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INVESTIGATIONS ON MESOPHOTIC CORAL ECOSYSTEMS IN CUBA (1970-1973) AND MEXICO (1983-1984)

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ABSTRACT. After a pioneering study of Jamaican coral reefs, the Cuban archipelago was the second to be surveyed by SCUBA for scleractinian corals and reef life to a depth of 90m, sampling all phenotypes. Regrettably, the published data on the mesophotic coral ecosystems (MCEs) of Cuba, collected 1970 to 1973, have been ignored. This is also true for the published data on the MCEs of the Mexican Yucatán Peninsula, collected 1983 to 1984. These two investigations described immense areas exhibiting a rich continuum of coral life, from shallow reefs into MCEs without scleractinian faunal break, and no depth-specialists species complex. Instead, a morphological changeover of three-dimensional corallum into two-dimensional corallum was observed and documented. The existing data on the Cuban and Mexican MCEs (now 45 and 34 years old, respectively) present a unique opportunity for long-term status and ecosystem trends analysis. MCEs require terminological clarification from collaborative efforts to effectively use the globally available data.

Keywords: Mesophotic coral ecosystems, Scleractinia, Cuba, Mexico.

Investigaciones sobre ecosistemas coralinos mesofóticos en Cuba (1970-1973) y México (1983-1984)

RESUMEN. Después de un estudio pionero en arrecifes de Jamaica sobre corales escleratinios y vida arrecifal, el archipiélago cubano fue el segundo que se estudió mediante buceo SCUBA a profundidades de hasta 90m, incluyendo muestras de todos los fenotipos. Infortunadamente, los datos publicados sobre ecosistemas coralinos mesofóticos (ECM), recabados entre 1970 y 1973 han sido soslayados, al igual que los datos publicados sobre los ECM de la Península de Yucatán, México, recabados entre 1983 y 1984. Ambas investigaciones describen áreas inmensas que exhiben un rico continuo de vida coralina, desde arrecifes someros hasta ECM sin ruptura en la fauna escleratinia y sin complejos de especies especialistas de profundidad. En vez de esto, se observó y documentó un reemplazamiento de formas tridimensionales de corales por formas bidimensionales. La información existente sobre ECM cubanos y mexicanos con antigüedades de 45 y 34 años, respectivamente ofrecen una oportunidad única para realizar análisis sobre estatus a largo plazo y tendencias de ecosistema. Los ECM requieren aclaración terminológica de esfuerzos de colaboración para utilizar efectivamente los datos disponibles globalmente.

Palabras clave: Sistema coralinos mesofóticos; Scleractinia, Cuba, México

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INTRODUCTION

To progress our understanding of mesophotic coral ecosystems (MCEs), we must avail ourselves of all existing relevant spatial and temporal knowledge and clarified terminology. After the exploration of Jamaican coral reefs by Thomas F. Goreau in the 1950s and 1960s (Wells, 1971), the immense Cuban coral reef system was the second on the planet to be investigated by SCUBA, examining Scleractinia life to a depth of 90m. Unfortunately, the resulting data on MCEs in Cuba, collected 1970-1973 (Zlatarski & Martínez Estalella, 1980, 1982, 2018), have been completely ignored. Unaccountably, even in their cruise work and report on Cuba, Reed *et al*. (2017) neglected the published data on MCEs. Similarly, the data collected 1983-1984 in neighboring Yucatán Peninsula, Mexico by Zlatarski (2008, with description of "mesophotic reefs," p.50) were never used, and a Final Report by Gress *et al.* (2017) was inaccurately titled "First characterization of mesophotic coral ecosystems (MCEs) in Cozumel, Mexico." The published results of the earlier Cuban and Mexican investigations contain valuable data on Scleractinia species richness, vertical distribution, qualified species diversity and the role of stony corals in the continuum of reef ecosystems in Cuba and Yucatán Peninsula, Mexico, and provide information about the borders of the upper part of mesophotic zone, coral health and the potential for long-term coral ecosystem comparisons.

Investigation in Cuba (1970-1973)

The Cuban exploration began at a time in which conventional wisdom held that the coral world disappeared in tropical waters deeper than 40m (Cousteau & Diolé, 1971). The data upended not only this understanding, but also revealed an extraordinary and surprising coral phenotypic variability, which was neglected by the conventional Caribbean Scleractinia taxonomy. Many of collected phenotypes "did not fit in the drawers" of the nominal species. Series of specimens demonstrated gradual morphological continuity between nominal species, and some coralla displayed in their different parts the characters of more than one species. This led to massive phenotypic sampling, as a first step toward reliable taxonomy. The usage of *forma* as an infraspecific category called into question the existing

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taxonomy. The conventional notion of coral species as a static unity excluded dynamism, its basic evolutionary character. The concept of phenoide as a graphic presentation of structure and dynamic of species population was introduced (Zlatarski & Martinez Estalella, 1980, 1982, 2018; Zlatarski, 2017).

Direct SCUBA day observations to 90m and sampling to 70m of 44 transects and 194 stations (Fig. 1, after Zlatarski & Martinez Estalella, 1982) resulted in the collection of 5,924 samples, 80% of which are maintained with pertinent data in Havana's Acuario Nacional (Anonymous, 2009). The taxa of each station were assigned to three categories in accordance with their abundance in the scleractinian community: present (found in locality), dominant (predominant by numbers or coverage of substratum), and highly dominant (predominant by more than half in numbers or coverage of substratum).

The boundary between shallow-water reefs and MCEs (30-40m.) was not marked by Scleractinia faunal break, nor by depth specialists species. Instead, a habitat-originated change of corallum morphology was observed, with a predominance in MCEs of platy, shingle-like and small mounds colonies. A shift of three-dimensional into two-dimensional corallum shape was evidenced (*corallum shift 3D into 2D*). Markedly, in MCEs, phenotypic corallum spectrum and the presence of bimorphic colonies were poorer. Species richness and abundance, together with vertical taxa distribution data (Figs. 2-7 after Zlatarski & Martinez Estalella, 1982; Figs. 2-4 and 7 are modified), were not indicative of a complex specific to the MCE. *Mycetophyllia*? *reesi* was the only scleractinian species observed only in the MCE, and was seldom found. Originally, this species was assigned to *Mycetophyllia* (Wells, 1973), but its lack of ridges and valleys evoked a question. Some dwellers in shallow reefs were not found in MCEs and could be considered as shallow-reef index (specialists) species. Such were: *Acropora cervicornis*, *A. palmata*, hybrid *A. prolifera*, *Favia fragum*, *Diploria labyrinthiformis*, *D. clivosa*, *D. strigosa*, *Solenastraea bournoni*, *S. hyades*, *Cladocora arbuscula*, *Phyllangia americana americana*, *Astrangia solitaria*, *Oculina diffusa*, *Oculina* spp., *Dendrogyra cylindrus*, *Eusmilia fastigiata* forma *guacanayabensis*, *Agaricia agaricites* forma *massiva*, *Siderastraea radians*, and *Tubastraea coccinea*. Their absence could be used as a suggestive sign for MCEs. Observed at a depth of 90m, an intensely red *Montastraea cavernosa* was the deepest found Scleractinia (Fig. 4). For the first time, the seamount Banco de San Antonio was visited and sampled—a location with strong current, favorable for MCE dwellers. At 28m, its top was inhabited by luxurious and diverse coral life (Fig. 7) and giant sponges, prompting expectations for impressive MCE at greater depth. In Cuba, the upper zone of the MCE varied vertically depending on geomorphology and local conditions. No epizootic phenomena were established.

Investigation in Mexico (1983-1984)

The investigation in Yucatán Peninsula, Mexico, 1983-1984, established another large Caribbean hot spot of coral and reef life. Because of this, the same sampling strategy was applied, with attention to coral variability and documentation of relative abundance as in the previous study in Cuba. Day and night SCUBA explorations were conducted from the coast to a depth of 60m, in 39 transects and 10 single stations, in a total of 141 sites and 174 stations (Fig. 8, Zlatarski, 2008). From the collected and studied 4,579 coralla, only 801 were preserved, with all pertinent data donated to Natural History Museum, Smithsonian Institution, Washington, D.C. Results of the investigation were published later (Zlatarski, 2008), but the manuscript of an atlas with 231 color pictures taken by José Manuel Castelló for scleractinian species characterizations, ecology and reef zonation was never published.

Local conditions, especially the presence of constant strong currents and the geomorphology of the Yucatán shelf, were predeterminative for MCE morphology and specificities in vertical distribution, in species richness and in abundance of Scleractinia taxa (Figs 8-14; Figs. 8, 10-14, Zlatarski, 2008). The cave-occupying azooxanthellate scleractinians at a depth of less than 4m made unreliable any comparison between numbers of zooxanthellate and azooxantellate species and their depth distribution. The steep slope and constant Gulf Stream (Yucatán current) off the west coast of the island of Cozumel favored luxuriant coral life. Spectacular mesophotic fringing reef formations between 25m and 45m, like northward "tilted coral cathedrals and castles," indicated the current's direction. After 55m, scleractinian corals were rare (Fig. 10, 11). At the steep west slope of Chinchorro Bank, to a depth of 45m, an *Agaricia lamarckiana* zone was observed (Fig. 12). At the south terrace edge of Chinchorro Bank, at 31m, colonies of *Acropora palmata* marked the deepest distribution of this species (Fig. 13). Northwest of Cayo Arenas, Gulf of Mexico, at a depth of 42m, a flat hard substratum was covered 10% by scleractinians, with *Montastraea cavernosa* dominating (Fig. 14).

The boundary between shallow coral reefs and MCEs could be delineated only loosely due to local conditions (geomorphology and currents). It was not marked by faunal break, but rather by a morphological changeover of *corallum shift 3D into 2D*. This transition was less clear in the deep fringing reefs west of Cozumel, where imposing coral reefs were constructed by coral colonies of different shapes. No MCEs index species (depth specialists)

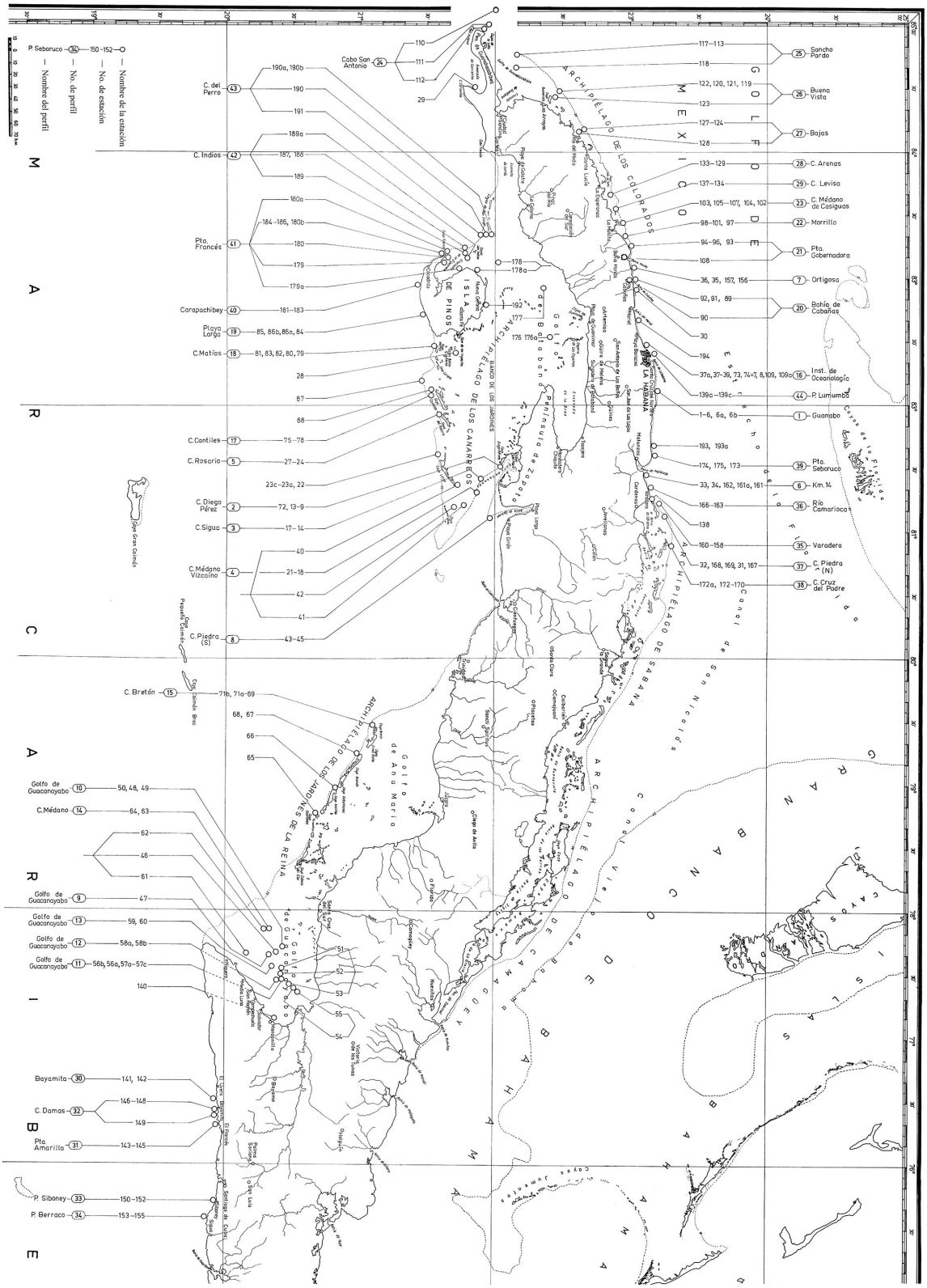


Figure 1. Map of Cuba showing studied transects and stations.

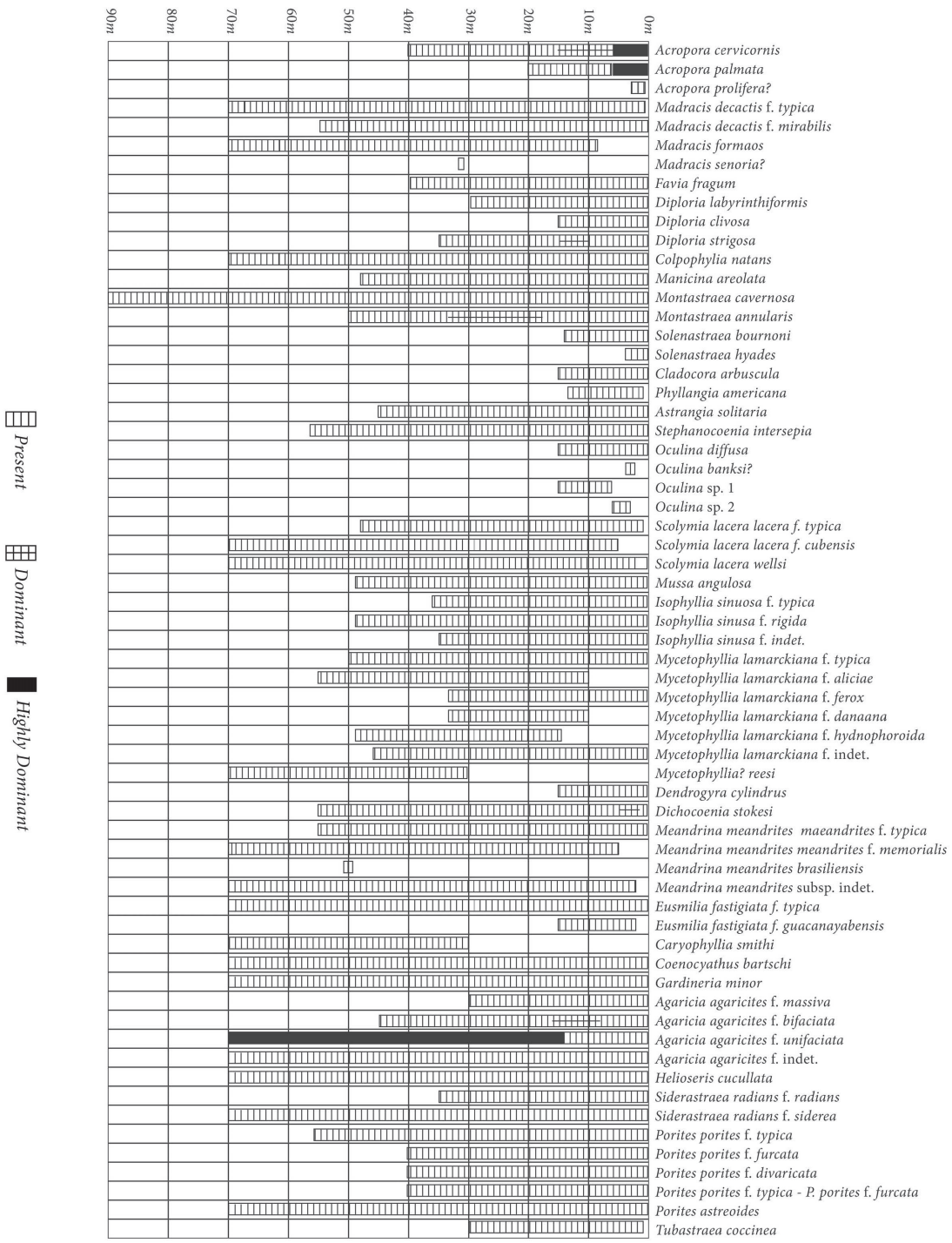


Figure 2. Bathymetric distribution of described Scleractinia.

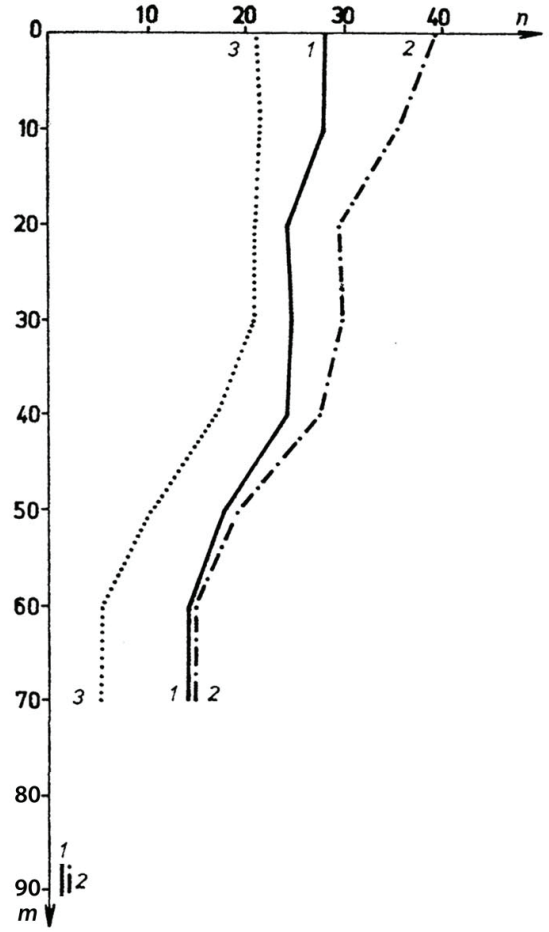


Figure 3. Distribution of number of taxa *(n*) in depth, in meters (*m*); number of genera (*1*), species (*2*) and forma (*3*).

were established. *Mycetophyllia*? *reesi,* the only scleractinian species found in Cuba solely in the mesophotic zone, was not observed. Scleractinian health did not show significant anomalies.

Later application of both investigations

The subsequent decades brought new knowledge supporting the unconventional approach to Cuban and Mexican scleractinians and led to taxonomic updating in the present Spanish version of the monograph on Cuban scleractinians (Zlatarski, 2017; Zlatarski & Martínez Estalella, 2018). The results of the investigation contributed to:

a) A holistic approach to scleractinian species (Zlatarski, 2007),

b) An integrative character of scleractinian taxonomy (Zlatarski, 2009),

c) Paleobiological perspectives on the variability and taxonomy of scleractinian corals (Zlatarski, 2010),

d) A review of past, present and future tasks in Scleractinia research (Zlatarski & Stake, 2012),

e) The proposal of a conceptual model of contemporary scleractinian research (Zlatarski, 2014),

f) The continuation of actuopaleontological studies on Cuban scleractinians and coral reefs almost half a century (Zlatarski, 2017).

A scientific documentary of the Cuban investigations was filmed in 1973 and is freely available on *YouTube*, as a two-way actuopaleontological tool for Anthropocene, in a new series called "Reefs of the Past" at https://youtu.be/ DMa-82-bIwU.

Future tasks

The existing extensive data for MCEs from Cuba and Mexico (now 45 and 34 years old, respectively) offer a rare opportunity for long-term status and trends ecosystem analysis. This should include use of the anticipated results of the recent Cuban twilight zone reef cruise (Reed *et al*., 2017). Further

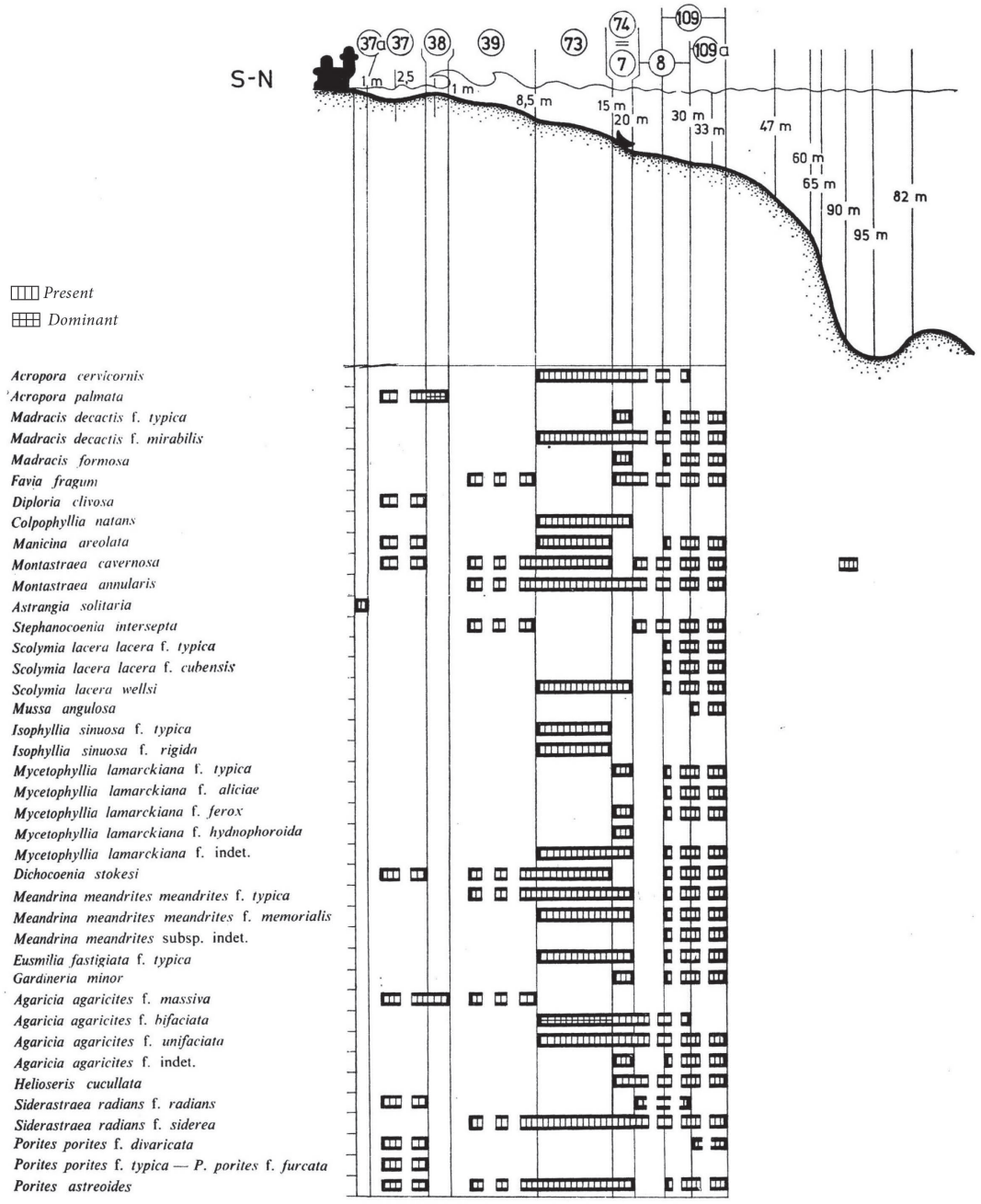


Figure 4. Transect Instituto de Oceanología.

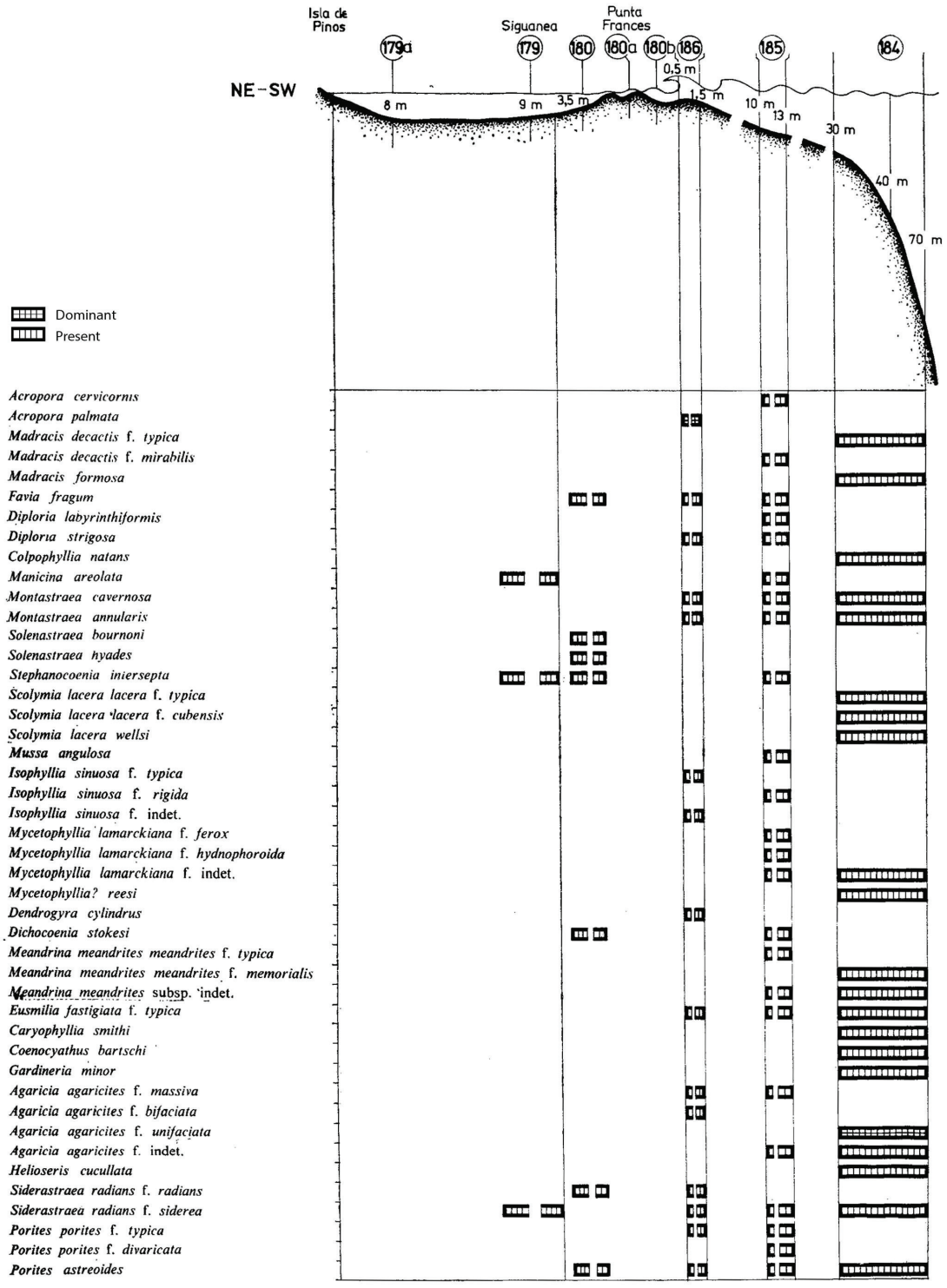


Figure 5. Transect Punta Francés.

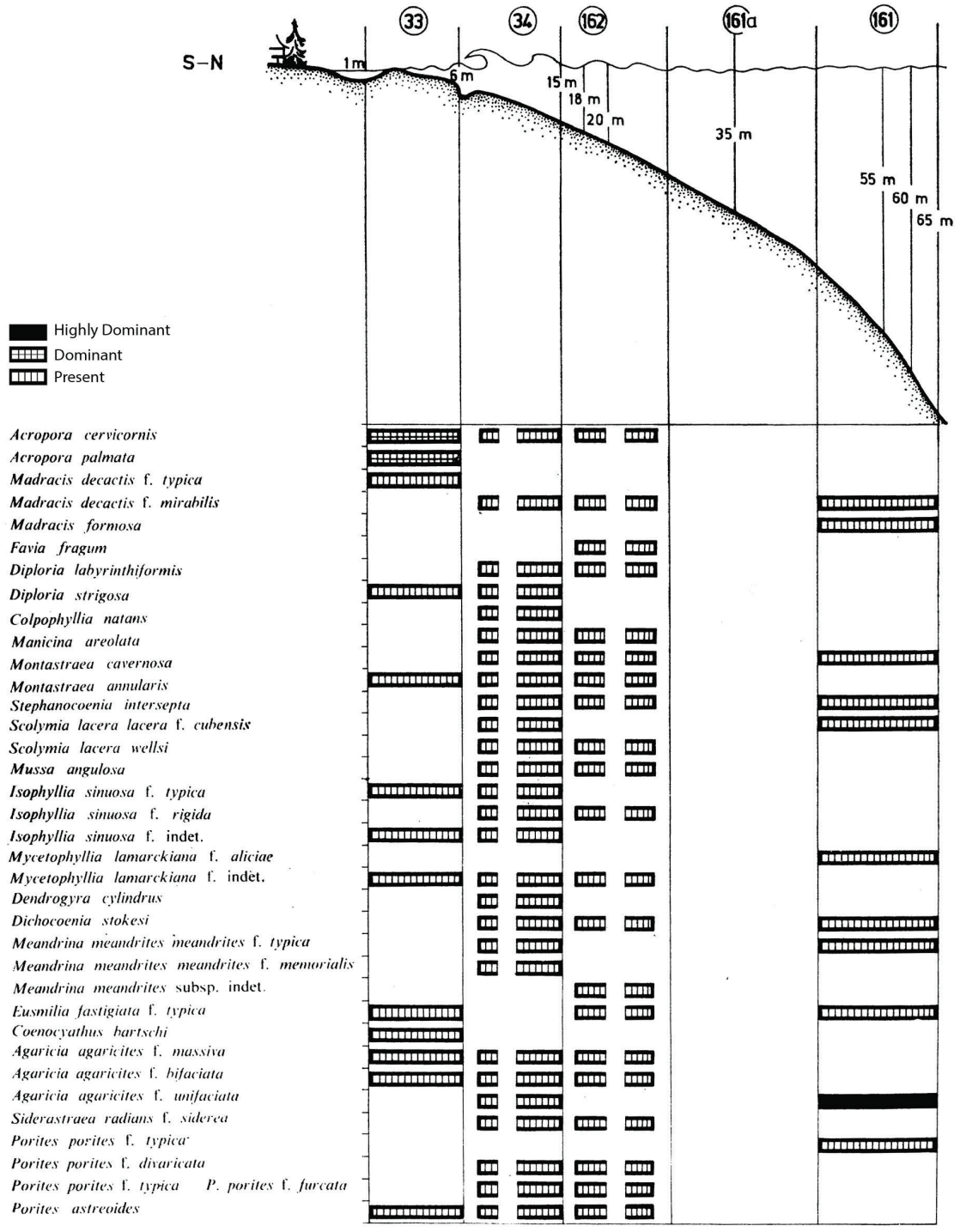


Figure 6. Transect Km 14.

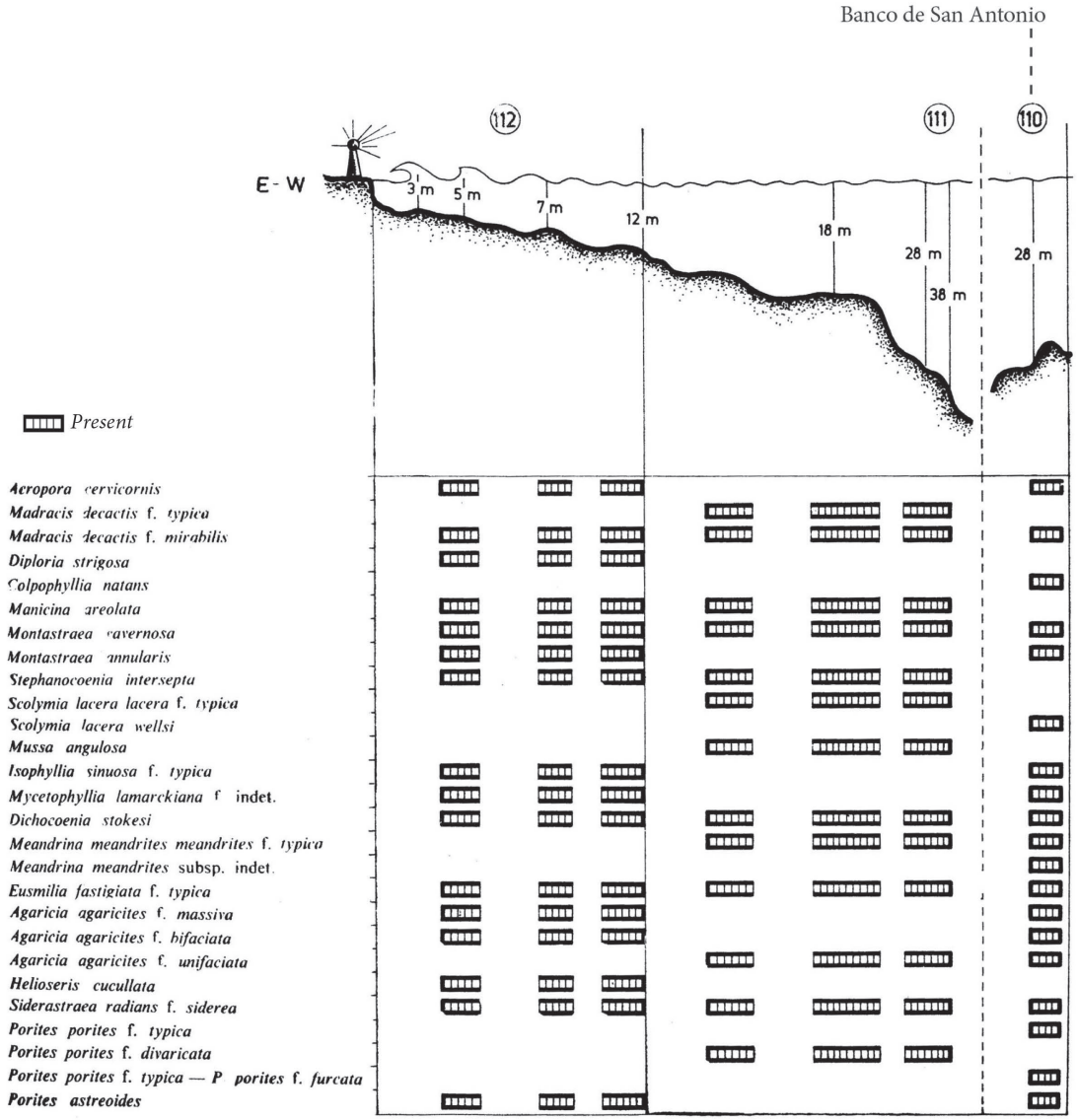


Figure 7. Transect Cabo San Antonio.

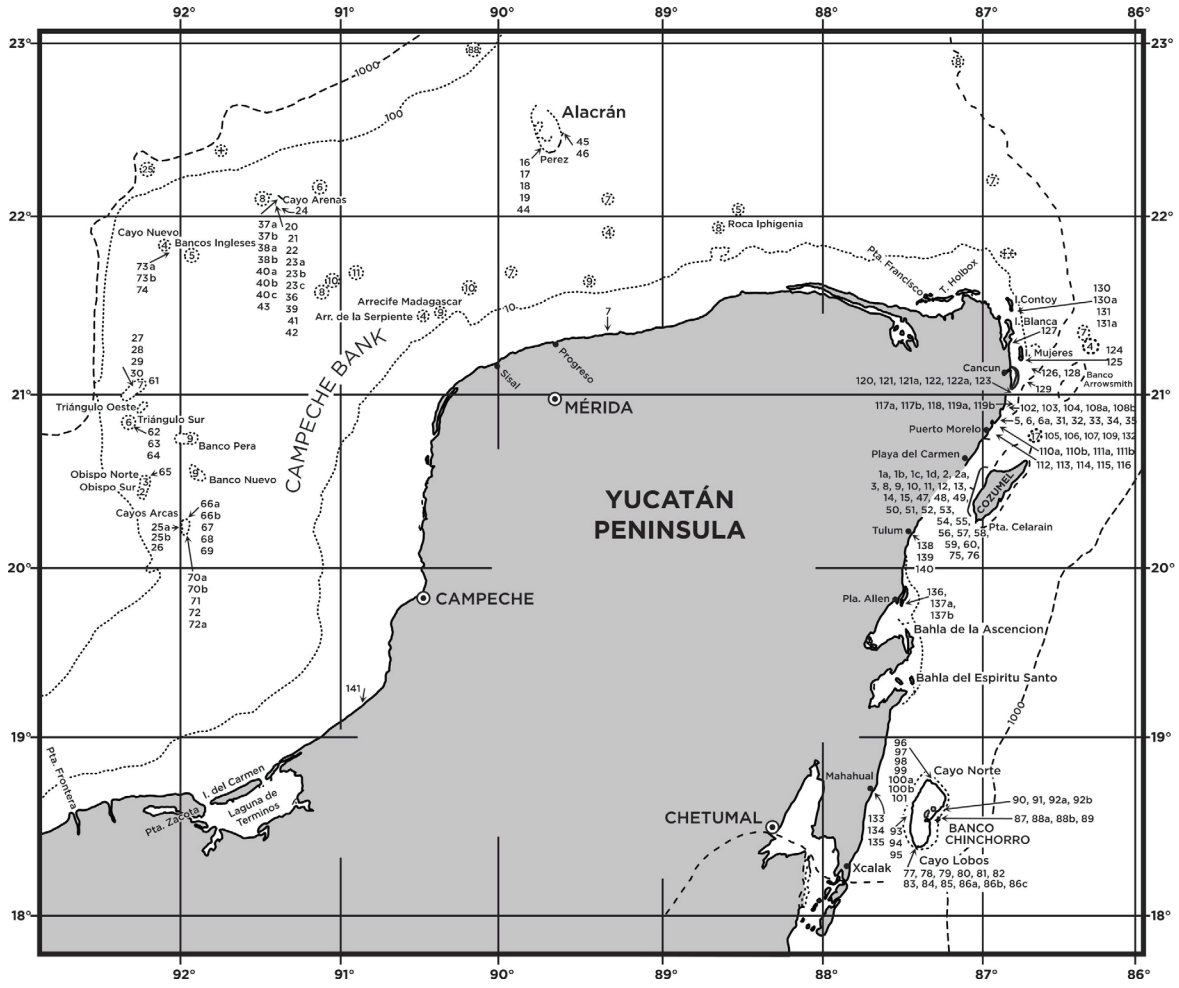


Figure 8. Map of Yucatán Peninsula, Mexico showing studied stations.

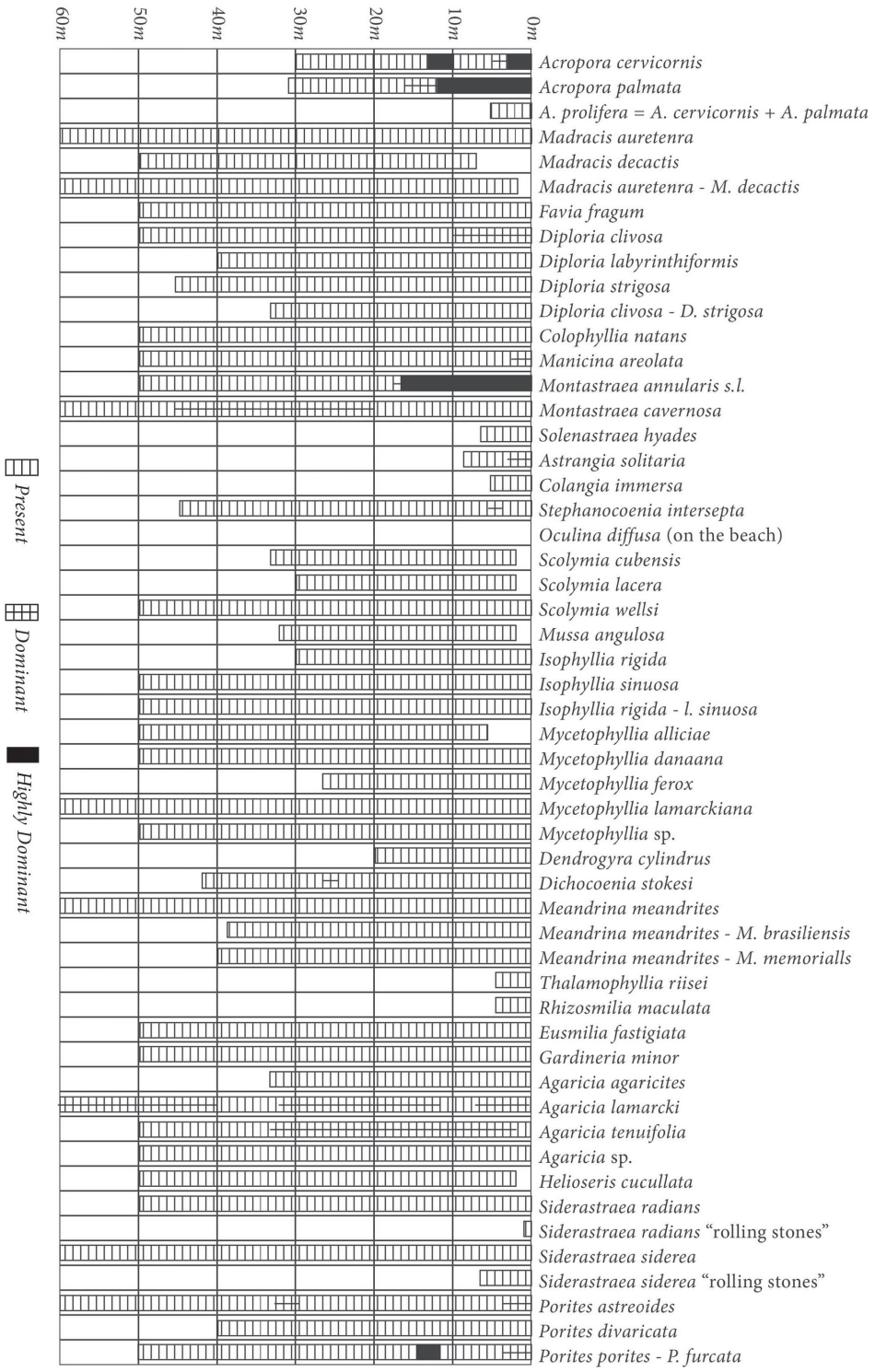
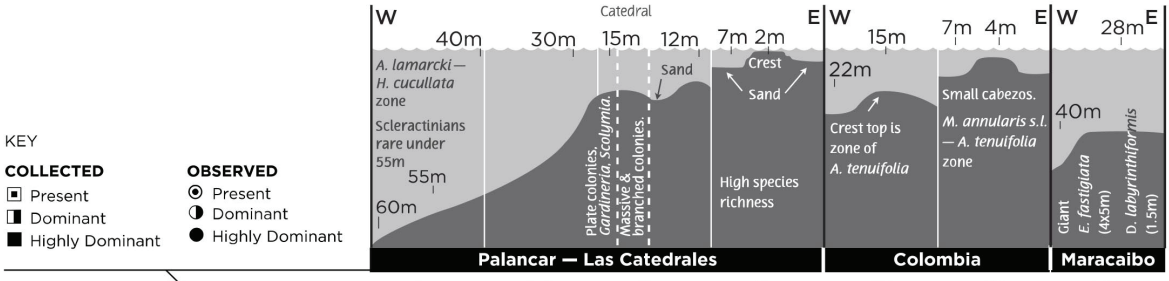
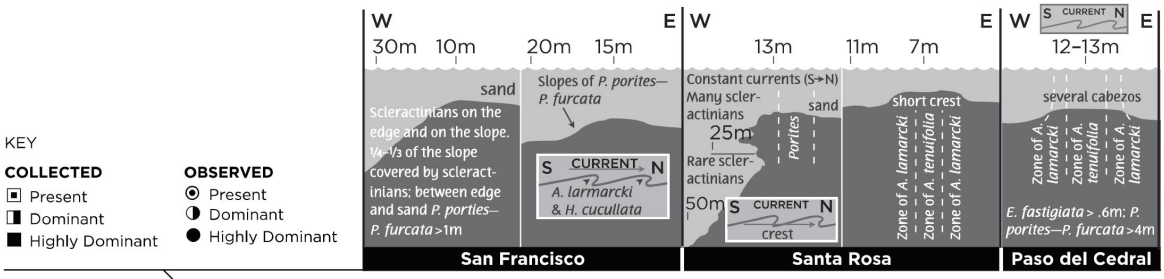


Figure 9. Bathymetric distribution of described Scleractinia.



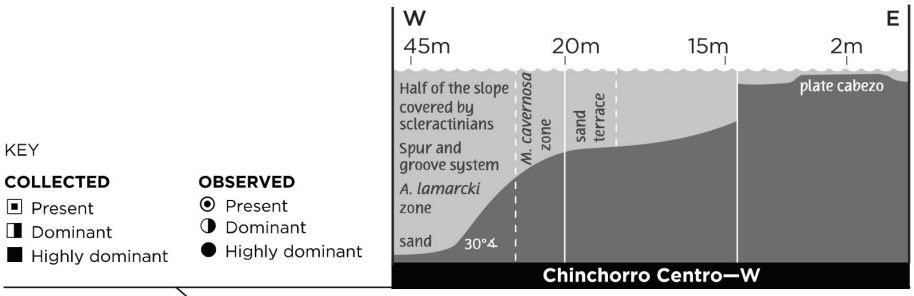
TAXON \ STATION	1c	1d	1a	1b	48	49	55
Acropora cervicornis				⦿			
Madracis auretenra	▣	▣	▣	▣	▣		▣
Madracis auretenra — M. decactis	⦿		⦿	▣		▣	
Favia fragum				▣	⦿	▣	
Diploria clivosa				▣	▣		
Diploria labyrinthiformis			⦿	⦿			▣
Diploria strigosa				▣			▣
Diploria clivosa — D. strigosa			⦿	▣			
Colpophyllia natans			▣	▣		▣	▣
Manicina areolata							▣
Montastraea annularis s. l.			▣	▣		◨	
Montastraea cavernosa	▣		⦿	▣	▣	▣	▣
Stephanocoenia intersepta				▣		⦿	▣
Scolymia lacera			▣				
Scolymia wellsi			▣			▣	⦿
Mussa angulosa			▣				
Isophyllia rigida			⦿	▣		▣	
Isophyllia sinuosa				⦿		▣	
Isophyllia rigida — I. sinuosa			▣	▣		▣	
Mycetophyllia aliciae			▣				
Mycetophyllia danaana			▣	▣		▣	
Mycetophyllia lamarckiana	▣		▣	▣	▣	▣	
Mycetophyllia sp.		▣	▣	▣	▣	▣	▣
Dichocoenia stokesi				▣	▣	▣	▣
Meandrina meandrites	▣	▣	▣	▣	▣	▣	▣
Meandrina meandrites — M. memorialis		▣					
Eusmilia fastigiata			▣	▣	▣	▣	▣
Gardineria minor			▣				
Agaricia agaricites			⦿	▣			
Agaricia lamarcki	◑		▣		▣	▣	⦿
Agaricia tenuifolia			⦿	▣	⦿◑⦿	◨	⦿
Agaricia sp.		⦿	▣	▣		▣	
Helioseris cucullata	◨	▣	⦿		▣	▣	▣
Siderastraea radians				▣		▣	
Siderastraea siderea	▣	▣	⦿	▣	▣	▣	▣
Porites astreoides		▣	▣	▣	▣	▣	▣
Porites divaricata			▣		▣	▣	▣
Porites porites — P. furcata			▣	▣	▣	▣	▣

Figure 10. Transects Cozumel (Palancar – Las Catedrales; Colombia; Maracaibo).



TAXON \ STATION	13	56	2	2a	54
Madracis auretenra	▣	▣	▣	▣	▣
Madracis decactis			◉	◉	
Favia fragum	▣	▣	▣	▣	▣
Diploria clivosa			▣		
Diploria labyrinthiformis				▣	
Diploria strigosa			▣	▣	
Diploria clivosa — D. strigosa		▣			
Colpophyllia natans			▣	▣	
Manicina areolata			▣	▣	▣
Montastaea annularis s. l.		▣	▣	▣	
Montastaea cavernosa	▣	▣	▣	▣	▣
Stephanocoenia intersepta	▣			▣	◉
Scolymia wellsi		▣	▣		▣
Isophyllia rigida	◉		▣		◉
Isophyllia sinuosa	◉		◉	▣	▣
Isophyllia rigida — I. sinuosa	▣	▣	▣	▣	▣
Mycetophyllia aliciae			▣	▣	
Mycetophyllia danaana			▣		
Mycetophyllia lamarckiana		▣	▣	▣	▣
Mycetophyllia sp.		▣	▣	▣	▣
Dichocoenia stokesi	▣	▣	▣	▣	▣
Meandrina meandrites	▣	▣	▣	▣	▣
Meandrina meandrites — M. memorialis		▣			▣
Eusmilia fastigiata	▣	▣	▣	▣	▣
Gardineria minor			◉		
Agaricia agaricites		▣			
Agaricia lamarcki	▣		▣	◑ ◑	◑ ◑
Agaricia tenuifolia	▣	▣	▣	◨	◨
Agaricia sp.	▣		▣	▣	
Helioseris cucullata	▣	▣	▣		▣ ▣
Siderastraea radians			◉	◉	▣
Siderastraea siderea	▣	▣	▣	▣	▣
Porites astreoides			▣	▣	▣
Porites divaricata	▣		▣	▣	▣
Porites porites — P. furcata	▣	▣	▣	▣	◉

Figure 11. Transects Cozumel (San Francisco; Santa Rosa; Paso del Cedral).



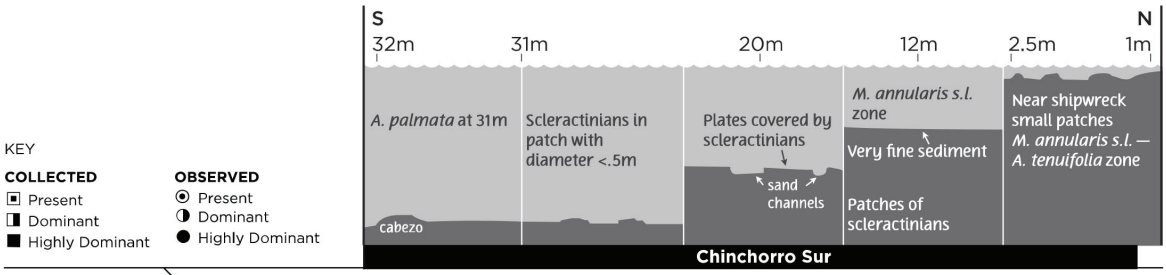
KEY

COLLECTED
- ▣ Present
- ◨ Dominant
- ■ Highly dominant

OBSERVED
- ⦿ Present
- ◑ Dominant
- ● Highly dominant

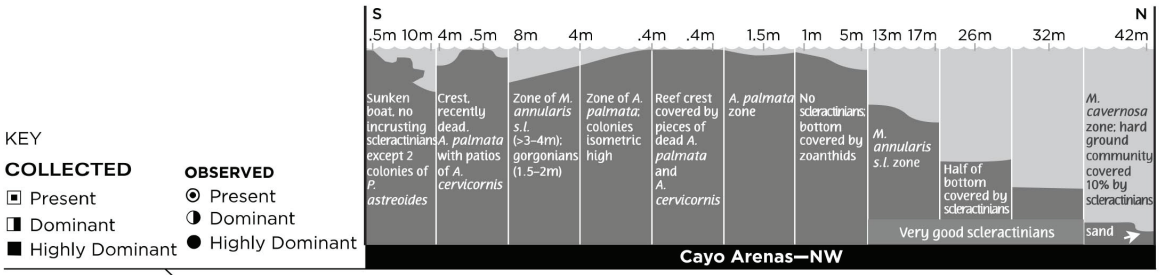
TAXON \ STATION	93	94	95
Acropora cervicornis			▣
Madracis auretenra		▣	
Madracis decactis		▣	
Madracis auretenra — M. decactis	⦿		
Favia fragum			⦿
Diploria clivosa			▣
Diploria labyrinthiformis			▣
Diploria strigosa			▣
Colpophyllia natans		⦿	
Montastraea annularis s. l.		▣	▣
Montastraea cavernosa	▣ ◨	⦿	⦿
Stephanocoenia intersepta			▣
Scolymia wellsi		▣	
Mussa angulosa		▣	
Isophyllia rigida			⦿
Isophyllia rigida — I. sinuosa			▣
Mycetophyllia aliciae	▣		
Mycetophyllia danaana		▣	
Mycetophyllia lamarckiana		▣	
Mycetophyllia sp.	▣	▣	
Dichocoenia stokesi		▣	▣
Meandrina meandrites	▣	▣	
Meandrina meandrites — M. brasiliensis		▣	
Meandrina meandrites — M. memorialis		▣	
Eusmilia fastigiata	▣	▣	
Gardineria minor		▣	
Agaricia agaricites		▣	⦿
Agaricia lamarcki	◨ ▣	▣	⦿
Agaricia tenuifolia	⦿		⦿
Agaricia sp.	▣	▣	
Helioseris cucullata	▣	▣	▣
Siderastraea siderea	▣		⦿
Porites astreoides			⦿
Porites divaricata		▣	
Porites porites — P. furcata		▣	▣

Figure 12. Transect Cinchorro Centro, West.



TAXON \ STATION	81	78	85	84	82
Acropora palmata	■				■
Madracis auretenra	■	■	■		
Madracis decactis	■			■	
Madracis auretenra — M. decactis		■			
Favia fragum			■		■
Diploria clivosa			■		
Diploria clivosa — D. strigosa					■
Colpophyllia natans	■	◉		◉	
Manicina areolata				■	
Montastraea annularis s.l.	■	■	■	◨	◨
Montastaea cavernosa	■	■	■	■	
Stephanocoenia intersepta	■	■	■		
Scolymia wellsi	■			■	
Mussa angulosa			■		
Isophyllia rigida			■		
Mycetophyllia lamarckiana		■	■	■	
Mycetophyllia sp.	■		■	■	
Dendrogyra cylindrus			■		
Dichocoenia stokesi	■		■	■	
Meandrina meandrites			■		
Meandrina meandrites — M. memorialis	■				
Eusmilia fastigiata			■	■	
Agaricia agaricites		◉		■	
Agaricia lamarcki	■	■	■		■
Agaricia tenuifolia					◨
Agaricia sp.	■	■			■
Helioseris cucullata	■				
Siderastraea siderea		■	■	■	
Porites astreoides				■	■
Porites porites — P. furcata				■	■

Figure 13. Transect Chinchorro Sur.



KEY

COLLECTED
- ▣ Present
- ◨ Dominant
- ■ Highly Dominant

OBSERVED
- ⦿ Present
- ◑ Dominant
- ● Highly Dominant

TAXON \ STATION	24	42	21	20	23c	23a	23b	22	36	39	41
Acropora cervicornis		◨	▣		◑						
Acropora palmata	▣	■	▣	■	◑	●					
A. prolifera = A. cervicornis + A. palmata		▣									
Madracis auretenra								▣	▣	▣	
Madracis decactis									▣	⦿	
Madracis auretenra — M. decactis									▣		
Favia fragum	▣		▣	▣							
Diploria clivosa	◨	▣	▣	▣				▣	▣		
Diploria labyrinthiformis			▣					▣	▣	⦿	
Diploria strigosa	◑		▣						▣	▣	
Diploria clivosa — D. strigosa		▣									
Colpophyllia natans			▣					⦿	▣	⦿	
Montastaea annularis s. l.	▣	▣	◨	▣				◨	◨	▣	
Montastaea cavernosa	▣		▣					▣	◨	▣	◨
Stephanocoenia intersepta	⦿	⦿						▣	▣	▣	▣
Scolymia wellsi			▣					⦿	▣	▣	▣
Mussa angulosa										▣	
Mycetophyllia aliciae											▣
Mycetophyllia ferox	▣							▣	▣	▣	
Mycetophyllia lamarckiana			▣					▣		▣	
Mycetophyllia sp.	▣							▣		▣	▣
Dichocoenia stokesi	▣		⦿						▣	▣	▣
Meandrina meandrites			▣						⦿		▣
Meandrina meandrites — M. memorialis									▣		
Eusmilia fastigiata								▣			
Agaricia agaricites	⦿		▣					▣			
Agaricia lamarcki	▣		▣					▣	▣		▣
Agaricia sp.		▣						▣	▣		
Siderastraea radians	▣	▣	▣						⦿		
Siderastraea siderea		▣	▣					▣	▣	▣	
Porites astreoides	▣	▣	▣	▣				▣	▣	▣	
Porites divaricata								▣		▣	
Porites porites — P. furcata		▣						▣			

Figure 14. Transect Cayo Arenas – NW.

globalization of MCE data requires terminological clarification in joint collegial efforts for efficient usage of all existing data.

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