Atlantic coast near Colón.

CONCLUSIONS

Perhaps the most obvious conclusion that can be made regarding the marine flora of Panama is that more work needs to be done. Basic surveys must be made to determine the composition of the marine flora of both coasts, and to lay a foundation for ecological work and other investigations. No morphological and no genetic studies have been made, but it is tempting to speculate on the results of experiments utilizing different species of the same genus from two oceans, or representatives of the same species from different oceans.

The Appendix lists 125 species of marine plants from the Atlantic coast of Panama and 90 species from the Pacific based on published records and personal collections. Seventeen new records are included for the Atlantic and 14 for the Pacific coast. For all of Panama, 195 species are reported, including 20 that are common to the two coasts.

Based on current information, it would appear that the flora of Atlantic Panama is more abundant and diverse than that of the Pacific. This impression may prove an illusion, however, and it is likely that careful exploration, with attention to seasonal change, will show diversity to equal or exceed that of the Atlantic.

ACKNOWLEDGMENTS

I wish to express my appreciation to the Smithsonian Tropical Research Institute, and most particularly, to Ira Rubinoff and Roberta Rubinoff for making possible much of my field work in Panama. I am indebted to the National Science Foundation for their support during cruises of the 11/V ANTON BRUUN. Special thanks are due those who joined me for field work, especially Giles W. Mead, Ira Rubinoff, Roberta Rubinoff, Joyce Redemske Young, and John McCosker. Harold J. Humm, Robert T. Wilce, and Joyce Redemske Young have kindly read and commented on the manuscript. Publication funds, provided by the Conservation Foundation, are gratefully acknowledged.

Essential laboratory and library work for this paper was accomplished at the Farlow Herbarium, Harvard University, and at the University of California, Berkeley, during research appointments, 1969–1971.

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APPENDIX

PRELIMINARY LIST OF MARINE PLANTS OF PANAMA

Most new records of species and the detailed locations of plants collected by S. A. Earle will be reported upon subsequently by Joyce Redemske Young for Atlantic Panama and by Earle for Pacific Panama; some of the species listed below are newly reported herein.

PLANTS OF ATLANTIC PANAMA

CHLOROPHYTA

t Acetabularia crenulata Lamouroux. Collected by Earle near Colon.

t Acetabularia sp. Collected by Earle at Holandés Cay.

Anadyomene stellata (Wulfen) C. Agardh. Taylor, 1929, 1942, 1960.

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t New record for Atlantic Panama.

Avrainvillea rawsonii (Dickie) Howe. Taylor, 1942.

tBoodleopsis sp. Collected by Earle at Holandés Cay.

†*Bryopsis* sp. Collected by Earle near Colon.

Caulerpa cupressoides (West) C. Agardh var. *mamillosa* (Montagne) Weber-van Bosse. Taylor, 1942, 1960.

Caulerpa fastigiata Montagne. Taylor, 1929, 1960.

†**_Caulerpa microphysa_ (Weber-van Bosse) J. Feldman. Collected by Earle near ColOn.

t **_Caulerpa peltata_ Lamouroux. Collected by Earle near Colon.

**_Caulerpa racemosa_ (Forskål) J. Agardh var. *clavifera* (Turner) Weber-von Bosse; var. *laetevirens* (Montagne) Weber-van Bosse; var. *uvifera* (Turner) Weber-van Bosse. Taylor, 1929, 1942, 1960.

**_Caulerpa sertularioides_ (Gmelin) Howe f. *brevipes* (J. Agardh) Svedelius. Taylor, 1929, 1942, 1960.

Chaetomorpha brachygona Harvey. Taylor, 1929, 1942, 1960.

Chaetomorpha linum (Muller) Kützing. Taylor, 1942, 1960.

Chaetomorpha media (C. Agardh) Kützing. Taylor, 1929, 1942, 1960.

Cladophora repens (J. Agardh) Harvey. Taylor, 1929, 1960.

**_Cladophoropsis membranacea_ (C. Agardh) Børgesen. Taylor, 1929, 1960.

Codium isthmocladum Vickers. Taylor, 1942, 1960.

Dictyosphaeria cavernosa (Forskål) Børgesen. Taylor, 1942, 1960.

t *Enteromorpha* sp. Collected by Earle near ColOn.

Halimeda discoidea Decaisne. Taylor, 1942, 1960.

Halimeda incrassata (Ellis) Lamouroux f. *tripartita* Barton. Taylor, 1960; Taylor, 1942, as H. *tridens* var. *tripartita.*

Halimeda monde (Ellis and Solander) Lamouroux. Taylor, 1942, 1960.

Halimeda opuntia (Linnaeus) Lamouroux. Taylor, 1929, 1942, 1960.

Halimeda simulans Howe. Taylor, 1942, 1960.

Halimeda tuna (Ellis and Solander) Lamouroux. Taylor, 1942, 1960.

Neomeris annulata Dickie. Taylor, 1942, 1960.

Penicillus capitatus Lamarck. Taylor, 1942, 1960.

Penicillus lamourouxii Decaisne. Taylor, 1942, 1960.

Penicillus pyriformis A. and E. S. Gepp. Taylor, 1942, 1960.

Rhipocephalus phoenix (Ellis and Solander) Kützing. Taylor, 1942, 1960.

Rhizoclonium hookeri Kützing. Taylor, 1929, 1960.

Siphonoclathrus stri Earle and Young. Earle and Young, 1972.

Udotea conglutinata (Ellis and Solander) Lamouroux. Taylor, 1942, 1960.

** Occurs on Atlantic and Pacific coasts of Panama.

Udotea *flabellum* (Ellis and Solander) Lamouroux. Taylor, 1942, 1960.
Ulva lactuca Linnaeus var. latissima (Linnaeus) De Candolle. Taylor, 1929, 1960.
Valonia utricularis C. Agardh. Taylor, 1929, 1960.
Valonia ventricosa J. Agardh. Taylor, 1942, 1960.

PHAEOPHYTA

Chnoospora *minima* (Hering) Papenfuss. Taylor, 1960; Taylor, 1929, 1942, as C. pacifica.
Cladosiphon occidentalis Kylin. Taylor, 1942, as Aegira zosterae. See Earle, 1969, p. 180.
**Colpomenia sinuosa (Roth) Derbès and Solier. Taylor, 1942, 1960.
Dictyopteris delicatula Lamouroux. Taylor, 1941, 1960; Taylor, 1929, as Neurocar*pus* delicatula and *N.* haukiana.
tDictyopteris plagiogrammus (Montagne) Vickers. Collected by Earle at Holandés Cay.
Dictyota bartayresii Lamouroux. Taylor, 1929, 1960.
Dictyota cervicornis Kützing. Taylor, 1929, 1942, 1960.
Dictyota ciliolata Kützing. Taylor, 1942, 1960.
Dictyota *dentata* Lamouroux. Taylor, 1929, 1942, 1960.
Dictyota *divaricata* Lamouroux. Taylor, 1942, 1960.
Dictyota volubilis Kützing sensu Vickers. Taylor, 1929, 1960.
t Ectocarpus sp. Collected by Earle near Colon.
**Lobophora variegata (Lamouroux) Womersley. Taylor, 1942, as Zonaria variegata; Taylor, 1960, as Pocockiella variegata.
Padina gymnospora (Kützing) Vickers. Taylor, 1942, 1960.
Padina vickersiae Hoyt. Taylor, 1929, 1942, 1960.
t Ralfsia sp. Collected by Earle at Holandés Cay.
Sargassum fluitans Børgesen. Taylor, 1941, 1942, 1960.
Sargassum polyceratium Montagne. Taylor, 1941, 1942, 1960.
Spatoglossum schroederi (Mertens) Kützing. Taylor, 1929, 1960.
Stypopodium zonale (Lamouroux) Papenfuss. Taylor, 1960; Taylor, 1929, as Zonaria zonalis.

RHODOPHYTA

Acanthophora muscoides (Linnaeus) Bory. Taylor, 1929, 1960.
***Acanthophora* spicifera (Vahl) Børgesen. Taylor, 1942, 1960.
Amansia multifida Lamouroux. Taylor, 1929, 1960.
Amphiroa fragillisima (Linnaeus) Lamouroux. Taylor, 1929, 1960.
Amphiroa hancockii Taylor. Taylor, 1942, 1960.
Amphiroa *rigida* Lamouroux. Taylor, 1929, 1942, 1960.
Amphiroa tribulus (Ellis and Solander) Lamouroux. Taylor, 1929, 1960.
t Antithamnion sp. Collected by Earle at Holandés Cay.

Archaeolithothamnion episporum Howe. Howe, 1918; Taylor, 1929, 1960.

Bostrychia binderi Harvey. Taylor, 1942, 1960.

t Botryocladia sp. Collected by Earle near Colon.

Bryothamnion triquetrum (Gmelin) Howe. Taylor, 1929, 1942, 1960.

tCaloglossa leprieurii (Montagne) J. Agardh. Collected by Earle near Colón.

Catenella repens (Lightfoot) Batters. Taylor, 1942, 1960.

**Centroceras clavulatum (C. Agardh) Montagne. Taylor, 1941, 1960.

tChondria sp. Collected by Earle at Holandés Cay and near Colón.

Contarinia magdae Weber-van Bosse. Taylor, 1942, 1960.

Digenia simplex (Wulfen) C. Agardh. Taylor, 1942, 1960.

Eucheuma gelidium (J. Agardh). J. Agardh. Taylor, 1929, 1960.

Fosliella farinosa (Lamouroux) Howe. Taylor, 1942, 1960.

Galaxura cylindrica (Ellis and Solander) Lamouroux. Taylor, 1929, 1960.

Galaxura lapidescens (Ellis and Solander) Lamouroux. Taylor, 1929, 1960.

Galaxura marginata (Ellis and Solander) Lamouroux. Taylor, 1929, 1960.

Galaxura oblongata (Ellis and Solander) Lamouroux. Taylor, 1929, 1960.

Galaxura obtusata (Ellis and Solander) Lamouroux. Taylor, 1942, 1960.

Galaxura rugosa (Ellis and Solander) Lamouroux. Taylor, 1929, 1960.

Galaxura squalida Kjellman. Taylor, 1942, 1960.

Gelidiella acerosa (Forskål) Feldman and Hamel. Taylor, 1942, 1960; 1929, as Gelidium rigidum.

Gelidium corneum (Hudson) Lamouroux. Taylor, 1929, 1960.

Goniolithon decutescens (Heydrich) Foslie. Taylor, 1942, 1960.

Gracilaria crassissima Crouan ex J. Agardh. Taylor, 1942, 1960.

Gracilaria ferox J. Agardh. Taylor, 1929, 1942.

Gracilaria foliifera (Forskål) Børgesen. Taylor, 1960; 1929, as G. lacinulata.

Gracilaria mammillaris Montagne) Howe. Taylor, 1942, 1960.

Gracilaria verrucosa (Hudson) Papenfuss. Taylor, 1960; 1942, as G. confervoides.

Grateloupia filicinia (Wulfen) C. Agardh. Taylor, 1929, 1960.

tHalymenia sp. Collected by Earle at Holandés Cay and near Colon.

**Herposiphonia secunda (C. Agardh) Ambronn. Taylor, 1929, 1960.

***Hildenbrandia* prototypus Nardo. Collected by Earle at Holandés Cay and near Colon.

Hypnea cervicornis J. Agardh. Taylor, 1942, 1960.
Hypnea musciformis (Wulfen) Lamoruoux. Taylor, 1929, 1942, 1960.
Jania capillacea Harvey. Taylor, 1929, 1942, 1960.
Laurencia gemmifera Harvey. Taylor, 1942, 1960.
Laurencia microcladia Kützing. Taylor, 1929, 1960.
Laurencia obtusa (Hudson) Lamouroux. Taylor, 1942, 1960.
Laurencia papillosa (Forskål) Greville. Taylor, 1929, 1942, 1960.
Liagora ceranoides Lamouroux. Taylor, 1942, 1960.
Liagora valida Harvey. Taylor, 1942, 1960.
Lithophyllum pustulatum (Lamouroux) Foslie. Taylor, 1960; 1929, as *Dermatolithon pustulatum.*
Lithothamnion sp. Collected by Earle at Holandés Cay.
Melobesia membranacea (Esper) Lamouroux. Taylor, 1942.
Meristotheca floridana Kylin. Taylor, 1960; Howe, 1911, as *M. duchassaignii.*
Ochtodes secundiramea (Montagne) Howe. Taylor, 1929, 1960.
Peyssonniellia rubra (Greville) J. Agardh. Taylor, 1929, 1960.
Polysiphonia sp. Collected by Earle at Holandés Cay.
***Polysiphonia howei* Hollenberg. Collected by Earle near Colon.
Porolithon sp. Collected by Earle at Holandés Cay.
***Spyridia filamentosa* (Wulfen) Harvey. Taylor, 1942, 1960.
***Wrangelia argus* (Montagne) Montagne. Taylor, 1942, 1960.
†***Wurdemannia miniata* (Draparnaud) Feldman and Hamel. Collected by Earle near Colón.

CYANOPHYTA

***Microcoleus lyngbyaceus* (Kützing) Crouan. Taylor, 1942, as *Hydrocoleum comoides* Gomont.
Schizothrix calcicola (C. Agardh) Gomont. Drouet, 1968.
***Schizothrix mexicana* Gomont. Drouet, 1968.

SPERMATOPHYTA

***Halodule wrightii* Ascherson. den Hartog, 1964, 1970.
***Halophila baillonis* Ascherson *ex* Dickie. den Hartog, 1970, as ***H.** baillonis* and *H. decipiens* Ostenfeld.
Syringodium filiforme Kützing. den Hartog, 1970.
***Thalassia testudinum* Banks *ex* Konig. den Hartog, 1970.

PLANTS OF PACIFIC PANAMA

CHLOROPHYTA

t t*Acetabularia pusilla* (Howe) Collins. Collected by Earle from the Perlas Islands.
Boodleopsis verticillata Dawson. Dawson, 1960.

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t t New Record for Pacific Panama.

Bryopsis hypnoides Lamouroux. Taylor, 1945.
Caulerpa sp. Dawson and Beaudette, 1959.
††***Caulerpa microphysa* (Weber-van Bosse) J. Feldman. Collected by Earle from the Perlas Islands.
*tt**Caulerpa peltata* Lamouroux. Collected by Earle from the Perlas Islands.
*t †**Caulerpa racemosa* (Forskål) J. Agardh. Collected by Earle from the Perlas Islands and the Bay of Panama.
††***Caulerpa sertularioides (Gmelin)* Howe. Collected by Earle from the Perlas Islands.
t tChaetomorpha sp. Collected by Earle from the Perlas Islands.
Cladophora panamensis Taylor. Taylor, 1945.
Cladophora sp. Dawson and Beaudette, 1959.
††***Cladophoropsis mebranacea* (C. Agardh) Kützing. Collected by Earle from the Perlas Islands.
Codium setchellii Gardner *prox.* Taylor, 1945.
Derbesia attenuata Dawson. Dawson, 1960.
Enteromorpha lingulata J. Agardh. Taylor, 1945.
Phaeophila engleri Reinke. Taylor, 1945.
Pilinia lunatiae Collins f. simplex Thivy. Taylor, 1945.
Rhizoclonium kochianum Kützing. Dawson, 1960.
ttUlva sp. Collected by Earle in the Bay of Panama.

PHAEOPHYTA

***Colpomenia sinuosa* (Roth) Derbès and Solier. Collected by Earle in the Bay of Panama and the Perlas Islands.
Dictyota sp. Dawson and Beaudette, 1959.
Dictyota flabellata (Collins) Setchell and Gardner. Taylor, 1945.
Ectocarpus sp. Dawson and Beaudette, 1959.
**Lobophora *variegata (Lamouroux)* Womersley. Dawson and Beaudette, 1959, as *Pocockiella.*
Padina sp. Dawson and Beaudette, 1959.
Ralfsia sp. Howe, 1910; Dawson and Beaudette, 1959.
Sargassum sp. Dawson and Beaudette, 1959.
Sphacelaria sp. Dawson and Beaudette, 1959.

RHODOPHYTA

†***Acanthophora spicifera* (Vahl) Børgesen. Collected by Earle from the Perlas Islands.
Amphiroa sp. Dawson and Beaudette, 1959.
Amphiroa crosslandi Lemoine. Lemoine, 1929.
Antithamnion breviramosus Dawson var. *breviramosus* Dawson. Dawson, 1960.
Antithamnion dumontii Dawson. Dawson, 1960.
Archaeolithothamnion howei Lemoine. Lemoine, 1929.

** Occurs on Atlantic and Pacific coasts of Panama.

Bostrychia calliptera (Montagne) Montagne. Taylor, 1945.
t tCaloglossa sp. Collected by Earle in the Bay of Panama.
Watenella sp. Collected by Earle in the Bay of Panama.
***Centroceras* clavulatum (C. Agardh) Montagne. Taylor, 1945.
Centroceras minutum Yamada. Dawson, 1960.
Chondria sp. Dawson and Beaudette, 1959.
Cruoriella dubyi (Crouan and Cruoan) Schmitz. Dawson, 1960.
Cruoriella fissurata Dawson. Dawson, 1960.
Digenia sp. Dawson and Beaudette, 1959.
Fosliella *minuta* Taylor. Taylor, 1945.
Galaxura sp. Dawson and Beaudette, 1959.
Galaxura ramulosa Kjellman. Taylor, 1945.
Gelidiella sp. Dawson and Beaudette, 1959.
Gelidium pusillum (Stackhouse) LeJolis. Taylor, 1945.
Goniolithon tessellatum (Lemoine) Setchell and Mason. Taylor, 1945.
Gracilaria *panamensis* Taylor. Taylor, 1945.
†*Grateloupia* sp. Collected by Earle in the Bay of Panama.
**Herposiphonia secunda (C. Agardh) Ambronn. Taylor, 1945.
**Hildenbranclia prototypus Nardo. Taylor, 1945.
Hypnea *ramosa* J. Agardh. Taylor, 1945.
Jania sp. Dawson and Beaudette, 1959.
t tLaurencia sp. Collected by Earle from the Perlas Islands.
Liagora sp. Dawson and Beaudette, 1959.
Lithophyllum sp. Lemoine, 1929.
Lithophyllurn bracchiatum (Heydrich) Lemoine. Lemoine, 1929; Taylor, 1945.
Lithophyllum (?) coibense Lemoine. Lemoine, 1929.
Lithophyllum divaricatum Lemoine. Taylor, 1945.
Lithophyllum (?) fetum Foslie. Lemoine, 1929.
Lithophyllum (?) *lividum* Lemoine. Lemoine, 1929.
Lithophyllum (?) *propinquum* Foslie var. cocosica Lemoine. Lemoine, 1929.
Lithophyllum *saxicolum* Lemoine. Lemoine, 1929.
Lithothamnion *mesomorphum* Foslie (?). Lemoine, 1929.
Lithothamnion *australe* Foslie. Taylor, 1945.
Lithothamnion indicum Foslie var. subtilis Foslie. Lemoine, 1929.
Melobesia fertilis Lemoine. Lemoine, 1929.
Mesophyllum australe Foslie var. tualensis Foslie; var. nzinutula Foslie. Lemoine, 1929.
†?*Nemalion* sp. Collected by Earle from the Bay of Panama.
tPeyssonniella sp. Collected by Earle from the Perlas Islands.
***Polysiphonia howei* Hollenberg. Taylor, 1945.
Porolithon cocosicum Lemoine. Lemoine, 1929.
Spyridia sp. Dawson and Beaudette, 1959.
***Spyridia* filamentosa (Wulfen) Harvey. Taylor, 1945.
Taenioma perpusillum (J. Agardh) J. Agardh. Dawson, 1960.

***Wrangelia* argus (Montagne) Montagne. Dawson, 1960.

**Wurdemannia miniata (Draparnaud) Feldman and Hamel. Taylor, 1945.

CYANOPHYTA

Entophysalis conferta Drouet and Daily. Drouet and Daily, 1954.

Entophysalis deusta Drouet and Daily. Taylor, 1945, as *Hyella* caespitosa Bornet and Flahault; Drouet and Daily, 1954.

***Microcoleus* lyngbyaceus (Kützing) Crouan. Taylor, 1945, as Lyngbya confervoides Gomont; Drouet, 1968.

Oscillatoria submembranacea Ardissone and Strafforello. Drouet, 1968.

***Schizothrix mexicana* Gomont. Drouet, 1968.

Spirulina *subsalsa* Oersted. Drouet, 1968.

SPERMATOPHYTA

Halodule *beaudettei* (den Hartog) den Hartog. den Hartog, 1960, 1964, 1970.

Halodule ciliata (den Hartog) den Hartog. den Hartog, 1960, 1964, 1970.

***Halodule* wrightii Ascherson (?). den Hartog, 1960, 1964, 1970.

**Halophila baillonis Ascherson ex Dickie. den Hartog, 1960, 1970.

**Thalassia testudinum Banks ex Konig (?). den Hartog, 1970; Setchell, 1935.

ECOLOGY AND SPECIES DIVERSITY OF CORAL REEFS ON OPPOSITE SIDES OF THE ISTHMUS OF PANAMA

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Within the Indo-Pacific region or within the Caribbean, corals tend to be widely distributed. This is due, perhaps, to the existence of planktonic larval stages in corals and the basic compatibility of most tropical shallow-water marine environments for their growth. Out of a combined total of some 100 hermatypic scleractinian genera, the Atlantic and the Pacific have in common only six: Acropora, Cladocora, Favia, Madracis, Porites, and Siderastrea. *Agaricia* and Solenastrea, known from the Caribbean, have been reported as well from the eastern Pacific, on the basis of questionable beach-worn specimens (Durham and Barnard, 1952). Out of a combined total of some 800 hermatypic species, the two oceans have, perhaps, one (Siderastrea radians) in common. Much less is known about the ahermatypic scleractinians, but so far, at least 20 of a combined total of roughly 150 ahermatypic genera appear to be represented in both oceans, with possibly several species in common (e.g., Tubastraea aurea and Madracis asperula). Good evidence is available (Vaughan and Wells, 1943) to suggest that the generic and specific similarity in the Atlantic and Pacific ahermatypic faunas increases with depth. In terms of their shallow-water coral faunas, however, these two oceans are very different. Work being conducted now in Panama allows us to be more precise about these differences and to report quantitative observations which can be repeated at some time in the future to recognize changes, either natural or those

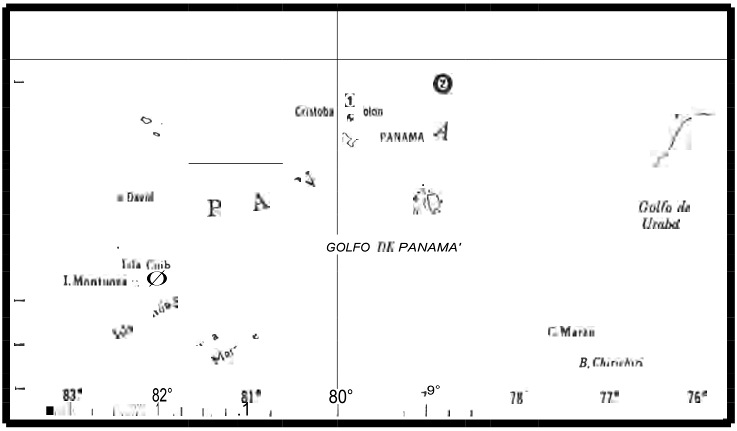

FIG. 1. Map of Panama showing the author's study localities listed in Appendices I and II. 1. Isla Galeta; 2. Islas San Blas; 3. Isla Taboga; 4. Islas Perlas; 5. Isla Naranjas; 6. Isla Coiba; 7. Islas Contreras; 8. Islas Secas; 9. Isla Parida.

caused by man. This must be the goal of any long range biological survey and is especially important in an area such as this, where unbiased monitoring of the marine environment is highly desirable.

The main body of this work was done at Galeta and the Islas San Blas, on the Atlantic side of Panama, with comparative observations from the islands of Taboga, Naranjas, Coiba, Contreras, Secas, and Parida, on the Pacific side (Fig. 1). The San Blas islands stretch from 86 km northeast of Colon, parallel to the coast, at a distance of not more than 15 km (usually much less), to within 48 km of the Colombian border, a distance of 175 km. In the region from the Golfo de San Blas to Isla Tigre (9°26'N; 78°30'W) many of the islands are protected on their seaward side by a particularly well-developed algal ridge (Fig. 2) constructed of crustose coralline algae and vermetid gastropods (Glynn, in press). In front of this impressive structure is an area devoid of coral growth, perhaps due to the tremendous wave action on these raised ramparts and to the shallowness of the bottom in this area (Fig. 3); but on the leeward side of the San Blas Islands,

FIG. 2. Algal ridge at Morotupo, Mauqui (Holandés Cays), Islas San Blas. Atlantic side.

steep drop-offs and strong currents combine to favor the growth of coral reefs (Fig. 4), as rich as any in the Caribbean. This can be said after personal observations in Bermuda, the Florida Keys, Jamaica, the Leeward Islands, Guadeloupe, Curaçao, and various localities in Panama. Between 30 and

FIG. 3. Looking up and across the barren zone at waves hitting the algal ridge, Mauqui (Holandés Cays), Islas San Blas.

Fig. 4. Coral reef at 20 meters off Arcuadargana (9°33'12"N; 78° 56'33"W), Islas San Bias, facing San Blas Channel.

50 meters depth, there is a sand bottom which supports isolated patches of Agaricia, Montastrea, and other corals (Fig. 5) and continues down to a maximum depth of 70 meters.

The number of species of corals in the San Blas is truly impressive (Appendix I). To date, 49 hermatypic and 16 ahermatypic scleractinians and four species of Millepora can be reported from the Caribbean side of Panama, and it seems certain that more will be found, especially among the ahermatypes, as work in this region continues. This compares favorably with the 52 hermatypes and approximately 20 ahermatypes currently known from Jamaica where Goreau (Goreau and Wells, 1967) and his co-workers have, over the last 16 years, discovered the greatest number of species for any single Caribbean area. The absence of Dendrogyra cylindrus in Panama is curious; this is a conspicuous coral present on most of the Caribbean islands and the Florida Keys, but absent from Panama and, apparently, also from Colombia (Pfaff, 1969; Geyer, 1969). If this species is actually confined to the north and central Caribbean, it represents the first case of restricted distribution among this normally widespread fauna. The presence of Solenastrea in Panama is still questionable and more collecting is necessary to confirm it.

FIG. 5. Agaricia lamarcki (spiraled), Montastrea *annularis* (bottom middle), and Porites astreoides (bottom left) on mud bottom at 35 meters off Suibirtupo, Islas San Blas.

In order to quantify the impression of diversity, I laid 2-meter square grids along a transect running from shallow- to deep-water and counted the number of species in each grid. The graph which results (Fig. 6) shows the uniformity of species distribution on the reef face. The graph compares favorably with the upper depth distribution of the same species in Jamaica (Goreau and Wells, 1967; see also Lang, 1970), but does not represent well their lower extensions, since 30 m was the depth limit imposed by a shortage of compressed air and time.

Even though the kinds of coral do not change greatly with depth, their relative abundances do; therefore, to be more

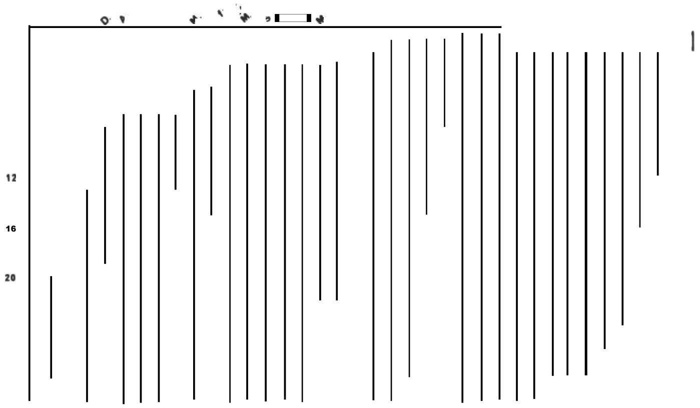

FIG. 6. Depth distribution of hermatypic reef corals based on 2-meter square transects down the reef faces at Isla Galeta and Islas San Blas, Atlantic, Panama.

precise, I devised the following method. A chain with links 1.3 cm long and with a total length of 10 meters was laid (Fig. 7) parallel to the depth contour at 3 meter intervals along the main transect line, shallow to deep, and the number of links covering each species of living coral was recorded. This method is particularly well-suited for such a study because it is easy to use with SCUBA and because, in compliance with current concepts of species diversity measurement (MacArthur, 1965), it records both the number of species and their relative abundances.

A direct analysis of the chain link data produced the diversity vs. depth graph shown in Figure 8. Diversity is here defined by the Shannon formula as adapted by Pielou (1966).

$$H' - p_i \log_2 p_i$$

where N is the total number of chain links covering s species of living coral, N_i is the number of chain links covering the ith species of coral, and $p_i = N_i / N$. Therefore,

$$N \quad N_i$$

FIG. 7. For measurement of species diversity, a chain was laid across the reef face and the number of links covering each species of coral was counted. Photograph from Islas San Bias.

The calculation of diversity and its various parameters was greatly facilitated by the use of the tables by Lloyd, Zar, and Karr (1968) and several especially constructed computer programs. As formulated, diversity has two major components: the number of species (species richness) and the evenness of distribution of individuals among these species (species evenness). Simply stated, high diversity would result from a sample having both a large number of species and an equitable distribution of the individuals among these species; low diversity, from a sample having a few species in which a few of these have a disproportionately large number of individuals.

From the graph (Fig. 8), at least two general trends are visible. Species diversity values increase from 0.0 at the surface to a peak of 3.2 at approximately 5 meters, continue between 1.5 and 3.5 down to about 25 meters, and then fall off to 0.0. Superimposed on this general trend is an increase in diversity toward cliff edges. Goreau and Wells (1967) noted that the most profuse coral growth generally occurs at the edges of steps, and, while they were referring to major geological features on the submerged Jamaican reef terraces, the same

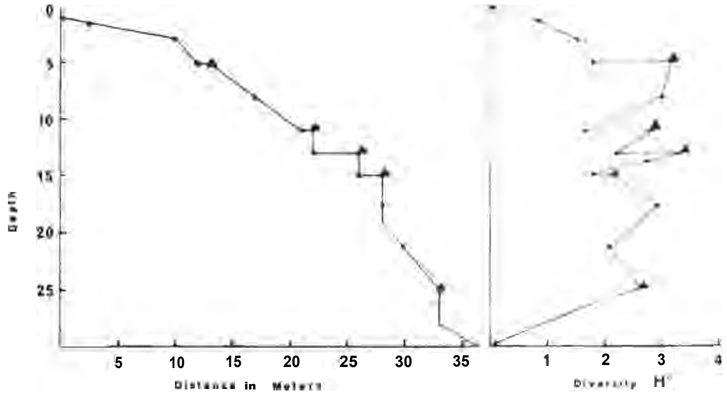

FIG. 8. (Right) The Shannon formula (H') in relation to depth on Arcuadargana, Islas San Blas. (Left) Cross-section of the transected reef. Chain transect positions designated by ▲ for cliff edge positions; • for all other reef face positions.

appears to hold here for the smaller buttress platforms of the San Blas. Preliminary evidence suggests this may be due to sedimentation in the back-shelf region, possibly an increase in turbulence (= food?) on the cliff edge, or, possibly, the amount of light impinging on the cliff. Experiments are being conducted to examine this phenomenon. Another parameter of the same transect data is shown in Figure 9. It appears that diversity correlates very well with the component of species richness, giving a regression coefficient of $r = 0.9028$, a highly significant value ($P < 0.001$). The best single indicator of species diversity in Atlantic reef corals is simply the number of species. This supports the same general finding reported by Johnson and Raven for plants (1970).

Limited work in the eastern Pacific in the summer of 1970 and March—April 1971, allows some tentative comparisons with the Caribbean region, but it must be stressed that basic field work in this region is still urgently needed. Elsewhere in this symposium, Dr. Peter W. Glynn has discussed several of the physical parameters influencing the environments of Atlantic and Pacific inshore areas. Two of these should be repeated with respect to the Pacific because of their special influence on corals. Not only is the average annual temperature of the

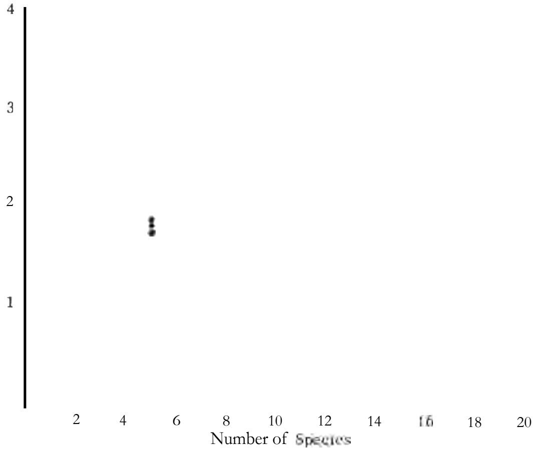

FIG. 9. Diversity (H') in relation to the component of species richness in chain transect counts from Arcuadargana, Islas San Bias.

eastern Pacific lower, 26.6°C at Balboa compared to 27.9°C at Cristóbal on the Caribbean side, but also, perhaps more important as far as corals are concerned, the temperature of the surface waters fluctuates a great deal more in the eastern Pacific, from 15° to 33°C at Balboa, but only from 24° to 31° at Cristóbal (Panama Canal Company, 1967; Rubinoff, 1968). Averages, however, can be misleading and work now in progress (Glynn and Stewart, unpublished) should give us more precise information about the distribution of physical phenomena and coral reefs on the Pacific side of Panama. Tidal ranges on opposite sides of the isthmus are strikingly different as well. During any one year the absolute range between the highest and the lowest water mark is 6.5m at Balboa on the Pacific, but only 0.7m at Cristóbal on the Atlantic. Further, Balboa, on the Pacific, averages a daily tidal change of 3.9m with a maximum daily range of 6.3m, whereas Cristóbal averages a daily tidal range of only 0.3m with a maximum daily range of only 0.5m (Panama Canal Zone Company, 1967; Rubinoff, 1968).

As Palmer (1928) and Crossland (1927) have pointed out for the eastern Pacific and the shallow-water environments near large land masses, sedimentation is probably a strong deterrent for corals and the formation of coral reefs. Its seems likely that even turbidity in the water could be a deterrent, and from April to November, Panama's rainy season, underwater visibility in this region is very poor (Secchi disc readings of 3m are common in Coiba in September). The deeper distributions of coral species, as well as those of reefs, might likewise be affected; in fact, it appears as if depth limits of corals of the eastern Pacific are less than those of the Caribbean.

The two oceans are very different biologically. In Appendix II the hermatypes and ahermatypes found so far during our shallow-water explorations in the eastern Pacific are listed. Despite the fact that fauna has been studied taxonomically (Boschma, 1948; Durham, 1947, 1962, and 1966; Durham and Barnard, 1952; Hertlein and Emerson, 1957; Marenzeller, 1904; Pourtalès, 1875; Vaughan, 1906 and 1919; and Verrill, 1864, 1865, 1866a and b, 1867, 1868, 1869a and b, and 1879a, b, and c) and, to some extent, ecologically (Squires, 1959), it remains poorly known. In recent collections, intermediates among the five forms of *Pocillopora* have been noted. Species-level distinctions within *Porites, Millepora,* and *Pavona* have also become difficult. I have retained the present classification because we have no taxonomic criteria available to deal with such intergrading forms and because, even if these species names designate polymorphic growth forms (either ecologically or genetically induced), under some conditions they are distinct. It is only when intermediates are found that identification becomes frustrating. These difficulties notwithstanding, at any taxonomic level, the affinities of this fauna clearly indicate an impoverished Indo-Pacific fauna, not at all Caribbean in nature. As many as 10 of the 21 corals listed in Appendix II may be conspecific with Indo-Pacific forms, and the one species that is common to both the eastern Pacific and the Caribbean, *Tuba straea aurea (= tenuilamellosa)* is pantropical in distribution.

A general description of the reefs of the Pacific side of Panama is now in progress (Peter W. Glynn, in manuscript), and only a small amount of background information is neces-

FIG. 10. Rocky lava point at 5 meters off Isla Uva (one of the Islas Contreras), Pacific side, Panama. The veneer of corals (Porites *panamensis* ? in center), gorgonians, and sponges is a common faunal assemblage in this region.

sary to place the diversity measurements in context. The paucity of species in this area has been commented on above. Further, in contrast to the Caribbean where much of the coast line is fringed by reefs, the Pacific shows a paucity of reef formations. The relative rarity of such structures caused them to be overlooked by early investigators, and a mystique developed in the literature concerning the absence of reefs from this region (Crossland, 1927; Wells, 1957). Certainly, however, one is almost constantly aware of the lava substratum of the eastern Pacific, which is much rarer on the Caribbean side (Fig. 10). Where reefs do occur, they are generally shallow

FIG. 11. Pocillopora reef top at Isla Uva (one of the Islas Contreras).

(> 10 meters) and are formed of Pocillopora banks, probably monospecific (Fig. 11), bound together by calcareous red algae (Fig. 12). As would be expected, low diversity values characterize these reef and nonreef areas. Diversity increases on the one hand due to the presence of corals, such as Tubastrea aurea, Porites spp., and Pavona varians, that live below or adjacent to the main branches of Pocillopora and, therefore, are eventually crossed by the transect line; on the other hand, increased diversity results from the presence of predominantly reef-top dwellers, such as Pavona clivosa or P. gigantea. The highest diversity value recorded so far is from the reef at Isla Uva, one of the Islas Contreras, with a Shannon (H') value of 1.81 compared to a maximum of 3.41 on the Atlantic side. This value is comparable to the shallowest and to the deepest areas in the Caribbean. These three areas, the eastern Pacific, the shallow and the deep Caribbean, are all characterized by severe physical stress: wave surge and possible desiccation in shallow-water in the Caribbean; heavy sedimentation in bottom areas in the Caribbean; and temperature and tidal rigors in the eastern Pacific. It is important to be cautious in this particular correlation of physical rigor and low diversity since, as pointed out above, the eastern Pacific reefs are

FIG. 12. Natural cross-section of monspecific *Pocillopora* bank at Islas Secas, Pacific, Panama, showing method of reef growth. Toppled block in the center measures 1.5 meters.

faunally Indo-Pacific, not Caribbean, and, possibly, very young compared to the Caribbean; thus, there may be a very strong historical component in the observed diversities.

Values of percentage coverage approaching 90% are common in the eastern Pacific; such high values are rarely found in the Caribbean. On one reef in the Islas Secas, 8.5 m to 9 m of the 10 m transect line covered living coral. These reefs represent well the repeated biological observation of low diversity corresponding to high abundance.

Another factor of importance in this area is the presence of the coral predator, *Acanthaster*, (Fig. 13). It does not appear to us to be in a plague situation, as has been reported for some areas in the Indo-Pacific (Chesher, 1969a), but further studies are needed. Its relationship to the proposed sea-level canal is obvious. The Caribbean corals, which have developed in isolation from this predator, can hardly be expected to have evolved resistance to it in the way that some Indo-Pacific species seem to have (Chesher, 1969b). In April, 1971, Dr. Glynn (personal communication) was able to feed the Caribbean corals *Porites furcata*, *P. asteroides*, and *Agaricia agari-*

FIG. 13. *Acanthaster* attacking Pavona ponderosa at Isla Uva (one of the Islas Contreras). White areas in upper middle and lower left of photograph are the exposed skeletons of incompletely digested Pavona colonies.

cites to a recently captured eastern Pacific Acanthaster. It proceeded to eat large portions of these colonies. How can one help but feel worried at the possible introduction of this animal into the Caribbean? Valid predictions, however, as to the outcome of such an introduction are impossible.

The interpretation of the geological history of this region has relied heavily on the data obtained from the study of fossil and recent coral reefs. Yet, major unanswered questions remain that are vital, not only for a reasonably complete picture of the history of this region, but also for an intelligent prediction of possible environmental effects of faunal exchange between the Caribbean and the eastern Pacific. To put the problem in perspective, it seems reasonable that the Isthmus of Panama is probably less important to the overall development of coral reefs in the tropical western hemisphere than either the Tethys Sea or the hitherto unexplained coral extinction (Newell, 1959) which took place in this hemisphere during the Miocene. It is felt that the route to the tropical western hemisphere prior to the Miocene was from the east across the Tethys Sea (Wells, 1956) and not from the west across the vast, islandless expanse of the East Pacific Basin. The Miocene extinctions in this region occurred simultaneously with the closing off of the Tethys Sea to the east, despite the fact that during this whole time there were no obstructions between this region and the species-rich Indo-Pacific to the west (Wells, 1969). Throughout a time span of some 10-15 million years, then, the Indo-Pacific with its rich coral fauna was not a source of recolonization and reinfusion for the Caribbean area. By the Pliocene, most of the important faunal changes had taken place, and the closing off of the Caribbean from the eastern Pacific by the emergence of the Isthmus of Panama in the late Pliocene (Whitmore and Stewart, 1965) seems, in retrospect, like closing off the back gate to an empty lot.

Problems remain, however. First of all, we know that the eastern Pacific is not an empty lot and that corals may come all the way from the Indo-Pacific and establish themselves, even in the harsh environment of the eastern Pacific. This is suggested by the apparent similarity, at the species level, between some of the present eastern Pacific coral faunas and those of the Indo-Pacific. Has there been a post-Pliocene introduction of some of this fauna from the Indo-Pacific?

Equally perplexing is the fact that some Indo-Pacific corals existed in the pre-isthmian Pliocene of the eastern Pacific (whether they were new immigrants or remnants from the old tropical western hemisphere fauna is not clear) but were not able to recolonize or even exist in the physically adjacent Caribbean at this time. A prime example is Pocillopora. This genus is common in Miocene reefs of both the Caribbean and the eastern Pacific, but has been restricted to the eastern Pacific since the Pliocene (Durham, 1966). I can understand why many corals became extinct when stranded west of the Panamanian isthmus: prior to the rising of the isthmus, this area had received a steady inflow of warm Caribbean water (Fell, 1967), and the corals which survived in or colonized the post-isthmian eastern Pacific had to withstand the stresses of tidal, temperature and salinity fluctuations encountered. But I cannot understand why the Indo-Pacific corals, and especially the Pliocene eastern Pacific forms, such as Pocillopora, were unable to contribute to the newly-isolated Caribbean area. A partial clue to the problem may lie in the persistence of Pocillopora in the north central areas of the eastern Pacific during the Miocene and the Pliocene, despite its extinction in the physically adjacent Caribbean. Should one suggest that the eastern Pacific fauna might have been a colder-water fauna, restricted to the region around Baja California? The difficulty of this idea is that it contradicts what we know about the distribution of recent corals. Wells (1955, 1969) has shown for the Great Barrier Reef and the Indo-Pacific, that, as one moves away from the main reef areas, the corals simply drop out and are not replaced by a colder-water fauna. The problem remains for Pocillopora, however, because it does appear to have been restricted, in some way, to the eastern Pacific, despite the fact that, as mentioned before, corals tend to disperse widely.

As mentioned above, the origin of the present eastern Pacific coral fauna is unclear. On the one hand, the apparent species-level similarity between it and the Indo-Pacific fauna argues in favor of a post-Pliocene introduction from the Indo-Pacific of at least some of this fauna. On the other hand, the generic-level similarity between the modern eastern Pacific fauna and the Tertiary fossils from this same region argues in favor of its being simply a relict remnant of the older pan-tropical Tethyan fauna. Perhaps both of these have interacted to produce the modern coral associations of the tropical eastern Pacific.

In any case, these are important questions since we might reintroduce, with a sea-level canal, these same corals which did not establish themselves in the Caribbean before. If they did not establish themselves before there was an isthmus, will they now, when the barrier is broken down? Likewise, there was occasion for the Caribbean fauna to invade and colonize the eastern Pacific before the rising of the isthmus. It, too, was unsuccessful.

The reduction of the Tethyan element in the Caribbean region during the Miocene and Pliocene, and the failure of the eastern Pacific forms to reestablish themselves there before the rising of the Isthmus of Panama, is particularly curious in the light of recent work by Lang (1970) on the competitive ability of scleractinian corals. She has shown that certain species of corals, when competing for space, can overcome the competing coral and then overgrow its dead skeleton. In experiments with Indo-Pacific species and Caribbean species, the species of the Indo-Pacific genus, *Lobophyllia,* always survives, even when competing with the most dominant Caribbean species. One is reminded here of Briggs' hypothesis of the evolution of competitive dominance among highly diverse faunas (Briggs, 1967) which caused him to suggest the possibility of a replacement of the Caribbean fish fauna by the Indo-Pacific inshore fish fauna of the eastern Pacific, if the sea-level canal were dug (Briggs, 1968). In the last analysis it is individuals, not faunas, which compete and, therefore, I would not wish to try to predict the outcome of experiments involving physical contact between eastern Pacific and Caribbean corals. Considering that the affinities of the corals of the eastern Pacific are Indo-Pacific and that Indo-Pacific corals which have been tested always survive over Caribbean corals, I would say that, at the very least, experiments are needed.

SUMMARY AND CONCLUSIONS

1. Of a combined total of 100 hermatypic scleractinian genera, the Caribbean and the Pacific have only six in common; of a combined total of some 800 species, they have perhaps only one in common. Of a combined total of approximately 150 ahermatypic scleractinian genera, the Caribbean and the Pacific have at least 20 in common, with, perhaps, several species also in common.

2. Forty-nine hermatypic and 16 ahermatypic scleractinians plus four species of *Millepora* are found on the Caribbean side of Panama. This makes it one of the richest areas in the Caribbean.

3. The eastern Pacific is, on any taxonomic level, an impoverished Indo-Pacific fauna, with only 16 hermatypic and one ahermatypic scleractinian and three milleporines in the areas sampled.

4. Using a chain transect method to obtain data for the precise measurement of diversity, two general trends are visible on San Blas coral reefs in the Caribbean. (1) Species diversity increases from 0 at the surface to a peak of 3.14 at approximately 5 meters, continues, thus, down to 25 meters (the lower limit of reef growth in the transect areas), and then falls off to 0. (2) Superimposed on this general trend is an increase in diversity toward cliff edges. Maximum diversity values approach 3.5. Despite the fact that diversity has several components, the best single indicator for species diversity in Atlantic reef corals is simply the number of species.

5. The extensive lava coasts and rarity of reefs in the eastern Pacific offer a striking biological and physical contrast to the limestone-coral coast of the Caribbean side. The eastern Pacific is also a high-stress environment, in terms of tidal, temperature, and salinity fluctuations, whereas the Caribbean is relatively stable for these factors. Maximum diversity values for the eastern Pacific approach only 1.81, but a comparison with Caribbean diversities must be cautious since divergent origins and geological histories of these two areas make the values difficult to interpret.

6. Several sources may have contributed to the origin of the modern eastern Pacific coral fauna. Apparent faunal similarities, at the species level, between the eastern Pacific and the modern Indo-Pacific fauna, suggest the recent post-Pliocene introduction of some of the eastern Pacific fauna. Similarities at the generic-level, between the modern eastern Pacific fauna and the Tertiary fossils from this same region, however, point toward the old pan-tropical Tethyan fauna as a source for the modern eastern Pacific fauna. The clear similarity between the modern eastern Pacific and Indo-

Pacific faunas, then, would be due to their common Tethyan origin rather than a recent migration from the Indo-Pacific to the eastern Pacific.

7. The reduction of the Tethyan element from the Caribbean, before the rising of the Isthmus of Panama, is perplexing in light of the demonstrated competitive superiority of some Indo-Pacific corals over Caribbean species. Further, since genetic interaction between these distinct faunas is not likely, further work should concentrate on ecologically equivalent genera such as *Porites* and *Pocillopora* or *Montastrea* and *Pavona,* and, especially, on their competitive abilities.

8. The coral predator, *Acanthaster,* exists in the eastern Pacific and its ability to eat corals, both Caribbean and eastern Pacific, has been demonstrated. This constitutes a real and exceptionally serious problem to be considered, concerning the joining of the oceans.

ACKNOWLEDGMENTS

I would like especially to thank Richard M. Lay of Yale College, my diving partner, for his continuous efforts on this project and Drs. Peter W. Glynn and Ira Rubinoff of the Smithsonian Tropical Research Institute, Balboa, Canal Zone for their advice and for the use of the R/V TETHYS. Dr. G. Evelyn Hutchinson, Dr. Willard D. Hartman, Yale University; Dr. John W. Wells, Cornell University; Dr. J. Wyatt Durham, University of California; and Dr. Peter W. Glynn and Dr. Charles Birkeland, Smithsonian Tropical Research Institute, have made helpful criticisms on this manuscript. I am further indebted to Dr. Thomas Siccama, Dr. Thomas Lovejoy and Richard Sage, for their help on computer problems, and to the late Dr. Thomas F. Goreau for a fruitful discussion on this project. This research has been supported by a Grant-in-Aid from the Society of Sigma Xi and grants from the Organization for Tropical Studies and from the Peabody Museum of Natural History of Yale University.

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APPENDIX I

SHALLOW-WATER CARIBBEAN CORALS OF PANAMA

"*" indicates ahermatypic species; "?" indicates the taxonomic confirmation is necessary; "P" refers to station numbers of R/V JOHN ELLIOTT PILLSBURY off Panama (Bayer, *et al.,* 1970); "LTW" refers to material in the collection of Mr. and Mrs. L. T. Williams (Bayer, *et al.,* 1970, Appendix, p. 1, *et seq.).*

Species	Isla Galeta	Islas San Bias	Other
Class: Anthozoa Ehrenburg			
Order: Scleractinia Bourne			
Family: Astrocoeniidae Koby			
Stephanocoencia michelinii Milne Edwards & Haime	X	X	
Stephanocoenia cf. michelinii ? (= No. 2 in Goreau and Wells, 1967)		X	
Family: Pocilloporidae Gray			
Madracis decatis (Lyman)	X	X	
Madracis mirabilis (Duchassaing & Michelotti)		X	
**Madracis asperula (Milne* Edwards & Haime)			P-336 (ca. 64-128 m)
**Madracis bruggemanni* (Rideley) ?			P-417 (51 m)
**Madracis pharensis* (Heller)			P-439 (18-22 m)
Family: Acroporidae Verrill			
Acropora palmata (Lamarck)	X	X	
Acropora cervicomis (Lamarck)	X	X	
Acropora prolifera (Lamarck)		X	
Family: Agariciidae Gray			
Agaricia agaricites (Linnaeus) forma *agaricites*	*X*	*X*	
Agaricia agaricites (Linnaeus) forma *danae*	X	X	
Agaricia agaricites (Linnaeus) forma *crassa*	*X*	*X*	
Agaricia agaricites (Linnaeus) forma *purpurea*	*X*	*X*	
Agaricia agaricites (Linnaeus) forma *humilis*	X	X	
Agaricia tenuifolia Dana	X	X	
Agaricia undata (Ellis & Solander)		X	
Agaricia lamarcki Milne Edwards & Haime (= No. 15 in Goreau and Wells, 1967)		X	
Agaricia fragilis Dana		X	
Agaricia cailleti (Duchassaing & Michelotti) ?			P-417 (51 m)
Helioseris cucullata (Ellis & Solander)	X	X	
Family: Siderastreidae Vaughan and Wells			
Siderastrea siderea (Ellis and Solander)	X	X	
Siderastrea radians (Pallas)	X	X	

APPENDIX I CONTINUED

Species	Isla Galeta	Islas San Blas	Other
Family Poritidae Gray			
Porites asteroides Lesueur	X	X	
Porites branneri Rathbun	X	X	
Porites porites (Pallas)	X	X	
Porites divaricata Lesueur	X	X	
Porites furcata Lamarck	X	X	
Porites sp., *cf. astreoides (*= No. 25 in Goreau and Wells, 1967)		X	
Family Faviidae Gregory			
Favia fragum (Esper)	X	X	
Diplora clivosa (Ellis & Solander)	X	X	
Diplora labyrinthiformis (Linnaeus)		X	
Diploria strigosa (Dana)	X	X	
Manacina areolata (Linnaeus)	X	X	
Colpophyllia natans (Muller)	X	X	
Colpophyllia amaranthus (Muller) (= *natans ?)*			
Colpophyllia breviserialis Milne Edwards & Haime	X	X	
Cladocora arbuscula (Lesueur)		X	
Montastrea annularis (Ellis & Solander)	X	X	
Monastrea cavernosa (Linnaeus)	X	X	
Solenastrea bournoni Milne Edwards & Haime ?			LTW
Family Rhizangiidae D'Orbigny			
**Astrangia solitaria* (Lesueur)	X	X	
**Astrangia* sp. 1			P-332-334 + 435 (48-57 m)
**Phyllangia americana* Milne Edwards & Haime			“Atlantic, Panama"
**Colangia immersa* Pourtalès			P-330 (64-128 m)
**Colangia* sp. 1			P-439 (18-22 m)
Family Oculinidae Gray			
Oculina diffusa Lamarck		X	
Family Meandrinidae Gray			
Meandrina meandrites (Linnaeus)	X	X	
Dichocoenia stokesii Milne Edwards & Haime	X	X	
Dichocoenia stellaris Milne Edwards & Haime? (= No. 45 in Goreau and Wells, 1967 ?)			LTW
Family Mussidae Ortmann			
Mussa angulosa (Pallas)	X	X	
Scolymia lacera (Pallas)	X	X	
Scolymia cubensis (Milne Edwards & Haime)		X	
Isophyllia sinuosa (Ellis & Solander)	X	X	
Isophyllia multiflora Verrill (= *sinuosa ?)*	X	X	
Isophyllastrea rigida (Dana)		X	

APPENDIX I CONTINUED

Species	Isla Galeta	Islas San Bias	Other
Mycetophyllia lamarckana Milne Edwards & Haime	X	X	
Mycetophyllia sp. A (see Lang, 1970)		X	
Mycetophyllia sp. B (see Lang, 1970)	X	X	
Mycetophyllia sp. C (see Lang, 1970)		X	
Family Caryophyllidae Gray			
**Caryophyllia flos* (Pourtalès)			P-405 (92-93 m)
**Cmyophyllia* sp. 1			P-405 (92-93 m)
**Paracyathus defilippi* Duchassaing & Michelotti			P-330 -I- 420 (51-128 m)
**Desmophyllum riisei* Duchassaing & Michelotti			P-405 (92-93 m)
Eusmilia fastigiata (Pallas)	X	X	
Family: Flabellidae Bourne			
**Gardineria* sp.			"Atlantic, Panama"
Family: Dendrophylliidae Gray			
**Balanophyllia floridana* Pourtalès			P-405 (92-93 m)
**Balanophyllia* sp. 1			P-403 405 (64-99 m)
**Tubastraea aurea* (Quoy & Gaimard)?			
Class: Hydrozoa Owen			
Order: Milleporina Hickson			
Family: Milleporidae Fleming			
Millepora alcicornis (Linnaeus)	X	X	
Millepora complanata Lamarck	X	X	
Millepora squarrosa Lamarck		X	
Millepora moniliformis (Dana)	X	X	

APPENDIX II

TENTATIVE LIST OF THE SHALLOW-WATER CORALS FROM THE PACIFIC COAST OF PANAMA

Tentative identifications by J. W. Durham (Scleractinia) and H. Boschma (Milleporina); serious taxonomic uncertainties exist within most of the genera below (see text); "?" refers to uncertain determinations or locality data; "*" indicates name written by Verrill on his labels (Peabody Museum of Natural History, Yale University) as the type variety of species *capitata,* but never used in print; "**" *fide* Durham and Barnard, 1952; "***" *fide* Durham, 1947; terms in quotes are for personal field identification.

Species List	Isla Taboga (8°50'N; 79°35'W)	Islas Perlas (8°10-40'N; 78°46'–79°10'W)	Islas Naranjos (7°15'N; 80°56'W)	Isla Coiba (7°17–40'N; 81°35-50'W)	Islas Contreras (7°49'N; 81°45'W)	Islas Secas (7°58'N; 82°01'W)	Isla Parida (8°08'N; 82°21'W)	Indo-Pacific
Class: Anthozoa Ehrenberg								
Order: Scleractinia Bourne								
Family: Pocilloporidae Gray								
**Pocillopora capitata* var. *capitata* Verrill [= P. *elegans* Dana, cf. Squires, 1959]	x	x	x	x	x	x	x	x?
Pocillopora capitata var. *pumila* Verrill 1870 [= P. *elegans* Dana, cf. Squires, 1959]	x	x	x	x	x	x	x	x ?
Pocillopora capitata var. *porosa* Verrill 1870 [= P. *verrucosa* (Ellis & Solander), cf. Squires, 1959]	x	x	x		x	x	x	x ?
Pocillopora capitata var. *robusta* Verrill 1870 [= P. *elegans* Dana, cf. Squires, 1959]		x		x	x	x		x ?

APPENDIX II CONTINUED

Species List	Isla T[illegible] (8°50'N; 79°35'W)	Islas Per[illegible] (8°10-40'N; 78°46'— 79°10'W)	Islas N[illegible] (7°15'N; 80°56'W)	Isla C[illegible] (7°17-40'N; 8P35-50'W)	Islas Contreras (7°49'N; 81°45'W)	Islas S[illegible] (7°58'N; 82°01'W)	Isla Parida (8°08'N; 82'21'W)	Indo-Pacific
Pocillopora lacera Verrill 1869 [= *P. damicornis* (Linnaeus); cf. Squires, 1959]	X	[illegible]		[illegible]	[illegible]	X	[illegible]	[illegible] ?
Family: T[illegible] Vaughan and Wells								
P.sammocora brighami (Vaughan 1907)		X		X	X	X		X
Psammocora sp. [illegible]. ?						?		
Family: A[illegible] Gray								
Leptoseris? sp. [illegible].?				[illegible]	X	[illegible]		
Pavona clivosa Verrill 1869	X	[illegible]	X	[illegible]	X	X	X	
Pavona ponderosa (Gardiner 1905)				[illegible]	[illegible]	[illegible]		[illegible]
Pavona sp. [illegible].?"[illegible]"				X				
Pavona varians Verrill 1864	X	X		X	X	X	X	X
Pavona gigantea Verrill 1869	X	X	[illegible]	[illegible]		[illegible]	[illegible]	
Family P[illegible] Gray								
Porites sp. [illegible]. ? "stagnant water"						[illegible]		
Porites lobata Dana 1846	X			X	X	X		[illegible]
Porites sp. [illegible]. ? "green [illegible]"			X	X	X	X	X	
Porites panamensis Verrill 1866		X	X	X	X	X	X	
Porites californica Verrill 1870						**		
Porites excavata Verrill 1870		*5*						

APPENDIX II CONTINUED

Species List	Isla T[illegible] (8°50'N; 79°35'W)	Islas Per[illegible] (8°10–40'N; 78°46'—[illegible] 79°10'W)	Islas N[illegible] (7°15'N; 80°56'W)	Isla C[illegible] (7°17–40'N; 81°35-50'W)	Islas Contreras (7°49'N; 81°45'W)	Islas S[illegible] (7°58'N; 82°01'W)	Isla Parida (8°08'N; 82°21'W)	I[illegible]-Pacific
Family D[illegible] Gray								
Tubastraea aurea (Q[illegible] & G[illegible]) [=*tenuilamellosa* (Milne Edwards & [illegible])]	X	X	X	X	X	X	X	X
Class: H[illegible] Owen								
Order: M[illegible] Hickson								
Family: M[illegible] Fleming								
Millepora intricata Milne Edwards 1857					X	X		X
Millepora platyphylla H[illegible] & Ehrenberg 1843				X	X	X		X
Millepora sp. [illegible].?				X				

ORIGIN OF THE EXISTING PANAMIC MOLLUSCAN BIOTAS IN TERMS OF THEIR GEOLOGIC HISTORY AND THEIR SEPARATION BY THE ISTHMIAN LAND BARRIER

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This symposium deals with the subject of environment and an effort to forecast the damage which might result to it through the construction of a sea-level canal across Panama, for such a canal might allow an interchange of oceanic waters from either side, as well as the transit through the canal system of harmful marine life. As a geologist and paleontologist, I will approach this problem from the standpoint of the Tertiary history of Panama and its adjacent lands and, also, from that of its fossils. The regional geology of Panama and Costa Rica is now fairly well-understood, especially on the basis of the distribution of the marine Miocene fauna. The Miocene was the time when our molluscan biotas, related to those of today, were evolved; a consideration of the Miocene forms from both the Caribbean and Eastern Pacific regions, therefore, is the clue to origin and present day distribution of the living faunas. Present day Panama and portions of northwestern Colombia and western Ecuador are but small remnants of a former, much greater land mass which once extended an unknown distance, far out into the Pacific. The evidence for the existence of such a land is geological and beyond the scope of this review. In pre-Tertiary times, the Panamic land functioned as the foreland of the Andean geosyncline of interior Venezuela and Colombia and contributed by its own erosional degradation to the sedimentary fill of that great South American structural feature. In Tertiary times, the Panamic land underwent nearly complete destruction and fragmentation both in the Caribbean and Pacific zones and major parts of it were flooded and foundered in the deeps. By Miocene times, the Panamanian portion had been reduced to an archipelago of large islands separated by sea-lanes between the Caribbean and Eastern Pacific through which marine life was free to pass and intermingle. Through geological exploration in Panama and nearby lands, mainly under the auspices of oil companies, the position of the main seaways or straits have been established. There were two main straits. The most westerly of these interoceanic connections lay across Costa Rica, much of whose foundational geology lies smothered under volcanic ejecta of more recent date. The easterly strait (the Bolivar geosyncline) lay along the present north-south connecting valleys of the Rio Atrato and the Río San Juan of northwestern Colombia, a region which is still low throughout much of its length. Both straits permitted free migration of marine life between the Caribbean and the Eastern Pacific and both straits were closed by uplift at the end of the Tertiary about 1,000,000 years ago.

The Costa Rican and Bolivar straits were generally open through the Tertiary and during the Miocene especially, a single faunal province extended from the Caribbean southward through the Bolivar geosyncline into the Eastern Pacific. Thus, Miocene species from Peru, Ecuador and southern Panama are generally related and often identical with common Miocene forms from the Caribbean-West Indian region as far northward as Florida. More than a century ago, malacologists engaged in describing Tertiary fossils from Hispaniola, Trinidad, etc., noted their general similarity to Miocene species from Europe and also to some of the common living species of mollusks on the Pacific side of Central and South America. The close similarities of our Neogene mollusks with the species now living on the Pacific side of Panama and, to a certain extent with European Miocene species, has been confirmed by all recent work. Thus, it becomes clear that the Miocene mollusks we find so abundantly throughout the Caribbean-West Indian region, and along the Pacific coast south to Peru, represent largely a unit development, mainly of Atlantic origin. There are naturally in both subprovinces (Caribbean and

Eastern Pacific) a few species which are endemic. We may note this situation amongst the Olividae which have quite different species on the two sides and in the Volutidae which have few species on the Pacific side but many in the Caribbean. Both situations apply to the fossils as well.

The Eastern Pacific subprovince today faces the open Pacific and a few elements amongst its mollusks are of Indo-Pacific origin such as species of Conus and Cypraea, all of apparently late arrival; several authors have recorded a much larger number of Indo-Pacific species on the outer, offshore islands. There are apparently no Indo-Pacific elements amongst our Miocene mollusks, either in the Caribbean or Eastern Pacific zones, that are clearly recognizable as such. This situation seems to imply that a barrier of sorts existed to the west as late as Pliocene times. At present, the location of this barrier is conjectural, but we can think of it as a fringe remnant of the old Panamic land barrier. A likely position is one over the submerged ridge extending southward from the Peninsula of Nicoya of Costa Rica to the Galapagos and from there eastward to the Manta Arch of middle western Ecuador. Such an outer land bridge between North and South America could well have served as the principal migration route for grazing animals (horses and camels) rather than one along the present Panamic Isthmus with its tropical forest growth.

Our information on the molluscan biotas of Panama is most complete for that of the Pacific side, the one better studied and more thoroughly and widely collected. We can conservatively estimate its size (Panamic-Pacific) as 4500 species for the Pelecypoda and Gastropoda, alone. For the inshore mollusks along the Caribbean side of Panama, our information is incomplete since there are so few places where good collections have been secured. Along the whole length of the Caribbean coast of Panama, we have sizable collections from only two places, namely Payardí (just east of the Canal Zone) and Bocas del Toro. The Payardí collections were made by R. H. Stewart, a Canal Zone geologist, from dredged material used as fill for the construction and elevations of a refinery site. The other sizable collection of mollusks is from Bocas del Toro in western Panama near the Costa Rican border. The Bocas collections were secured through discriminating shore collecting and, especially, from the picking of highly selective beach drift, thus yielding a high percentage of the small to minute species, usually neglected by other collectors. The combined collections from Payardí and Bocas del Toro comprise about 650 species, a number comparable with the tabulation of the Porto Rican mollusks prepared by Dall and Simpson in 1901. For the entire molluscan fauna of the inshore and shelf areas throughout the West Indian-Caribbean region, we may, for the present, estimate its size to be about 1000 species, a number far below that of the Eastern Pacific. Of the two molluscan biotas on each side of Panama, that of the Pacific is far richer with a general ratio of 5 to 1.

The closing of the isthmian straits at the end of the Tertiary was brought about by a general regional uplift throughout the Caribbean region contemporaneous with that in many other parts of the world. It served also to mark the beginning of the general impoverishment of the present Caribbean molluscan fauna from its former richness in the Tertiary. The uplift brought about a general retreat of marine waters from all major coastal areas where sedimentation had been going on, and the emergence of many shallow, platform areas, aggravated still further by a lowered sea-level during periods of maximum glaciation in the north, during the Pleistocene. The general result was the partial or complete extinction of many important groups of Caribbean, benthic, inshore and shelf mollusks. On the Pacific side the effects of the Quaternary orogenics were minor and their impact on the environment less significant. The molluscan biota of the Eastern Pacific (the Panamic-Pacific faunal province), therefore, retained the richness and diversity developed during Tertiary times.

There are considerable differences in the environmental settings on the two sides of Panama. The large, daily fluctuation in tidal levels on the Pacific side, its large stretches of mangrove swamps coupled with colder waters due to strong upwellings, are a few examples. On the Caribbean side of Panama the tidal changes are small and of no account. The coastal perimeter of the whole Caribbean is sedimentary and its waters are warmer. These environmental conditions are favorable to the growth of reef corals and associated marine life, whose remains are abundant throughout Tertiary formations (wholly lacking in the Eastern Pacific Tertiaries). These environmental differences may well prove to be effective barriers to many forms of marine life which by chance might secure a transit through the proposed canal system. Since the Caribbean and Eastern Pacific biotas are so clearly of the same unit origin, it seems needless at this time to detail the varying similarities and differences between the molluscan families in the two faunal provinces as shown today.

SUMMARY

The origin and relationships of our living animal and plant communities is rooted in the historical geological past. We have approached this problem of origin of the Panamanian marine faunas by an analysis of both the present molluscan biotas on the two sides of Panama and of the fossils and the geological history of the Isthmian lands.

Fossil molluscan shells are abundant in the Tertiary formations in both the Western Atlantic and Eastern Pacific regions and the compositions of these faunas have been well-studied and documented. The Miocene mollusks, in particular, lend themselves to such an analysis, being the ones most directly related to our Recent forms.

The Caribbean mollusks of shallow water habits suffered great impoverishment through the effects of repeated orogenies during the Quaternary and general sea-level lowering during the periods of Pleistocene glacial advances in the north. The molluscan biota in the Eastern Pacific with similar environmental habits was not similarly affected and retained its original Tertiary richness and diversity. The ratio of species abundance between the Caribbean and Eastern Pacific molluscan biotas is to the general order of 1 to 5.

To the paleontologist, the living mollusks of the Panamic-Pacific fauna have the aspect of a relict fauna stranded and divorced from its homeland in the western Atlantic by the isthmian land uplift at the end of the Tertiary, about 1,000,000 years ago.

Both molluscan biotas of Panama (Caribbean and Pacific) are fundamentally of Atlantic origin, and each development has special species which are endemic and give to each of them their distinctive characters. If this analysis of origin is true for the mollusks, it should be also for most other groups of marine life in the two now-separated faunal provinces.

The damage to the environment which may ensue through the construction of a sea-level canal across Panama on the part of the mollusks seems negligible. The case may be different with other invertebrates. The greatest danger would seem to be from elements of Indo-Pacific origin, new arrivals in the Eastern Pacific region.

Proper assessment of future damage to the marine environment is dependent upon full knowledge of our existing plant and animal communities. For the mollusks additional exploration is needed along the whole length of the Caribbean coast, less so in the Pacific side of Panama. Special attention should be directed to inlets and shore environment, including the stretches of mangrove swamps.

In the final analysis, the selection of the route of the canal is most important and it should not be decided upon on political or engineering considerations alone. From a geological standpoint, the selected route should be across solid, unbroken rock formation, as far as possible, to insure earth stability and freedom from slides, such as those which have plagued the maintenance of the present canal from the very start. From a biological standpoint, the possible impact of the proposed canal on the environment should be better understood, both along its course and at its terminal ends in the sea. In all these matters of concern, the regional geologist and the biologist must work together and both must have a recorded voice in the selection of the canal route.

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COMPARATIVE HABITAT DIVERSITY AND FAUNAL RELATIONSHIPS BETWEEN THE PACIFIC AND CARIBBEAN PANAMANIAN DECAPOD CRUSTACEA: A PRELIMINARY REPORT, WITH SOME REMARKS ON THE CRUSTACEAN FAUNA OF PANAMA[1]

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"The time is still far in the future when a tropical marine ecologist can identify the components of an ecosystem or a food chain from his handy pocket guide" (Chace, 1969). This statement is as true for the crustaceans of Panama as it is for most other marine groups. There is, with the exception of some decapod and stomatopod groups, virtually no information available on the crustaceans of Panama. This report reviews a few of my own observations on the crustaceans of Panama and then presents preliminary data on a study of habitat diversity and faunal relationships of the Panamanian Decapoda.

STATUS OF SOME CRUSTACEAN GROUPS IN PANAMA

The American cumacean fauna is virtually unknown. Jones (1969) in a study of the distribution of the known cumaceans does not list a single species from the Panamic region in 0-200 meters depth. Yet the group is not uncommon in the shallow waters of Panama (personal observations).

In many areas of the Bay of Panama stomatopods are the dominant benthic invertebrates in terms of both biomass and numbers of individuals (personal observations). The more common species in the Bay of Panama were treated by Schmitt

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(1940). They have not been dealt with since then. In the western Atlantic and Caribbean, 38% of the species studied by Manning (1969) were previously undescribed, and more undescribed species are still being collected (Manning, 1970). A similar situation may be expected when the eastern Pacific species are studied.

The isopods and amphipods of Panama, although quite abundant, have yet to be studied. Papers dealing with these groups in Panama have dealt mainly with the description of new species. Even the faunas of regions such as Puerto Rico and California, which were surveyed during the early 1900's, have been shown in subsequent studies to be poorly known. For example, Menzies and Glynn (1968), during only one month of field work, were able to increase the number of marine isopods known from Puerto Rico by 338%. This included the description of three new genera and 32 new species. In California Barnard (1969) lists 155 intertidal species. Of these 57, or about 37%, were described as new by that author. The density of some of the undescribed species reached 2,677 individuals per square meter and other species were found in comparable densities. These animals were collected in an area which had been studied by biologists for years.

The decapods appear to be the best known of the crustaceans, yet, as Chace (1969) pointed out, nearly 20% of the Caribbean shrimps taken by recent expeditions were undescribed. This 20% figure is not unreasonable for the total amphi-American decapod fauna, where easily half of the named species are so incompletely known that any identification is tentative at best. For example, the most common shrimp in the tidepools of the Bay of Panama is undescribed (Abele, in press, b). One of the more common crab species present in the Panama Canal, only recently recognized, has apparently been introduced from the freshwaters of Iraq (Abele, in press, a). Of the nine species of Hippidea collected in Panama only one was previously recorded from the area, and half of the remaining species may be undescribed. It was possible to identify only eight of the approximately 22 species of Pacific Alpheidae collected, and half of these identifications are tentative. Of the 11 species of Atyidae collected, only three were previously recorded from the area. The percentages improve somewhat in the palaemonids, porcellanids and some brachyurans (due largely to the works of Holthuis, 1951, 1952; Haig, 1960; Rathbun, 1918, 1925, 1930, 1937; Crane, 1941, 1947; Garth, 1946, 1948, 1958; Garth and Stephanson, 1966), but the list could go on and on.

There is no reason to expect that the crustacean fauna of Panama is any better known than that of regions which have been studied, such as Puerto Rico and California. It is highly probable, in fact, that only the most common of the intertidal decapods have been collected. Experience in less diverse temperate areas, such as North Carolina, suggest that 50 years of collecting is necessary to bring a faunal list of decapods, alone, to a reasonably complete level (Williams, 1965). The number of Panamanian plant species, for instance, has increased by 85% since the groups involved were monographed in the middle 1900's (Dressler, this symposium). Meyers (this symposium) estimates that it required about 10 years of collecting to compile a reasonably complete list of the reptiles and amphibians of Panama. A sampling program in Panama must begin soon to assure us of a reasonable level of base line data prior to the completion of a sea-level canal.

HABITAT DIVERSITY AND FAUNAL RELATIONSHIPS OF THE PANAMANIAN DECAPODA

My own work in Panama (on which the previous remarks are based) began in 1968 when a program was initiated to study the decapod fauna of Panama. The study (still in progress) involves comparing the decapod fauna of a particular habitat on the Pacific coast with the decapod fauna of the same habitat on the Caribbean coast. After an initial field survey, the following five habitats were selected for comparison: sandy beach, freshwater stream, mangrove, rocky intertidal, and coral reef. These habitats were selected because they are widespread on both coasts (sandy beach, freshwater stream, and mangrove) or are widespread on each coast (the lava flow, rocky intertidal of the Pacific coast and the Caribbean coral reef habitat).

A total of 119 stations (primary sampling areas are

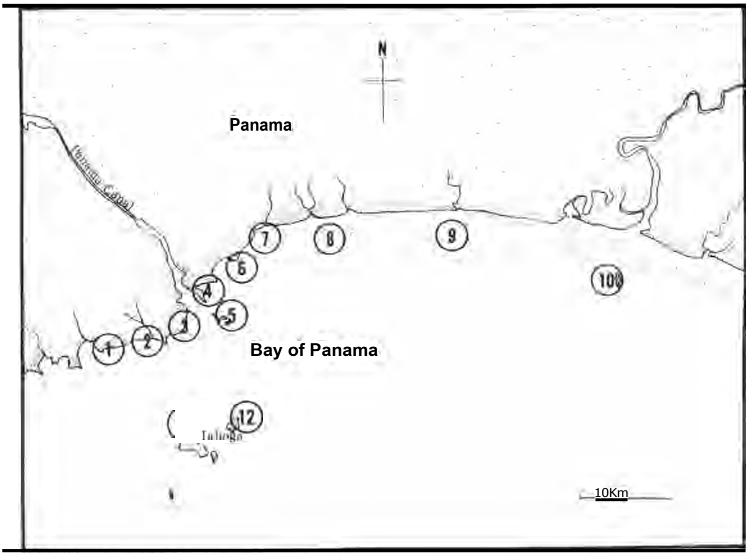

FIG. 1. Primaiy sampling areas on the Pacific coast of Panama. 1, Vera Cruz. 2, Punta Bruja. 3, Venado-Kobbe. 4, Fort Amador. 5, Naos Island group. 6, Punta Paitilla. 7, Panama Vieja. 8, Juan Diaz. 9, South of Pacora. 10, Isla Chepillo. 11, Isla Taboga. 12, Isla Taboguilla.

shown in Figures 1 and 2) were sampled during a period of 15 months. An attempt was made to sample each station until the accumulated-species curve became asymptotic and then the number of individuals of each species was to be recorded. The species curve has not yet leveled off for the subtidal coral reef habitat of the Caribbean. Additional sampling of this habitat is planned. Over 6,000 specimens representing an estimated 485 species have been collected to date. Approximately 325 of these species, and over 5,100 of the specimens, are involved in the habitat comparisons below, after eliminating species collected in areas, such as intertidal mud flats, which were sampled initially but were not included in the habitat comparisons. An index of faunal similarity was calculated for each habitat. This is the percentage of faunal elements common to the same habitat on both coasts. Common faunal elements include both conspecific and closely related congeneric species which seem to occupy the same or similar

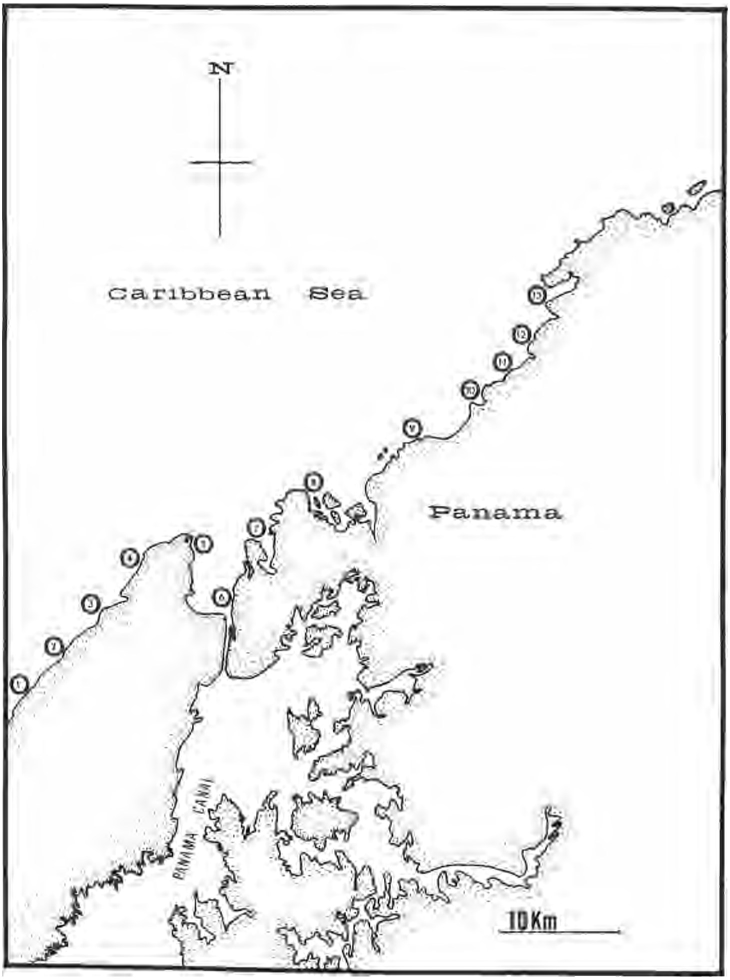

FIG. 2. Primary sampling areas on the Caribbean coast of Panama. 1, Piña. 2, Beyond Rio Piña. 3, Beyond Río Chagres. 4, Fort San Lorenzo. 5, Fort Sherman. 6, Cristóbal. 7, Coco Solo. 8, Isla Galeta. 9, María Chiquita. 10, Punta Gorda. 11, Beyond Rio Gorda. 12, Five miles SW of Portobelo. 13, Portobelo.

niche on the opposite coast. The faunal index and the number of species reported for each habitat are the summed totals of the fauna of different localities of the same habitat. The results are presented in Table 1.

Table 1. Comparison of number of species, number of common faunal elements, and Index of Faunal Similarity (IFS) among five decapod communities of Panama.

Habitat	No. of Species		No. of Common Faunal Elements	IFS	
	Pacific	Carib.		Pacific	Carib.
Sandy Beach	17	8	4 pairs	25%	50%
Freshwater Stream	17	15	10 pairs	60%	66%
Mangrove	20	17	10 pairs	50%	60%
Coral Reef	55	30?	—	—	—
Rocky Intertidal	78	67	27 pairs	35%	40%

The Sandy Beach Fauna

Beaches were sampled in the area of Piña, Fort San Lorenzo, Shimmey (Fort Sherman) and Maria Chiquita on the Caribbean coast. Beaches were sampled in the area of Río Mar, Farallón, and Naos Island on the Pacific coast.

This habitat was the least diverse of those sampled with a total of 25 species collected: 17 on the Pacific coast and eight on the Caribbean coast. On the Pacific coast about 50% of the species, including at least three undescribed species, were new records for the area. The situation is similar on the Caribbean coast which also had three apparently undescribed species, one of which has recently been treated (Abele and Efford, in press). A mole crab, Emerita rathbunae Schmitt was the most abundant species on the Pacific coast, accounting for over 50% of the individuals collected. On the Caribbean coast another mole crab, Hippa testudinaria (Herbst) (= H. cubensis) was the most abundant species, accounting for over 50% of the individuals collected on that coast. These genera are in the same family and are somewhat similar, ecologically. The genera Gecarcinus, Ocypode (both supratidal), Albunea, and Emerita (both intertidal) contain closely related species pairs in this habitat pair. The faunal index is 4/17, about 25%, for the Pacific fauna and 4/8, 50%, for the Caribbean.

Utilizing only the six Caribbean and 14 Pacific intertidal species, the faunal index drops to 2/6, 33%, for the Caribbean and 2/14, about 14%, for the Pacific coast. The dissimiliarity between the faunas of this habitat pair seems to be related to differences in the substratum in the study area. The Pacific quartz sand beaches are stabilized by mud, whereas the Caribbean calcareous sand beaches are subjected to much shifting during the dry season's high winds and irregular tidal cycles. Apparently correlated with the stability of the Pacific beaches is the presence of several burrow-inhabiting species of *Callianassa, Pinnixa,* and *Ambidexter* which were not found on the Caribbean beaches.

The Freshwater Stream Fauna

Freshwater streams of both drainages were sampled in a large number of areas. Stations included streams from slightly above sea level to over 1,000 meters elevation. All streams were less than two meters in depth. Primary sampling areas were the Río Chagres (Caribbean) and Pedro Miguel (Pacific) drainages.

In this habitat an approximately equal number of species were collected on both coasts: 17 in Pacific and 15 in Caribbean drainages. Four families, the Palaemonidae, Atyidae Grapsidae, and Pseudothelphusidae accounted for all but one *(Callinectes toxotes* Ordway) of the species. About 40% of these had not been previously recorded from the area. A small atyid shrimp, *Potimirim glabra (Kingsley),* was the most abundant species in both drainages (although the Caribbean populations may be specifically distinct). The genera *Macrobrachium, Atya, Potimirim, Sesarma, Potamocarcinus,* and *Pseudothelphusa* contain closely related species pairs in this habitat pair. The faunal index for the Pacific coast is 10/17, about 60%, and is 10/15, about 66%, for the Caribbean coast. As indicated by the high faunal indices, the faunas of this habitat pair are quite similar.

The genera *Potimirim, Potamocarcinus,* and *Pseudothelphusa* are American in distribution, but the genera *Macrobrachium, Atya* and *Sesarma* contain closely related species on the West African coast (as well as containing circumtropical species).

The Mangrove Fauna

Mangrove habitats were sampled at Aquadulce, Diablo, and Farfán on the Pacific coast. Mangrove habitats were sampled at Galeta and Fort Randolph on the Caribbean coast.

Mangroves of both coasts were composed primarily of the red mangrove, Rhizophora mangle Linnaeus.

As in the preceding habitat an approximately equal number of species were collected on both coasts: 20 species on the Pacific coast and 17 on the Caribbean coast. Crane (1947) listed and gave notes on most of the Pacific brachyuran crabs and Chace and Hobbs (1969) treated a portion of the Caribbean fauna. Abele (1970) reported on a semi-terrestrial shrimp, Merguia rhizophorae (Rathbun), found on Caribbean red mangroves. Twenty-five percent of the Pacific species are undescribed, including a species each of both Petrolisthes and Sesarma which were among the most abundant Pacific mangrove decapods collected. Other abundant decapods of the Pacific mangroves included Petrolisthes zacae Haig, Eurytium tristani Rathbun, and Sesarma rhizophorae Rathbun. The arboreal mangrove crab, Aratus pisonii (H. Milne Edwards), was the most abundant species occurring in the trees on both coasts. Only a single species on the Caribbean coast appears be undescribed. A grapsid crab, Sesarma rhizophorae, previously considered to be a Pacific species, was collected on the Caribbean coast. The most abundant species of the Caribbean mangrove fauna included Panopeus herbstii H. Milne Edwards, *Merguia* rhizophorae (Rathbun), Uca rapax (Smith) and Sesarma curacaeoense De Man. The genera Sesarma, Uca, Panopeus, Eurytium, *Clibanarius*, Aratus, Goniopsis, *Cardisoma* and Ucides contain closely related species pairs in this habitat pair. The faunal index for the Pacific coast is 10/20, 50%, and 10/17, about 60%, for the Caribbean coast.

These faunas, as in the preceding habitat, are quite similar. Nine of the 12 Caribbean genera have closely related species pairs in this habitat. In addition to the close relationship between the Pacific and Caribbean faunas, there exists a close relationship between these two faunas and the mangrove fauna of the West African coast. The genera Cardisoma, Goniopsis, Sesarma, Uca, Panopeus and Pachygrapsus (Caribbean only) have closely related species on the West African coast.

The Coral Reef Fauna

The Pocillopora coral habitats of the offshore islands of Taboguilla, Taboga and certain of the Perlas group were sampled, as coral reefs do not occur along the Pacific coastline in the study area. Coral reefs were sampled at Galeta, Maria Chiquita, and Portobelo on the Caribbean coast. Primary effort was toward sampling only Porites associations of the Caribbean to get a single coral comparison (Pocillopora vs. Porites), but the effects of adjacent Caribbean coral species could not be eliminated.

There was a significant increase in the number of species in this habitat compared to the three other habitats. Fifty-five and at least 30 (sampling of the Caribbean reefs is not yet completed) species were collected from Pacific and Caribbean subtidal coral, respectively. Many of the species (slightly under 50%) were previously unrecorded from the area and about 25% of these appear to be undescribed. The most abundant decapod species of the Pocillopora habitat included Petrolisthes haigae Chace, an undescribed species of Pagurus, Trapezia cymodoce ferruginea Latreille, Harpiliopsis *depressus* (Stimpson), Heteractaea lunata (H. Milne Edwards and Lucas) and *Alpheus* lottini Guérin. One of these, T. cymodoce ferruginea, is an ectoparasite on the coral (Knudsen, 1967). Approximately one-third of the decapod fauna of the Pocillopora coral appear to be obligate commensals. Further sampling of the Caribbean coral is needed before a discussion of that habitat is warranted.

However, there is probably very little similarity between the Caribbean and Pacific coral decapod faunas, due to the fact that Pocillopora, with about one-third of its fauna obligate commensals, does not occur in the Caribbean. Garth (1968) postulated a close relationship between some coral-inhabiting xanthid crabs of the eastern Pacific and eastern Atlantic as a result of extinction of the genus or species group in the western Atlantic following the late Miocene closure of the Panama Portal by the Isthmus of Panama. He then stated that the most closely related species to a tropical West American coral-inhabiting species of crab (or shrimp) was to be looked for on the tropical West African coast. The situation, however, appears to be more complex, with about 14% of the eastern Pacific Pocillopora fauna having either the same or a closely related species occurring in the Indo-West Pacific, but absent from the West African coast.

The Rocky Intertidal Fauna

Comparison of rocky intertidal communities presented a problem because true intertidal lava flow, so characteristic of the Pacific coast, is sparsely distributed in the Caribbean study area. Intertidal fossil coral reefs with coralline rubble and cobble stone, present near María Chiquita on the Caribbean coast, were sampled, in addition to intertidal fossil reefs near Fort Randolph. The justification for this comparison of hard substrata is borne out by the faunal similarity of the Caribbean to the Pacific (faunal index: 40%, which included the more abundant species of both coasts).

This was the most diverse habitat studied, with 78 and 67 species being collected from the Pacific and Caribbean coasts, respectively. Crane (1947) treated part of the Pacific brachyuran fauna, but this fauna, for the most part, remains to be adequately described taxonomically. The most abundant shrimp of the Pacific intertidal is still undescribed. The two most abundant hermit crabs, Clibanarius *albidigitus* Nobili and Calcinus obscurus Stimpson, the former occurring in densities up to 100 individuals per m^2, were not adequately described until 1954 (Holthuis, 1954). The systematic status of the most abundant crab species, Xanthodius *sternberghii* Stimpson, is unsettled. The above three and Petrolisthes armatus (Gibbes) were the most abundant decapods of the Pacific coast. The most abundant species of the Caribbean coast included *Calcinus* tibicen (Herbst), Paraliomera dispar (Stimpson *Clibanarius* antillensis Stimpson, Cataleptodius floridanus (Gibbes), Pachygrapsus transversus (Gibbes) and Clibanarius tricolor (Gibbes). Three of these were not adequately described until 1959 (Provenzano, 1959). The genera *Clibanarius*, Calcinus, Cataleptodius, Pachygrapsus, Eriphia, Paguristes, Petrolisthes, Geograpsus, Penaeus, Grapsus, Menippe, Callinectes, *Alpheus*, Synalpheus, Thoe, Pilumnus, Pachycheles, Hexapanopeus, and Eurypanopeus contain closely related species pairs in this habitat pair. The faunal index for the Pacific is 27/78, about 35%, and that for the Caribbean is 27/67, about 40%.

HABITAT DIVERSITY OF PANAMANIAN DECAPODA

A complete discussion is more appropriate for a final report, which is now being prepared, but a few trends should be mentioned.

(1) There are a few more species, represented by more individuals, in the same habitat on the Pacific coast than on the Caribbean.

(2) The number of species per habitat increases in the same sequence on both coasts: sandy beach, freshwater stream, mangrove, coral reef (Pacific, only, completed) and rocky intertidal.

(3) For the marine habitats the increase in the number of species per habitat corresponds to an increase in the structural complexity of the habitats.

(4) A high degree of dominance exists in all of the habitats with only a few species accounting for over half of the individuals: one species in the sandy beach, one species in the freshwater stream, four species in the mangrove, five species in the Pacific coral reef, and six in the Caribbean and four in the Pacific rocky intertidal.

(5) The taxonomic relationships between habitat pairs range from about 14% (sandy beach intertidal) to about 66% (freshwater stream) similarity. Not surprisingly, this corresponds with the similarity in physical structure between the habitat pairs.

(6) For the total decapod fauna of Panama, estimated to be approximately 1,400 species, about 45% comprise species pairs. More than half of all Panamanian decapods remain to be adequately described.

GENERAL DISCUSSION

There is, as already pointed out, almost no information available on the majority of the crustaceans of Panama. There is a real need for a sampling program which would take into consideration the alpha level of the knowledge of the groups concerned. In addition to taxonomic studies, work on food preferences, food web structures, predator-prey relationships, etc., must be carried out.

These latter studies should include the several species of shrimp involved in Panama's fishing industry. Shrimp constitute that country's third largest export item, amounting to over 9 million dollars a year and contributing approximately 2% to Panama's Gross National Product (Anonymous, 1970). Further, the social structure of almost every small village depends, in a large part, on fishing. The most important species, *Penaeus occidentalis* Streets, occurs along the Pacific coast of Central America. This species is larger and more abundant than its Caribbean congener *Penaeus schmitti* Burkenroad, which is not fished to any extent on the Caribbean coast of Panama. It is, of course, not possible to predict the outcome of any species interactions, nor do I wish to imply any possible outcome, should these two species (or any species) attain sympatry upon the completion of a proposed sea-level canal. However, because of the economic and social importance of certain species, all possible results of species interactions must be taken into consideration, including the potential loss of a commercially important species.

Acknowledgments

This work was supported by research grants NSF-GB-19384 and NSF-GB-7075X from the National Science Foundation. I especially thank Dr. Robert J. Menzies, Florida State University, for guidance and encouragement throughout this study. Thomas Biffar was kind enough to offer constructive criticism of this manuscript. Facilities were provided by the Smithsonian Tropical Research Institute and the University of Panama. I also thank Dr. Raymond B. Manning, who suggested I give this paper, and Dr. Meredith L. Jones, for the privilege of attending this symposium.

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THE STATUS OF KNOWLEDGE OF PANAMANIAN ECHINOIDS, 1971, WITH COMMENTS ON OTHER ECHINODERMS

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Through the works of A. Agassiz, H. L. Clark, T. Mortensen and others, echinoids are, taxonomically, one of the best known invertebrate groups. Recent intensive investigation throughout the West Indian Faunal Province has yielded only a four percent increase in known species. Probably another three percent remain to be discovered. The Eastern Pacific echinoid fauna is less well-known. Exploration by the research vessels ALBATROSS, VELERO, and PILLSBURY obtained a substantial number of new echinoid species. Based on results of intensive search efforts elsewhere, and the amount of collecting in the Eastern Pacific, I estimate the known Pacific species comprise about eighty percent of the actual fauna.

Based on this assumption, the presently known echinoid fauna (Table 2) can be used to establish relationships between the West Indian Faunal Province (Atlantic) and the Panamic[2] Faunal Province (Pacific).

AFFINITIES OF SPECIES

Table 1 shows a comparison of echinoid genera occurring in the two regions, in depths less than 50 meters. Table 2 shows a comparison of echinoid genera from all depths. Eighty-one to eighty-five percent of the shallow-water genera are repre-

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[2] Editor's note: "Panamic", as used in this paper, refers to the Panamic Faunal Province, *i.e.,* the faunal region on the Pacific side of the Central American landmass.

Table L—Number of tropical American echinoid species from shallow-water (< 50 m).

Genera	Atlantic spp.	Pacific spp.	General Distribution
Agassizia	1	1	Tropical Americas
Arbacia	1	1	Atlantic-Western Americas
Astropyga	1	1	Tropical
Brissopsis	1	1	Tropical
Brissus	1	1	Tropical
Cassidulus	1	1	Tropical (Relict)
Clypeaster	2	2	Tropical
Diadema	1	1	Tropical
Echinometra	2	1	Tropical
Echinoneus	1		Tropical
Encope	1	5	Tropical Americas
Eucidaris	1	1	Tropical
Leodia	1		Tropical Americas
Lovenia		1	Tropical Indo-Pacific
Lytechinus	2	1	Atlantic-Western Americas
Mellita	1	1	Tropical Americas
Mellitella		1	Tropical-Western Americas
Meoma	1	2	Tropical Atlantic-Western Americas
Metalia		1	Indo-Pacific
Moira	1	1	Tropical
Paraster	2		Tropical (except Western Americas)
Plagiobrissus	1	1	Tropical Atlantic-Western Americas
Toxopneustes		1	Indo-Pacific
Tripneustes	1	1	Tropical
Total No. of species	24	27	
Number of genera	20	21	
Amphiamerican genera	17	17	
Percentage of generic interrelationship	85	81	

sented on both sides of the Panama isthmus. When genera from all depths are compared, only forty-two percent of West Indian and sixty-four percent of the Panamic fauna are represented on both sides. The six deep-water echinoid genera which occur on both sides of the isthmus are cosmopolitan and probably achieved their present distribution through deep-sea basins. Accordingly, the echinoid genera occurring at depths greater than 50 meters probably did not move through the Panamic seaway when it was open one million years ago.

With a few exceptions, present day littoral and sublittoral genera were part of a homologous gene pool in the Tertiary Caribbean Province described by Woodring (1966). Morphological divergence has been so slight since the Panama isthmus interrupted these gene pools that it is often impossible to identify specimens at the species level without first knowing the place of collection. Most of the specific names were originally designated on the basis of locality. Attempts to find "key characters" for species identification have been unproductive and most, if not all, characters recommended by Mortensen (1928-1951) are invalid.

Examination of morphology and fossil history in the genus *Meoma* (Chesher, 1970) showed that specimens of *Meoma grandis* from the Pacific side of Colombia could not be separated morphologically from specimens of *M. ventricosa* from the Atlantic side of Colombia. Morphological clines were discovered in both populations, and specimens from both sides of the isthmus could be separated with about eighty percent assurance. After analysis, the geminates of *Meoma,* which so perfectly agree with the concept of geographic subspecies suggested by Mayr, *et al.* (1953), were reduced to subspecific level (Chesher, 1970).

Separation of the geminates *Brissus unicolor* and *B. obesus* from one another was attempted using a series of 50 *B. unicolor* from Panama, Florida, Jamaica, and the Bahamas ranging in size from 5.5 to 53 mm test length. The resulting biometric summary is presented in Table 3. These data were compared to specimens of *Brissus* collected from the Bay of Panama and Lower California. While two significant differences were found between specimens from the Atlantic and from the Gulf

Table 2. Number of tropical American echinoid species from all depths; "*" indicates taxa which have been recorded previously from localities near, but not in, Central America; "**" indicates taxa which probably occur near Central America but have not been recorded there, as yet; unmarked taxa are known from the Central American coasts.

Genera	Atlantic	Pacific	Distribution Range
**Aceste*	*1*	*1*	Cosmopolitan
**Aeropsis*	*1*	*1*	Cosmopolitan
Agassizia	*1*	*1*	Tropical Americas
Aporocidaris	–	*1*	Pacific Abyssal Antarctic
Araeosoma	*1*	–	Cosmopolitan (except Western Americas)
Arbacia	**1*	*1*	Atlantic-Western Americas
Astropyga	*1*	1	Tropical
**Brisaster*	*1*	2	Cosmopolitan
Brissopsis	4	2	Tropical
Brissus	*1*	*1*	Tropical
***Caenopedina*	*1*	1	Indo-Pacific-Atlantic-archibenthal
**Calocidaris*	*1*	–	West Indies
**Cassidulus*	*1*	*1*	Americas
**Centrostephanos*	*1*	–	Tropical (except Western Americas)
***Cidaris*	3	–	Atlant.-Med. Sea-Indo-Pacif.
Clypeaster	6 (+ 5**)	3	Tropical
Coelopleurus	*1*	–	Tropical (except Western Americas)
**Conolampas*	*1*	–	West Indies
**Cystocrepis*	–	*1*	Panama
Diadema	*1*	1	Tropical
Dilithocidaris	–	*1*	Panamic deep sea
***Echinocardium*	*1*	–	Tropical (except Western Americas)
Echinometra	2	1	Tropical
Echinoneus	*1*	–	Tropical (except Western Americas)
Encope	*1*	5	Tropical Americas
Eucidaris	1	1	Tropical
**Genocidaris*	*1*	–	Atlantic
**Gracilechinus*	*1*	–	Western Atlantic slope

Table 2. (Continued).

Genera	Atlantic	Pacific	Distribution Recent
*Habrocidaris	1	–	Central Pacific-Caribbean
Hemiaster	*	1	Cosmopolitan
Hesperocidaris	–	2	Western Americas
**Histocidaris	2	–	Tropical
Homolampas	1	*	Cosmopolitan
Hypselaster	1	–	Cosmopolitan
Kamptosoma	–	1	South Eastern & Central Pacific Asyssal
Leodia	1	–	Tropical Western Atlantic
Linopneustes	1	–	Tropical
Lovenia	–	1	Indo-Pacific
Lytechinus	2	(+ 2**) 1	Tropical & subtropical Americas
Mellita	1	1	Tropical Americas
*Mellitella	[illegible]	1	Eastern Pacific
Meoma	1	2	Tropical Atlantic-Western Americas
Metalia	–	1	Indo-Pacific
Moira	1	*1	Tropical
**Palaeotropus	1	–	Atlantic
***Paleobrissus*	1	–	Tropical Atlantic
Paleopneustes	2	–	Tropical Atlantic
Paraster	2	–	Tropical Atlantic (except Western Americas)
Phormosoma	1	–	Cosmopolitan (except Western Americas)
*Pilematechinus	–	1	Panama-Antarctic
Plagiobrissus	1	*	Tropical Atlantic-Western Americas
***Plesiodiadema*	1	–	Indo-Pacific-Atlantic-archibenthal
**Plexechinus*	–	1	Cosmopolitan
**Podocidaris*	1	–	Tropical
Pourtalesia	1	–	Cosmopolitan
***Pseudoboletia*	1	–	Tropical (except Western Americas)
*Pseudomaretia	–	1	Indo-Pacific

Table 2. (Continued).

Genera	Atlantic	Pacific	Distribution Recent
**Rhynobrissus*	1		Tropical (except Western Americas)
**Salenia*	1		Indo-Pacific-Atlantic-archibenthal
**Salenocidaris*	2		Indo-Pacific-Atlantic-archibenthal
**Schizaster*	1		Tropical (except Western Americas)
***Stereocidaris*	1		Cosmopolitan
Stylocidaris	2		Tropical
Toxopneustes		1	Indo-Pacific
Tretocidaris	1		Tropical Atlantic
Tripneustes	1	1	Tropical
Tromikosema		1	Tropical
Total No. of species	78	46	
Number of genera	54	36	
Amphiamerican genera	23	23	
Percentage of interrelationship	42	64	

of California (U. S. National Museum E957, E877), specimens from the Bay of Panama differed in having fewer plates between the mouth and the posterior petal (15 to 16 compared to 17 to 19 in *B. unicolor)* and in having the lateral portion of the peripetalous fasciole farther from the apical system (30 to 31 percent of the test length, compared to 21.69 ± 1.86 percent of the test length in *B. unicolor* from the West Indies). The specimens from the Gulf of California, however, matched the Atlantic specimens in these features and were well within range of all other characters measured. *B. obesus* may exist in the Bay of Panama. More specimens must be measured to decide if the differences are consistent. The Gulf of California specimens must be considered typical *B. unicolor* and, thus, *B. unicolor* becomes the first echinoid species known to occur on both sides of Central America.

Table 3. Measurements of specimens of Brissus, given as percentages of the length of the test, except *tl* (mm), apw (ratio, apw:ap), and *ppw* (ratio, ppw:pp). Chesher (1970, fig. 1) shows the following measurement characters, diagrammatically: ae, distance between ends of anterior paired petals; ap, length of anterior petal from the ocular plate to the last pore-pairs; apw, width of anterior petal measured at the widest point from the outer periphery of the two pore-zones; aw, width of the periproct; ax, distance from the center of the apical system to the anterior portion of the test; d, width of the plastron; ff, distance from the apical system to the frontal portion of the peripetalous fasciole; h, test height; l, length of the labrum; *lf*, distance from the apical system to the lateral portion of the peripetalous fasciole; *lp*, distance between the anterior tip of the labrum and the posterior portion of the test; pa, distance from the anterior portion of the peristome to the anterior portion of the test; pe, distance between the ends of the posterior paired petals; *pf*, distance from the apical system to the posterior portion of the peripetalous fasciole; *pl*, length of the plastron; pp, length of posterior petal; ppfl, length of the peripetalous fasciole, as measured by "walking" a measured set of calipers along its length; *ppw*, width of posterior petal; *safl*, length of subanal fasciole; safw, width of the area enclosed by the subanal fasciole; *tl*, test length; tw, test width; I, II, III, IV, and V, ambulacra; 1, 2, 3, 4, and 5, interambulacra.

	B. unicolor (Atlantic)		B. unicolor (Gulf of Calif.)	B. obesus? (Bay of Panama)
Character	Mean (N = 50)	Std. Dev.	Mean (N = 5)	Mean (N = 4)
tl	23.79	12.09	37.9	38.5
tw	77.26	1.71	77.8	74.0
h	56.86	2.45	56.0	57.5
ax	26.61	3.57	29.0	30.0
pa	19.90	1.64	18.6	19.5
lp	69.41	3.17	72.6	72.8
ap	27.78	3.76	31.2	31.5
apw	27.47	5.47	24.6	22.3
pp	33.16	6.12	36.0	39.5
ppw	23.31	6.26	20.6	17.8
ff	32.33	1.75	35.5	33.0
pf	30.84	3.26	30.0	26.0
lf	21.69	1.86	20.4	30.6
ppfl	215.76	23.02	—	214.0
ae	54.69	4.54	55.0	55.3
pe	30.45	3.33	33.0	31.0
safw	41.73	1.98	39.2	42.6
safl	111.22	8.44	—	114.5
l	2.78	0.65	2.2	1.8

Table 3. (Continued).

	B. *unicolor* (Atlantic)		B. *unicolor* (Gulf of Calif.)	B. *obesus?* (Bay of Panama)
Character	Mean (N = 50)	Std. Dev.	Mean (N = 5)	Mean (N = 4)
pl	43.94	2.75	47.0	45.0
	37.80	2.28	40.8	39.7
aw	13.98	2.54	12.5	14.5
Plates on which pen-petalous fasciole found:	III b, 9+10 3 a, 4 (5) 3 b, 3+4 IV a, 11+12 (13) 4a, 6+7 (5 to 8) 4b, 6+7 (8) V a, 17+18 5 a, 11 (12)		IV a, 13+14 V a, 16+17	IV a, 12 to 14 V a, 16
Plates on which sub-anal fasciole found:	V b, 6 to 10 5 a, 3 to 6		V b, 6 to 10 5 a, 3 to 6	V b, 6 to 10 5 a, 3 to 6

Moira atropos probably cannot be morphologically separated from M. clotho. After a study of the morphological variation in several hundred specimens of Moira atropos from Brazil to North Carolina, three specimens of M. *clotho* were compared to the Atlantic data. The character given by Mortensen (1951) to separate these geminates (the dimension of the plastron) is invalid. Another character may be the distance from the apical system to the posterior portion of the peripetalous fasciole relative to the distance from the apical system to the lateral portion of the peripetalous fasciole. In the Pacific specimens, the former distance is half the latter, while in the Atlantic the posterior fasciole distance is about eighty percent of the lateral distance. Several specimens in the Atlantic were found with the same ratio (1:1) and there will certainly be considerable overlap when more specimens of M. clotho become available. Based on this information, M. *clotho* can be considered no more than a geographic subspecies of M. atropos or possibly even identical with M. atropos.

Diadema antillarum can be separated from D. mexicanum on the basis of the characters shown in Figure 1. Other char-

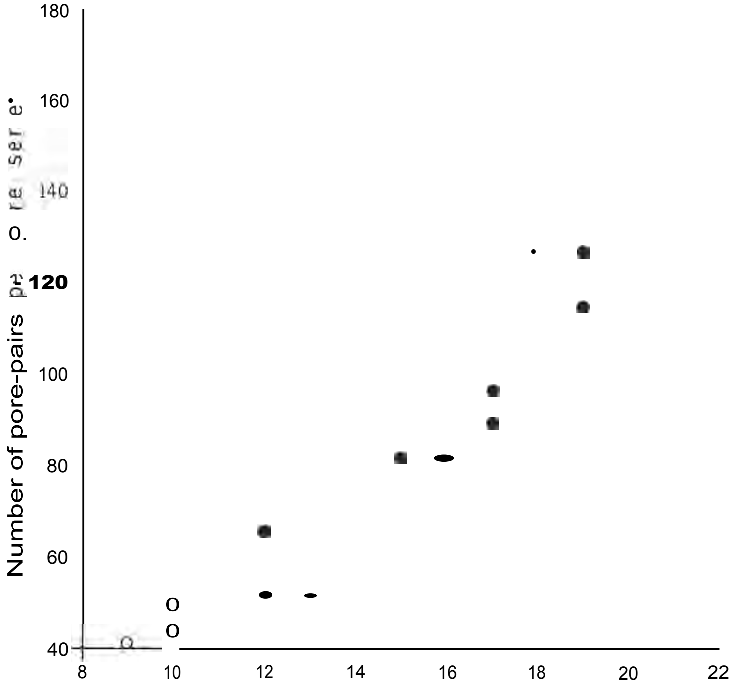

FIG. 1. Comparison of number of pore-pairs per ambulacral pore series to number of interambulacral plates in Diadema *mexicanum* ○ and Diadema antillarum ●.

acters given by Mortensen (1940) were found to be invalid upon examination of a large series of specimens. Similarly, the geminates of Eucidaris cannot be distinguished on the basis of Mortensen's (1928) comments. Figure 2 shows a technique for separating them.

Mayr (1954), Agassiz (1904), and Mortensen (1940) stressed that changes have been slight in some genera since the formation of the Panamic landbridge, whereas other genera today show changes which probably began long before the raising of the land barrier. An example of two stages of evolution in isolated echinoid populations is seen in the genus Meoma (Chesher, 1970). Meoma ventricosa ventricosa, M. ventricosa

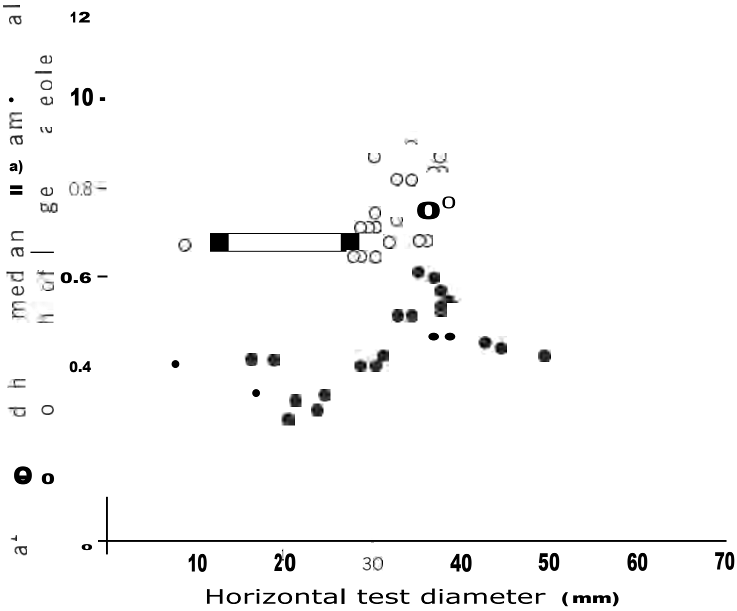

FIG. 2. Metric comparison of Eucidaris thouarsii ● and Eucidaris tribuloides ○.

grandis and M. frangibilis evolved from a common ancestor, but the M. frangibilis-M. ventricosa divergence is considerably older (about 10 million years) than the M. ventricosa grandis and M. ventricosa ventricosa split (about 1 million years). The minor morphological changes between the two subspecies of Meoma are indicative of the amount of evolution in that genus which occurred in one million years.

Mayr (1954) outlined the geographic distribution and speciation of shallow-water West Indian echinoids, and considered the Eastern Pacific Basin to be the greatest geographic barrier to echinoid distribution. Indeed, all of the shallow-water Panamic echinoid genera originated in the West Indies, except for three genera which have invaded the Panamic Province from the Indo-West Pacific since the uplift of the Central American landbridge. Lovenia is primarily an Indo-Pacific genus, not represented in the West Indian fossil record. Toxopneustes and Metalia are tropical Indo-Pacific genera and, also, are represented in the West Indian fossil history (Mortensen, 1943a and 1951). All three genera would probably establish populations in the West Indies should access to that area become available to them.

Two genera with nearly circumtropical distributions are missing from the Panamic Province; Echinoneus and Paraster. Echinoneus is a very old echinoid genus and is present as West Indian fossils predating the isthmian uplift. Its absence from the western coast of Central America is, therefore, probably due to unsuitable environmental conditions or to incomplete faunal sampling. Paraster, one species of which inhabits a niche similar to Echinoneus (in sand under rocks on shallow-water coral reefs), also, either has failed to establish itself in the Panamic region or has simply not been found yet. As both Atlantic Paraster species were discovered in the 1960's (Chesher, 1972), it is very probable that Pacific counterparts exist but remain to be found. *Paraster* rotundatus does occur in the Galapagos Islands and Chesher (1966) has compared P. rotundatus to P. floridensis on a meristic basis, and has shown them to be geminate species.

The echinoid genera Leodia and *Arbacia* have unusual geminate distributions, each with one widespread Atlantic species and a Pacific species located along the western coast of South America, from Ecuador to Chile, but not reaching into the tropical Pacific region. Mortensen (1935) considered Arbacia spatuligera to be the geminate of A. punctulata. It is possible, however, that A. stellata is derived from an even older A. punctulata stock which split prior to the separation of A. spatuligera and A. punctulata. Thus, with the exception of Echinoneus, all shallow-water West Indian echinoid genera are represented on the Eastern Pacific, but only eighty-five percent are present in the Panamic fauna.

ECOLOGY OF ECHINOIDS

Many shallow-water West Indian echinoids have been the subject of recent ecological studies (Table 4). Except for preliminary observations by Mortensen, Clark, and Chesher, no ecological studies have been made on Panamic echinoids. The information which is available suggests, however, that

Table 4. Geminate, shallow-water echinoid species, ecological observations on Atlantic species, and specific characters. Pacific species occupy habitats similar to those of the Atlantic, unless otherwise indicated; "p" indicates species not extensively studied ecologically; "*" indicates species for which habitats are unknown; taxa for which specific characters are considered reliable are printed in boldface.

Genus	Atlantic sp.	Pacific sp.	Ecological Observations	Characters for Discriminating Species
Agassizia	**excentrica*	***scrobiculata***	Atlantic: mud, over 30 m. Pacific: sand or mud.	Posterior petals of A. *excentrica* poorly developed and anterior series rudimentary, compared to equally well-developed pore-series in A. *scrobiculata*.
Arbacia	*punctulata*	**stellata*	Rock zones, grass beds. Harvey, 1956; Chesher, publ.	*A. punctulata* with no conspicuous red spots on aboral interambulacra, as in A. *stellata*, Mortensen, 1935, p. 575. (Note: Mortensen considers A. *spatuligera*, Ecuador to Chile, as A. *punctulata's* geminate).
Astropyga	**magnifica*	**pulvinata*	5 to 50 m, sand and rubble environment. Chesher, unpubl.; Kier and Grant, 1965.	Mortensen 1940, p. 181; A. *magnifica* with fewer interambulacral plates and with primary interambulacral tubercles parallel to interambulacral midline. A. *pulvinata* with tubercles parallel to ambulacra in adults and with more interambulacral plates.
Brissus	**unicolor*	**obesus*	Shallow coral reefs in sand. Chesher, unpubl.	*B. unicolor* with peripetalous fasciole on plates 4a (17 to 19) and 21.6% of test length laterally from apical system, compared to ***B.** obesus* (15 to 16) and 30 to 31%.

Table 4. (Continued).

Genus	Atlantic sp.	Pacific sp.	Ecological Observations	Characters for Discriminating Species
Cassidulus	**caribaearum*	**pacificus*	Shallow lagoon sand. Lowell P. Thomas, pers. comm.; Mortensen, 1948.	Test of C. *caribaearum* lower, and pits of naked sternal space larger, than C. *pacificus*. Mortensen 1948a, p. 198.
Clypeaster	**subdepressus*	**rotundus*	10 to 50 m, sand flats. Chesher, unpubl.; Kier and Grant, 1965.	*C. subdepressus* is longer than wide and pentagonal, compared to the more rounded *C. rotundus* which is about as wide as long. Mortensen 1948b, p. 109.
Diadema	*antillarum*	* *mexicanum*	Littoral and sublittoral coral reef, rock zones, grass, and sand beds. Lewis, 1966; Bauer, 1970.	*D. antillarum* with fewer pore-pairs per pore-series when compared to the number of interambulacral plates (see Fig. 2), than *D. mexicanum*.
Echinometra	*lucunter*	**vanbrunti*	Littoral rock and coral zones. McPherson, 1969.	*E. lucunter* with pronounced vertical "tag" on symphysis of auricles which support the muscles for the lantern. Low, poorly developed tag in *E. vanbrunti*. Mortensen 1943b, p. 362.
Encope	**emarginata*	**micropora*	Intertidal or shallow-water sand. Chesher, unpubl.	Posterior lunule of *E. emarginata* larger than that of *E. micropora*, Mortensen 1948b, p. 436.
Eucidaris	*tribuloides*	*thouarsii*	Coral reef, rocky zones, grass. McPherson, 1968.	In *E. tribuloides* percentage of interambulacral tuberculated midzone relative to width of largest primary tubercle areole larger (64-115%, mean 79%) than *E. thouarsii* (30 to 59%, mean 45%) (see Fig. 1).

Table 4. (Continued).

Genus	Atlantic sp.	Pacific sp.	Ecological Observations	Characters for Discriminating Species
Lytechinus	***williamsi**	**** *panamensis***	***L.*** *williamsi,* coral reefs. Chesher, 1968b.	Adult *L. williamsi* with less than 14 interambulacral plates per series, pedicellariae purple compared to brown pedicellariae and more than 14 plates per series in *L. panamensis,* Chesher 1968b.
Mellita	**lata*	**longifissa*	Intertidal sand beaches. Chesher, unpubl.	Posterior lunule of *M. lata* shorter (28% test length) and broader (14% lunule length) and pore-pairs per pore-series fewer in petals (41 in *IIIa*, in 62 mm specimen) than *M. longifissa* (37%, 8%, and 56, in 69 mm specimen).
Meoma	*ventricosa ventricosa*	**ventricosa grandis*	Sand, 3 meters to 100 m. Chesher 1969a.	In *M. v. ventricosa* distance from subanal fasciole to anal system equal to or greater than the vertical diameter of the anal system, color light to dark reddish brown, tubercles small and uniform size, compared to the same distance being less than the vertical diameter of the anal system, a dark brown to black pigmentation, and coarse tuberculation in M. *ventricosa grandis,* Chesher 1970.
Moira	*atropos*	**clotho*	Mud, intertidal to 160 m. Moore and Lopez, 1966.	Characters given by Mortensen, 1951, invalid, no adequate information available for reliable separation.

Table 4. (Continued).

Genus	Atlantic sp.	Pacific sp.	Ecological Observations	Characters for Discriminating Species
Plagiobrissus	*grandis	**pacificus*	Sand, intertidal to 50 m. Chesher, unpubl.; Kier and Grant, 1965.	Anterior ambulacrum of P. grandis forms a distinct notch along the ambitus in adults (not in juveniles), whereas P. *pacificus* lacks such a notch. Mortensen 1951, p. 494.
Tripneustes	ventricosus	*depressus	Coral and rock zone, *Thalassia* beds. McPherson, 1965.	Plates of buccal membrane of T. ventricosus few, scattered, compared to numerous plates on buccal membrane of T. depressus. Difference in tridentate pedicellariae possible. Mortensen 1943a, p. 500.

most of the Pacific members of geminate pairs inhabit ecological niches similar to their Atlantic counterparts and would probably live in similar habitats if the populations were intermixed.

Echinoid species occasionally hybridize in nature. Chesher (1968a) described a Brissopsis elongata x B. atlantica hybrid, Swan (1953) described hybrids among three species of Strongylocentrotus, and Mortensen (1943b) described hybrids of Echinus esculentus with E. acutus, E. elegans, and even with Psammechinus miliaris.

Despite occurrence of natural hybrids, closely related echinoids are able to maintain specific identity when living sympatrically. Cogeneric echinoid species often overlap in their geographic ranges and some species exist sympatrically in exactly the same ecological niches (cf. Chesher, 1968a). Mayr (1954) speculated that the sympatric species of Diadema in the Indo-Pacific were the result of a double invasion of the geographic range. Chesher (1968a) postulated a similar double invasion to explain the sympatric species of West Indian spatangoids.

Ecological conditions are much more rigorous for the Pacific littoral echinoids, especially in the Bay of Panama where rate of siltation is high and temperatures are low. Tidal fluctuations are much greater than the Atlantic geminates experience and the Pacific intertidal species of Echinometra, Diadema, Eucidaris, Encope, and Mellita are often exposed to the air for some hours without harm. On the Atlantic coast of Panama, these genera are seldom, if ever, fully uncovered by low tides. Bathymetric and geographic distributions are poorly known for the Pacific species, as are the more intricate aspects of their ecology. When the ecology of different species of closely related echinoid genera are compared, they are generally very similar. The major points of difference usually are bathymetric distribution and reproductive periodicity. Methods of feeding, nutrient selection, behavior patterns, fecundity, parasites, and environmental sensitivity, generally can be deduced from studies of closely related species.

FUTURE RESEARCH ON ECHINOIDS

Taxonomic analyses of geminate pairs are needed to establish techniques for separating the individual species. Should the geminates become intermixed, it would be of great biological interest to observe the movements of their populations. Presently, only about fifty percent of the species pairs can be separated without locality data. Characters which are now available to separate geminate species are listed in Table 4. Those which are based on a large series or for which there are usually reliable characters are printed in boldface type. The other morphological characters need verification and are probably inadequate to separate the species without locality data.

Additional exploration is needed along the whole of the Central American coastline to establish bathymetric and geographic distributions of echinoids. New species records and species new to science are almost certain to emerge from such studies. Additional collections are needed to resolve taxonomic problems in the genera Encope, Mellita, Clypeaster, Brissopsis and Brisaster. Two of these genera have remained taxonomic enigmas in the West Indian area, even though Brissopsis was examined by Chesher (1968a) and Clypeaster by Serafy (1970). Brisaster, from the northeast Pacific, was examined briefly by McCauley (1967).

Ecological studies are needed on at least some of the Panamic shallow-water species to determine how the animals compare with their Atlantic counterparts. Preferably, those genera which have been well-studied in the Atlantic should be considered first. Experiments on reproductive periodicity and environmental tolerances should take precedence, followed, perhaps, by studies of hybridization and larval development.

COMMENTS ON OTHER ECHINODERMS

No faunal list has been prepared for the other classes of echinoderms, but those specimens collected by the various Panamic expeditions, including the collections of the R /V PILLSBURY, have been identified (Bayer, et al., 1970).

The shallow-water asteroids, at least, show a much lower number of geminate pairs (three), and a much higher number of species (37) in the Panamic region, compared to the West Indies (18). Most of the species in the Panamic fauna appear to have invaded the tropical Eastern Pacific from the Indo-Pacific, sometime after the landbridge became established. Two of these genera, *Nidorellia* and *Acanthaster,* are of more than passing interest. Both genera are efficient coral predators and *Acanthaster,* at least, has the potential to cause severe ecological disturbances should it successfully invade the West Indies and undergo a population increase (Chesher, 1969b). It is presently uncertain how many species of *Acanthaster* inhabit the western coast of Central America. Caso (1962) records *A. ellisii* and *A. ellisii pseudo planci* and also presents characters which differentiate these two forms from *A. planci,* which is known to occur from the Red Sea to the Central Pacific Islands. The actual distribution of *Acanthaster* along the Central American Pacific coast is questionable, but it has recently been reported in the Bay of Panama (Sylvia A. Earle, personal communication[3]) and elsewhere (Peter W. Glynn and James W. Porter, this symposium). *Nidorellia* also occurs in the Bay of Panama.

Conversely, the crinoid fauna of the West Indies is strikingly larger than that of the Eastern Tropical Pacific. The R/V PILLSBURY, for example, collected eight species of comasterids in the Western Caribbean, but none at all in the Bay of Panama. Only two species of crinoids are known from the Bay of Panama (Clark, 1915, p. 51), whereas there are about fifty species of crinoids in the West Indian region (Clark, 1923).

Similarly, the ophiuroid fauna of the West Indies greatly exceeds the Panamic fauna. The R/V PILLSBURY, for example, took 51 species of ophiuroids in the Western Caribbean and only ten species in the Bay of Panama. Holothuroids collected by the R/V PILLSBURY comprised 20 species in the Panamic area and 23 in the West Indian area.

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[3] Editor's note: Field notes for this sight record of *Acanthaster* by Dr. Earle have been kindly supplied by her. They are: "Isolate Valladolid, near Isla Taboga: 8°40'26" N; 79°35'26" W, 6 April 1967, Water temp. 74°F, Station No. M[useum of] C[omparative] Z[oology] -19." Unfortunately, the specimen was not collected, and a search for a second specimen in June, 1971, was fruitless.

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THE STATE OF KNOWLEDGE OF THE COASTAL FISH FAUNA OF THE PANAMIC REGION PRIOR TO THE CONSTRUCTION OF AN INTEROCEANIC SEA-LEVEL CANAL[1]

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The only checklist of the fish fauna of the tropical shores of North America is that encompassed in the broad work by Jordan, Everman and Clark (1930) on fishes found in America north of Venezuela and Colombia. Because of the species described subsequently to 1930, as well as the initial inclusion of numerous nominal species, now regarded as synonyms, this work is so systematically out of date that any attempt to derive from it a meaningful list of fishes that may or may not occur in the Panamic region would be useless exercise. Meek and Hildebrand's (1923-28) three volume treatise on Panamanian fishes was based on few collections and is, again, so incomplete, extremely so with regard to the Atlantic section, as to be useless as a workable list of fishes of the region. The recent literature is voluminous but widely scattered in systematic reports, and in faunal reports from the periphery of the region in question.

The Panamanian fish fauna first should be examined relative to that of the larger tropical American region. Robins (1971) estimated that between 2000 and 2500 species comprise the fish fauna of the tropical Atlantic. This includes all forms from the estuaries to the deep sea. Coastal fishes comprise

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the largest single group, probably about 60 percent, and they are the species most likely to be involved in any change effected by construction of a sea-level canal.

For this reason this report concerns coastal fishes only (i.e., those occurring from the estuaries to the edge of the Continental Shelf). Also, most attention is given the Atlantic section, because its fish fauna is richer, because the situation there is somewhat more complex, and because there is much more published information available.

Elsewhere (Robins, 1969 and 1971) I have divided the shorefish fauna into two segments, which, although describable in geographic terms, have discrete ecological requirements. These faunas are termed insular and continental.

The distinctive and species-rich island fish fauna requires clear waters, buffered environmental conditions, and bottom sediments largely of calcium carbonate. In areas of steep drop-offs, clear ocean waters pound sediment-free rocky cliffs or wash variously developed fringing reefs, providing habitat along the mainland for island species. This fauna occurs from the Bahama Islands south to the islands off South America, such as Curaçao, Cubagua, and Los Roques. This faunal element is acentrically distributed, for it is in the north, in the vast expanse of the shallow waters that comprise the Bahamas, that it is best developed. Within the island area, species diversity depends on the extent of the shelf area and the nature of its habitat; the most impoverished islands are those with precipitous underwater profiles and with only limited and compact fringing reef development, and the richest are those with a broad, shallow-water environment, with grass beds, sand and coral flats and luxuriant reefs of various types. The Florida Keys, particularly along the border of the warm Florida Current, receive many elements of the insular fauna and, thus, form a mixing ground for continental and island species, an important factor contributing to the richness of Florida's fish fauna.

Other mixing areas are in Cuba, Hispaniola, Jamaica and along Central America from Yucatan to Colombia. Here, in coastal waters that never cool much, one finds an island fauna along the reefs that fringe areas where the shelf is very narrow and estuaries are absent. A continental fauna occurs in the bays and estuaries and in areas of broad shelf where muds are common.

Continental species require environments where change is a way of life; change due to seasonal shifts in continental climates unbuffered by broad stretches of ocean, change due to run off from large rivers, and change due to turbidities caused by winds that stir rich bottom sediments. Broad muddy embayments are common and estuarine influence is strong. Species characteristic of continental waters may be divided into northern and southern types, though some occur through both sections.

Geographically, and with regard to tropical and subtropical fishes or at least to fishes of tropical origin, this fauna extends from Cape Canaveral, on Florida's east coast, south to the tip of Florida, around the Gulf of Mexico to Yucatan, and through Cuba, in diminishing representation, to Hispaniola and Jamaica. During summer months species of this group may extend their distributions north along the southeastern coast of the United States to the Carolinas or beyond. Southern species occur along Brazil's north coast, the Guianas, and Venezuela, and in pockets in the mud shadows of the river mouths from Colombia to Nicaragua. These pockets show a mixture of southern and northern types, the shift being largely complete south of Mexico. Southern types also reach Jamaica in small numbers and mix there with northern continental types.

The reason for the inclusion of Cuba and Hispaniola and, to a lesser extent, Jamaica, in the ranges of the continental species lies in the high mountains that these islands possess, with consequent high rainfalls, permanent river systems and broad muddy embayments. Thus, we can expect continental species to predominate on the large, high islands where shelf waters are broadest and most influenced by run-off. Such areas include the Gulf of Batabano in southern Cuba and the Gulf of Gonaives in western Haiti.

Not all coastal species can be defined as insular or as northern or southern continental, but the only important exception is the group of ubiquitous shore fishes found nearly throughout the region and, thus, provides a common element to both sections of the tropical western Atlantic fauna.

Panama thus occupies a key mixing area. Its continental fauna, though largely southern, contains northern species and steep-profile sections of its coast permit colonization by insular elements. The insular element has been little sampled and recent collections using fish poisons demonstrate that we can expect to discover many species of this type in Panama. Obviously any sampling program aimed at assessing the fish fauna of the area must be extended outward in all directions, at least to Trinidad, the Greater Antilles and Honduras (and preferably Yucatan) if meaningful results are to be obtained in a short period of time. Starck (1968) recorded 517 species (389 inhabitants of coral reefs) from the limited environment of Alligator Reef, Florida, but hundreds of days of field work over a period of ten years was involved and species were still being added at the end.

Collections have been made by Miami's ship, R/V PILLSBURY, whose cruises were referred to earlier by Dr. Voss, and by National Oceanic and Atmospheric Administration, National Marine Fisheries Service vessels, especially R/V OREGON. Coverage provided by these vessels is good between 10 and 200 meters, especially in the southern and northeastern sections and for smooth or moderately smooth bottoms. Trawl operations on rough-profile areas below routine diving depth are important and rewarding but they result in heavy loss of gear and are time-consuming. Such operations must be increased. We have yet to make a single successful tow in such areas without collecting new species of fishes. Such areas are inadequately sampled.

Except for a small area at Tortuguero Lagoon, Costa Rica, whose fishes were studied by Gilbert and Kelso (1971), and at Cubagua Island, Venezuela, by Cervigón, there has been no thorough and systematic collection of fishes from the estuaries and shore regions anywhere along the continental margins. Island areas, in contrast, have been much better collected. Yet it is precisely this fauna, from the estuaries, muddy embayments, and inshore rocky coast that stands to be most involved in the effects of an isthmian sea-level canal.

The fish fauna of the coastal regions of the eastern Pacific has been the subject of important early surveys and reports, *e.g.,* the classic work of Gilbert and Starks (1904). Further, the Panamanian fisheries are concentrated in the Pacific and, as a result, much more material was available to Meek and Hildebrand from the Pacific than from the Atlantic. Shore collections have largely been the province of scientists from UCLA and Scripps Institution of Oceanography, but their efforts, understandably, have been concentrated in the north along the Mexican coast and especially in the Gulf of California where the fauna is perhaps the richest. Collections to the south have been much more based on opportunity than design. The R/V PILLSBURY sampled the Gulf of Panama but, because of gear failure, was unable to work the Continental Slope. The consistencies of the collections so far analyzed lead us to believe that the fishes in this muddy bay replace each other in depth, as an upper, middle and deep shelf fauna (Bayer *et al.,* 1970). PILLSBURY did not work the shore areas, either of the mainland or the Pearl Islands, nor was any estuarine work done. Collections are especially needed from the Coiba-Secas area. Again estuarine regions and isolated embayments away from Panama Bay, itself, are very poorly sampled.

Comparisons of the fish faunas of the two sides yield results that contrast sharply with those of such invertebrate groups as the echinoderms. Excluding pantropical species, there are very few fish species common to the eastern Pacific and western Atlantic. If these common species represent those elements that were exchanged during the opening of the most recent natural portals, then that exchange was very ineffective and involved only estuarine and continental types. In dealing with geminate species in Jordan's sense of the word (twin species of immediate common ancestry) the list is still small and, again, concerns estuarine and continental forms.

In making this statement I restrict my attention to families and genera that have been reviewed recently. In fish genera that prefer the reefs, clear waters and other conditions that we termed insular for the Atlantic, reviewers have stated that species groups do not cross the isthmus, but have their relations within the western Atlantic or Eastern Pacific. I can only conclude that the most recent series of southern portals across Central America did not exchange such elements and that their common ancestry was in much older and, perhaps, deeper and more extensive portals. It follows that construction of a sea-level canal, much smaller than the natural portals, will not result in exchange of elements of the insular fish fauna.

The list of transisthmian pairs of fishes will increase when genera that dwell in the muddy embayments and estuarines are studied and reported on.

Although there are many ichthyologists in the United States, few have concerned themselves largely with the tropical American fauna. Much has been done with regard to group revision, but, even here, few authors will say that problems do not remain in their study group. As might be expected, interest in diving and poisoning in clear water areas has been much greater than in the shore, bay and estuarine areas and this factor is compounded by the difficulty in moving along the shores of Central America. Thus, the systematically unworked or most poorly known groups are those of such inshore areas. Yet this is the fish fauna that stands to be most affected by a sea-level canal and, in part, has no doubt already been somewhat altered by movement through the present canal.

The biology and ecology of the inshore fishes, even those of importance to man, is unknown, except for a few dozen species, and in these, such studies have been conducted only in distant areas, such as the Gulf of California and southern Florida.

Virtually nothing is known of the biology or distribution of Panama's freshwater fishes. Scientists from Florida State University have made collections but few have been studied and no revisions have been published. A sea-level canal will effectively divide the fresh waters of Panama. No doubt the present canal has affected some fresh water fishes, but lack of baseline studies obviates additional comment.

With regard to fishes I conclude with the following observations.

1) It is urgent that an intensive collection program be inaugurated that will continue and expand existing efforts and

broaden participation. The facets of this program should be: a) continuation of surveys of shelf and upper slope waters on both coasts, with proper funding, so that geographic gaps may be filled, and rapidly so; b) development of a collection program with divers, poison and seines in inshore, bay, and estuarine situations—this effort will need to be sea-based with houseboats, barges, and small collection boats, for travel along the mainland is not possible—since the entire coast can not be worked, it is important to select a series of sites for very detailed effort in all habitats for about ten days each; and c) give urgent consideration to a large scale collection program within the present canal system and its entrances.

2) Collection programs must not end with the obtaining of material, but major support must be sought for all participating institutions for the handling, processing and study of it and for the publication of results.

3) In systematics research, funds should be made available specifically for study of the Clupeidae, Engraulidae, Ariidae, Gerreidae, Sciaenidae, Eleotridae and other fish families that history has shown to be most likely to move through a sea-level canal.

4) Ecological and community studies are particularly desired. If we do not yet know what species occur in these waters we surely know little about their life histories and interrelationships. Biologists situated in Central and northern South America are in a particularly good position to do this work. Because of its long term nature it must be started quickly.

5) It is particularly desirable to involve ichthyologists from countries of Central and northern South America. A training program for them would be a desirable adjunct to the work and would help insure interest in the natural resources of these countries and the study of them.

ACKNOWLEDGMENTS

This report stems from a program of research on oceanic fishes supported by the National Science Foundation (NSF-GB-7015X) and by the Maytag Chair of Ichthyology. Travel funds to participate in this symposium were provided by the National Museum of Natural History. I am also indebted to my colleagues Gilbert L. Voss and Frederick M. Bayer with whom this subject has frequently been discussed.

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THE MARINE FISHERIES OF PANAMA

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The principle fisheries of Panama are based on shrimp and industrial fish. As in the United States, they are the most valuable and produce the greatest tonnage, respectively. They both are produced mainly for export markets, however, and contribute little to the protein base of the Panamanian diet.

The third largest fishery is for miscellaneous marine species that are marketed within the country. The landings are made by local independent fishermen (the so-called "canoe fleet"), by several small fishing cooperatives, and by shrimpers who retain a portion of their associated fish catch for sale on the local fresh fish market. The most important of these include corbina, red snapper, Spanish mackerel, groupers, jacks, snook, and mullet (Lucas, 1946 and Sever, 1966).

The fourth largest fishery is for spiny lobster and, again, the bulk of production is exported.

Except for shrimp, the fishery resources of Panama are believed to be considerably in excess of present production. A preponderance of these are located on the Pacific coast where both abundance and availability are markedly affected by seasonal environmental phenomena. Although limited amounts of processed fish products, chiefly bacalao, are imported to supplant the fresh fish caught locally, there is no doubt that national demand could be met by local production capability, if suitable refrigeration, transportation, and marketing facilities were available.

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[1] Read by Walter R. Nelson, National Marine Fisheries Service.

THE RESOURCE BASE—PACIFIC COAST

While it is easy to argue in either direction with Gulland's (1970) recent summary of the fishery resource base, we generally support his estimates for the Panamanian region and rely on his figures as they can be extrapolated for the Panama Pacific coast.

Coastal *Schoolfish*

The anchoveta (Cetengraulis mysticetus) and four species of thread herring (Opisthonema libertate, 0. *bulleri*, 0. medirastre, and 0. berlangai) constitute a large resource of coastal schoolfish. Gulland estimates the potential yield of these stocks in the region between the Gulfs of Fonseca and Guayaquil to be from 0.5 to 1 million tons. Based on the observations and studies of Bayliff (1966 and 1969) and Forsbergh (1969), he constructs a likely potential yield for the Gulf of Panama (as the richest part of this area) to be to the order of 150,000 to 250,000 tons annually.

Tuna

The tuna resources of the region are harvested at present by nations other than Panama, chiefly by the United States. In the Panama Bight, beyond the 100-fathom isobath, yellowfin tuna (Thunnus albacares) and skipjack tuna (Katsuwonus pelamis) are taken by high-seas tuna fleets. The nature of the resource in proximity to Panama can be described as follows.

Most fishing effort occurs between Piñas Bay and Cape Mala. The maximum catch rates occurred from this area to south of Piñas Bay, approximately off Buenaventura, Colombia, or about latitude 5°N. Until about 1962, yellowfin and skipjack tuna were caught almost exclusively by the bait boats fishing from California. After 1962, most of this fleet was converted to purse seining and tuna are now caught chiefly by large purse vessels operating out of both California and Puerto Rico. Forsbergh (1969) indicated that the abundance of tuna in the northern part of the Panama Bight is high in April and May, which may be related to the abundance of food. Earlier, Alverson (1963) showed that zooplankton comprise a considerable portion of the stomach contents of yellowfin and skipjack tuna. Observations from a fixed station in the Gulf of Panama showed that zooplankton concentrations might be expected to peak during the May–June period. He felt that other factors being equal, it is undoubtedly advantageous for the fish to arrive at a given area at a time when food is abundant and to depart when abundance declines.

Fink and Bayliff (1970) recently suggested, on the basis of tagging data, that migration patterns for yellowfin and skipjack in the eastern Pacific support Forsbergh's hypothesis. They indicated that in March both species concentrate between the equator and latitude 10°N., which is offshore and north of the Galapagos Archipelago. By April, they are concentrated northeast of Malpelo Island, and by May they have split into two branches. The minor branch is directed to the northwest and the major one is directed toward the Gulf of Panama and then southward along the coast of Colombia.

Demersal Finfish and Shellfish

The demersal stocks on the Pacific coast of Panama have been estimated to yield 30,000 to 60,000 tons of fish byproducts from shrimp trawling activities (Gulland, 1970). Based on personal experience in the area, we would support that estimate and add that the total potential demersal production of finfish might be from 50,000 to 100,000 tons. Approximately 10 percent or 5,000 to 10,000 tons would constitute high value food fishes such as grouper and snapper.

Most of the locally consumed fresh fish is a mixture of demersal species such as snapper, grouper, corbina—the choice sciaenid—and catfishes. The larger coastal pelagic fish, such as mackerels (Scomberomorus spp.) and dolphin (Coryphaena sp.), also find a ready market. Resource assessments of these stock elements do not exist and landing data are wholly inadequate for extrapolation. In the local markets, these species appear to be available for most of the year so one must assume that an adequate, if not rich, supply is available to the fishermen.

Additional resources have been identified on the Pacific coast that are not being fished. An exploratory spiny lobster fishing survey was undertaken by the U. S. Agency for International Development in 1963 and 1964, utilizing the R/V PELICAN along both Caribbean and Pacific coasts. Bocas del Toro, Chiriquí Gulf, and San Carlos were the areas considered to have greatest commercial potential for spiny lobsters. In addition to the Pacific spiny lobster (Panulirus gracilis), concentrations of sand lobsters (Evibacus princeps), that proved available to trawling, were located in the Gulf of Panama.

THE RESOURCE BASE—CARIBBEAN COAST

Knowledge of the resources of the Caribbean coast is more fragmentary and less encouraging. Small quantities of brown shrimp (Penaeus aztecus and P. braziliensis) occasionally appear off Cabo Tiburón, at the mouth of the Darien Gulf, and in the western Gulfo de los Mosquitos, near Laguna de Chiriquí. We have observed an occasional Panamanian trawler working in both of these areas, although there are no production statistics indicating a Caribbean coast shrimp fishery.

Coastal Schoolfish

Coastal pelagic schoolfishes include a number of anchovy and herring species as well as scad, jacks, and Spanish mackerel. Assessment data are too meager to more than note their presence. Personal knowledge of experimental purse seining operations near the Panama-Colombia borders a few years ago indicates that schools of thread herring (Opisthonema oglinum) of up to 10 tons per school can be caught, but the incidence of schools of this size is too infrequent to encourage commercial development. Gill netting experiments have also yielded large Spanish sardines (Sardinella anchovia) in small numbers.

Tuna

Offshore there are several species of tunas, none of which is being fished at the present time. Troll captures and school sighting just beyond the Continental Shelf have encouraged some very limited experimental tuna fishing by United States purse seine vessels (under charter by the Commonwealth of Puerto Rico). No catches, however, have been made.

Demersal Fin fish

Demersal fishes on the Continental Shelf are also less abundant than on the Pacific coast. Although incidental species in shrimp trawl catches include many desirable market species, such as grunts, snapper, and corbina, the catch rates experienced are not encouraging for development.

RESOURCE ASSESSMENT PROGRAMS

The Republic of Panama is receiving further technical assistance from the Food and Agriculture Organization of the United Nations through a regional project for fishery development which was established in November 1966. Objectives of this project are: (1) to investigate potential commercial fisheries; (2) to develop management for existing fisheries; (3) to improve processing and marketing methods; and (4) the regional consolidation of fishery planning. The FAO project is in its fourth year and has completed intensive studies on the purse seine fishery for anchoveta in the Gulf of Panama, a description and management plan for the shrimp fisheries, and exploratory fishing for shrimp and the fishery resources along the north coast in the Laguna de Chiriquí.

PRESENT FISHERIES

The purse seine fishery in the Gulf of Panama is based upon anchoveta and thread herring, which are converted to meal and oil. There are two reduction plants; one at Puerto Caimito and the other on Isla Tobago. Small local fisheries also utilize anchoveta as bait for tuna and other fish. Shrimp trawlers take small amounts of anchoveta but discard them at sea. One center of abundance for anchoveta is the Gulf of Panama. As the United States tuna fishery gradually extended southward during the 1930's and 1940's, the ready availability of anchoveta in the Gulf of Panama was identified. The area remained the prime source for the tuna live bait fleet until about 1958. A subsequent decline in the catch of anchoveta was a result of the conversion of most live bait tuna vessels to purse seining. Now anchoveta is exploited preponderently by the purse seine fishery for reduction purposes.

The anchoveta fishery is conducted in all parts of the Gulf of Panama where fishing is permitted, except along a 50 km stretch of sandy beach between Bahía de Parita and Puerto Chame. Most fishing in the Gulf of Panama occurs in the Isla Verde and Panama Vieja areas.

Initially, reduction plants were located in the Isla Verde area and it was seldom necessary to travel far to catch fish. During 1964-67 the Isla Verde vessels extended throughout the Gulf of Panama; however, today the vessels rarely fish beyond Puerto Mangle. Part of the fleet concentrates fishing to the southwest of Isla Verde where catches consist almost entirely of thread herring.

Six purse seiners were active in 1966 and this fleet has now expanded to 15 vessels. Anchoveta inhabit the shallow mud flats along the coast of the Gulf of Panama and are rarely found beyond 8 km from the shoreline. They occur in Bahia Parita and almost continuously from Puerto Chame to Bahía San Miguel. So purse seining in the Gulf of Panama takes place almost entirely on mud bottom areas between Puerto Chame and the entrance of the Panama Canal. From Puerto Chame to Bahía Parita, the bottom is sandy and is not suitable for anchoveta. Consequently, Puerto Chame forms a natural boundary to the fishery.

Spawning occurs principally in November and December. Young-of-the-year reach catchable size for the purse seine fishery in April or May and are the main source of supply for the fishery through the summer and fall. During the fall and winter, availability decreases rapidly so that year-old fish make up only a minor portion of the catch by late winter and early spring. In March, April, May, and June, young-of-the-year and older fish tend to school according to size so fish caught in a single set are almost entirely of one age group. Later in the season, mixed age groups arc commonly caught in single sets. From October to December, anchoveta are more difficult to catch because of behavior changes associated with spawning. At the same time, thread herring become more available so fishing effort is diverted from anchoveta to thread herring. In December, the catches of anchoveta again improve and fair catches may be made in January. There is usually little fishing in February and March due to the difficulty of catching fish and to the tendency of the young-of-the-year to gill in seine netting. At this time, plant and vessel maintenance takes place and some purse seining for snapper, *Lutjanus* sp., is conducted in deeper waters with large mesh nets; at this time, schools of snapper are occasionally found near the surface and juvenile anchoveta occur at the surface out over depths of 60 meters. The adult anchoveta are found more inshore, from the bottom to the surface, out to about 10 meters. Juvenile anchoveta are found in relatively clear water while adults are on mud flats where the water is turbid. Forsbergh (1969) estimated the stock of anchoveta in the Gulf of Panama at 39,000 metric tons in December increasing to 169,000 tons in April; the incoming year class causes the increase in biomass.

Reduction fishing reached a peak in 1966 with 53,000 metric tons of anchoveta and almost 13,000 metric tons of thread herring. It decreased drastically to a total of only 23,880 short tons in 1969. The industry attributed the low catches to temporary changes in the coastal currents caused by unusual weather conditions (Anon., 1970). We do not have information on the 1970 catch that would permit further evaluation.

Shrimp

The shrimp fishery was initiated in Panama shortly after World War II and experienced dramatic growth during the 1950's; the fleet expanded from 8 to 220 vessels. Shrimp has become the most valuable fishery resource and total annual production has stabilized at 10 to 15 million pounds. In 1969, exports exceeded 9.5 million pounds and was valued at $9.9 million.

Three species of Pacific white shrimp, Penaeus occidentalis, P. stylirostris, and P. vannamei, comprise 30 to 50 percent of the shrimp production. Seven other species are also caught commercially (see Table 1).

White shrimp are usually fished near the coast in 4 to 12 fathoms (Obarrio, 1959) and the principal fishing grounds are in the Gulf of Panama and the Gulf of Chiriquí. Major portion of the catch is from the Panamá-Darién area and the eastern part of the Gulf. Penaeus occidentalis accounts for more than 90 percent of the white shrimp catch in this area.

Table 1. Scientific and vernacular names of commercially important shrimp from the Central Eastern Pacific.

Scientific name	English	Spanish
Penaeus vannamei	White	blanco, camaroncillo
P. occidentalis	White	blanco, camaroncillo
P. stylirostris	White	blanco, camaroncillo
P. californiensis	Brown or white	Cafe o blanco
P. brevirostris	Red	Rojo
Trachypenaeus byrdi	Tiger, seabob	Tigre, carabali, camarón
T. similis pacificus	Tiger, seabob	Tigre, carabali, camarón
T. faoea	Tiger, seabob	Tigre, carabali, camarón
Protrachypene precipua	Seabob	Titi, camaroncillo
Xiphopenaeus riveti	Seabob	Titi, camaroncillo

West of the Panama Canal P. vannamei and P. stylirostris dominate the catches, with very few P. occidentalis present. Bayliff (unpublished paper) described the procedures used in Panama to determine the catch per unit of effort for white shrimp and presented these data from 1954 to 1967. Forsbergh (1969), using Bayliff's data, suggests that the annual apparent abundance of white shrimp in the Gulf of Panama may be related to the degree of upwelling in the year. He also found that mean monthly catches of shrimp in the Panama Bight are greatest in May and July, about three to five months after peak upwelling, and that monthly catches of all kinds of shrimp in the Gulf of Panama are inversely, and significantly, correlated with mean sea level at Balboa, Canal Zone. He concluded that the life cycle of shrimp in the Panama Bight appears to be related to the seasonal cycle of upwelling and enrichment. According to Bayliff, the catch per unit of effort of white shrimp has decreased since 1954. During the mid-1950's, catch per unit of effort was about 200 pounds per day. It decreased in 1957 to 148 pounds per day and to 80 pounds per day in 1958. It increased to about 120 pounds per day for the next several years. The annual catch of the three species of white shrimp since 1954 has only increased slightly more than 1.5 million pounds. In 1954, the catch for these species was 3.2 million pounds and recently the catch has fluctuated between 4.5 and 4.7 million pounds annually. The great increase in fishing effort and small increase in catch indicate that this resource is being used at maximum level.

Production of Pacific red shrimp *(Penaeus brevirostris)* grew dramatically after 1956 when this resource was found in commercial concentrations. Production reached a peak of more than 4 million pounds in 1968. Since 1961, annual production has fluctuated between 2.5 and 4.25 million pounds. Red shrimp are primarily caught during January through March and August through September. During the January—March period, when upwelling occurs in the Gulf of Panama, the shrimp occur in concentrations which may last from a few days to three months. They are normally caught near the coastline during this period. During August and September, peak production is reached and the shrimp are found between 5 and 35 fathoms throughout the Gulf of Panama.

Production of the seabob, or "tití" (*Xiphopenaeus riveti*), started in 1954 and, during the last few years, landings have leveled off at around 5 million pounds. During 1969, production peaked in November and December, but in previous years this usually occurred in June and July. The other species important to the local fishery is the "carabali" or tiger seabob (*Trachypenaeus byrdi*) with a limited annual production of less than 0.5 million pounds; this species is caught throughout the year.

The shrimp fleet is limited by law to 232 vessels, but only 227 vessels are known to be fishing the Pacific coast of Panama. This law restricts the amount of fishing effort by limiting the number of boats.

Spiny Lobsters

Several attempts have been made to develop the spiny lobster resources of both sides of the Panamanian Isthmus. Stimulated by the adjacent Costa Rican production of some 4 million pounds in 1960-61, commercial, government, and United States technical assistance programs have been directed at resource assessment and fishing development. The resources described earlier (Butler and Pease, 1965) have not been fished to date. Some limited production of both spiny and sand lobsters during shrimp trawling operations in the Gulf of Panama has been noted by Panamanian fishery officials.

Presently, spiny lobster fishing is concentrated on the Caribbean side in the Bocas del Toro Archipelago. The season extends from February to May when spiny lobsters enter the rocky shoals of the Chiriqui Lagoon. In other areas where lobsters are fished—San Bias on the Atlantic coast and San Carlos, Veracruz, and Los Santos in the Pacific—year-round fishing is practiced. It is estimated that about 60 fishermen on the Pacific and 100 on the Atlantic are actively engaged in lobster fishing. About 80 boats are used, mostly canoes and other small boats. The price to the fisherman for live spiny lobsters is about 45 cents to 60 cents per pound. In the Pacific, trammel nets are used for lobsters, while in the Bocas del Toro and San Blas regions, lobsters are fished by divers during low tides. The UNDP /FAO R /V ORION recently conducted an exploratory survey in Laguna de Chiriqui and Almirante Bay on the Caribbean coast, but very few lobsters were taken.

Incidental Fisheries

The Republic of Panama does not keep statistics on the number of local fishermen who either actively pursue fishing commercially or those who catch fish for personal use and sell excess quantities. There are large numbers of fishermen who use dugout canoes and hand lines for various species of snapper, corbina (*Cynoscion* sp.), jacks, and other fishes. In the San Carlos area in the Gulf of Panama, there are several fishing villages and cooperatives which employ beach seines with either powered or unpowered skiffs to catch various coastal species. In most cases, these fish are either sun-dried or salted but, occasionally, they are delivered to market in the fresh state. Here it is possible to juggle estimates of production to your heart's content without serious challenge. Most estimates of the indigenous utilization of localized, small-unit production fall within a range of 2 million to 5 million pounds. This seems reasonable to us.

On a final note, we believe that the production of snapper, groupers, and seatrout could be increased with modest effort. In addition to the potential for spiny lobsters, there are other latent resources which could be developed, such as scallops. We would observe that, in general, Panamanian fisheries are in a healthy state and contribute significantly to the national well-being.

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TERRESTRIAL PLANTS OF PANAMA

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It is generally felt that residents in the tropics are in a poor position to write floras, because we lack the necessary library and museum facilities. I hope, though, that we may be well-qualified to evaluate the floras which are written elsewhere. In the case of Panama, a flora is being published, and this gives a very good idea of what is currently known of the vascular plants of Panama.

The Missouri Botanical Garden acquired a station in the Canal Zone in 1926, and this very naturally channelled their activities toward the isthmus. The first of a series entitled "Contributions toward a Flora of Panama" was published by Dr. Woodson and his colleagues in 1937, and the first fascicle of the Flora of Panama appeared in 1943. According to the original plan this flora would be made up of about ten parts, but "Part I," with the introductory material, has been left until "later." The publication was at first in systematic order within each part, but this procedure has been abandoned, so that completed manuscripts would not have to remain shelved until preceding families were ready. At the present the Flora is almost exactly three-quarters done, in terms of families. The families remaining to be published include several large and important groups, such as the Acanthaceae, Bignoniaceae, Gesneriaceae, Guttiferae, Malpighiaceae, Rubiaceae, Solanaceae and Verbenaceae. Thus, though the Flora may be a bit less than three-quarters done in terms of species, the staff of the Garden is working hard at its completion, and I believe we may expect the vascular plants to be finished within a few years. The Flora of Panama, thus, stands a fair chance of being the first completed modern flora for any sizeable area in tropical America.

The question is, of course, "How well does the Flora of Panama represent the flora of Panama?" and this is a question of how well the flora has been sampled. I have been told that the flora of Panama is one of the best known in the American tropics, but I sincerely hope that my informants were wrong. As Dr. Walter Lewis has indicated (1968), the sampling for the Flora of Panama has been at best somewhat spotty. I have chosen five groups of flowering plants about which I have some knowledge, personal or borrowed, to compare the treatments in the Flora of Panama with what I know to occur. My knowledge is somewhat biased toward the monocots, and strongly biased toward the area of central Panama.

We may start with the oldest part of the Flora; Part II, Fascicle 1, including the family Gramineae, was published in 1943. My personal knowledge of the grasses is virtually nil, but I have given special attention to the tribe Olyreae since Dr. Cleofé Calderón visited Panama in early 1968. These are usually forest grasses, with quite wide leaves. Their flowers are not at all showy, but no conscientious general collector would neglect them. Dr. Calderón had planned to stay only two or three days in Panama, because the Flora indicated that she would find very little. On our first field trip we found two unexpected species of *Cryptochloa,* one of *Olyra,* and one which still remains unidentified for lack of fruit or flowers; Dr. Calderón postponed her departure for several days. We did not find all of the six Olyreae listed in the Flora, but we did find at least eight additional species, giving an increase of 133% with only a few days of collecting. The biggest contributor was *Cryptochloa,* of which we have found five additional species.

The Marantaceae are usually large or very large herbaceous monocots with quite showy flowers. They can scarcely be overlooked by the collector, though he may prefer to devote his energies to plants which are easier to press and dry. The treatment of this family was published in 1945 and included 22 species. Miss Helen Kennedy, of the University of California at Davis, has been studying the ecology of this group and has devoted considerable effort to their taxonomy, as well. In the last couple of years she has spent several months in Panama and has found thirteen additional species of *Calathea* and *Ischnosiphon.* This represents an increase of about 60% over the Flora treatment.

The largest family of flowering plants, the Orchidaceae, are my special interest. The showier members of the family are much sought after by orchid growers, but these activities only occasionally contribute well-documented specimens for botanical study, and the plants of many species either are small and inconspicuous or bear tiny flowers. The majority of tropical species are epiphytes, and these are undoubtedly difficult to sample. The Orchidaceae in the Flora of Panama were published from 1946 to 1949, and the published account lists 470 species, a rather puny figure when compared with the thousand or so known for Costa Rica. I have tried to bring together the new records published since that time, and have added enough of my own recent new records to list a hundred additions to the flora (Dressler, in press). I do not have enough new records on hand to publish another "century" of additions just yet, only about eighty so far, bringing the known orchid flora up to about 650, an increase of nearly 40%. This is, proportionately, the smallest increase of the five groups we are sampling here.

As the orchids supply the largest lot of new records we will discuss here, it may be of interest to consider their geographic affinities. Many of these additions are species previously known from Costa Rica or other parts of Central America, about 38%, while only about 12% were previously known only from Colombia or other regions of South America. This is undoubtedly somewhat skewed; it is much easier to identify the species known from Costa Rica than those known from Colombia. About 18.8% of the additions to the flora were previously known from both Central and South America, and, thus, were to be expected in Panama. About 8.7% of the additional species were definitely undescribed, while about 20% remain nameless, but may be either undescribed or species known from other areas but still unidentified. This does not quite total 100%, as I have included a couple of naturalized species and a couple of species previously known from Panama but omitted from the Flora. The orchids' reputation for narrow endemism seems to be largely fallacious; many of the new species described within the last 10 or 15 years are already known from Nicaragua, Costa Rica, Colombia or all three.

I am not sure that herbaceous plants, whether huge terrestrials or tiny epiphytes, will be accepted as a good measure of a flora's completeness. Trees are the dominant element in tropical forests and are economically important. For many purposes, our knowledge must be evaluated in terms of how well we know the forest trees. While the trees can scarcely be "overlooked" by collectors, their sampling is very difficult. Even if one has a crew of tree-cutters or tree-climbers, only a small proportion of the trees are in flower or fruit at any given time, and these may be very difficult to distinguish from the ground.

The Lecythidaceae seem to me one of the most interesting of the woody families in the American tropics. These are usually trees of primary forest; both the flowers and the fruits are quite distinctive, and both need to be sampled for an adequate taxonomy. The features of the foliage may help a good deal in matching fruiting and flowering specimens of the same species, but the leaves differ largely in size and more subtle features of texture and posture, features which do not sound very convincing when written into a description. The Lecythidaceae were treated in the Flora in 1958, with 17 species listed. Since then, several additional species and one additional genus have been recorded (Brizicky 1958, Dwyer 1965). Our attention was drawn to this family in late 1967 when Scott Mori, then a student at the University of Wisconsin, visited the isthmus seeking lecythids. We were soon quite bewildered by the abundance of *Eschweilera* species, especially in the hills near the Caribbean coast. We have matched one of these with a previously described species, and a couple of the others could be the same as previously described species, but we seem to have at least fourteen species of Eschweilera in Panama. We have also a distinct new Gustavia, which is rather widely distributed in central Panama, and we have three quite distinct species of Couratari, one of which is presumably C. panamensis. My enumeration of named and nameless Panamanian Lecythidaceae totals 39 at the present, giving an increase of about 130% over the treatment in the Flora.

The only other woody group for which I have good data near at hand is the genus Ficus, which forms an important element in nearly all tropical forests. Mr. William Ramírez, now a Smithsonian pre-doctoral fellow, is working on the fascinating relationships between Ficus and the wasps of the family Agaonidae, and he has, of necessity, learned a good deal about fig taxonomy. The figs have the disadvantage that the rather diverse fruits shrivel to identical, nearly formless lumps upon drying, obscuring many of the best taxonomic features. Thus, some of the species which we enumerate here were surely sampled before the treatment of Ficus was prepared for the Flora (1960), but the distinctions were not readily evident in the dried specimens. Mr. Ramírez' experience shows, however, that these are thoroughly "good" species, often with wide and overlapping geographic ranges, with different habitat preferences, with different and highly specific pollinators, and consistent differences in fruit morphology, leaf venation and stipule form. The treatment of Ficus in the Flora listed 18 species for Panama, plus one other in the "to be expected" category. Mr. Ramírez' work has revealed 28 species in Panama, without counting two of those listed in the Flora, giving us a total of 30 species, or an increase of about 66%.

The five groups which we have sampled show an average increase of about 85% over the number of species listed in the Flora of Panama (Table 1). One may feel that our sampling is biased, in spite of the habital diversity of the plants involved. Certainly, we do not usually take a special interest in any group which is monotonously easy to identfy, but I do not know of any sizeable group in that category in Panama. There are, in fact, several groups which are as bad as, or worse than, those we have sampled, such as Heliconia, Myrtaceae and the taxonomically chaotic Araceae. The treatment of the Euphorbiaceae was published in 1968, yet the authors are already planning a supplement. I recently sent a lot of Gesneriaceae to Mr. Hans Wiehler; nine of the 21 collections represented undescribed species.

One may ask why this supposedly well-collected area is

Table 1. Comparison of number of species of various plant groups now known, to numbers listed in the Flora of Panama.

	In "Flora of Panama":			
Plant group	Date of treatment	Number of species	Number of species now known	Percentage increase
Graminae/Olyreae	1943	6	14	133
Marantaceae	1945	22	35	59
Orchidaceae	1949	470	650	38
Lecythidaceae	1958	17	39	129
Moraceae (Ficus)	1960	18	30	66
			Average:	85

so poorly sampled. I believe that there are two major factors involved here. One of these is the simple factor of accessibility. Panama has one major all-weather highway running from the Costa Rican border through the heavily settled Pacific slope to Chepo, about 50 km east of Panama City, with several side-roads, also in heavily settled areas, and the Trans-Isthmian Highway from Panama City to Colon. The floristically rich Atlantic slope is almost totally without roads except for the banana and cacao producing area of Bocas del Toro and the region near Colon. The higher elevations are exceedingly rich in plant species, but they are easily reached only near Boquete, Volcán and Cerro Punta, in extreme western Panama, and near El Valle de Anton, Cerro Campana and Cerro Azul in central Panama. The much greater areas between Boquete and El Valle and between Cerro Azul and Colombia remain virtually untouched. In this respect, I must emphasize that the field experience on which my evaluation is based is also virtually limited to the few areas mentioned above. The flora of Panama will almost certainly prove to be at least twice as rich as indicated by the published Flora.

While there have been many plant collectors in Panama— Dr. Dwyer lists about 175 and guesses over 200 (1964), very few of these collectors remained long in Panama. Paul Allen and Henri Pittier are about the only ones who might be called resident collectors. The obvious result is that all Panamanian plants are strange to most of these collectors, and the same common or striking species are collected repeatedly; one can still find novelties in the most heavily collected areas. Few of these collectors have had the time to reach new or undisturbed areas, and the available collections are heavily biased toward the edges of the Pan-American and Trans-Isthmian highways. Even the very heavily visited Barro Colorado Island has revealed numerous new records with the systematic and persistent efforts of Mr. Robin Foster and Dr. Thomas Croat. Dr. Croat tells me that the vascular flora of this relatively small island (nearly 4,000 acres) seems to be "levelling off at about 1,300 species.

There is no easy way to create or promote an adequate number of resident collectors. Costa Rica has long had both a physical and an intellectual climate which are attractive to professional and amateur biologists, and there have been over a dozen resident collectors, which supports my hope that some other areas in the American tropics are better known than Panama. While we cannot easily duplicate Costa Rica's climate or history, we can promote botanical collecting in various ways. Probably the best all-around system is to place graduate students in the field for long periods (6-24 months). Graduate students are at the peak of their energy and collect many more specimens per day than later ontogenetic stages, and their upkeep is relatively inexpensive. At the same time, their field work is valuable professional experience which contributes to their later careers.

If, on the other hand, the number of plant specimens per dollar spent is the only consideration, I would recommend the training of native collectors. Do not, in any case, seek potential collectors in the city, or even in small towns, but look for persons who are at home in the forest. Some degree of literacy may be a requisite, but, in most areas, requiring proficiency in English will exclude 90 to 100% of the best potential collectors.

If I may, I would like to add a few words about current activities which may advance our sampling of the Panamanian flora. The University of Panama now has a small but actively growing herbarium, in the capable hands of Miss Mireya D. Correa A. Both Miss Correa and Professor Novencido Escobar are always eager to collect, though teaching eats heavily into their available time. The Missouri Botanical Garden once again has a station in the Canal Zone, a cooperative effort with the Panama Canal Company at Summit Gardens. At the present Dr. Croat is in charge of this station and continues his efforts toward a revised flora of Barro Colorado Island. Hopefully, it will be possible to keep a resident botanist at this station for the foreseeable future. My own institution, the Smithsonian Tropical Research Institute, is largely oriented toward ecological and evolutionary problems, though some of us collect whenever we have an opportunity, and we often serve as host for visiting collectors.

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THE ENTOMOLOGY OF PANAMA

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The insects of Panama are that group of animals with the greatest number of species, and many investigators have been engaged in describing this fauna. It was insects which prevented the first attempts to complete the Panama Canal. In the present brief survey, included as usual subjects for entomologists, are related arthropods such as ticks and mites.

Because of the success of Major Walter Reed of the U. S. Army and his associates, including W. C. Gorgas, an Army surgeon, in attacking yellow fever in Cuba, Gorgas was assigned the task of eliminating insect-borne malaria and yellow fever in the Panama Canal area. Only then could the Canal excavation work be effectively pursued.

The Indians of Middle America took insects in stride. As their populations in Panama increased before the arrival of Europeans, it may be assumed that their agricultural practices had some effect on various insect species. This relationship of man to insects may well be considered to be "natural." It was not until the advent of Europeans, after Columbus came in 1502, that insects became noteworthy. When citrus, banana and other cultivated plants were brought here, insects became conspicuous as defoliators and transmitters of plant and human disease.

The systematic study of Panama insects began in the late 19th century. It was not until the *Biologica Centrali-Americana* was published in 52 volumes that the basis for a monograph of the biological life of Central America was possible. The Insecta included many volumes, of which the ants by A. Forel comprised Vol. III of the Hymenoptera. This series included many

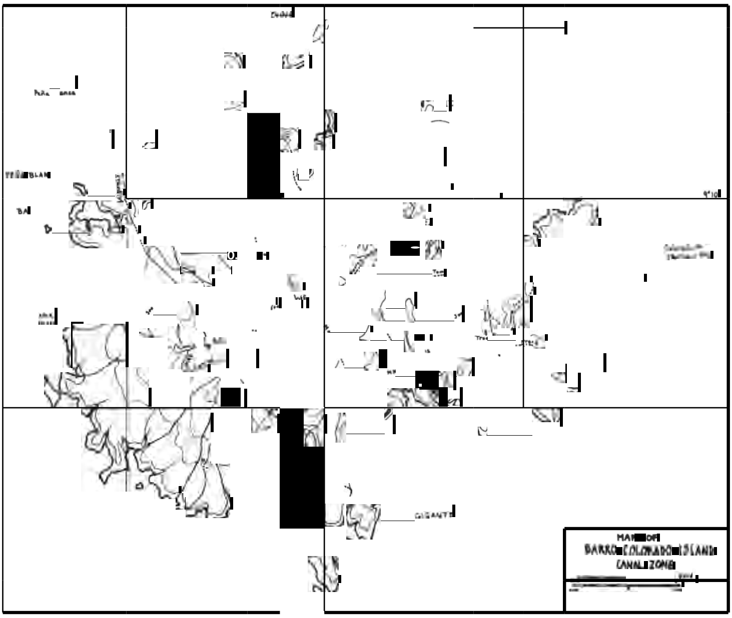

FIG. 1. A map of Barro Colorado Island, Panama Canal Zone, showing the trail system in dotted lines. Each 100 meters is marked by a numbered post along the trail. Contour lines are at 100 foot intervals. The shore is approximately 85 feet above sea level. Map, courtesy of the Barro Colorado Island Laboratory.

Similarly marked trails are advocated for other Panama biological reserves to facilitate continuing ecological and other studies.

Panama records and tended to relate the Central with the South American faunas.

Two local institutions have had a profound effect in promoting the study of Panama insects, the Barro Colorado Island Laboratory on the island of that name in Gatún Lake and the Gorgas Memorial Laboratory of Tropical and Preventive Medicine in Panama City.

The book "William Morton Wheeler, Biologist" by M. A. and H. E. Evans (1970) describes the beginnings of the Barro Colorado Island Laboratory. Wheeler's letter of 21 March 1923 to his fellow Harvard professor, Thomas Barbour, is quoted in part and summarizes good reasons for starting the laboratory.

He suggested James Zetek for the post of resident director and the latter did, in fact, assume this post and proved to be indispensable for the rest of his life. The book contains an account of the founders of the laboratory and a photograph of nine men there in 1924, including several founders.

Due in part to Barbour, Barro Colorado Island was preserved for scientific purposes by the Governor on 17 April 1923. His friends, Wheeler and the plant explorer, David Fairchild, were among the first-rate scientists who developed sound principles for the preservation and conservation of this island. A system of trails numbered at 100-meter intervals was created that made it possible to determine exact locations of particular study areas or records of observations (Fig. 1). For example, three, named respectively after Zetek, Wheeler and Barbour, cross the island from west to east. I would suggest that such a system of marked trails might well be introduced into other biologically conserved areas in Panama, including the western savannah.

Barro Colorado Island was originally established by Congress to maintain permanent primeval sites for biological and other research and was placed under the administration of the Smithsonian Institution in 1947. The first report of the Smithsonian for the year ended 30 June 1947 noted the appearance of 603 individual published articles of which the greatest proportion was on insects. The bibliography of 1960 by the Smithsonian consisted of 65 mimeographed pages, including 34 pages on arthropods. The authors of the publications include a large share of active United States entomologists. They comprised international authorities and, in later years, graduate students who acquired their first exposure to tropical life here. My own first visit was in 1938.

Changes in the flora and fauna of Barro Colorado Island since the creation of the laboratory clearing in 1924 have affected the insect life. Wheeler (1925) noted the felling of trees then and the resulting hordes of ambrosia beetles (Platypodidae). The grass of the present clearing came later and, by 1938, it was a regular site for sweepings by the nets of entomologists. Numerous species of insects are probably still known on the island only at this site. Similar present and future invasions of insects are probable as grasslands areas are created by man.

The Gorgas Memorial Laboratory of Tropical and Preventive Medicine has long been in the forefront of investigations of arthropods of medical importance. W. M. Wheeler played a role here, as in the Barro Colorado Island Laboratory, for in 1922 he had been appointed to the Board of Directors of the Gorgas Memorial Institute of Tropical and Preventive Medicine, located in Washington, D. C. In 1923 he attended the laying of the cornerstone of the Laboratory in Panama City. S. J. Carpenter, G. B. Fairchild, P. Galindo, M. Hertig and H. Trapido have been prominent among those who worked on such topics as the general Diptera fauna, tree-hole breeding mosquitoes, yellow fever mosquitoes and biting flies.

Aside from the mosquito vectors of yellow fever and malaria, there are other noteworthy disease carriers or pests. For example, some 65 species of sandflies (*Phlebotomus*), vectors of leishmaniasis, are known from Panama and six or eight of these commonly bite man (Thatcher and Hertig, 1966). The different species have different ecological requirements. While some species are primarily forest species, breeding in cavities in wood, it may be suggested that they or others could breed in artificial cavities and migrate more widely.

Blowflies, tabanids, stable flies and others play significant roles and many less conspicuous types are important as parasites of other arthropods, as scavengers and as pollinators. Ecologically significant midges at the opposite ends of the Canal have been examined by Wirth (1970). I have lost a fair number of hours of sleep to mosquitoes in the venerable Tivoli Hotel.

The Smithsonian Institution and the United States Department of Agriculture have played a vital role in encouraging work in entomology in Panama and in furnishing most of the experts who could do the actual work of determination of species. The support of the universities to the Barro Colorado Laboratory by financial contributions aided many of their staff in coming to the laboratory. Frequently this was their first contact with the tropics and it may be said that laboratories in Costa Rica and other tropical countries have benefited from this heritage.

The concentration of the soil fauna (mainly arthropods) in the soil litter of the Panama forest was indicated by a study (Williams, 1941) of 29 quadrats, either one meter (11) or 25 centimeters (18) square. There were 5 phyla, 12 classes and 37 orders present and the Acarina, Collembola and Formicidae (ants) made up 81-88 percent of the fauna; there were up to 19,474 animals with an average biomass of 15.5 grams per square meter. This type of forest canot be considered to be primitive, after a history of over 400 years of human activity since Europeans arrived, but does reflect the extreme exuberance of the Central American fauna.

The nests of social insects such as termites, bees and ants are often conspicuous and long-lived structures. Schwarz (1934) refers to captures of the bee, *Lestrimellita limao,* over a period of four years from the same Barro Colorado Island nest and a colony of *Trigona fulviventris* nested in the "Allee" tree for at least five years. Conspicuous nests of the ant, *Atta,* were located at known sites along the marked trails of the same island in the period 1938-1966 (Weber, 1969). The large, gray carton nests of the ant, *Azteca,* that are suspended from the branches of trees are also readily identifiable and the ants are often the dominant form of animal life in such trees (Fig. 2). They may pasture insects that puncture plant tissues and weaken the plants or transmit pathogens. Conspicuous wasp nests, such as those of *Polybia,* may be associated with them. The large nests of *Amitermes medius* of Panama (Emerson, 1938) must take years to develop to their three meter or more height. These can now too easily be razed by bulldozers and protection of them should be considered because of their ecological role.

In general, populous nests of these social insects harbor many other types of animals, especially arthropods, in various degrees of relationships and are major ecological habitats for them.

Goldman and Zetek (1926), referring to the construction of the Panama Canal said "This gigantic undertaking involving the destruction of formerly unbroken forest and the creation of Gatun Lake along a transcontinental belt has had a profound

FIG. 2. Nests of two social insects close together on a tree on Barro Colorado Island. The larger is the ant, *Azteca,* and the smaller is the wasp, *Polybia* (probably *P. rejecta).* Such associations have not been thoroughly studied and have much to teach us about ecological relationships. They will disappear from disturbed or urbanized areas although the two animals may survive separately. The *Azteca* ants are small (about 2 or 3 mm) and have no sting but are well-protected by anal and mandibular excretions which have properties well-worth investigating for repellent and other pheromone characteristics.

effect on the local fauna and flora. Species restricted to the original forest interior are replaced by those of widely different associations which thrive on forest borders or in cleared spaces where grasses, herbaceous vegetation, and a multitude of shrubs and vines of low growth are the first to secure a foothold."

A low-level additional Panama Canal, such as one to the west of the present site, would further reduce the forests and create a man-made pathway for the transit of xerophytic and mesophytic insects. Adaptable insects will move freely across the Isthmus as they use the concrete and other pathways. Some will find the necessary resting and nesting sites on the green margins of the roads and walks. Migrations of insects may be more common than generally realized. Sylvan yellow fever apparently crossed from eastern Panama through the Canal Zone area into western Panama and Central America after 1948 (Galindo, *et al.,* 1956). The annual abundance cycles of arboreal mosquitoes are dependent on rainfall and suitable breeding sites and while man cannot do much about rainfall, he does regularly have an effect on breeding sites of many types of animals.

The position of Panama in the distribution and ecology of the fungus-growing ants (Attini) is instructive and may be duplicated in other primarily neotropical groups of insects (Weber, 1941). They occur from approximately 44° South to 40° North Latitude and are neotropical in origin. They have invaded deserts and semi-deserts, as well as grasslands and wet forests. The distribution of the leaf-cutting species of *Acromyrmex* and *Atta* is comparatively well-known.

The widespread *Atta sexdens,* so important to the economy of Brazil for its defoliation of agricultural crops, occupies grasslands, parklands and the margins of forests through much of South America. Other species such as A. *cephalotes* are more characteristic of tropical forests. A third, A. *colombica,* was described from mountainous Colombia. All three extend into Panama but usually occupy distinct ecological niches (Weber 1966, 1969). The drier and more western part has A. *sexdens* and, as humans have practiced slash and fire culture over the centuries (Bennett, 1968), A. *sexdens* has probably kept pace and extended its range. As human populations waned and forests crept into formerly open lands, A. colombica tonsipes in turn has extended into these forests, as it now does along the Panama Canal, as far toward the Pacific side as the grounds of the Tivoli Hotel. The Plaza de Lesseps in Panama City, at the foot of Ancón Hill, had flourishing colonies of Atta sexdens until the government's major building program of the 1950's extinguished its sites. Even under urbanized conditions in 1938, the A. sexdens nests of the Plaza de Lesseps had 14 aggregates of craters, some of which were 30 cm in diameter and 10 cm high. At the opposite side of the Panama Canal at Colon, A. colombica tonsipes was the common Atta, at least to 1966, but a colony of the third Atta, A. cephalotes isthmicola, then was found in the midst of A. colombica tonsipes, illustrating a constant tendency for many species to extend their ranges in the Isthmus. A. cephalotes isthmicola appears to be originally an ant of the dense forests of the hilltops, such as Barro Colorado Island and Cerro Campana. At the base of the latter range is Atta sexdens. A. cephalotes isthmicola occurs also in Colombia.

The golf course at Summit has been plagued by young colonies of Atta colombica tonsipes that arise from females settling here from their nuptial flights. These arise from parental nests in nearby patches of forest. Manicured grasslands do not seem an impediment to the spread of this species.

The tourist attraction of the ruins of Old Panama, sacked by the buccaneer Morgan, had Marsh's Zoo nearby in 1938. This had a large colony of A. colombica tonsipes. These ants had populous files going through the cages of birds, cats, rodents and other animals and carried leaf sections from near-by trees. They also took corn and other food that was given to the animals. A notable tourist site such as this should be rechecked periodically for evidence that Atta sexdens replaces A. colombica tonsipes during dry cycles or as urbanization becomes developed.

No species of the typically grasslands and semi-deserts Acromyrmex, subgenus Moellerius, is known from Panama, but one, A. (M.) versicolor, is common from northern Mexico into adjacent semi-arid parts of the United States. None of the common species in South America, especially the grass-cutting A. (M.) landolti, appears to have migrated into Panama from the llanos of Colombia and Venezuela. There is no continuous pathway for them, but western Panama would appear to be suitable, should the species be introduced. In this case it could be a significant addition to the grass-cutting insects. The widespread A. (Acromyrmex) octospinosus represents the genus in Panama and is a common urbanized ant that is a pest in gardens.

The bull-horn, Acacia costaricensis, with its aggressive Pseudomyrmex ants (Wheeler, 1942, Janzen, 1967 and 1969) is a feature of the western Panama savannahs. These bushes or low trees are among the plants that have withstood fire caused by humans over the millenia and are of particular ecological interest for their resistance to fire and for their relations with animals. Although they seem superficially to be a scrubby type of vegetation, they deserve to be conserved.

The weed tree, Cecropia, will soon invade new clearings in the Isthmus, carrying their Azteca and other ants with them.

Species of insects to be watched for, include the notorious fire ant, Solenopsis saevissima, that would find an entirely suitable habitat in lawns and cultivated areas along the Panama Canal. This common South American ant showed rapid expansion when introduced into the southwestern United States. In the states of Rio Grande do Sul, Brazil and Corrientes, Argentina it is abundant in much the same type of habitat that occurs in the vicinity of Juan Diaz, Panama, low, occasionally wet, grassland. Their mounds enable them to escape flooding by concentrating their brood in the upper cells of the nest.

SUMMARY AND RECOMMENDATIONS

The conscious inclusion of some insects and, certainly, of optimum habitats for most insects, should be considered in any plans for conserving biological areas. The need to maintain Barro Colorado Island and other areas, such as Cerro Campana, has become pressing because of the general trend to modify natural habitats with increasing human populations. Scientific and technological advances, including the synthesis of pheromones such as sex attractants, are creating sudden hazards to many insects and a potential hazard to others. There is no justification for exterminating such attractive features of the forest as the brilliant blue Morpho butterflies, because we have the capability. It is important to realize that the vast majority of insects are an indispensable and desirable feature of all habitats, except the most completely urbanized.

Additional man-made corridors across the Isthmus of Panama, such as a sea-level canal or added highways, should be preceded by a thorough survey of the existing vegetation and the major insect groups that are clearly associated with them. Nests of insects, such as Polybia wasps, bees and Azteca ants, that are found in forests could be included in such surveys. In the case of conspicuous nests of social insects, particularly Amitermes termites and Atta sexdens ants on the Pacific savannah, their present distribution within proposed disturbed areas should be mapped, together with their occurrence in adjacent areas which will sooner or later be affected by man. This opportunity will not occur again.

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THE STATUS OF HERPETOLOGY IN PANAMA[1]

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Few regions in the world support such a diversity of terrestrial life in such a small area as the Isthmus of Panama, illustrated, for example, by my estimate that 4 per cent of the world's living species of amphibians and reptiles occur there.[2] The principal reasons for this diversity now seem evident, even though the details are complex and incompletely understood. There is, of course, the deceptively simple fact that humid tropical mainlands seem almost inherently to have great numbers of species; and there is the historical closing of the Tertiary seaways, with the subsequent mixing of biotas that had evolved in long isolation. Two additional factors, which only recently have begun to be fully appreciated, are the alternation, in Pleistocene and post-Pleistocene time, of wet and dry climatic periods that allowed different biotic assemblages access to the region at different times, and, finally, the maintenance in present-day Panama of markedly different types of climates and habitats, thus permitting preservation of the diverse historical elements and encouraging the evolution of new forms through isolation (Haffer, 1967, 1970; Myers, 1969). The present report briefly considers the state of knowledge of the Panamanian herpetofauna, and emphasizes the correlation between habitat diversity and faunal size. A few guidelines are then presented

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[1] Based on work initiated at the Gorgas Memorial Laboratory in Panama City, with support from National Institutes of Health Grant No. GM-12020 and, subsequently, from National Science Foundation Grant No. GB-8139 (W. E. Duellman and C. W. Myers, co-investigators).

[2] For comparison, only about 5 per cent of the living species occur in the vastly greater area of the United States.

for estimating the effort that must be put into a sampling program on an interoceanic canal route.

Several hundred publications relate more or less directly to the amphibians and reptiles of Panama, with the vast majority being taxonomically oriented. Nonetheless, it is a rare paper that can be used by a nonspecialist to identify specimens, and then usually only for a single group, and few papers contain any attempt at synthesis. All of the combined literature proved inadequate for the purpose of drawing up a faunal list that was reasonably complete and which did not record the same species under more than one name. This is a statement of fact and not a disparagement of past work, which provides an essential base and which was by necessity limited to single collections or restricted geographic areas. Some important geographic regions have only recently been sampled, and a few areas are biologically unexplored, even at this time. But, even though the taxonomic base has not yet attained the desired firmness, the Panamanian fauna has stimulated other kinds of work that enrich the biological literature. Thus, there are preliminary studies of tropical amphibians and reptiles in relation to human health (Craighead, et al., 1962; Kourany, et al., 1970); analyses of anuran skin toxins that are of protective value to the amphibian and of potential importance in biomedical research (Daly and Myers, 1967; Daly, et *al.*, 1969; Fuhrman, et al., 1969; Shindelman, et *al.*, 1969); discussions of the influence of the human population on faunal distributions (Bennett, 1968; Heatwole, 1966); demonstrations that populations of some tropical species can be as large as populations of common temperate-zone species, and can fluctuate just as much (Heatwole and Sexton, 1966; Sexton, 1967; Sexton, et *al.*, 1963); estimates of the relative abundance of different kinds of snakes, based on the extraordinary snake census made by the Gorgas Memorial Laboratory (Dunn, 1947, 1949, 1954; Dunn and Allendoerfer, 1949); and a growing number of other ecological, life history, behavioral, and evolutionary studies (e.g., Ballinger, et al., 1970; Breder, 1946; Davidson and Hough, 1969; Duellman, 1966a, 1966b; Fouquette, 1960; Myers, 1966, 1969; Myers and Rand, 1969; Rand, 1968; Rand and Marx, 1967; Rubinoff and Kropach, 1970; Sexton, et al., 1964; Sexton and

Ortleb, 1966; Stultifer, 1970; Trueb, 1968; Zweifel, 1964a, 1964b).

A survey of the amphibians and reptiles of Panama was initiated in 1964 by Professor William E. Duellman and me; full-time collecting was carried out for a period of three years, especially in remote areas of the republic, and continues on an intermittent basis. Various taxonomic problems remain to be solved, and new species to be described, before the objective of an exhaustive catalogue can be attained, but it is now possible to make a reasonable estimate of the number of species actually occurring in the Republic of Panama (Table 1). Of the total of 357 species, 40 per cent are amphibians and 60 per cent are reptiles. The anurans comprise 80 per cent of the amphibians, and 32 per cent of the total fauna. The major order of reptiles is the Squamata, of which the snakes make up 36 per cent of the total herpetofauna and the lizards 19 per cent. Therefore, an overwhelming 87 per cent of the herpetofauna is comprised of snakes, frogs, and lizards. Allowing for the probability that Savage's (1966, p. 719) estimate of 625 species for all of Central America (Guatemala through Panama) is conservative, it would seem that over half of the entire Central American herpetofauna occurs in Panama.

Of course, not all of the amphibian and reptile fauna of Panama occurs in any one part of the republic, but a surprisingly large 28 per cent can exist in an area as small as Barro Colorado Island (Table 2). The Barro Colorado figures probably are the most complete count available of the herpetofauna of a humid, tropical mainland locality, and the relative numbers of species in the different groups are indicative of the kind of ecological diversity to be expected in most humid, lowland forests in Panama. However, the actual tally of species can be geographically altered within amazingly short distances, both horizontally and vertically. Thus, there is an important faunal change in the wet Atlantic-side forest between the Bocas del Toro region and the present Canal Zone, and then a discernible change between the Atlantic and Pacific sides of the Zone itself; these changes are correlated with a seasonal shift in rainfall distribution that seems to be reflected more noticeably in the actual biota than in the physiognomy of the

TABLE 1. Number of Amphibians and Reptiles in Panama.'

Group	Families	Genera	Species
Caecilians	1	4	11
Salamanders	1	2	17
Frogs and Toads	9	26	115
Turtles	6	10	14
Crocodilians	2	2	2
Amphisbaenians	1	1	3
Lizards	7	29	67
Snakes	6	55	128
Totals:			
Amphibians	11	32	143
Reptiles	22	97	214
Grand Totals	33	129	357

These figures include species (both named and unnamed) not formally reported from the country; the several marine species also are included. The species estimates are, nonetheless, conservative and eventually will have to be revised upward, but probably not to such an extent as to greatly alter conclusions based on present figures.

forest. Areas of tropical "savanna" climate on parts of the Pacific side of the isthmus support a fauna that is notable in being not only distinct from that of the moist forests but also in having a particularly strong South American aspect. Such species as *Leptodactylus fuscus (L. sibilatrix, auct.), Pleurodema brachyops, Dryadophis pleei, Lygophis lineatus,* and others, occur in the Pacific-side savannas as relicts that are widely separated from conspecific populations in the dry country of northeastern South America. Dunn (1940) pointed out this peculiarity of Panamanian zoogeography, where part of the Pacific-side fauna is allied to that of the Atlantic lowlands of northern South America and the Atlantic-side fauna to that of the Pacific lowlands of northwestern South America; but it bears emphasizing that the "Panamanian X" is a broken one and is the result of present-day climatic diversity as well as historical factors. In the eastern half of Panama, the situation is complicated by the concurrent increase of humid-forest amphibians and reptiles from South America, and striking physiognomic changes in the lowland forests; here, on the nearly base-leveled plains of the Chucunaque and Tuira rivers, we find extensive river-swamp forests and large expanses of

TABLE 2. Number of Amphibians and Reptiles on Barro Colorado

Group	No. species on island	As a per cent of Panamanian fauna[b]
Caecilians	1	9
Salamanders	2	12
Frogs and Toads	29	25
Turtles	5	56
Crocodilians	2	100
Amphisbaenians	1	33
Lizards	21	31
Snakes	39	31
Totals:		
Amphibians	32	22
Reptiles	68	33
Grand Totals	100	28

• Based on Myers and Rand (1969), and on Table 1.

[b] The marine turtles and the sea snake are excluded from these calculations.

monsoon rain forest that is peculiar in being dominated by a single species of tree (Myers, 1969, p. 7). Panama is a mountainous country, and the effects of the highlands on moisture-laden air partly accounts for the diverse lowland habitats. The montane habitats are also varied, and the several disjunct highland regions, with their different histories, add many species to the faunal list that do not occur in the lowlands.

The preceding remarks hint at the variety of environments on the Isthmus of Panama and suggest a partial explanation as to why the terrestrial fauna is so diverse. But diversity implies more than mere numbers of species. We scarcely have any knowledge at all of the dynamic aspects of tropical diversity, and we have only begun to acknowledge the existence of rapid temporal changes in populations of tropical amphibians and reptiles (Sexton, 1967; Myers and Rand, 1969). Even in tropical rain forest there is more short-term environmental variation, and biological response to that variation, than some writers have led us to believe.

Thus, even though the approximate numbers and kinds of species in Panama are becoming fairly well known, the extent of our ignorance also is more evident. The Panamanian fauna varies in a complex manner, both geographically and in time; we lack the information needed to do more than very generally predict the changing composition of the herpetofauna in any given transect across the isthmus. Any biotic survey of a new canal route should certainly provide for adequate sampling of the amphibians and reptiles, many of which are sensitive indicators of ecological conditions and zoogeographic events and some of which are of potential significance in the area of public health.

A great potentiality for evolutionary studies might seem almost inherent with the creation of a new sea barrier across the Panamanian isthmus, but such potential was largely nullified by the Canal Study Commission's choice (announced late in 1970) of "route 10," which is situated only about 10 miles west of the present canal. The existing fresh-water canal, as well as ecological disturbance on either side, already provides a barrier of variable effectiveness to most wingless terrestrial animals. For example, Myers and Rand (1969, p. 6) note the increasing insular effect on the fauna of Barro Colorado, a 60-year old island formed in Gatun Lake by construction of the present canal, and observed that it seems easier for a resident population to become extinct than for overwater colonization to occur. A number of isthmian species have a distributional break in the region of the Canal Zone, and a similar gap also separates a few pairs of closely related species. Although few of these discontinuities are well studied, many seem correlated with topographic features and probably are the result of climatic fluctuations that antedate the present canal, but the circumstances are complex and some significant distributional breaks possibly have occurred in this century. It is unlikely that we shall ever be able positively to ascribe a cause and effect in the majority of such cases; thus, the appearance of a salt-water strait will reinforce an already existing barrier whose effects cannot be determined because of the inadequacy of precanal data. I do not mean to imply that there will be no chance at all of gathering new data that are relevant to evolutionary zoogeography, particularly in the case of non-forest and "edge" species, but the situation is a distressing example of what opportunities can be lost by the failure to conduct thorough surveys of a biota threatened with major disturbance. Most biologists would be genuinely shocked at how little we really know about the biota of the *present* Canal Zone, and, surely, an informed scientist could not have been responsible for the statement (Commission, 1971, p. 59) that the ". . total effects [of a new canal] upon land ecology can also be estimated with confidence . .."! The complexity of tropical ecosystems was scarcely appreciated when construction was started on the present canal, and the "Biological Survey" of 1911-1912 was, in retrospect, woefully deficient; it is fervently to be hoped that the mistake will not be made a second time.

An assessment of herpetology in relation to a sea-level canal would be incomplete without mention of *Pelamis platurus,* the sea snake, which is being ably studied by Dr. Ira Rubinoff and his associates at the Smithsonian Tropical Research Institute. The possibility of sea snakes migrating to the Atlantic Ocean through a sea-level canal is a subject of frequent concern (*e.g., The New York Times,* December 13, 1970, p. E-12; *Congressional Record, House,* January 21, 1971, pp. 22–26). Because of tidal differences, a freely floating object would take only about two and a half days to transit an unobstructed canal from the Pacific side to the Atlantic (Commission, 1971, p. V-96), and, if the object were a sea snake, it probably would find favorable habitats off the Atlantic coast, although predation from native Atlantic predators initially might be high (Rubinoff and Kropach, 1970). That sea snakes would indeed enter the canal is indicated by the pertinent fact that they sometimes even occur in Panamanian rivers—I found two specimens that were actively swimming in the Río Jaqué (Darien), about 2 kilometers above its mouth, where the snakes presumably had been carried by tidal currents. The possible consequences of migration of sea turtles should also be considered, particularly in light of their economic importance and endangered status.

A basis for estimating the effort required in a terrestrial sampling program is given in Figure 1, in which collecting success is plotted against the time expended in building up a faunal list. Myers and Rand (1969, pp. 8, 9) concluded that at least 80 per cent of the herpetofauna of a lowland, humid forest locality could be determined by ". . . a party of several

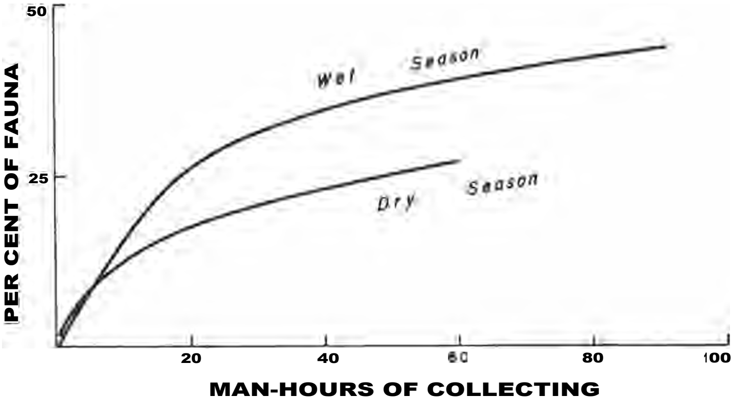

FIG. 1. Collecting success as a function of time, for species of amphibians and reptiles on Barro Colorado Island—a humid, lowland forest locality. "Per cent of fauna" also can be read as "number of species," since the total herpetofauna is comprised of an estimated 100 species. Adapted from Myers and Rand (1969).

people working intensively for a month or two in one wet season plus a week or so in one dry season." Such a program, of course, would have to be repeated in each major physiographic and vegetational region and in different parts of any climatic gradiant. At the same time, an attempt should be made to determine relative abundance of species and, if possible, the actual population densities of those species sufficiently abundant for such a task. The mistake should not be made, however, in thinking that sampling techniques required for determining population densities will be adequate for censusing the entire fauna. For determining the variety of species present, there is no substitute for hours of patient "cruising," during which many microhabitats are explored both by day and night; however, quadrate sampling *(e.g.,* Heatwole and Sexton, 1966, p. 50, fig. 2) and utilization of such devices as open trenches and turtle traps are likely to add some secretive species that might not otherwise be seen. The rate at which species are discovered in different habitats, and the relative abundance of species and comparison of their ecological roles, might provide some solid data on the relationship between environmental carrying capacity, biomass, and that aspect of diversity reflected by numbers of species. Indeed, a systematic sampling program on any transect across the isthmus could usefully contribute a variety of data to the study of biological diversity in a tropical region. This is a field in which formulation of theory has outdistanced factual evaluation, which would be all right—except, that, given the rate at which tropical environments are being altered, we may soon be left with only the theories.

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THE BIRDS OF THE ISTHMUS OF PANAMA

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The long, narrow Panamanian Isthmus is definitely tropical in the variety of its birds, with 865 species recorded within the limits of its 29,306 square miles, and the seas adjacent. The number may not seem impressive until it is recalled that in the vast region of North America north of Mexico only 800 living kinds are known. The overall relationship of the resident Panamanian avifauna is to southern Central America and northern South America, in particular to Costa Rica on the west and Colombia to the south. In the latter, with sixteen times the land area and far greater expanse in the higher elevations, 1,592 species of birds, or less than twice the number in Panama, are recorded.

In the Panamanian list 145 kinds are migrant visitors that come annually in their escape from northern winter. Part of these are birds of passage through Panama, to and from wintering grounds in South America, but many remain to add their number for a period of months to the population of the resident avifauna. In addition to those from the north, there are at least six kinds that arrive annually in June or July as migrants from southern South America in escape from the southern winter season. Two of these are species of swallows that may appear in considerable number.

Other than the migrants and a few casual visitors, there are 670 species of birds that are definitely resident on the Isthmus. Aside from aquatic species and others of wide distribution, few of these appear northern in origin. The exceptions include the meadowlark, pipit, and grasshopper sparrow of the savannas; the junco on the Chiriquí volcano; the hairy woodpecker of the western mountains, the mourning dove, and the red-tailed hawk. Ancestral stock of the others appears mainly of tropical origin. Numerous kinds of the resident birds found in the tropical zone range widely throughout the lowlands on both Caribbean and Pacific sides of the isthmus, wherever the habitat is favorable. Their main restriction toward general range is found in the open savannas of the western half on the Pacific side. Here true forest species are absent because of the lack of tree-covered habitat. The mountainous areas of the western half mark the southern terminus of the great ranges of the north that begin in North America and continue through Central America. Near the Costa Rican boundary the highest mountain in the Republic, the great Volcán Barú (the Chiriquí Volcano), rises in an isolated peak to 3,475 meters. On its temperate zone summit range five species of birds not found elsewhere in Panama: a hummingbird (Selasphorus flammula torridus), a wren (Thryorchilus browni browni), the sooty robin (Planesticus nigrescens), the large-footed finch (Pezopetes capitalis), and the Irazú junco (Junco vulcani). These directly, or as closely related subspecies, occur also on the high volcanoes nearby in Costa Rica.

To the east there are limited, less elevated areas in eastern Chiriquí and Veraguas that have birds of the subtropical zone, some of them continuing as far as Cerro Campana, which rises abruptly to a thousand meters from the central lowland area where the Panama Canal crosses between the two oceans. In these lower mountains there is a highly interesting avifauna of 20 or more species related to those of southern Central America.

Beyond the Canal Zone in eastern Panama the highlands are less elevated and are not continuous. Adjacent to the Colombian border Cerro Pirre and the Serranía de Tacarcuna rise as mountainous islands, outliers of the northern Andean chain which terminates in Colombia.

In the subtropical zone of Chiriquí, numerous kinds of birds are like those of adjacent Costa Rica. Some of these species occur also on Cerro Pirre and Tacarcuna in Darien, though usually differing sufficiently to be recognized as separate subspecies. There are also others allied to those of Colombia, a number of them differing also at the subspecific level. As especially interesting there may be mentioned the Tacarcuna wood quail (Odontophorus dialeucos), found through a space of a few kilometers along the slopes of Tacarcuna, and several small flycatchers and some others that barely enter Panama on the higher slopes of these eastern mountains.

Of peculiar occurrence in the lowlands to the east of the Canal Zone is a small flycatcher, the pied water-tyrant (Fluvicola pica pica). This is found locally in a limited area on the marshy coastal lands from the lower Río Juan Diaz east for about 35 kilometers to near the Rio Bayano, only ranging inland for 5 kilometers or so from the sea. The occurrence in this limited area on the northern shore of Panama Bay marks an isolated colony of a species that ranges widely in northern and eastern South America, the nearest known being along the Rio Simi in northwestern Colombia, distant about 400 kilometers.

The Pearl Islands in the Gulf of Panama have an abundance of birds, including one outstanding anomaly in a small ant-bird (Formicivora grisea alticincta) recorded from the five major islands of the group and restricted in range to them, being recorded nowhere on the mainland of the isthmus. Its nearest relative is the closely similar subspecies Formicivora grisea hondae of northwestern Colombia.

The race of the Choliba screech owl, recorded in this archipelago, on Rey and Pedro Gonzalez islands, is another interesting anomaly as it differs from the subspecies (Otus choliba luctisonus) widespread along the Pacific slope of Panama. The birds of the Pearl Islands have larger size and darker coloration, in this resembling the race (Otus choliba crucigerus) of the upper and middle Magdalena valley of northwestern Colombia.

As the Bay and Gulf of Panama are relatively shallow, these islands may be supposed to have had direct land connection when the sea was lowered in Pleistocene time. The ancestral ant-birds and the owls that seem to have Colombian affinities may have become established at that period.

Of interest also in this eastern area of Panama is a hummingbird (*Goldmania* violiceps) restricted to the subtropical zone of four of the mountain tops. Another (Goethalsia bella), lives only on the ridge of Cerro Pirre. A number of other kinds of birds related closely to those of Colombia are found, especially on Pirre and Tacarcuna.

Two of the Panamanian islands that lie off the western half of Panama are especially interesting. Escudo de Veraguas, with an area of about 5 square kilometers, distant only 18 kilometers off the base of the Valiente Peninsula in the Province of Bocas del Toro, was named by Columbus on his fourth voyage in 1502, as its shape suggested a shield. Among the birds, a subspecies of manakin (Manacus vitellinus amitinus), and one of a bay wren (Thryothorus nigricapillus odicus), are generally similar to races of the adjacent mainland, but differ significantly in their larger size, and also in their color. A hummingbird, Amazilia handleyi, is more remarkable. It is a distinct species related to the common, widely distributed Rieffer's hummingbird, but decidedly darker in color and somewhat more than 16 per cent larger. Its bulk among its smaller relatives is impressive. A distinct species of small mammal, a spiny rat (genus Hoplomys) is also found only on Escudo.

The island is located on a submarine bank, where the surrounding sea is shallow, separated from the adjacent mainland by a narrow trench with a depth of 24 to 35 fathoms. It may be assumed that during the late Pleistocene, when sea-level was low, it was part of the mainland. At this time the parent stock of these birds may have become resident, to be isolated later with return of the ocean waters.

Isla Coiba, in the Pacific off the western end of the isthmus, is also interesting. It is a large island over 35 kilometers long by 21 wide, with a semicircular bay indenting much of the eastern side. It lies 25 kilometers off the coast of Veraguas, separated by a channel from 40 to 55 fathoms deep. It is, thus, fairly remote, with no indication of connection with the mainland at any recent period. Birds are abundant, so that my list for a five-week intensive survey, aided by two competent assistants, included 133 species. Of this total 36 kinds were migrants, and three others were casual wanderers from the mainland, leaving 94 considered to be normal residents. In these, eight major families, common and widely distributed on the mainland, were not represented, i.e., tinamous, currasows, trogons, motmots, jacamars, puffbirds, toucans, and woodhewers. Several others had minor representation of only one or two species.

The island is well-watered, covered by great forests rising from coastal mangroves and shrubs bordering the beaches to inland stands of trees from 100 to 200 feet tall. Until recently there were few clearings.

One of the bird species, small, slender, the only representative of the tropical ovenbird family on the island, the rusty spinetail, Cranioleuca vulpina dissita, has its closest relative in southeastern Colombia and the Orinoco valley of Venezuela, 1200 to 1500 kilometers distant. The only other member of the genus in Panama, found in the subtropical zone of Chiriquí, is of another species. Twenty-one of the other resident birds of Isla Coiba differ from the species elsewhere in Panama in being darker colored. One of these, a small dove, *Columbigallina* talpacoti nesophila, is like the population of the Pearl Islands, differing, as stated, from the mainland population in its darker coloration. Another, a flycatcher, Elaenia flavigaster sub pagana, darker than the population of the Panamanian mainland, in this, resembles the race of Costa Rica. The remaining nineteen all are darker when compared to their counterparts in mainland Panama.

As an interesting variation in habit, the barred ant-shrike, the only species of its family on this island, always a bird that lives in thickets on the mainland, on Coiba ranges also in the sun, but in the top of the tree crown of the heavy stand of forest, high above the ground.

Further additions to the list of 865 species now recorded on the Isthmus may be expected in birds that range the sea, especially in the Gulf of Panama. There are certain to be others in the forests of the high mountains in northwestern Bocas del Toro, and probably also in the Serranía de Tabasará in eastern Chiriquí. Others are to be expected in the ranges in Darien that mark the international boundary with Colombia.

The future of the native species of the Panamanian avifauna is uncertain. With steady growth in population, the demand for more land for human use increases annually, leading to constant encroachment on the forests. Certain of the birds adjust to this, and continue in scattered tree shelter, or in areas recovered by second growth. Many of the true forest birds, however, are few in number and, with loss of their primitive cover, disappear. To save them it is important to establish reserves under national care where no cutting is permitted so that these remnants of the original avifauna may be preserved from total loss.

MAMMALOGY IN PANAMA

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Early in the dry season of 1964 a Smithsonian mammal survey group climbed the steep slopes of the Serranía del Darien to Cerro Tacarcuna on the Colombian boundary. En route one of the Cuna Indian pack bearers found a small rat struggling up a vine-clad tree beside the trail. The animal proved to be a vesper rat, *Nyctomys sumichrasti,* a species and genus of the Central American highlands. A few more miles along the ridge and this animal would have been in South America, a continent on which it is unknown.

As recently as 1920, E. A. Goldman, in culminating the Smithsonian's first mammal survey of Panama, wrote that the southern limit of the vesper rat's known distribution was Boquete, in the Chiriquí highlands near the Costa Rican boundary, whence six specimens had been obtained in 1900. Since then this rat has been found: at a higher elevation, within the frost zone, on the slopes of Volcán de Chiriquí; across the divide in Bocas del Toro, on one of the rainiest slopes in Latin America; on Water Key off the Caribbean coast; in mountains on the Azuero Peninsula; in dry deciduous forest near sea-level on the Pacific coast in the Canal Zone and along the Rio Teta a short distance to the west; beside Madden Lake and on Cerro Azul east of the Canal Zone; and, finally, in the Serranía del Darien near the Colombian boundary.

Thus, in the brief span of fifty years the known status of

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the vesper rat in Panama has changed from one of rare occurrence at a single marginal locality to one of some abundance, possibly throughout the Republic, at all elevations, and in both wet and dry situations. Either the vesper rat has extended its geographic distribution, as the facts suggest, or else most pre-1920 collectors overlooked it. Since recent collectors have not especially sought this animal, the first alternative probably has at least some validity.

The example of the vesper rat is not an isolated phenomenon. Goldman's 1920 "Mammals of Panama" reported the occurrence in the Republic of 138 kinds of mammals that are now recognized as species (some of Goldman's species have been reduced to the rank of subspecies). In 1971 the species of mammals in the fauna of Panama are known to number at least 227, an increase of 65 per cent over the 1920 count.

It must be admitted that the increase is not quite so dramatic as at first glance it appears to be. Most of the increase is in bats, from 44 to 109 species, due largely to improved collecting techniques and greater collecting effort. Nine of the species are whales and porpoises, which Goldman did not attempt to list. One species, the brown rat, *Rattus norvegicus,* has been introduced since 1920. The more significant increases in the known fauna have been among: the opossums, from nine to eleven species; shrews, from one to four species; monkeys, from seven to eight species; rabbits, from one to two species; mice and rats, from 46 to 52 species; carnivores, from seventeen to eighteen species; and hoofed mammals, from five to six species. Only among the sea cows and the edentates (anteaters, sloths, and armadillos) have no additions been made since the days of Goldman, and it is improbable that additions will be made in the foreseeable future. In fact, in these groups, the most likely change will be the extermination in Panama of two of their eight species (the manatee and giant anteater) .

These figures indicate progress in Panamanian mammalogy. Actually, estimates of the composition and distribution of the mammalian fauna have now been sufficiently documented to inspire some confidence in their reliability. To the present time most of the research on mammals in Panama has been concerned with this documentation. Lionel Wafer included mammals in his 17th Century treatise on Panama, and a few mammals reached museum collections from western Panama in the 19th Century, but systematic collection and study did not begin until about 1900. In the ensuing decade the faunas of Chiriquí, the Pearl Islands, and other Pacific coastal islands were described by Oldfield Thomas, Outram Bangs, and J. A. Allen. The next decade saw Goldman, H. E. Anthony, Thomas Barbour, and W. H. Osgood collect and describe the mammals of the Canal Zone and nearby areas; and during the same period Goldman and Anthony made major collections in Darien. Goldman's "Mammals of Panama," published in 1920, was a landmark ending an era of great exploration and discovery.

Early in the 'twenties Barbour extended studies of the fauna of Darien, and, at the end of the decade, R. K. Enders began his work on Barro Colorado Island and in Chiriquí which still continues. He was one of the first to use Panama as a natural laboratory, and many students have learned biology while collecting Panamanian mammals under Enders' tutelage. During the 1930's B. P. Bole, Jr., collected on the Azuero Peninsula and 0. P. Pearson followed up Goldman and Barbour's work in southeastern Darien. Only a few small collections were made in the 'forties and early 'fifties.

An era of epidemiological, virological, and other medically-oriented projects, in which mammals were studied because of their role as hosts of disease organisms, was initiated in the post-war years by Herbert Clark and continued by Carl Johnson, Pedro Galindo and Eustorgio Mendez of the Gorgas Memorial Laboratory; by C. M. Keenan and various officers of the United States Army Preventive Medicine Survey Detachment in the Canal Zone; and by K. M. Johnson, C. E. Yunker, M. L. Kuns, P. A. Webb, and R. B. Tesh at the Middle America Research Unit.

A spin-off of these studies of the natural history of disease was the Smithsonian's Mammals of Panama Project, supported financially at first by the Gorgas Memorial Laboratory and later by the National Science Foundation (Grant No. G19415) and the Smithsonian Research Foundation. The Project's objectives were to amass detailed data on the distribution, ecology, and systematics of mammals and to bring together all of the accumulated knowledge in a new "Mammals of Panama." Between 1957 and 1966 Project personnel, including C. 0. Handley, Jr., T. H. Fleming, E. L. Tyson, F. M. Greenwell, B. R. Feinstein, and D. I. Rhymer, surveyed Panama. Few areas were missed. An interim report, "Checklist of the Mammals of Panama," was published in 1966. Since the completion of the field phase of the Smithsonian's project other organizations have collected mammals in connection with sea-level canal surveys.

Enough material and data are now at hand to map, with a fair degree of accuracy, the distribution and geographic variation of mammals in Panama and to define their relationships with ectoparasites. Less is known about ecology, and very little is known of behavior, reproductive biology, population dynamics, and other aspects of natural history of most species. However, a promising start has been made in these areas of mammalogy, until now largely neglected in Panama.

Recent investigators have paid increasing attention to ecology. Where Goldman would have had to be content to say, "At Cana, in the mountains of eastern Panama . . . among rocks in second growth forest," the 1966 Checklist could at least extend this to, "Rare; at medium elevations (1500-4000 feet), possibly throughout Panama, in suitable habitats; has been trapped on the ground, and on or under logs in moist fog forest." Fleming's 1965-1966 comparative study of seasonal variation in marsupial and rodent populations on live-trap grids in an evergreen forest and in a deciduous forest in the Canal Zone was perhaps the first study of its kind anywhere in the American tropics. Enders, Fleming, and D. E. Wilson have accumulated a significant amount of detailed reproductive data for a few species and a great deal of generalized data have been gathered for a number of others. Landmark studies of the natural history of howler monkey, spider monkey, white-faced monkey, and coatimundi have been made in Panama by C. R. Carpenter, J. R. Oppenheimer, and J. H. Kaufmann.

Taking into account its small geographic area, Panama has an astonishingly large and complex mammalian fauna. Indeed, it probably has few equals anywhere in the world.

Its topographic and climatic diversity, as well as its brief history as part of a bridge between two major faunas, account for the size of its fauna. Until a few million years ago the isolated South American continent had an ancient mammalian fauna consisting largely of marsupials, edentates, endemic ungulates (now all extinct), and a specialized group of rodents, the hystricomorphs. North and Central America, on the other hand, with their intimate connection to much of the remainder of the world's land mass, teemed with a large and progressive fauna. When emergence bridged the waterways separating Central America and South America and provided an avenue between them, the northern fauna rushed into the relative vacuum in South America, radiated, and some derivatives began to return northward. Together with a few species of the South American ancient fauna they made Panama a two-way street. This is the situation today. Probably there is movement in both directions.

Mammals are quite mobile animals, and in the absence of barriers, such as competitors or unfavorable terrain, climate, or vegetation, they can extend their distribution surprising distances in remarkably short periods of time. This phenomenon is well-documented in the fossil record of mammals and in their present patterns of distribution, as well as by observations on the movements of living faunas, particularly in North America and in Europe.

Very little is known of dispersal rates or factors governing dispersal of mammals in the tropics. However, it is known that some land, at least island arcs, was present in Central America through much of the Miocene and Pliocene, that the entire region has been tectonically very active, with much rise and fall, and that present patterns of mammalian distribution undoubtedly must be quite young, and still labile. Vulcanism certainly has been a factor in the dispersal of some highland forms, and climatic variation and consequent shifts in vegetative zones must have had tremendous influence on the distribution of the entire fauna.

Panama's position is unique. Geographically it is Central American, but faunally it is as close to South America as it is to Central America. It has more South American species than any part of Central America, and, conversely, it has more Central American species than any part of South America. About 40 per cent of the species of indigenous land mammals of Panama are recognizably South American in origin, 27 per cent are Central American, 32 per cent are of indeterminate tropical origin, either South American or Central American, and 1 per cent are North American.

In the absence of a significant fossil record, the place of origin of a mammalian species may be inferred in a number of ways. The vesper rat is known to occur from Mexico to Panama. Its supposed relatives live in Central America. The vesper rat surely reached Panama from Central America. The white bat, Diclidurus albus, is known to occur from Mexico to Brazil. Apparently no other species of its genus occurs in Central America, but three other species of Diclidurus are sympatric with D. albus in South America. Probably it had a South American origin. Species that are particularly mobile or which may have been among the earliest to move across the Isthmus can be difficult to place. Many of them occur now throughout tropical America. The larger spotted cats, the common brocket, many of the sac-winged bats, and the vampire bats, for example, seem to fit this category.

The South American element in the Panamanian fauna can be split three ways. Presumably from the lowlands east of the Andes came 61 per cent of it, including the brown four-eyed opossum, night monkey, sloths, capybara, and crab-eating raccoon. The Andes provided 27 per cent (e.g., short-tailed opossum, *Monodelphis* adusta; red squirrel, Sciurus granatensis; and white-breasted rat, Oryzomys albigularis). Most of the Andean species occur only at high elevations in Panama. Twelve per cent probably originated in the Chocó region of northwestern South America and southeastern Panama. The woolly opossum, Caluromys derbianus; black spider monkey, Ateles fusciceps; gray spiny pocket rat, Heteromys australis; and thick-spined rat, Hoplomys gymnurus; are members of this fauna.

Many of the species of Central American origin are highland inhabitants that have quite limited distribution in Panama. In this fauna are several species of shrews (Cryptotis); the black fruit bats, *Artibeus aztecus* and A. *toltecus;* the groove-toothed squirrel, *Syntheosciurus brochus;* several species of white-footed mice *(Peromyscus);* and the ringtail, *Bassariscus sumichrasti.*

Unquestionably other species eventually will immigrate into Panama from the north or south. Predictably some of these may be species whose ranges now approach, but do not reach, Panama. The sac-winged bat, *Balantiopteryx plicata;* brown squirrel, *Sciurus deppei;* silky climbing rat, *Ototylomys phyllotis;* coyote, *Canis latrans;* and spotted skunk, *Spilo gale putorius;* among others, range southward to Costa Rica but are as yet unknown in Panama. Similarly, in the Andes just across the Rio Atrato from Darien are several species of mouse opossums of the genus *Marmosa;* white-eared opossum, *Didelphis azarae;* big-eared bat, *Histiotus montanus;* hoary bat, *Lasiurus cinereus;* several species of mice of the genera *Thomasomys* and *Akodon;* and spectacled bear, *Tremarctos ornatus;* as well as other species unknown in Panama at the present time.

Central America has had a significant effect as a land barrier on the distribution of marine mammals. Most, such as the baleen whales, sperm whale, false killer whale, and goose-beaked whale, occur in both oceans with little or no differentiation. Supposedly the bottle-nosed porpoise, *Tursiops truncatus,* has different subspecies on the Caribbean and Pacific sides of the Isthmus, while the long-nosed porpoise, *Stenella,* is represented by distinct species, S. *plagiodon* (Caribbean) and S. *graffmani (Pacific)*. Eared seals are known only in the Pacific, while manatees are only in the Caribbean. Monk seals evidently passed through the straits before the land barrier was complete, for related species now occur around the Hawaiian Islands and in the Caribbean.

Alternation of pluvial and arid climates, at least since the beginning of the Pleistocene, accounts for much of Panama's present faunal diversity. Rainy intervals produced continuous forest on the Isthmus and effectively blocked immigration of savanna-inhabiting mammals. Dry intervals inhibited the movement of rain forest dwellers. Not only did such changes block the advance of northern and southern species not yet in the Isthmus, but more importantly they split populations of species already in passage. Consequent isolation and interrupted gene flow produced a classic situation for evolution. Perhaps no other place in the New World has been responsible for so much speciation in the terrestrial mammalian fauna as Panama.

At this moment the Isthmus apparently is coming out of an arid interval. Savanna extends along the Pacific coast from Central America across Panama to just beyond the Rio Bayano and begins again on the north coast of Colombia and in southwestern Ecuador. Evergreen forest occupies the gap. Savanna-loving species such as the leaf-chinned bat, Mormoops megalophylla; Florida cottontail, Sylvilagus floridanus; cotton rat, Sigmodon hispidus; and gray fox, Urocyon cinereoargenteus; occur on both sides of the gap. Their separate populations are at most subspecifically distinct. In all, about twenty species of mammals appear to have disjunct populations in Central and South America.

Among these, the cotton rat is of particular interest because it and its ancestors evidently have immigrated across the Isthmus several times when suitable savanna conditions existed there. A number of species of cotton rats now live in Mexico and in South America, but only Sigmodon hispidus inhabits Central America. From Central America S. hispidus has moved northward into the United States and southward into South America, to occupy the savannas in northern Colombia and western Venezuela. It is absent from large blocks of savanna further eastward and southeastward. Three previous stages of cotton rat evolution are represented by a strongly differentiated species, Sigmodon *alstoni*, in the grasslands of northern Brazil and eastern Venezuela; by a fairly distinct species, S. peruanus, in the deserts and adjacent grasslands of northwestern Peru and southwestern Ecuador; and by a poorly differentiated species, S. inopinatus, in high elevation grasslands in Ecuador. It may be possible to demonstrate similar degrees of differentiation among the Mexican species.

Based on the distribution and relationships of mammals, a number of faunal units can be recognized in Panama. The primary division is between highland and lowland faunas. There are two sharply distinct highland faunas. One, at high elevations along the continental divide in western Panama, is an extension of the Costa Rican Highland Fauna. It reaches into Panama at least to Boquete in Chiriquí, but its eastern limit is unknown. Its relationships are strongly Central American. The other, the Darién-Chocó Highland Fauna, occurs at high elevations in the eastern edge of Panama, in the Darien, Pirre, and Sapo ranges. It has a South American character. A few of the species of the highland faunas occur on the lower mountains in central Panama, which, however, are populated mostly by lowland species. The isolated mountains on the Azuero Peninsula harbor a peculiar fauna which may merit recognition as a separate highland unit. Another isolated mountain mass, the Sierra de Majé, behind Chimán on the Pacific coast of eastern Panama, has not been explored for mammals.

The lowland fauna has two main divisions, xeric and mesic. The xeric unit, the southeastern extreme of the Central American Savanna Fauna, extends into Panama along the Pacific coast almost to Chimán. Most of its species are Central American, but a few from South America have reached it. The mesic unit has three subdivisions, the Bocas del Toro Lowland Fauna and the San Blas Lowland Fauna, both with strong Central American affinities, and the Darien Lowland Fauna, with South American relationships. As would be expected, in the absence of barriers in central Panama, the four lowland faunas merge there without distinct boundaries.

Assuming that the classic survey technique has made its contribution and reached the point of diminishing returns, future work on the mammals of Panama should focus upon the phenomenon of the Isthmus as part of a living land bridge. Most of our knowledge of land bridges is based upon inferences drawn from the observable effects of former bridges, such as the Bering Bridge, or the effects of an existing bridge, such as the Central American. But to dwell upon effects is to miss the truly unique opportunity to study process and function. It is unfortunate that this realization should come to the fore only when fears are raised that environmental modifications, such as the construction of a canal, might damage or destroy the bridge. Crash programs to provide precise base line data on pre-construction distribution are relatively ineffective, as shown by the Smithsonian's 1911-12 survey, since they reveal little more than the presence of the most easily collected species.

However, such surveys can become very valuable if they are comprehensive and if they are followed up at regular intervals over a long period of time by new programs designed to reveal various sorts of changes. Aside from being a general compendium from which several generations of compilers have drawn distributional data, the most useful feature of Goldman's 1920 "Mammals of Panama" was what he said about the mammals of two localities where he collected intensively: Gatún in the Canal Zone and Cana-Pirre in Darien. Since Goldman's survey, both of these localities and their faunas and floras have changed drastically, but in different ways: Gatún from flooding, urbanization, and constant disturbance; Cana from reversion to wilderness (it had been a metropolis in Spanish colonial days, was a small mining town in 1912, and now, not even a trail leads to its site). The extensive collections that Anthony made at Tacarcuna in Darien in 1915 are, likewise, priceless. Once a large Indian village, only a few families lived at Tacarcuna in 1915, and 45 years later, when the Smithsonian group collected for several months at the site, it required a considerable search to find evidence that it had not always been trackless jungle. Species which Anthony did not find at all in 1915, but which were common in 1960, and species which were numerous in 1915, but uncommon in 1960, must represent real change and faunal movement.

The recent Smithsonian survey has left a legacy of a dozen well-collected stations throughout Panama, of the caliber of the Cana-Pirre, and Tacarcuna surveys. A manual is in preparation that describes the fauna and ecology of each site. Periodic restudy of these stations, once each decade, or at least once each quarter century, would reveal changes in species composition, changes in populations, changes in ecology, changes in parasite faunas, and, eventually, rates of change and, possibly, reasons for change.

Related studies should consider subjects such as: evolution of species and subspecies; the barrier effect of interspecific competition where niche-equivalents from different faunas meet; the filter effect of the narrow isthmus, selectively allowing passage of some species but blocking others; pressures and circumstances that initiate and perpetuate emigration; speed of immigration and reasons for variation; habitat preferences; differential altitudinal tolerances in various habitats; response to environmental modification; and precise definition of faunal areas. Continuous long-term studies at one or two stations should concentrate on local populations and movements, reproduction and survival, natural history of individual species, and seasonal and annual variations and cycles.

For mammals, at least, the construction of another canal should have little, if any, effect on distribution and movement. It is more likely that barriers will be produced by other large scale environmental modifications, such as deforestation or urbanization. These are foreseeable. The very smallness and narrowness that make Panama such a neat, manageable unit for study, make it eminently fragile and destructible. If we are to seize the opportunity to unravel some of the basic mysteries of biogeography that lie here, we must begin now.

THE ANTHROPOLOGY OF EASTERN PANAMA

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As part of the feasibility studies for a sea-level canal, the author conducted intensive field work in the eastern region of the Republic of Panama during the years 1966-1968.

The area studied comprises the eastern portion of the Province of Panama, the Province of Darien, Archipelago of San Blas in the Atlantic, and the Islands of Las Perlas in the Pacific. The territory covers approximately 26,938 square kilometers, corresponding to a third of the total area of the Republic of Panama (77,882 km^2).

DEMOGRAPHIC DATA

Jungle vegetation occupies most of the area and the human population density (1.8 inhabitants per square kilometer, in Darien) is low. The National Census of 1960 indicated a total of only 33,145 people in this region. The current population (Table 1) surpassed the estimate of 41,206, extrapolated from the highest and lowest population growth rates observed in the area (Table 2).

The human population of the area was divided, for this study, into five groups, as follows:

Group A: San Blas Cuna Indians who inhabit the islands between Ailigandí and Anachucuna.

Group B: Cuna Indians who live on the upper Chucunaque River and the upper Bayano River.

Group C: Chocó Indians who are scattered throughout

Table 1. Current population of the study area based on the National Census of 1970.

Political Division	Number of inhabitants
Comarca de San Blas	24,681
Province of Darien	
District of Chepigana	13,767
District of Pinogana	8,918
Province of Panama	
District of Chepo	14,469
District of Chimán	1,678
District of Balboa	2,756
Total current population	66,269

the Province of Darien and also are found in the district of Chimán in the Province of Panama.

Group D: Negroes and "mestizos" who are found chiefly around the Gulf of San Miguel.

Group E: Colonists from western Panama (the Provinces of Chiriquí, Herrera, Los Santos and Veraguas) who have settled at several points in the Province of Darien and in the District of Chimán.

To obtain up to date demographic data for this area, precoded questionnaires were distributed to 9,000 individuals in 1,400 houses. These data were used to estimate the rates of natality and mortality, as well as other demographic variables, for each human group. The results of this study are summarized in Table 2.

The infant mortality rate and the death rate are highest among the Cuna Indians of the upper Bayano and Chucunaque Rivers (Group B), where the possibility of receiving medical assistance is virtually nil. The lowest death rates and infant mortality rates occur among the Negroes and Colonists (Groups D and E), who live closer to communities, such as La Palma and El Real, where modern medical facilities are available.

As shown by the gross rates of reproduction, all groups have high levels of fecundity. The rate shown is the number of

Table 2. Results of the demographic survey of the present study. Cultural groups are described in the text and in the legend of Table 3.

Demographic parameters	Cultural groups				
	A	B	C	D	E
Reproduction rate (children per female)	2.7	2.7	3.4	3.4	3.1
Child mortality rate (deaths per year per 1,000 live births)	156	206	187	96	92
Life expectancy at birth (years)	46	38	42	56	58
Birth rate (b = births per year per 1,000 pop.)	40	40	47	45	42
Death rate (d = deaths per year per 1,000 pop.)	19	25	21	13	13
Natural growth rate (b — d)	21	15	26	32	29

children that a newly-born female may have during her reproductive years if existing conditions remain the same. Women of the five groups have the highest rate of fecundity between the ages of 20 and 25.

ECOLOGICAL PATTERNS AND HUMAN POPULATION

The populations of the study area can also be subdivided according to the kinds of habitats (estuarine, coastal, insular, fluvial) from which they derive part or all of their food, water, and other materials required for subsistence. For example, based on the National Census of 1960, there were about 7,500 people, mostly non-Indians, who lived on the shores of the Gulf of San Miguel and, thus, had access to various estuarine ecosystems. About 11,800 people, including the majority of the Chocó Indians, some Negroes, and some Cuna Indians, lived inland along rivers and, thus, obtained part of their food from riverine (fluvial) ecosystems. Some of the Negroes (Puerto Obaldia on the Caribbean and Garachiné on the Pacific, for example) lived in coastal habitats, while others occupied insular habitats (Las Perlas Islands, for example).

SUBSISTENCE CULTURE

In all the different cultural groups and in the different habitats, the subsistence economy of the area is uniform. It depends primarily on shifting agriculture and secondarily on fishing in the rivers and marine habitats available. The raising of livestock and poultry ranks third, while hunting and the gathering of wild fruits rank fourth and fifth as methods employed in these different subsistence activities, and the species utilized by the different cultural groups depend to a significant extent on the kinds of environments in the different areas.

Agriculture

The agricultural systems employed by the different cultural groups are: shifting cultivation, riverine agriculture, plantation agriculture and dooryard agriculture. The characteristic type of agriculture, shifting cultivation of the slash-burn type, does not produce high yields because the native population lacks the technology required to utilize the land to its maximum advantage; the condition of the soil and the lack of plows and fertilizers contribute greatly to the migratory character and the low yields of shifting agriculture. In spite of this, agricultural products account for 70 to 90% (Table 3) of the total diet.

The Cuna Indians of the San Blas Islands have coconut plantations along the coast and on some islands, but the principal areas of cultivation are along the mainland rivers and on the sides of the low mountains bordering the Caribbean coast. Dooryard agriculture is limited because of the small size and poor soil of the islands.

These four agricultural systems are practiced by all the groups. While shifting cultivation is the most important, plantation agriculture is very important among Chocó Indians and Negro farmers, who are engaged in the intensive cultivation of plantain and banana for commercial purposes. The colonists combine shifting agriculture with cattle-raising which takes them inland and away from the river banks. The cleared lands belonging to these people are becoming anthropogenic savannahs due to the establishment of pastures to further livestock raising.

Fishing

Fishing in the rivers, estuaries, and oceans of the area is the most frequent and expedient way of obtaining animal protein.

Table 3. Percentages of food consumption with respect to source and populational group, based on total weekly intake of food by adult males. Populational groups are as follows: A, Cuna Indians of the San Blas Islands; B, Cuna Indians of the Bayano and Chucunaque Rivers; C, Chocó Indians; D1, Negroes (estuarine ecosystem); D2, Negroes (fluvial ecosystem); D3, Negroes (coastal ecosystem); D4, Negroes (island ecosystem); and E, Colonists.

Foods	Group A	Group B	Group C	Group D1	Group D2	Group D3	Group D4	Group E
Agricultural Products	81.9	86.4	83.7	76.3	83.9	73.9	72.0	88.9
Fishing (Sea Fish)	11.3	—	—	10.7	—	11.3	17.2	—
Fishing (River Fish)	—	6.3	7.6	—	6.9	—	—	1.0
Hunting	1.7	7.2	5.9	—	1.0	3.3	4.3	1.2
Cattle & Poultry Products	—	—	1.6	1.7	5.4	6.6	2.4	7.7
Imported Products	4.9	—	0.9	11.0	2.7	4.9	4.0	1.0

Fig. 1. Typical Cuna dwellings in the San Blas Islands.

Maritime fishing by natives of the study area is rather limited, but shrimp boats from the Gulf of Panama often bring part of their rich cargo to the towns bordering the Gulf of San Miguel to sell or simply give away to the people. With the exception of the colonists, who are primarily cattle-raisers, sea and river fish are the most important sources of animal protein. As can be seen in Table 3, fish account for 6 to 17% (by weight) of the diets of the other subpopulations.

Hunting

Although less important than fishing, hunting also provides a source of protein in the form of birds and mammals. Group B shows a higher percentage consumption of game than the other groups; this reflects the greater availability of birds and mammals in the upper Bayano and upper Chucunaque areas. Usually, game is consumed fresh; but when the hunting is good, excess meat may be preserved by salting, smoking, or sun drying.

Animal Husbandry

Domesticated animals such as chickens, ducks and pigs are common throughout the area. Their basic nourishment is corn and rice, but pigs are also fed plantain, squash, and root crops.

FIG. 2. Cuna woman working at the fireplace, Mulatupo, San Blas.

It is customary in the region to allow domesticated animals to run wild, allowing them to complement their nourishment with worms, insects, human and animal residues, and wild plants.

Livestock-raising is becoming commercially and locally more important. This is due primarily to the tendency of colonists to combine agriculture with cattle-raising. The result is a general movement of the population inland, away from the rivers, as more and more forest areas are cleared and converted to artificial pasture.

Gathering

The gathering of wild fruits is a seasonal practice, which contributes very little to the total diet. Raicilla (Ipecac) is the only item gathered for commercial purposes.

Potable Water

Water for drinking, cooking, and the preparation of beverages is usually obtained from rivers or creeks. In a few places, such as La Palma, Puerto Obaldia, and Garachiné, there are rudimentary aquaducts. Artesian wells are limited in number

FIG. 3. Cuna Indians of the mainland, Bayano River, Panama.

and a few people in some parts of San Blas and in La Palma collect rain water, especially during the rainy season.

Transportation

The means of transportation utilized by the different human groups are related to their habitat and cultural associations. The many rivers of the area are the major routes of transportation, and the dugout canoe is the most common vehicle, but other types of boats are also fairly common. Recently colonists have introduced horses and oxcarts, but roads are virtually non-existent. Travel between the upper Bayano and the San Blas Islands is still by foot, but transportation by air is available between Panama City and many points in the study area.

MATERIAL CULTURE OF THE HUMAN GROUPS

The Cuna Indians (Groups A and B)

These groups represent one culture and one language but they are found in two different habitats. Group A is found in the coastal-insular region known as the Comarca de San Blas (Figs. 1 and 2). In the Census of 1960 the San Blas population was approximately 19,340. Group B, the Cuna Indians of the

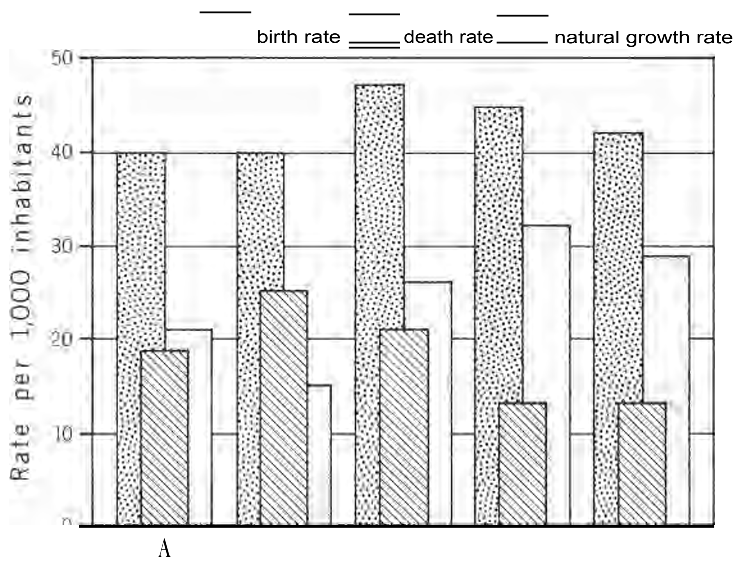

Fig. 4. Natural growth, birth, and death rates among human groups of Eastern Panama, 1967. A: San Blas Cuna Indians (insular); B: Cuna Indians (mainland); C: Chocó Indians; D: Negroes; E: Colonists.

Chucunaque and the Bayano Rivers, consists of about 1,500 people. Their habitat is typical of the tropical jungle, and most of them live in riverside settlements (Fig. 3). The presence of the Cunas in two different habitats justifies the recognition of two different groups. Group B, because of its isolation, is culturally conservative and shows little evidence of either acculturation or cultural progress. Group A, on the other hand, is culturally progressive. It has eagerly accepted the efforts of governmental and charitable organizations to establish educational and medical facilities on the islands. The people carry on a lively trade (exporting coconuts, avocados, and other seasonal fruits and importing various trade goods) with Colombian trading vessels. They have encouraged tourism by building small hotels and opening landing fields for light aircraft on several of the islands.

The San Blas Cuna population is relatively static; the natural growth rate is only 21 per 1,000 (Fig. 4). The 1960 Panamanian Census report suggested that the population of San Blas will

FIG. 5. Coming from a successful hunt, two peccaries are transported by the hunters.

diminish by 1970 to 18,860. The decline of the Chucunaque and Bayano population (Group B) may be even greater because the natural growth rate is only 15 per 1,000 inhabitants (Fig. 4). The endemic and epidemic illnesses that have swept the region are undoubtedly the principal causes for this situation.

Almost everything required for the subsistence of these two groups is extracted from their immediate environments. The principal agricultural products are plantain *(Musa paradisiaca)* and bananas *(Musa sapientum).* Both plantain and banana are common in the upper Bayano-Chucunaque area, but plantain is relatively rare in the San Blas area. The weekly adult consumption of plantain/banana amounts to 12.5 kg in the Bayano-Chucunaque area, and 9.0 kg in the San Blas area. The second and third most important agricultural products are corn and rice, but more than two dozen other plant species (including root crops such as manioc, yam, and sweet potatoes,

FIG. 6. Chocó girls in Darien.

and fruits, such as avocado, cacao, and papaya) are commonly cultivated.

As shown in Table 3, hunting is much more important in the Bayano-Chucunaque area than in the San Blas area. The collared peccary (Fig. 5), agouti, and tapir are among the commonest mammals taken, while the most frequently hunted birds are curassow, guan, and parrot. The relative unimportance of game in the San Blas diet reflects the increasing dependency of this group on imported foods and the difficulty of hunting excursions to the mountains. Due to their inland location, maritime products are not available to Group B; but sea fish and other marine food species account for 11.3% (by weight) of the San Blas diet (Fig. 3). By the same token, the San Blas do little or no fishing in rivers, while the Bayano-Chucunaque group makes extensive use of fluvial food sources.

The isolation of these two groups is not great. They communicate by means of paths cut through the San Blas mountain range. Especially during the dry season, the Cuna from

Fig. 7. In close relationship with the habitat, the Chocó Indians like spider monkeys (*Ateles*) as pets.

the continental region visit the San Blas Islands to sell smoked meat, agricultural products such as cacao, and cosmetics made from the seeds of achiote *(Bira orellana)*. Such visits are profitable and the visitors buy manufactured articles such as clothing, cooking oil, flour, salt and other "luxury" items. During the dry season the San Blas Cuna follow the same paths and visit relatives that live in the Bayano-Chucunaque area: at the same time, they may buy tobacco or go on hunting excursions. These hunts are granted by permission of the political chief of the mainland region.

Contact between the mainland Cuna (Group B) and the other human groups of the study area is rare, and this is due more to volitive reasons than to geographical isolation. The rivers of the region should facilitate such contact, but the Cuna community voluntarily maintains its isolation and expressly denies admission to the vehicles of acculturation.

FIG. 8. Typical Chocó dwelling.

The Chocó Indians (Group C)

In 1960 there were 5,475 Chocó Indians in the region of study (Figs. 6, 7, and 8). Mostly, they are dispersed along the upper reaches and tributaries of the most important rivers in the region: the Jaqué, Sambú, Tucutí, Chucunaque, and Tuira. The subsistence economy, based on shifting agriculture, is supplemented by the intensive cultivation of plantain and rice for commercial purposes. As with the other groups, plantain and banana, especially the former, are the main elements of the diet. In order of importance, these are followed by rice, corn, and root crops. The consumption of agricultural products accounts for 83.7% of the total diet.

River fish, mollusks, and crustaceans are the main sources of animal protein. There is remarkably little selectivity displayed in regard to fishing, and virtually everything caught goes into the pot. As shown in Table 3, river fish account for some 7.6% of the Chocó diet. Small groups of Chocó living around the Gulf of San Miguel consume similar quantities of sea fish.

Certain mammals such as agouti *(Dasyprocta punctata),*

FIG. 9. A coastal village of Negro population in Darien.

white-lipped peccary *(Tayassu pecari)*, collared peccary *(Tayassu tajacu)*, and brocket deer *(Mazama americana)* are preferred, but other animals, such as monkeys, various kinds of birds, iguanas, and a few other reptiles, also are taken. Chickens and pigs are raised to a limited extent. As shown by Table 3, the consumption of game and domestic animals is about equal to the consumption of fish and other aquatic organisms.

There is a close relationship between the Chocó Indians and their habitat, not only in regard to diet, but also in regard to the collection of wild plants used in house construction, as medicines, or as cosmetics. Virtually everything they require for subsistence is available in their immediate environment. The only imported items commonly seen in Chocó homes are articles of clothing, household utensils, such as aluminum pots, and transistor radios.

The Negro Population (Group D)

The Negro population of the study area, approximately 17,041, has the highest growth rate (32 per 1,000) of all the

FIG. 10. Plantain-trade boats in Darien.

groups studied (Fig. 4). The death rate is one of the lowest (13 per 1,000) and the birth rate is one of the highest (45 per 1,000). Demographically, this is the most important group of the region. Its geographical distribution is largely estuarine or coastal because many of the larger and economically more important Negro villages, such as La Palma, Rio Congo, Garachine, and Chepigana, are located on the Gulf of San Miguel (Fig. 9). Another segment of the Negro population shows a fluvial (riverine) distribution in villages such as El Real, Pinogana and Yaviza. Population data for these non-Indian inhabitants of the area show that 56% live in estuarine or coastal zones, while 32% live along the principal rivers of the region. The insular subgroup of the Negro population, about 12%, is confined to Las Perlas Islands.

The economy of this group is also based on the slash-burn type of shifting agriculture. The principal agricultural products, in order of the importance in the diet, are: rice; plantain (Fig. 10); corn; and edible roots such as yams, manioc, and sweet potato. The Negroes of fluvial habitats are somewhat more dependent (Table 3) than those of other areas on agricultural products.

The relationship between habitat and diet is perhaps best

FIG. 11. Traditional hut of colonists settled in Darien.

illustrated (Table 3) by the proportions of river fish (plus other freshwater organisms) and sea fish (plus other marine organisms) in the diets of different groups. The consumption of river fish (6.9%) by Negroes living near rivers (Group D2) is comparable to that of the riverine Indian population (Groups B and C). The same relationship holds in regard to the consumption of seafood by the Negroes of Las Perlas Islands (Group D4), which is significantly higher (17.2%) than that of any other group.

The hunting of game animals and wild birds contributes less to the diet of Negro populations than it does to those of inland Cuna and Chocó Indians, but the consumption of domestic animals such as chickens, hogs, and cattle is generally more important. In La Palma, for example (not shown in Table 3), 14.2% of the diet is made up of poultry, pork, and beef; the latter comprises 8.4% of the diet. In this particular case, the high rate of domestic animal consumption is related to the relatively high level to which a money economy has developed. La Palma is the capital of the Darien Province and a relatively large percentage of the population is composed of salaried government workers, merchants, and tradesmen who have enough money to purchase the poultry, pork, and beef raised in other parts of the region and brought to La Palma for butchering and sale.

The development of a money economy is also responsible for the fact that the consumption of foods imported from outside the study area—items such as canned meats, canned fish, carbonated beverages, beer, rum, bread, crackers, cookies, etc. —is also relatively high, ranging from 2.7% among the Negroes of fluvial habitats to 15.3% of the total diet of the urban population of La Palma. In fact, the consumption of imported products (Table 3) seems to be a fair indicator of the extent to which the different population groups are or are not dependent upon their immediate environment to provide the items required for subsistence.

Historical and political factors are also involved in the gradually decreasing dependency of these groups upon their immediate environment. The building of primary and secondary schools by the federal government, the establishment of two hospitals, and the existence of national agricultural agencies, etc., have all contributed to rapid cultural progress and the transition from a subsistence economy to a money-based economy and a mode of life with semi-urban characteristics.

The Colonists (Group E)

Recent settlers from the western part of Panama (about 1,300 people) constitute a minority of the population, but they are bringing about some serious ecological changes in the region. They have brought with them the agricultural practices which are characteristic of the region of their origin (the Azuero Peninsula and the central provinces of Panama and Chiriquí). They are rapidly clearing large areas of jungle for agricultural purposes, especially for the planting of pastures and the establishment of cattle.

In their culture, cattle-raising is not just an economic undertaking, it also imparts a high degree of social prestige. Under their influence, cattle-raising has been popularized throughout the region, and "small cattlemen" have begun to appear among the Negro and Chocó Indian populations as well. The colonists are the only group in which the consumption of milk and dairy products is of any importance. It is also the group (Table 3) in which the average consumption of cattle and poultry products is highest (7.7%).

This group is also strongly influenced by the environment, not so much because of present cultural patterns, but, because they live in incipient colonies (Fig. 11) and are economically poor; they must take maximum advantages of natural resources and keep to a minimum the consumption of purchased products. This explains the high percentage of agricultural products (88.9%) and the low percentage (1.0%) of imported products in the average diet. Likewise, fishing and hunting contribute little to the colonist's diet because the work of raising crops and cattle leaves little time for such activities.

EXPORTS

Another matter of some importance in regard to radiological-safety feasibility studies is the export of vegetable and animal products from this region to other provinces of the Republic of Panama and even to different parts of the world. The principal agricultural exports are plantain, rice, and yarn. The region under study supplies most of the plantains consumed in the Province of Panama and in some of the central provinces as well; plantain is an element of daily consumption throughout the Republic. Exportation of rice and edible roots is also important and helps to fill requirements of other parts of Panama. The vast timber lands of the region are continuously exploited for exportation purposes. It is estimated that 7,000,000 board feet of lumber for fine furniture and construction purposes are shipped every year to the Province of Panama from the Darien Province. Shrimp fishing, while not confined to the study area, is common throughout the Gulf of Panama and the Gulf of San Miguel. Most of the 12 to 15 million pounds of shrimp taken annually is exported to the United States.

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THE NATIONAL ACADEMY OF SCIENCE COMMITTEE ON THE ECOLOGY OF THE INTEROCEANIC CANAL

By WILLIAM A. NEWMAN
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The Panama Canal is a lock canal too small to accommodate many of the larger ships travelling between the Atlantic and the Pacific Oceans today. In the foreseeable future it will be unable to satisfy the increasing demand for ordinary ship transits.

The canal requires a considerable amount of water to operate. A single complete transit by a ship utilizes 52 million gallons of fresh water, or enough to supply a large city for a day. Presently the canal can handle up to some 40 ships a day, or 14,000 ships a year, when enough water is available.

Fresh water is the principal factor limiting the canal's operation. But even if water needs are satisfied, there would always be the limitation of the locks. Improvements can increase their capacity somewhat but, even so, it is estimated that maximum capacity set by the rate ships can be passed through locks would be reached in the next thirty years or so. Because of this the United States Government decided to look into the feasibility of a new canal, preferably a lockless one at sea level.

In 1964, the United States Army Corps of Engineers, the Atomic Energy Commission and the Panama Canal Company completed a study of 30 possible routes for a sea-level canal, with special reference to nuclear excavation. In 1965, President

Lyndon Johnson appointed a five-man commission of citizens from private life to study the overall situation, as well as the sites surveyed. The commission was called the Atlantic-Pacific Interoceanic Canal Study Commission, (hereafter referred to as the Commission). Members were: R. B. Anderson, (Chairman) M. S. Eisenhower, Gen. K. E. Fields, R. A. Hill and J. P. Sheffey (Executive Director). The Battelle Memorial Institute, Columbus, Ohio (hereafter, BMI), was contracted by the Commission to carry out a number of environmental studies on a sea-level canal. The Commission was reappointed by President Richard Nixon and its report was to be presented to him in October of 1970.

In 1969, the National Academy of Sciences (NAS) was requested by the Commission to appoint a committee of biologists to review what had been accomplished and to make recommendations to the Commission by April of 1970 with regard to the ecological problems surrounding a sea-level canal. The new committee, called the Committee of Ecological Research for the Interoceanic Canal (CERIC) was charged with the following responsibilities: Examination of ecological issues implicit in the construction of a sea-level canal, with special reference to the marine environment, and the outlining of a program of research that might appropriately be done in the period before, during, and after the construction of such a canal. Further duties were to assess the ecological impact of the canal and to recommend ways of minimizing damage that might, in fact, occur. Evaluation of the need for a canal, and the wisdom of constructing it, were explicitly excluded from CERIC's task—deliberations were to be carried out under the assumptions that a canal would be built, that it would probably be located in the vicinity of the Panama Canal, and that construction would probably be by conventional means. CERIC consisted of: Ernst Mayr, Harvard University (Chairman); Máximo Cerame-Vivas, University of Puerto Rico; David Challinor, Smithsonian Institution; Daniel Cohen, Bureau of Commercial Fisheries (BCF), Washington, D. C.; Joseph Connell, University of California, Santa Barbara; Ivan Goodbody, University College of the West Indies, Jamaica; W. Newman, Scripps Institution of Oceanography (SIO); C.

Ladd Prosser, University of Illinois; Howard Sanders, Woods Hole Oceanographic Institution; E. 0. Wilson, Harvard University, and Donald Wohlschlag, University of Texas.

Two ad hoc committees were subsequently appointed by NAS and CERIC. One on Oceanography included: Alan Longhurst, BCF, La Jolla, (Chairman); W. H. Bayliff, E. Forsbergh, Forrest Miller and Merritt Stevenson, all of BCF, La Jolla; D. Inman and B. Taft, SIO and C. Rooth, University of Miami. The other, on Hydrology, included: Luna B. Leopold, United States Geological Survey (USGS), Washington, D. C., (Chairman); Walter B. Langbein, USGS, Washington, D. C.; Thomas Maddock, Jr., USGS, Tucson; Robert H. Meade, USGS, Woods Hole.

The following considerations are my understandings of the bases of deliberations of these committees:

The Panamic Isthmus has separated the tropical American marine biotas, of approximately 8,000 Pacific and 7,000 Caribbean species, for three to five million years and this period of isolation has allowed them to diverge markedly from whatever similarities they originally held. A 10% similarity between the Recent biotas has been estimated. Despite claims to the contrary, CERIC observed that the Panama Canal has not allowed significant interchange between the two oceans because Gatún and Miraflores Lakes form a fresh water barrier between them.

An unbarriered sea-level canal would allow biotic interchange, the consequences of which are unknown. There would be two types of problems: those of scientific and those of economic importance. The latter of course cannot be separated wholly from the former and separation here is quite arbitrary. Consequences of scientific import include the disruption of fresh water and marine communities before they have been adequately studied and the concomitant interactions that would follow. Those problems that presently can be identified as economically important include effects on fisheries, recreational resources, and general living conditions within the areas affected. What is apparently happening to the eastern Mediterranean sardine fishery, presumably a result of the Aswan Dam, is a recent example of what can occur when large ecological changes are made. Furthermore, the extensive studies required to understand the collapse of the California sardine industry were in good part necessitated by the lack of previous knowledge. It would be far better to have population dynamics of Panamic fisheries well-understood before a sea-level canal were built. Without background information, attempts to understand and explain changes that occur after a canal is completed would have serious shortcomings.

Transfer of undesirable marine organisms, undesirable in any terms one likes, but affecting recreational, fisheries and other economic resources, is a distinct possibility. The Yellow-bellied sea snake and the Crown-of-Thorns starfish are two Pacific forms that might get into the Caribbean, should an unbarriered sea-level canal be built. The risk of introducing parasites and pathogens was also considered by CERIC, and there are undoubtedly many other kinds of interactions of which we are not aware.

CERIC, therefore, considered an unrestricted breaching of the Panamic Isthmus by a sea-level canal totally unacceptable because of what has been experienced when comparable barriers have been eliminated or all but eliminated in the past. It will be recalled that the Suez Canal remained an ineffective connection between the Red Sea and the Mediterranean, until recently, because of the hypersaline barrier formed by the Bitter Lakes. The same might be said of the Panama Canal because of the fresh water barrier formed by Gatún Lake. We can also recall what an effective barrier Niagra Falls formed before ship canals by-passed them, letting the sea lamprey into the Great Lakes. Therefore, the establishment of an antibiotic barrier within an interoceanic canal was recommended by CERIC.

Bubble curtains, electrical weirs, ultrasonic screens, etc., were among the physical barriers considered. All need much research and each has drawbacks. Perhaps an effective combination of two or more could be worked out. Such physical barriers were not highly recommended by CERIC, for, as with chemical barriers, CERIC claimed no expertise in this field.

CERIC went on to consider treating the waters contained within the canal in some way. However, maintenance of a parcel of treated water in the sea-level canal would not be a simple matter. There is a marked difference in sea-level and tidal amplitude between the two oceans. The Pacific side has a tidal range of 21 feet and is on the average 0.7 feet higher than the Caribbean which has a tidal range of but a few feet. A modern sea-level canal would have a cross-section of some 50,000 square feet, which, under these conditions, would allow an average flow of approximately 1 foot per second. This would result in a net transport of about 50,000 cubic feet of water per second from the Pacific to the Caribbean, an amount equivalent to about half the discharge of the Nile before the Aswan Dam. Peak currents of eight feet per second, or about five knots, would occur about 10% of a tidal cycle. During the remainder of the time, currents would range between some moderate negative value and four knots. Such strong currents would make the maintenance of a parcel of treated water within the canal virtually impossible. However peak velocities would not be realized because, for navigational purposes, tidal barriers were deemed necessary by the canal engineers. Therefore, CERIC recommended the tidal barriers be so arranged as to keep the net flow to a minimum, so that the contained waters could be treated and maintained in an appropriate way, as an antibiotic barrier.

CERIC concluded that a fresh water barrier was among the least objectionable. But there would be no possibility of supplying the amount of fresh water needed to form a hyposaline barrier unless the tidal barriers kept the flow very low. If the flow could be kept to a minimum, CERIC considered a fresh water barrier worthy of investigation by the engineers. CERIC also considered that if a parcel of water within the canal could be warmed sufficiently, an efficient thermal barrier could be formed. Nuclear or conventional power plants probably would be needed in the new canal zone and CERIC suggested perhaps the waste heat could be used to supply the thermal barrier.

CERIC recommended that fresh water and thermal barriers be combined. The effectiveness of fresh water and thermal barriers would be much enhanced when used together due to the synergistic relationship between them. Virtually all marine organisms would be killed by a residence time of 48 hours in 0.5-1.5% (< 5%) seawater. Temperatures of 45°C, alone, for the same period, would also be lethal. When salinity and temperature are combined for 48 hours the gradient can be less severe. For temperate forms, a salinity of 10% (3.4‰) and a temperature of 37-38°C was tentatively considered to be satisfactory. Research would have to be performed to see if these figures would be applicable because they are based on experiments carried out on relatively hardy temperate species. In general, tropical organisms are more sensitive to change, especially in temperature, so an even less severe gradient might be practicable.

General conclusions were that researches should begin well in advance of the canal's construction. Laboratory work in physiology should include research on osmotic and thermal tolerances, reproductive cycles, and life histories. Additional collecting of the biota for taxonomic studies, as well as detailed work in systematics, would also be required. Field studies should include work on nearshore communities, such as mangrove swamps, mud flats, soft bottoms, and coral reefs, as well as oceanographic studies. Oceanic work considered included biological, chemical, physical and geological oceanography. The pursuit of these researches would require funding, space, ships, and administration.

In view of its findings, CERIC recommended that a *Commission on the Ecology of the Interoceanic Canal* be established. A distinguished governing board of North, Central and South American scientists would be required, and the principal administrative office for this board would probably best be situated in Washington, D. C.

One major 120-150 foot ship, two 65 foot trawlers, and an assortment of small craft were considered necessary to support field operations. Ten principal international investigators, plus a supporting staff of at least 20 junior scientists, technicians and secretaries, would be resident personnel. Space and funds for visiting investigators should be available. Two laboratories, one on the Caribbean side and a major one on the Pacific side, would be needed for physiological, marine biological, systematic, and oceanographic work. Subsidiary laboratories, especially in the Caribbean, would also require support, especially after the canal was operational.

An itemized initial capital outlay was estimated to be approximately 4 million dollars with an annual operating budget of about 2.5 million dollars. It should be borne in mind that 22 million dollars were spent looking into the feasibility of nuclear excavation (now considered impractical), and that the construction of a sea-level canal by conventional means, at 1970 price-levels, is to the order of 3 billion dollars. The ecological studies, then, represent but a small fraction of the total capital outlay and operational costs of a sea-level canal.

To summarize, the principal problem before CERIC was to evaluate existing knowledge on the effect of mixing two previously separated biotas by creating an interoceanic connection across the Panamic Isthmus. The literature on the subject is scattered and varied, and conclusions range from "catastrophe" on one hand, to "no significant, or even beneficial, effects" on the other.

CERIC viewed the situation in the following way: Specifically what would happen by allowing the two biotas to mingle cannot be predicted, but experience indicates that undesirable events have followed virtually every ecological disruption and barrier-removal in the past. Reduction or removal of the terrestrial and fresh water barriers that presently separate the Panamic marine biotas would obviously lead to exchange, and the exchange would not be negligible. The effects of the exchange would not be limited only to the areas immediately adjacent to the canal openings, but would be far reaching. Therefore, CERIC took the stand that, since undesirable consequences are likely, exchanges of these biotas must be prevented as much as possible.

CERIC recommended that an antibiotic barrier be installed. A sea-level canal would require tidal barriers for navigational purposes. Engineers informed CERIC that these barriers would probably be submarine gates restricting, but not closing, the channel during periods of peak flow. CERIC, therefore, suggested that these gates be designed in such a way as to reduce the net flow to a minimum, so as to contain a thermo-hyposaline barrier, or any other effective antibiotic barrier, within the canal. The nature of the barrier was not strictly stipulated. Studies of the synergistic effect of heat and dilution necessary to kill representative samples of marine invertebrates, fishes, plants, etc., of the area would be needed, if a thermo-hyposaline barrier were utilized, since available data are based primarily on studies of organisms of the temperate region.

CERIC recommended that the oceanography and marine biology of the region should be thoroughly studied, beginning as much as ten years before the opening of a sea-level canal, and that the situation should be monitored and studied afterwards, in order to check on the effectiveness of the barrier and to identify the causes of biotic changes likely to occur if the barrier were not being properly maintained.

CERIC recommended that a commission be established to administer the funds, facilities and research concerning the Panamic sea-level canal. It further recommended, in general terms, the kinds of research to be carried out.

CERIC's report and recommendations went to the Atlantic-Pacific Interoceanic Canal Study Commission in April, 1970. Reverberations were immediately forthcoming. Two letters, one from Mr. Sheffey (Executive Director of the Commission) to Gerald Bakus, (NAS Staff Officer for CERIC), and another from Brigadier General R. H. Groves, (Engineering Agent for the Commission) to Dr. J. S. Coleman, (Executive Officer, NAS), were circulated among members of CERIC. These letters give the tenor of the philosophy of the Commission. The following are my own responses to some of their assertions and queries, paraphrasing my letter of May 28, 1970 to Dr. Coleman, with copies to the aforementioned Commission members and to members of CERIC. At least two colleagues in CERIC, namely from Puerto Rico and Woods Hole, also submitted letters in reply to the aforementioned, reflecting much the same feelings.

In his letter of May 18, Mr. Sheffey stated that the "CERIC report . .. is oriented almost entirely toward the alarmistic view point," implying that CERIC had taken an extreme stand. Actually it is Mr. Sheffey who has taken an extreme stand,

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[1] Editor's note: Another viewpoint of the subsequent events may be found in Boffey, P. M., 1971, "Sea-level canal: How the Academy's voice was muted." Science, 171: 355-358.

for he says that nothing need be considered in allowing free interchange between the tropical American biotas beyond factors strictly associated with engineering practices because he believes the ecological consequences involve little or no risk. Actually CERIC's approach was, that "while ecologically undesirable, if a sea-level canal were deemed necessary for national purposes, it should be designed in such a way as to minimize ecological effects," and CERIC recommended an antibiotic barrier be installed. I hardly think this an alarmistic or extreme approach, any more than would be the recommendation that fish ladders and diverters be included in the construction of certain dams.

In this same letter Mr. Sheffey went on to imply that he could rally a group of biologists that would back up his assertion that there would be essentially no undesirable ecological consequences connected with a sea-level canal and who would place their names on a document disavowing recommendations for preventing free interchange of tropical American marine biotas. Could such a group, acceptable to a quorum of ecologists, be assembled? It seems very doubtful that a knowledgeable person would allow himself to be held responsible for the undesirable consequences that could result from the introduction of such organisms as the Indo-Pacific starfish, *Acanthaster,* or the Eastern Pacific sea snake, into the Caribbean. Considering the wide range of conditions under which these organisms presently thrive, there appears to be no compelling reason to suspect that they could not become successfully established in the Caribbean and, that they would remain dynamically neutral in their new environment, would be most unlikely indeed. Such considerations have been discussed with informed people outside of CERIC, and have evoked agreement rather than arguments to the contrary.

We are not faced here simply with the responsibility for the economic losses that might occur. The free mixing of tropical American marine biotas would enact irreversible changes, not only locally, but, eventually, throughout the Indo-Pacific and tropical Atlantic, that virtually no amount of might nor money could significantly alter. Experience in the past strongly suggests that some of these interactions are likely to be quite undesirable and the potential threat, as regards a sea-level canal, cannot be ignored.

Mr. Sheffey has had an elastic collision with knowledge in his argument that the Crown-of-Thorns starfish (and, therefore, presumably many other organisms of which we know little or nothing) already would have established itself in the Caribbean were conditions there favorable for it. Such a statement only displays an ignorance of the facts and of the principles of zoogeography and elementary ecology.

General Groves, while taking a more sober approach than Mr. Sheffey, in his letter of May 11, 1970, also queried CERIC's considerations, as though, somehow, the significance of the biological and physical data at CERIC's disposal had escaped CERIC. His major points were of two types. The first concerned CERIC's judgments on the "desirability and feasibility of a sea-level canal." There is nothing known to be ecologically desirable about the sea-level canal. Virtually anything is possible, of course, but the probability of desirable ecological effects is extremely remote. On the other hand, ecological changes are certain and, for the most part, irreversible, and the probability that some of these would be undesirable is great enough to warrant concern by all. From a purely ecological point of view, no canal should be built, and this is, perhaps, the recommendation an uncompromising conservationist would feel compelled to make. Desirability can only be couched in economic terms, for a number of reasons ranging from world commerce to defense, and these were neither within the purview nor competence of CERIC to assess. If, for various non-environmental reasons, a sea-level canal were deemed essential, in order that it be ecologically tolerable, CERIC considered that the canal must be designed and constructed in such a way as to have as little ecological impact as possible, and must include mechanisms for the prevention of exchange of marine organisms between the tropical Americas when in operation. To prevent exchange CERIC recommended an antibiotic barrier be installed. CERIC had no expertise on how acceptable barriers could be implemented; decisions of feasibility would come from engineering studies. This was all in the report to the Commission, yet we have heard virtually nothing of what feasibility problems this recommended restraint would impose.

As to assessing the "significant and rather extensive movement of marine life through the present canal" mentioned again by General Groves, and often reiterated by Mr. Sheffey, there is no documentation of this. There are a few fouling and euryhaline organisms, most of which have undoubtedly gotten through from the Caribbean to the Pacific, but these are neither numerous nor wholly marine. If it were known that a spectrum of marine organisms had been getting through the existing canal, primarily in ships' ballast tanks, it would be well that measures be taken to stop the transport, but there is no evidence that successful transports of this kind have been made. CERIC also recommended against salination of Gatim Lake, for even though the degree of salination probably would not be sufficient to permit passage for most oceanic organisms, it would nullify a good deal of the effectiveness that this fresh water barrier presently has in preventing the exchange of hardier shallow water forms. The impact that salination would have on the fresh water organisms of the region is another matter.

General Groves' second question concerned ecological information gathering and the research program needed, should a sea-level canal be built. Most if not all of the information needed to answer this was contained in the CERIC report, although it might not all be readily identifiable without a complete reading. Therefore, one can only agree wholeheartedly with the General's suggestion that a five to ten page abstract of the CERIC report be published with the Commission's report (see below as to what was published).

In consideration of CERIC's recommendations, one would have thought the Commission would have started exploring the kinds of antibiotic barriers that would do the job effectively and economically. There are a number of possibilities and, if appropriate minds were brought together to work on the problem, it is likely a reasonable solution could be developed that would provide little or no interference with the operation of the canal, at negligible cost.

The Commission's report went to President Nixon in Octo-

[illegible] of 1970. Copies were not received by this and, presumably, other members of CERIC. The report contains a four-page chapter on "Environmental Considerations," and only through the special efforts of Alan L[illegible], Chairman of CERIC's Oceanographic Subcommittee did I receive a copy of it. The recommendations of CERIC are not cited in the chapter. The CERIC report is mentioned, but only to the extent that it is to be found in Appendix 16 to Annex V, "Study of Engineering Feasibility," of the Commission's Report—that is, somewhere back in the archives presumably supporting the principal text.

The Commission's chapter on "Ecological Considerations" does contain better than a page-long summary of BMI's conclusions which, while minimizing the effects of [illegible] tropical biotic exchange, appear to stand somewhere between those of CERIC and the Commission, especially with regard to barriers. The BMI summary states: "Environmental conditions [illegible] to] the [sea-level] canal would constitute barriers to the migration of both plankton and nekton, and effectiveness of these barriers could be enhanced by engineering manipulations of fresh water inputs to the canal and other artificial means." The Commission follows by saying that "it would be possible to install a temperature or salinity barrier." However, the Commission feels that "the risk of adverse ecological consequences stemming from construction and operation of a sea-level Isthmian canal appears to be acceptable" and "no such barrier was included in the design, because the need for anything in addition to tidal gates has not been established." Their recommendation to our President, without further ado, is to build a sea-level canal without an antibiotic barrier despite CERIC's strong recommendation to the contrary. One wonders on whose judgment CERIC's primary recommendation was so summarily dismissed.

The short shrift given the year-long studies and deliberations presented in the CERIC report is particularly disappointing because the resulting recommendations stem from well-considered analyses of the situation by some of the most intelligent and reasonable men with whom I have ever had the privilege to work. Mr. S[illegible]'s accusations imply a [illegible]-

tion between BMI and CERIC. This was not the case and personal communications with BMI were most satisfactory.

Mr. Sheffey erred in dealing with CERIC recommendations as though they represented an untenable extreme. Little could be further from the truth. In light of existing knowledge and experience, the idea of connecting the tropical American marine biotas by a seaway without an effective antibiotic barrier is presently indefensible. Surely further serious international deliberations on this subject are in order, regardless of who builds a sea-level canal across Central America.

ACKNOWLEDGMENTS

Many colleagues have helped me rationalize the difficult problems expressed here. While my desire is to acknowledge them all, they are so numerous that I am sure I have forgotten some for the moment. For any omissions I apologize. I would like to begin by thanking Robert Hessler, Richard Rosenblatt and Thomas Dana (Scripps Institution of Oceanography); Meredith Jones (Convenor of this symposium); members of CERIC—especially Ernst Mayr (Chairman), Alan Longhurst (Chairman, Oceanographic Subcommittee), Daniel Cohen, Ivan Goodbody, Máximo Cerame-Vivas and C. Ladd Prosser; Peter Glynn and Ira and Roberta Rubinoff (Smithsonian Tropical Research Institute), all for instructive conversations and critical advice. I also would like to acknowledge Mrs. Ann A. Newman and Mrs. Carol Kourtz Platt (my research assistant of many years), for kindly keeping me abreast of developments appearing in the mass media.

SUMMARY

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More work remains to be done—that is the scarcely surprising conclusion to be drawn from this series of papers. Over all, I am not certain which is most impressive, how much is known, or how little is known. But it is to the latter that this Symposium is chiefly addressed, and I have tried to emphasize this in my summary.

In his Introduction, Jones states the objectives of The Society in convening this Symposium: to examine the present knowledge of the Central American biota.

Two papers, those of Challinor and Newman present overviews of the canal problem. The former discusses some of the political and diplomatic considerations which attended the excavation and operation of the present Panama Canal and points out difficulties that may precede the excavation of a new canal. In Newman's summary of the work of the National Academy of Sciences Committee on the Ecology of the Interoceanic Canal, he mentions the difficulty of making predictions based on presently available data. Partly on the basis of the Suez and Welland Canals he warns that a sea-level canal could result in undesirable biological consequences. Directions for further study and the provision of barriers to dispersal are recommended.

Two papers, those of Sheffey and Harleman, discuss physical characteristics and particularly the flow of water through the proposed sea-level canal. They leave no doubt that an unobstructed canal would constitute a wide avenue for biotic dispersal. However, both stress that tidal gates would greatly decrease the interchange of water between the two oceans and Sheffey mentions the possibility of other kinds of barriers to dispersal.

Three papers, those of Glynn, Voss, and Bullis and Klima treat ecological assemblages on both sides of the isthmus. Glynn discusses several coastal communities (coral reef, rocky intertidal, sandy beach, mangrove shores and fouling), which are particularly important as they are most likely to be affected by faunal interchange. He presents a comparative account of selected aspects of the physical environment that may play a role in shaping biotas, and he also gives general comparisons of communities. Although considerable differences exist in the physical environments and biota of the regions generally adjacent to the proposed canal mouths, Glynn feels there is insufficient information available to allow accurate prediction of the results of an interoceanic sea-level canal.

Voss describes the survey work of the University of Miami, which, early on, had realized the need for additional research on the isthmian biota. On the basis of field work centered in deeper waters than those discussed by Glynn, Voss concludes that faunal interchange would be small. He postulates considerable similarities in the two faunas and predicts that adverse affects are unlikely as the consequence of a sea-level canal. Voss nonetheless recommends additional studies, as well as the inclusion of a barrier.

Bullis and Klima describe the marine fisheries of Panama as a significant resource, both as a direct source of protein and for international exchange. The major part of the fishery is in the Pacific. Except for shrimp, the fishery resource is at present probably under-exploited. Species from several habitats are available. Shrimp from the benthic mud-bottom community are particularly important, as are onshore and offshore epipelagic species of scombroid and clupeoid fishes. Demersal species of grouper, snapper and spiny lobster are taken, as well as numerous other species.

Porter and Cheshire, treating corals and echinoids, respectively, present data on two relatively well-known groups of animals; both authors note that some taxonomic problems remain and that further exploration may reveal undescribed species. Reef-building stony corals, in particular, are well enough known so that Porter has been able to compare faunas from both sides of the isthmus. He finds them very different and suggests reasons based on historical zoogeography. For the less well-known solitary stony corals, similarities in the two faunas increase with depth. Cheshire finds exactly the opposite situation in echinoids, with a decrease in faunal similarity as depth increases. Geminate species of echinoids are discussed and suggestions are given for further research. Cheshire also presents a brief summary of knowledge of other less well-known echinoderm groups. Porter discusses his work on coral communities, the long-term continuation of which would be particularly desirable. Both echinoids and corals are examples of groups especially well-suited for continuing qualitative and quantitative monitoring. Neither Porter nor Cheshire are sanguine about the effects of the coral eating starfish Acanthaster, should it become introduced onto Caribbean reefs.

Papers by Earle on marine plants, Olsson on mollusks, Abele on decapod crustaceans, and Robins on fishes, all agree on one point, the biota is very poorly known, even on a qualitative basis. Earle suggests that the total known marine flora of 191 species for both sides of the isthmus may double, at least, with further collecting. She finds few species common to both sides, and most of these are cosmopolitan. Olsson takes an historical approach and presents an analysis of the origins of the present mollusk fauna, which he finds to be in the Atlantic; however, he estimates the Panamanian Pacific fauna to be about five times the size of the Panamanian Atlantic fauna. He suggests that the mollusks of the inlets, the shore and the mangroves, precisely the habitats most likely to be affected by a sea-level canal, are the least well-known. He concludes that a canal will have little effect. Abele reports at least 485 species of decapod crustaceans, for which he compares four kinds of marine habitats from both sides of the isthmus, as well as for freshwater. Robins divides the shore fishes into two groups, the insular, clear-water fauna which has a smaller likelihood of dispersing through a sea-level canal, and the continental fishes of more turbid waters. The latter, which are more likely to transit a canal, are not well-known taxonomically or ecologically, and Robins suggests some particular groups from this fauna for immediate attention.

Dressler reports on the Panamanian terrestrial flora and finds it poorly known; the same is true of the insects as surveyed by Weber, who suggests that further clearing of forests attendant on the excavation of a new canal would broaden the highway for the trans-isthmian dispersal of certain kinds of insects. He recommends a thorough entomological survey along the canal route. Myers finds the herpetofauna relatively well-known. He suggests that the present canal is already a barrier to dispersal and doubts that a sea-level canal would significantly increase isolation. Myers also proposes a survey as a contribution to evolutionary zoogeography. He discusses the distinct possibility of the dispersal of the venomous eastern Pacific sea snake through a sea-level canal. Both Wetmore for birds and Handley for mammals treat diverse and well-known faunas. They make the point, shared by virtually all of the contributors on terrestrial groups, that a sea-level canal is an example of modern man's increasing pressure on the environment and its biota. The same conclusion can surely be drawn from the account by Torres de Araúz of the indigenous peoples of eastern Panama.

Further to the conclusion stated at the beginning of this summary, some few other generalizations can be attempted. For marine organisms, most participants were strongly of the opinion that insufficient base-line data is available to allow predictions as to the possible effects of a sea-level canal on the plants or animals that they study. For those few groups which are relatively well-known, ecological studies are clearly in order. Information on the historical origins and the geographical relationships of various taxonomic segments of the biota are obviously of great importance in attempting to frame a rationale for chosing significant problems for further study. The nearly unanimous need for more collections and an increased level of taxonomic study lends particular significance to Cowan's consideration of curatorial problems, and some possible solutions, occasioned by extensive biological surveys.

Two contributors have emphasized the need for overall planning and coordination. Voss's vivid description of his trials and tribulations, as he hurled himself against one bureaucracy after another in search of support, lends credence to the need for a body such as the proposed Commission on the Ecology of the Interoceanic Canal described by Newman.

The Society would like to take this occasion to thank each and every author for their contributions. We also thank the Conservation Foundation and the Smithsonian Institution for their support.

Finally, we all join with Llano in saluting Waldo L. Schmitt, who has contributed mightily in thought and deed to man's urgent task of cataloging the record of life on the increasingly unstable surface of the globe.

PELAMIS PLATURUS AS A POTENTIAL COLONIZER OF THE CARIBBEAN SEA[1]

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Recently much attention has been given by the press to the question of sea snakes and to the result of their possible movement into the Caribbean in the event that a sea-level canal is constructed across the Isthmus of Panama. Two major views are expressed: one claims that the sea snake, Pelamis platurus, is a deep-water species which does not come close to shore and is not likely to spread into the Caribbean, thus, dismissing the need for further discussion of the problem; the other emphasizes great physical and psychological danger to humans on Caribbean beaches and hazards to economically important marine organisms. Occasionally, the view is expressed that a fresh water lake might act as a barrier to sea snakes.

The facts which have emerged from my studies on Pelamis platurus differ from both views. Sea snakes appear in large groups in the Gulf of Panama along surface slicks and drift lines (Kropach, 1971), indicating that they are greatly influenced by surface currents. Although Pelamis is pelagic, its distribution in the Gulf is unpredictable, and the greatest probability of encountering them is along the slicks and drift lines which may develop close to land or far out at sea. Thus, I was able to collect as many as 60 sea snakes in an hour at the Pacific entrance of the present Panama Canal. Further, in-

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Editor's note: These comments were made from the floor of the Symposium by Mr. Kropach. They are included here because there seems to be a dearth of objective evaluations of the potential effect of sea snakes in the Caribbean. Mr. Kropach collaborated with Dr. Ira Rubinoff, Smithsonian Tropical Research Institute, during the tenure of a one-year pre-doctoral study of *Pelamis.*

dividual snakes occasionally are washed ashore on local beaches, which suggests their nearshore presence. From this, the presence of snakes close to the mainland, and the fact that they are influenced by currents, it is clear that the differential tidal ranges and presumed net flow of a sea-level canal (John P. Sheffey and Donald R. F. Harleman, this symposium) will facilitate the movement of sea snakes into the Caribbean.

The tendency of the snakes to aggregate would insure the movement of large numbers of snakes, approximately half of which would be females. It has been noted that a female *Pelamis* may carry up to six embryos (Visser, 1967; personal observation). In terms of a successful colonization of the Caribbean, the implication of these facts would seem to be most clear.

Pelamis platurus, at least for short periods, appears to be a euryhaline species. Snakes have been kept in fresh water for more than nine months with no apparent ill effects. Some sea snakes of the Indian Ocean are known to frequent estuaries and may ascend 100 to 200 miles up rivers (Smith, 1926). Considering the short distance between the two oceans across the Isthmus, the near-normal salinities which would be encountered along an appreciable length of a sea-level canal, and the length of time that *Pelamis* can survive fresh water, it can be concluded that a fresh water lake will not constitute a barrier for sea snakes.

In the Gulf of Panama, *Pelamis* feed on any pelagic fish small enough to be taken, and no choice of a specific food item is discernible. Although there is probably no great effect on the Pacific fisheries, among the fish found in the stomachs of *Pelamis* were *Lutjanus, Coryphaena, Mugil,* scombrids, and carangids, all commercially important. The effects of sea snakes on similar economically important species in the Caribbean can not be estimated.

The factors controlling populations of *Pelamis* in the Pacific are not known. Predators have not been discovered in the Bay of Panama (Rubinoff and Kropach, 1970), and, if a predatory species is preying on the snake population outside the Bay, it is quite possible, indeed, probable, that such a predator will be absent from the Caribbean. This is yet another problem involved in attempting to predict the fate of *Pelamis* after an invasion of the Caribbean.

The danger of *Pelamis* to humans has been pointed out by Halstead (1970). In order to evaluate the degree of danger from a given species one should consider the potency of the snake's venom, the efficiency of its injection mechanism, and its behavior, *i.e.,* degree of aggressiveness. *Pelamis* venom is highly potent, but I have been unsuccessful in finding accounts of human fatalities from bites of *Pelamis* in Central America. Further, I am aware of six incidents of *Pelamis* bites where there was no effect, whatsoever. The *Pelamis* injection mechanism is, perhaps, not very efficient, certainly not in comparison with that of the viperine snakes. These sea snakes are very docile animals and will bite only when provoked. Panamanians of the Pacific coast neither show fear of them nor consider them to be dangerous.

In summary, *Pelamis platurus* appear to exhibit several characteristics which would enable them to invade the Caribbean through a sea-level canal. Whether they will be successful in colonizing it is a matter of speculation, but the odds are good. I feel, however, that no great danger to humans is to be expected.

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