

Gulf of Mexico Origin, Waters, and Biota

Volume 1, Biodiversity



Harte Research Institute for Gulf of Mexico Studies Series

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John W. Tunnell Jr., General Editor

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Edited by

Darryl L. Felder and

David K. Camp

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Cover: The orange-cup coral, *Tubastraea coccinea* Lesson, 1829. The beautifully delicate live polyps featured here represent a nonindigenous species of current concern, exemplifying the urgent need for the biodiversity baseline provided in this volume. Native to the Indo-Pacific region, this species has been introduced into the Western Atlantic and the Gulf of Mexico by the activities of man (Global Invasive Species Database, www.issg.org/database). Photograph by Harley Moody.

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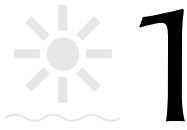
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An Introduction to Gulf of Mexico Biodiversity Assessment

Darryl L. Felder, David K. Camp, and John W. Tunnell Jr.

Assessment of natural resources is fundamental to managing their sustainable use and conservation, especially against a backdrop of ongoing global environmental change. Large-scale, species-level inventories are particularly important for understanding and managing biodiversity, but they are also extraordinarily difficult to prepare, considering the broad range of expertise required, the scope and heterogeneous quality of applicable literature, and the limited number of taxonomic specialists available to undertake compilations of this nature. The aforementioned challenges clearly apply to major baseline assessments for large geographic regions, as in the present work, but also to the ongoing monitoring of diversity on a regional scale that is essential for documentation of potential changes as they occur. In our collective research experience, focused on a diverse set of marine groups, the absence of authoritative, up-to-date, and reasonably comprehensive biodiversity treatments for marine waters of the world has proven to be a major impediment to comparative regional biotic assessments. In addition to their utility in evaluations of marine ecosystem health and biogeography, such species-level inventories are also a necessary resource in any research subdiscipline that may require a readily available portal to current knowledge regarding taxonomy, diversity, habitat restriction, and geographic distribution of marine biota. This, without question, applies to studies in marine ecology, evolutionary phylogenetics, environmental physiology, development, and dispersal, to name but a few.

As noted in the foreword to this series, its focus on the

Gulf of Mexico (hereafter abbreviated GMx) was originally framed to follow by 50 years the publication of “Bulletin 89” (Galtsoff 1954). Our present effort to compile a thorough account of the Gulf of Mexico biota was not motivated, however, by a wish to simply build on this earlier biotic account. Rather, it was to fill a contemporary need for comprehensive treatment of marine biodiversity within a region in which we had extensive first-hand experience, a highly qualified set of international colleagues to draw upon, and growing reasons for environmental concern. Given a wealth of relevant literature published since 1954, the coverage of biota for this large region at least appeared to be tractable, despite the obvious challenge that its compilation represented.

Were it not for the timely establishment of the Harte Research Institute (HRI) for Gulf of Mexico Studies, with a mission remarkably suited to our perceived needs, it is unlikely that the present work would have gone forward. The Harte Research Institute was developed under a generous endowment to support and enhance long-term sustainable use and conservation of the Gulf of Mexico, as well as to foster cooperation and collaboration within and between the United States, Mexico, and Cuba in order to achieve this mission (Tunnell and Earle 2004). Determining the total species diversity of the Gulf of Mexico Large Marine Ecosystem (LME) became an early goal of HRI in 2003 (Tunnell, Felder, and Earle 2004, Tunnell 2005). Thus, HRI and its visionary sponsors became the launching pad for the present effort, as well as other volumes to appear in this series.

Biodiversity, simply stated, is the variety of life (Reaka-Kudla 1997). The Convention on Biological Diversity (Article 2) defines biodiversity as the variability “within species, between species, and of ecosystems,” which thus embraces structural and functional variation among individuals, populations, species, communities, and ecosystems (Costello 1998). Protecting and conserving biodiversity is now viewed to be important not only by scientists but by the general public as well, with many citizens now viewing its conservation as an ethical obligation of Earth stewardship (Reaka-Kudla 1997, Costello 1998, Bouchet 2006). While public concern appears to be growing of late, it has historically ebbed and flowed. The underpinnings of public interest are diverse, in some instances rooted in histories and beliefs of native cultures, in others relating back to the checkered early history of educated European explorers who set forth by sea with blessings of church and crown. Representing the advanced cultures of their time, some of the early contributors to our knowledge of global marine diversity went forth solely to exploit, whereas others put science and technology in the context of their faith. So was said to be the case for Captain James Cook, who in quest of discoveries sought wonders that “spoke to the glory of God.” At least this was so observed by the Bishop of Whitby, when this great but controversial explorer’s discoveries were recently commemorated

in Yorkshire (Horowitz 2002), in an address that quoted lines from Psalm 107: “They that go down to the sea in ships, that do business in great waters. . . . These see the works of the Lord and His wonders in the deep.” Notwithstanding the Church’s primary interests in the subversion of pagans over the course of those explorations, the search for such wonders produced valuable early perspectives on both biotic and cultural diversity, albeit with lasting and often troubling impacts on the cultural and biological health of the regions visited. As for interests of the Crown or governments in general, the Cook expeditions also serve to reflect historical foci: Funding was driven heavily by a search for economic opportunities and intentions of laying claim to newly discovered commercial resources, this serving to justify the collection of many species new to science. Until recently there was little appreciation for just how ephemeral some of those biological and cultural resources would prove to be over an ensuing few hundred years, but a modern retracing of Cook’s voyages in popular literature (Horowitz 2002) puts the scope of that change into a historical context that resonates with environmental scientists and layman stewards of nature alike.

The case for conservation of biodiversity can be argued from economic, ecological, moral, and legal standpoints (Table 1; Costello 1998). On a global scale, the need for

Table 1. Ten economic, ecological, moral, and legal reasons why society needs to protect and manage biodiversity (modified from Costello 1998).

Economic

1. It is essential for the assimilation and recycling of wastes derived from human activity.
2. It is the source of food for humans and domestic animals.
3. It provides valuable recreational resources.
4. It contains biotechnological resources of increasing commercial importance.
5. It produces nonliving resources of commercial importance such as maerl and coral.

Ecological

6. It supports economic resources through the food chain and interaction between species.
7. It maintains local-to-global ecosystem health through its interaction with the physical and chemical environment (e.g., atmospheric carbon dioxide, oxygenation) and can buffer the world against climate change.

Moral and Ethical

8. It is generally accepted that other life forms have a right to exist, and that man has a responsibility of stewardship to protect our natural inheritance for future generations. Indeed, a review of history suggests that we can have little idea of what uses and values future generations may discover in biodiversity.
9. The production of unnecessary waste and thus pollution can be considered immoral.

Legal

10. The Convention on Biological Diversity and other laws now place a legal obligation on most countries and their citizens to protect and sustainably use biodiversity. This is essential because some people will either not have the ability or willingness to understand the importance of biodiversity, or their short-term selfishness and greed will result in their activities reducing biodiversity.
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action at the international level is encouraged by the (Rio) Convention on Biological Diversity (Costello 1998), which urges efforts to:

- Develop national plans for biodiversity management
- Use biodiversity in environmental assessments for planning and development
- Manage resource harvesting in ways that do not diminish biodiversity
- Identify, monitor, legally protect, conserve, and restore biodiversity
- Provide education and training in biodiversity
- Conduct research in biodiversity
- Establish biodiversity-rich protected areas
- Take measures to control alien and genetically modified species

Scientific and public concern is increasing over the continued loss and decline of biodiversity due to over-exploitation and the degradation of habitats by humans (Reaka-Kudla 1997), as is more recent social anxiety over global climate change and unsustainable development (Bouchet 2006). Yet, accurate accounts of biodiversity are lacking on most geographic scales. Twenty-five years ago scientists believed that there were about 1.6 million described species and that these represented about half of the biota on Earth. Today there are about 1.7 to 1.8 million described species, but new findings with modern technological approaches suggest that these represent only a fraction of the potential 10 to 100 million or more that remain to be discovered (Bouchet 2006). Estimates of the total number of bacterial species alone range from millions to hundreds of millions, with the number of yet-to-be-discovered marine prokaryotic microbes potentially enormous (Pedrós-Alió 2007). Perhaps comparable to the taxonomic diversity of marine prokaryotes are a tremendous variety of extremely small, newly discovered marine eukaryotic cells, many of which comprise components of marine picoplankton and some perhaps deserving treatment as new divisions or phyla (Not et al. 2007). Without question, the recent realization of both diversity and abundance among these groups has grown from advancements in molecular approaches. Continued application of these tools is rapidly bringing the diversity of marine microbes into focus at the same time it serves to clarify the diversity and relationships of higher eukaryotic forms.

As the scientific community has refocused on assessment of marine biodiversity, species inventorying and its taxonomic underpinnings have evolved from under-

valued and somewhat “neglected scientific activity to a timely cutting-edge mega-science” (Bouchet 2006, 33). The new priority allocated to these activities is rooted in concerns over global climate change, declining global biodiversity, overexploitation of living resources, habitat destruction, and other unsustainable practices (Reaka-Kudla 1997, Bouchet 2006). If we are to follow a new paradigm of informed regional focus and ecosystem-based management, as promulgated by the U.S. Commission on Ocean Policy (USCOP 2004), the President’s Ocean Action Plan (Council On Environmental Quality [CEQ] 2004), and the Ocean Research Priorities Plan and Implementation Strategy (Joint Subcommittee on Ocean Science and Technology [JSOST] 2007), we must first prove our ability to conduct authoritative species-level marine inventories.

Fundamental to all such efforts is the inventory of species present within an ecosystem, no matter its size and thus the scope of the undertaking. A complete list or inventory of species subsequently allows scientists to ask questions regarding the long-term sustainable use and conservation of biodiversity. Such questions might include:

- How many species reside in the defined area?
- How are those species distributed in and outside the area, and are there diversity hotspots?
- What depths and habitats do they occupy?
- What is the pertinent ecological and taxonomic literature?
- Who are knowledgeable experts?
- Are any species endangered, threatened, invasive, extinct, or endemic?
- Is diversity changing in the region, and if so, how and why?
- Where should future efforts focus—taxonomically, geographically?

All of these questions are best addressed by first establishing an updated all-taxa inventory for marine species. The purpose of the present project is to do exactly this for the Gulf of Mexico, while providing at least some fundamental accompanying data on the habitat, biology, depth range, distribution, systematics, and the sources of records for each species, to the extent possible in such a massive undertaking.

Regional marine species inventories have been previously undertaken for some other areas of the world (Table 2), although these vary in scope and taxonomic coverage. The largest and most complete inventories

Table 2. Selected regional marine species inventories comparing total number of species and size of geographic area covered.

Geographic region	Number species	Geographic size	Source
Europe	26,927	21.8 million km ²	Costello, Emblow, and White (2001)
Hawaii	6,150	2.2 million km ²	Eldredge (2006)
Gulf of Mexico	15,419	1.5 million km ²	Present work (2009)
South Africa	10,836	576,000 km ²	Gibbons (1999)
China	20,000+	ND	Huang (2001)
Guam	6172	ND	Paulay (2003)

ND = No data.

include those for Europe (Costello, Emblow, and White 2001), China (Huang 2001), Hawaii (Allison and Miller 2000, Eldredge and Evenhuis 2003, Eldredge 2006), and South Africa (Gibbons 1999). Smaller geographic studies with relatively comprehensive taxonomic coverage include Bermuda (Sterrer 1998), Guam (Pauley 2003), and Cuba (Claro 2006). While none of these can be considered exhaustive accounts, they do provide some group-by-group baseline assessments against which to measure our present effort and also allow comparisons to world marine biodiversity estimates (Table 3).

The Approach

From the outset, we realized what could be asked of the largely volunteer contributors to this volume must be limited, both to keep the task manageable and for it to result in a document of publishable length. Beyond that we were also aware of the need to enforce, to the extent possible, standards of uniformity among the varied contributors. To this end, a rather detailed set of guidelines and required formats were created. Some elements, like defining clear limits to what we considered waters of the Gulf of Mexico, were discussed and agreed upon following an early meeting of invited contributors at a State of Knowledge Workshop, hosted by HRI in October 2003.

For purposes of this volume, biota of the Gulf of Mexico (Figure 1) was defined as that documented to occur in marine habitats, coastal waters, and tidal wetlands west of Cabo Catoche, Quintana Roo, Mexico (21°33'N, 87°00'W), that in waters north of a line from Cabo Catoche, Mexico, to Cabo de San Antonio, Cuba (21°51'N, 84°57'W), that from coastal waters and tidal wetlands between Cabo de San Antonio and Punta Hicacos, Cuba (23°12'N, 81°08'W), and that from waters and tidal wetlands of the Florida Straits and Florida Keys on or

west of a line from Punta Hicacos, Cuba, to the vicinity of Key Largo, Florida (25°06'N, 80°26'W). This delineation thus included all marine waters and tidal wetlands extending to the eastern extreme of Florida Bay. It excluded Cay Sal Bank as well as the extensive system of islands and estuaries east of Punta Hicacos, Cuba.

Except for a closing chapter that deals with an overview of biogeography, the chapters in this volume treat phylogenetically defined sets of species (usually at the order, class, or phylum level). We sought to limit information entries for each species to one or two lines in a checklist table, which constitutes the bulk of most chapters. In each case, chapter titles define the taxonomic coverage of the checklist table, be it an entire phylum or some component group thereof. In each case, the checklist table is preceded by a short introduction that briefly defines the group under treatment, provides a tabular quantitative overview of the group's composition in the Gulf of Mexico, reviews the overall history of major works bearing on the group in this region, explains any departures from the protocol of other chapters in the volume, and defines abbreviations and other conventions used in the checklist. Within this introduction, full author and date citations are used for reference to literature.

The checklist itself consists of columns rigidly defined in width, limiting the number of printed characters that can be used in a single line. The first (left-hand) column is labeled Taxon and typically lists the species name with the authority and date for that name, with as much consistency in format between chapters as could be imposed upon contributors accustomed to varied styles. Even for this column, allowances were made to accommodate deeply rooted traditions for specialists working on some groups. Authors were asked to restrict taxa listed in this column to those documented to occur within our defined boundaries of the Gulf of Mexico by credible publication, archived museum specimen, or other authoritative source

Table 3. Compared assessments of large-scale/regional marine biodiversity, represented as number of described species by phylum.

Taxon	Gulf of Mexico (present work)	Europe (Costello et al. 2006)	Hawaii (Eldridge 2006)	South Africa (Gibbons et al. 1999)	Estimated worldwide (Bouchet 2006)
Bacteria	UD				4800
Cyanophyta/Cyanobacteria	45		58		1000
Ciliophora	574				
Radiolaria	NL				550
Fungi	54				500
Chlorophyta	195				2500
Foraminifera	951	1167			10,000
Bacillariophyta	948				5000
Phaeophyta	86				1600
Rhodophyta	392				6200
Plantae	380				
Dinoflagellates	644				
Porifera	339	1640	122	289	5500
Placozoa	UD				
Cnidaria	792	1224	412	842	9795
Ctenophora	18	38	8	11	166
Platyhelminthes	705	2398	676	28	15,000
Dicyemida/Rhombozoa	7				82
Orthonectida	UD				24
Nemertea	42	478	49	17	1180–1230
Rotifera	23	139	3		50
Gastrotricha	42	240			390–400
Kinorhyncha	2	41	1	1	130
Nematoda	190	1837		338	12,000
Nematomorpha	UD	3	2		5
Acanthocephala	33	67	5		600
Entoprocta	2	45	2	6	165–170
Gnathostomulida	19		8		97
Priapulida	1		1	1	8
Loricifera	UD				18
Cycliophora	NL				1
Sipuncula	27	44	14	47	144
Echiura	7		6	21	176
Annelida	866	1848	324	766	12,000
Pogonophora	UD	23	2	1	148
Tardigrada	14	76	33		212
Crustacea	2579	7082	1320	2333	44,950
Chelicerata (nonarachnid)	59	146	15	101	2267
Mollusca	2455	3353	1294	3062	52,525
Phoronida	3	9	5		10
Bryozoa/Ectoprocta	266	724	168		5700
Brachiopoda	26	18	3	31	550
Echinodermata	522	648	309	410	7000
Chaetognatha	24	42	9	28	121
Hemichordata	5	17	3	11	106
Urochordata	102	393	74	220	4900
Cephalochordata	5	2	3	1	32
Vertebrata	[1975]	[1478]	[1221]	[2271]	[16,585]
Pisces	1541	1349	1197	2000	16,475
Reptilia	9	5		1	
Aves	395	74		222	
Mammalia	30	50	24	43	110
Total	15,419	26,927	6,150	10,836	224,787

NL = Not listed in comparable grouping; UD = Listed in work but number undetermined to date; [] = Sum of vertebrate constituent groups.

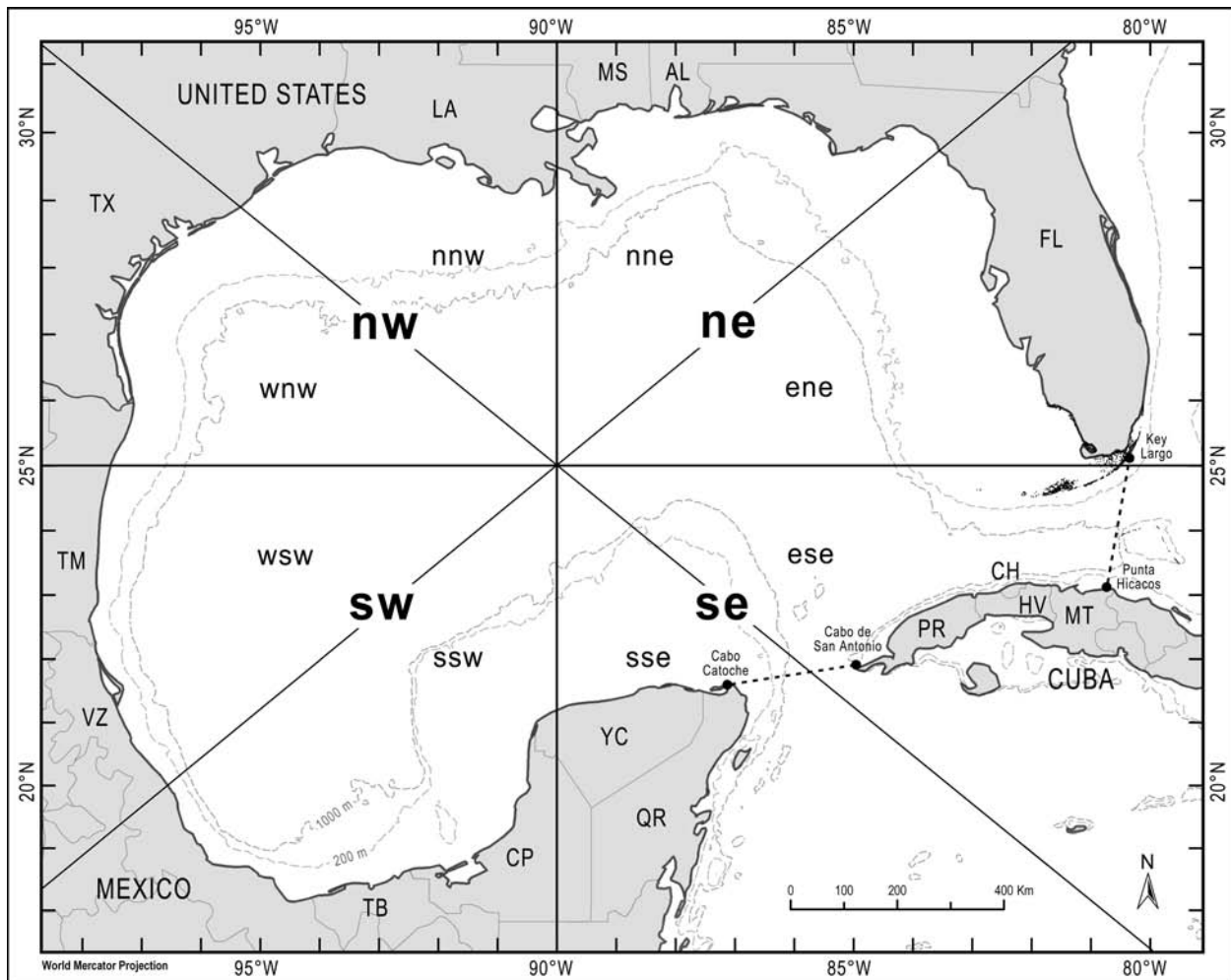


Figure 1. The Gulf of Mexico, delimiting the geographic boundaries considered in this work. Abbreviations for the states (counterclockwise) from Florida: FL = Florida, AL = Alabama, MS = Mississippi, LA = Louisiana, TX = Texas, TM = Tamaulipas, VZ = Veracruz, TB = Tabasco, CP = Campeche, YC = Yucatán, QR = Quintana Roo, PR = Pinar del Rio, CH = Ciudad de la Habana, HV = La Habana, MT = Matanzas. Map by Fabio Moretzsohn.

of documentation. Authors were encouraged to update to current taxonomy, but were left to make their own experienced decisions regarding the adoption or rejection of any controversial revisions or records.

Ideally, columns to the right of Taxon are successively labeled Habitat-Biology, Depth (in meters), Overall geographic range, GMx range, and References/Endnotes. Because of restricted column widths, contents depend heavily on abbreviations, all of which should be defined in closing paragraphs of the introduction to each chapter. Given limited space for printed characters, each of these columns is limited in the level of detail furnished. Depths are usually stated as a range, but may be presented either in italic type (depth range as known over the entire world distribution) or in roman type (depth

range as known within specifically the Gulf of Mexico). Indicators of habitat-biology are somewhat generalized, picked from defined sets of abbreviations. Global distributions are likewise generalized in most instances, rather than precise, and often indicated by abbreviations. Distributions within the Gulf of Mexico are shown by listing of abbreviations for up to 8 sectors of the Gulf (Figure 1), thus indicating in only broad terms the geographical distributions for known records, without implying any biogeographic significance in making these sector assignments. In the course of determining which localities occur within each of these sectors, close calls were left to the authors and no corrections were required for curvature of the Earth or other minor errors inherent to sector delineation in the map projection.

The final (right-hand) column is of key importance in many chapters, providing essential references that serve to document the taxonomic treatment for each entry, as well as information sources concerning biology, habitat, and distributions for that entry. In most cases, the taxon entry in the first column is justified by the information presented here. Published records are in general supported by the references listed, while museum catalog numbers, other documentation of record sources, and taxonomic interpretations are presented as endnotes. References are here listed numerically in italic type, correlating to numbered references in the alphabetical list of literature cited that follows the introduction of each chapter. Endnotes, appearing here in superscript roman type, refer the reader to explanations regarding taxonomic issues, previously unpublished records, unresolved controversies, and a host of other possible subjects. While the endnotes are usually written in abbreviated style, literature may also be cited within endnotes, by author and date, as in the introduction. For some chapters, these endnotes offer critically important background information and may comprise a total text that rivals the references section or the checklist itself in length.

Having stated this, it should be noted that some exceptions to this format were allowed on a case-by-case basis. One or more columns may have been dropped where considered illogical (as for depth in the case of marine avifauna) or where there was wholesale absence of information for certain categories of data (several columns for microbes). Likewise, some parasitic groups required special allowances, as simultaneous treatments of host species could not be avoided. In each case, such departures from the standard format are explained in the respective chapter introductions.

While every attempt was made to enforce uniform standards, it is undeniable that the authors contributing to this volume have varied in the degree to which they have questioned and culled records, adopted controversial systematic revisions, or included (with endnote documentation) previously unpublished records. We accept this as an unavoidable limitation of the overall effort, imposed by the way in which practice varies between taxonomic specialties, the varied personalities of the authorities mustered to join this effort, and—ultimately—the need for the editors to bring this effort to a timely conclusion. The passage of time alone has in the end proven to be our greatest nemesis on many fronts, limiting our efforts to impose further standardization for purposes of the present treatment.

Time has also driven us to ultimately abandon our envisioned ideal of full and uniform coverage of marine biotic groups in the Gulf of Mexico, an objective that we nonetheless closely approached. While progress was made early toward filling the gaps that at this point remain, a few of the originally chosen authors either abandoned efforts or ultimately exceeded our ability to grant further time extensions for manuscript submissions or revisions. In some cases, we were able to enlist alternate authors to provide at least an abbreviated treatment with a list of references, but this was not true in all cases. Yet more time extensions to bring full coverage of additional groups into the present volume would have only further eroded the value of chapters submitted months ago by other authors in accord with deadlines, so we opted to limit losses and move forward.

Among the gaps in coverage are a few apparently minor groups for which we are personally aware of only unpublished or pending reports from the Gulf of Mexico, some of which cannot yet be assigned with certainty to known genera or species. This, for example, is the case with rare specimens that appear to represent pterobranchian hemichordates and the nectonematoidean marine nematomorphs. For comparatively low-diversity groups like pentastomid parasites, marine oligochaetes, and marine cladoceran crustaceans, limited records are available in literature, but no authority could be found to undertake a Gulf-wide treatment. In the case of freshwater nematomorph worms, stages that parasitize insects are periodically released into ephemeral freshwaters of tidal shorelines along the Gulf of Mexico, but to include parasites of insects was illogical, as we were unable to include the host insects themselves. Clearly, insects and some arachnids loom large as constituents of coastal wetland assemblages, but with only very rare representation in high-salinity aquatic habitats. As groups that are primarily terrestrial and freshwater in adaptation but that do range widely into upper estuaries and wetlands, or which may migrate or be otherwise transported on winds well out to sea, it was extremely difficult to delimit which were and were not associated with the Gulf of Mexico. In the end, no qualified contributor was found to take them on. Their omission is in no sense intended to dismiss the obvious importance of flies, ants, beetles, moths, butterflies, bugs, grasshoppers, spiders, mites, and other of these generally terrestrial groups living throughout Gulf of Mexico coastal environments, some as parasites on other organisms we have treated, and it requires that corrections be made to the biodiversity counts that we provide.

Certainly of no less magnitude in diversity, the parasitic nematodes also have not been covered, again due to a lack of willing contributors. In the opinion of those approached to treat this group, the limited state of knowledge and the massive work yet to be done in the Gulf of Mexico region made coverage of this group impractical for the present treatment. The same was said of parasitic copepods, despite the existence of a substantial literature base. There are also a number of groups historically treated as protists or fungi for which we could not include coverage, some of these encompassing even a few high-profile pathogenic taxa, such as those now treated as the Mesomycetozoa, that were not encompassed in the coverage of the following chapters. While definitely known to occur in the Gulf of Mexico (Blaylock, Bullard, and Whipps 2004), the remarkable Myxozoa is a unique group that falls through phylogenetic cracks at present (Jiménez-Guri et al. 2007); current evidence indicates them to be of cnidarian affinity, basically being medusozoan worms. Earlier concepts of the Protista encompassed yet other higher taxa that our treatment has omitted, some of these all but lost in recent revisions of higher classification. Notable among them are microsporideans, now placed among the pathogenic fungi, and other groups treated historically among sporozoans or other protistan phyla, some being of major significance as pathogens in marine and estuarine waters of the Gulf of Mexico (Overstreet 1978). Myriad groups of symbiotic and free-living protists remain subjects of intensive study, and future account must be taken of their diversity along with that of untold numbers of prokaryotes, the latter of which we can only touch upon superficially in the present treatment.

In terms of higher groups, even coverage of vertebrates has not encompassed many species of fishes, reptiles, amphibians, birds, and mammals that occupy coastal, tidally influenced wetlands of the Gulf of Mexico, despite some authors doing so in the course of covering other taxonomic groups. For anyone familiar with these habitats, it is readily obvious that there is no clear demarcation to separate widely ranging terrestrial and freshwater vertebrate populations from those that occasionally or routinely occupy coastal brackish waters and wetlands. The same could actually be said for a number of primarily inland plants as well, just as for our earlier mention of insects and arachnids. For the present treatment, we have made no concerted attempt to fully account for the diversity of this biota, and must call attention to the substantial diversity that it may represent.

Because submission dates and completion dates have

varied chapter by chapter, as indicated after the references section of each chapter, users of this volume should not hold authors accountable for recent literature of which they could not have been aware at the time their chapter was completed. In our original charge to the authors, we requested that treatments be current through 15 October 2004. Many if not most contributors have made updates on the basis of at least some publications since that date, usually in the course of revising chapters to accommodate editorial recommendations, but none have been required to do so.

Content Overview

This work encompasses 79 chapters, prepared by a total of 140 contributors representing 80 institutions in 15 countries. These chapters provide an inventory of about 15,419 species distributed among over 40 phyla inhabiting the Gulf of Mexico as we define it. We say “about” this many, as there clearly remains much question as to how we might best count species among some groups—for example, such groups as genetically defined strains of microbes. From species counts for each of the systematic subdivisions that we have adopted in this work (Tables 3 and 4), and our estimates of species numbers for the groups we have not included (assuming those to be numerically dominated by insects and nematodes that occupy Gulf of Mexico habitats), we deduce that the present inventory covers roughly 80% to 85% of the known (described) Gulf eukaryotic taxa. For multicellular eukaryotes (macrobiota), we can only speculate how many additional species remain to be discovered, either as undescribed taxa or yet-to-be-documented Gulf occurrences of known species. Having a grasp of undescribed species in our own laboratories and those of selected colleagues, we roughly estimate that our present coverage of Gulf of Mexico macrobiota is no better than 80% of what actually exists, with this estimate varying widely across phylogenetic groups. Certainly, higher percentages of large and historically well-sampled macrobiota may be known for the Gulf, but far less is known of small, rare, symbiotic or cryptic groups, especially those that are taxonomically problematic. There are especially large numbers of Gulf of Mexico nematodes, polychaetes, copepods, and amphipods yet to be named. Furthermore, it is likely that our coverage encompasses only a small percentage of what will eventually be found to comprise the prokaryotic and eukaryotic microbial assemblages of the Gulf of Mexico, and that these species will massively out-

Table 4. Compared species numbers by phylum in Bulletin 89 (Galtsoff 1954) and the present work, including endemic* and nonindigenous species, where known.

Taxon	All species (Galtsoff 1954)	All species (present work)	Endemic* species (present work)	Nonindigenous species (present work)
Viruses	NL	UD		
Bacteria	6	UD		
Cyanophyta/Cyanobacteria	4	45		
Ciliophora	52	574		
Sarcomastigophora	24	NL		
Fungi	NL	54	1	
Chlorophyta	30	195		
Foraminifera	160	951	35	
Bacillariophyta	31 (500)	948		
Phaeophyta	20	86		
Rhodophyta	28	392	9	
Plantae	111	380	7	33
Dinoflagellates	24 (36)	644		
Porifera	13	339	109	
Cnidaria	440	792	62	94
Ctenophora	11	18		
Platyhelminthes	300	705	191	
Dicyemida/Rhombzoa	NL	7	4	
Orthonectida	NL	UD		
Nemertea	17	42	10	
Rotifera	NL	23		
Gastrotricha	NL	42	7	
Kinorhyncha	NL	2	1	
Nematoda	75	190	126	
Nematomorpha	NL	UD		
Acanthocephala	7	33	8	
Entoprocta	NL	2		
Gnathostomulida	NL	19	2	
Priapula	NL	1		
Loricifera	NL	UD		
Sipuncula	11	27		
Echiura	1	7	4	
Annelida	59	866	120	181
Pogonophora	NL	UD		
Tardigrada	1	14	1	
Arthropoda**	166	2638	388	20
Mollusca	125	2455	257	11
Phoronida	NL	3		
Bryozoa/Ectoprocta	(170)	266	55	
Brachiopoda	16	26		
Echinodermata	448	522	31	
Chaetognatha	13	24	2	
Hemichordata	3	5		
Chordata	248	2082	81	2
Total	2444 (706)	15,419	1511	341

Note: NL = Not listed in comparable grouping; () = Number species mentioned but not listed by name; UD = Listed in work but number undetermined to date.

*As here listed, these are potentially endemic species presently known from only the Gulf of Mexico; additional collecting may eventually document their wider distribution.

**Sum of Crustacea, Pycnogonida, and Merostomata, thus excluding insects and arachnids.

number macrobiotic species once their diversity is fully appreciated.

This effort has been truly multinational, with the contributing authors being based in the following countries (by number from each): United States (90), Mexico (31), Cuba (3), Canada (2), Denmark (2), Norway (2), Russia (2), Argentina (1), Australia (1), Bermuda (1), Chile (1), The Netherlands (1), New Zealand (1), Spain (1), United Kingdom (1). It is remarkable to note that, while no Mexican authors were included as contributors to Bulletin 89 (Galtsoff 1954), 31 were authors on chapters in the present volume. Without question, knowledge of marine biota in Mexican waters has improved more dramatically over the last few decades than that for any other region of the Gulf of Mexico, and a Mexico-based corps of expertise is now essential to studies of biodiversity in the entire Gulf region. Similarly, colleagues in Cuba have contributed markedly to this effort, even though a comparatively small region of Cuban waters is included in the Gulf of Mexico proper.

While we clearly intended for this volume to serve as a 50-year update to Bulletin 89, it is important that readers regard it as a 50-year update of the knowledge base for the biota, and not an authoritative documentation of changes that may have taken place in the composition, abundance, and distribution of biota since 1954. In fact, taken too casually, the listings themselves could actually obfuscate such changes, since the compiled records of occurrences include those from well before 1954, sometimes going back to the earliest credible records from the Gulf. For some such records, there may have been no subsequent evidence of the organism's occurrence in the Gulf of Mexico, and it is even plausible that a few may no longer occur in the geographic region we have defined. However, proving absence is extremely difficult for most groups of organisms that we have treated, so we can only state that previous reports give reasonable expectation for the presence of some lesser-known organisms that may be here reported. In many cases, references to literature may provide a means to actually date the record upon which listing of a species was based, but that is not to imply the absence of additional GMx records in other literature that was not herein cited.

The taxonomic lists of species herewith furnished are thus cumulative over the full course of recorded scientific inquiry in the Gulf of Mexico, although a listing of all records for all Gulf species is well beyond the scope of the project. The accumulating records are added to slightly by introductions of species that are in the fol-

lowing chapters identified as nonindigenous, and at least some (if not most) of those appear to have been introduced since 1954. In addition, some records likely accrue for the Gulf of Mexico purely because of an ever longer history of observation, during which chance observations or infrequent dispersal events may conspire to add reports of rare or extralimital occurrences. However, it is largely an enhanced effort over time, more comprehensive geographic coverage, exploration of unique niches, improved techniques, growing literature, and an expanding cadre of expertise that accounts for change in the Gulf of Mexico biodiversity knowledge base over the last 50 years. In particular, one cannot overlook the last 5 decades of attention to systematics within all taxonomic groups we have covered, this in many cases resulting in either splitting or lumping of taxa, although more commonly the former. Both the actual names applied and the numbers of those species names (i.e., the reported species diversity) have changed in part for this reason since 1954, more markedly in some groups than others. For example, a number of species that were formerly believed to be wide-ranging warm-temperate forms extending from "Carolinian" waters of the Atlantic coast into at least the northern Gulf of Mexico are now recognized or pending recognition as separate sister taxa, with distributions completely or incompletely separated across the Florida Peninsula (see Felder and Staton 1994, Staton and Felder 1995). Sometimes, ranges of the now-separated sister taxa both extend into the Gulf of Mexico, with one of the two representing an endemic distribution in the Gulf. Biogeographic dynamics of such separations are treated in the closing chapter of this volume, but it should also be realized that taxonomic recognition of these biogeographic separations impacts Gulf of Mexico biodiversity estimates. In addition, many other taxonomic separations have come about through recognition of niche specializations and underappreciated regional population separations that were not yet known in 1954.

With the advent of improved techniques for both morphological and genetic analyses in systematics and the impact of this on the resurgent field of taxonomy, species counts for the Gulf of Mexico have grown, which likely would have been the case even without broadened sampling coverage over the last 5 decades. However, in an effect common to the progress of science, the very development of such modern techniques has also driven renewed efforts in exploration and sampling of the Gulf of Mexico biota. Most recently, major efforts have been mounted to secure fresh samples appropriate for use

in DNA sequence analyses, just as are also sometimes required in preparation, staining, labeling, or embedding for optimal light and electron microscopic analyses. Returned as live, cryologically stored, ethanol preserved, or otherwise fixed samples, many new collections result from efforts to represent known species or populations that were not favorably archived in years past. Efforts are also now made to thoroughly sample across putative variant populations or distribution breaks within species and to more finely explore unique niches and assemblages previously intractable to comprehensive and definitive systematic study. In the course of all these activities, new taxa are being discovered, new distributional records are accumulating, and problematic systematic issues are being resolved, all with impacts on the measurement of Gulf of Mexico biodiversity. We foresee this pattern to continue, even as we conclude present efforts to compile benchmark Gulf of Mexico biodiversity accounts for future workers to build upon.

The Future

Early in the development of this project, we committed to production of both a hard copy (paper version/benchmark) and a digital version of this compendium. Preparation of the present hard copy has been labeled Phase I, and we are now proceeding with Phase II, the conversion of these listings into digital formats for placement on the World Wide Web. The plans call for listing of this information on GulfBase (www.gulfbase.org) and on OBIS, (www.iobis.org) the Ocean Biogeographic Information System. In addition, we look forward to instituting programs that will allow authoritative augmentation and updating of Gulf of Mexico checklist contents, as the need and opportunity arises.

References

- Allison, A., and S. E. Miller. 2000. Hawaii Biological Survey: museum resources in support of conservation. Pp. 281–290 in P. H. Raven and T. Williams, ed. *Nature and Human Society: The Quest for a Sustainable World*. National Academy of Sciences and Natural Research Council, Washington, D.C.
- Blaylock, R. B., S. A. Bullard, and C. M. Whipps. 2004. *Kudoa hypoepicardialis* n. sp. (Myxozoa: Kudoidea) and associated lesions from the heart of seven perciform fishes in the northern Gulf of Mexico. *Journal of Parasitology* 90: 584–593.
- Bouchet, P. 2006. The magnitude of marine biodiversity. Pp. 31–62 in C. M. Duarte, ed. *The Exploration of Marine Biodiversity: Scientific and Technological Challenges*. Fundación BBVA, Barcelona, Spain.
- Briggs, J. C. 1994. Species diversity: land and sea compared. *Systematic Biology* 43: 130–135.
- CEQ (Council on Environmental Quality). 2004. U.S. Ocean Action Plan; The Bush Administration's Response to the U.S. Commission on Ocean Policy.
- Claro, R., editor. 2006. *La biodiversidad marina de Cuba*. Instituto de Oceanología, CITMA, Havana, Cuba. [Preliminary version of book in preparation.]
- Costello, M. J. 1998. To know, research, manage and conserve marine biodiversity. *Océanis* 24: 25–49.
- Costello, M. J., and E. V. Berghe. 2006. "Ocean biodiversity informatics": a new era in marine biology research and management. *Marine Ecology Progress Series* 316: 203–214.
- Costello, M. J., C. S. Emblow, and R. White, editors. 2001. *European register of marine species. A check-list of the marine species in Europe and a bibliography of guides to their identification*. *Patrimoines naturels* 50: 1–463.
- Costello, M. J., P. Bouchet, C. S. Emblow, and A. Legakis. 2006. European marine biodiversity inventory and taxonomic resources: state of the art and gaps in knowledge. *Marine Ecology Progress Series* 316: 257–268.
- Eldredge, L. G. 2006. Numbers of Hawaiian species. *Bishop Museum Occasional Papers* 88: 62–79.
- Eldredge, L. G., and N. L. Evenhuis. 2003. Hawaii's biodiversity: a detailed assessment of the number of species in the Hawaiian islands. *Bishop Museum Occasional Papers* 76: 1–28.
- Felder, D. L., and J. L. Staton. 1994. Genetic variation in trans-Floridian species complexes of *Sesarma* and *Uca* (Crustacea: Decapoda: Brachyura). *Journal of Crustacean Biology* 14: 191–209.
- Galtsoff, P. S. 1954. *Gulf of Mexico, Its Origin, Waters, and Marine Life*. Fishery Bulletin 89. Fishery Bulletin of the Fish and Wildlife Service, Vol. 55, Washington, D.C.
- Gibbons, M. J., et al. 1999. The taxonomic riches of South Africa's marine fauna: a crisis at hand. *South African Journal of Science* 95: 8–12.
- Hammond, P. M. 1995. The current magnitude of biodiversity. Pp. 131–138 in V. H. Heywood and R. T. Watson, eds. *Global Biodiversity Assessment*. Cambridge University Press, Cambridge.
- Horowitz, T. 2002. *Blue Latitudes—Boldly Going Where*

- Captain Cook Has Gone Before. Henry Holt and Company, New York.
18. Huang, Z., editor. J. Lin, translator. 2001. *Marine Species and Their Distribution in China's Seas*. Krieger Publishing Company, Malabar, Florida.
 19. Jiménez-Guri, E., H. Philippe, B. Okamura, and P. W. H. Holland. 2007. *Buddenbrockia* is a cnidarian worm. *Science* 317: 116–118.
 20. JSOST (Joint Subcommittee on Ocean Science and Technology). 2007. *Charting the Course for Ocean Science in the United States for the Next Decade: An Ocean Research Priorities Plan and Implementation Strategy*. Final Report. Washington, D.C. Available from http://ocean.ceq.gov/about/docs/jsost_chartcourse_083006.pdf
 21. Not, F., K. Valentin, R. Khadidja, C. Lovejoy, R. Massana, K. Tröbe, D. Vaultot, and L. Medlin. 2007. Picobiliphytes: a marine picoplanktonic algal group with unknown affinities to other eukaryotes. *Science* 315: 253–254.
 22. Overstreet, R. M. 1978. Marine Maladies? Worms, Germs and other Symbionts from the Northern Gulf of Mexico. MASGP-78-021. Mississippi-Alabama Sea Grant Consortium. Ocean Springs, Mississippi.
 23. Paulay, G. 2003. Marine biodiversity of Guam and the Marianas: overview. *Micronesica* 35–36: 3–25.
 24. Pedrós-Alió, C. 2007. Dipping into the rare biosphere. *Science* 315: 192–193.
 25. Reaka-Kudla, M. L. 1997. The global biodiversity of coral reefs: a comparison with rain forests. Pp. 83–108 *in* M. L. Reaka-Kudla, D. E. Wilson, and E. O. Wilson, eds. *Biodiversity II*. Joseph Henry Press, Washington, D.C.
 26. Staton, J. L., and D. L. Felder. 1995. Genetic variation in populations of the ghost shrimp genus *Callinectes* (Crustacea, Decapoda, Thalassinoidea) in the western Atlantic and Gulf of Mexico. *Bulletin of Marine Science* 56: 523–536.
 27. Sterrer, W. 1998. How many species are there in Bermuda? *Bulletin of Marine Science* 62: 809–840.
 28. Tunnell, J. W. Jr. 2005. Biodiversity of the Gulf of Mexico Project. Pp. 285–286 *in* P. Miloslavich and E. Klein, eds. *Caribbean Marine Biodiversity: The Known and the Unknown*. DEStech Publications, Pennsylvania.
 29. Tunnell, J. W. Jr., and S. A. Earle. 2004. Harte Research Institute for Gulf of Mexico Studies: initiatives in marine science research. Pp. 132–141 *in* *Proceedings of 55th Annual Gulf and Caribbean Fisheries Institute, Xel-Ha, Quintana Roo, Mexico*.
 30. Tunnell, J. W. Jr., D. L. Felder, and S. A. Earle. 2004. El Golfo de México: Pasado, presente, y futuro. Una colaboración entre Estados Unidos de América, México, Cuba. Pp. 361–371 *in* M. Caso, I. Pisanty, y E. Ezcurra, compiladores. *Diagnostico Ambiental del Golfo de México*. Instituto Nacional de Ecología, México, D. F.
 31. Tunnicliffe, V. 1992. Biodiversity: the marine biota of British Columbia. *In* M. A. Fenger, E. H. Miller, J. A. Johnson, and E. J. R. Williams, eds. *Our Living Legacy: Proceedings of a Symposium on Biological Diversity*. Royal British Columbia Museum, Victoria, Canada.
 32. USCOP (U.S. Commission on Ocean Policy). 2004. *An Ocean Blueprint for the 21st Century, Final Report*. Washington, D.C.

List of Abbreviations Provided to Authors

acc	accidental	nek	nektonic
ben	benthic	ner	neritic
bns	bay and nearshore	neu	neustonic
bsl	beach and shoreline	nid	nonindigenous to Gulf of Mexico
bur	burrower or borer	ocs	outer continental shelf
bys	byssate	orf	oyster reef
cas	casual	osp	oceanic surface and epipelagic
cen	central	par	parasitic
cep	coastal surface and epipelagic	pin	potentially invasive
cmp	circumpolar	ple	pleustonic
cmt	circumtropical	plg	pelagic
com	commercially important in GMx	plk	planktonic
crr	coral reef	poh	polyhaline
csp	cosmopolitan	pth	potentially pathogenic
cst	coasts	rbl	rubble
dem	demersal	rit	rocky intertidal
dps	deep sea	riv	rivers
ebn	epibenthic	ses	sessile
end	endemic solely to Gulf of Mexico	sft	soft substrates
epi	epibiotic	sgr	seagrass
est	estuarine	shl	shell hash
eur	euryhaline	shw	shallow water
evg	emergent vegetation	slp	slope
hcs	hydrocarbon seep	smr	salt marsh
hlar	holarctic	sth	stenohaline
hsb	hard substrate	str	subtropical
htv	hydrothermal vent	sub	subtidal
hys	hypersaline specialist	svg	submergent vegetation
iif	inlet influenced	sym	symbiotic
inf	infaunal	tbi	tubicolous
ins	interstitial	tem	temperate
isb	breeding on islands	tft	tidal flat
isl	island, islands	tre	transequatorial
itd	intertidal to semiterrestrial	trp	tropical
lvb	live bottom	THR	threatened or endangered
msp	mangrove swamp	unk	habitat unknown
mul	mud lump	vag	vagrant