Species Discovery of Deep-Water Corals and Sponges in U.S. Waters (2007-2016)

Chapter 2 in The State of Deep-Sea Coral and Sponge Ecosystems of the United States Report

Recommended citation: Cairns SD, Stone RP, Berntson EA, Pomponi SA (2017) Species Discovery of Deep-Water Corals and Sponges in U.S. Waters (2007-2016). In: Hourigan TF, Etnoyer, PJ, Cairns, SD (eds.).

The State of Deep-Sea Coral and Sponge Ecosystems of the United States. NOAA Technical

Memorandum NMFS-OHC-4, Silver Spring, MD. 18 p.

Available online: http://deepseacoraldata.noaa.gov/library.



SPECIES DISCOVERY OF DEEP-WATER CORALS AND SPONGES IN U.S. WATERS (2007-2016)

I. Discovery of Deep-Water Corals

In order to understand biodiversity and to conserve a biota, or to simply converse about it in a meaningful manner, one must know the names of the units being discussed – the species. The 2007 "State of Deep Coral Ecosystems" report (Lumsden et al. 2007) concentrated on the most ecologically important species - the structure-forming deep-water corals (highlighted in Appendices 1.1, 1.2, and elsewhere). In seven articles, each on a different region of the United States (U.S.), the authors dutifully included detailed lists of the deepwater coral species found within each region, sometimes subdividing their regions into smaller subunits. Yet, there was never a comprehensive synthesis or grand tally of how many deep-water coral species occur in U.S. waters in the 2007 report.

Admittedly, a 'comprehensive synthesis' requires some time and effort, but this can initially be accomplished by comparing the seven previously published regional lists (Lumsden et al. 2007) with the new online regional species lists associated with this report (Online Annexes). Taking into account revisions in taxonomy and eliminating duplicate entries, i.e., those species occurring in two of more of the seven regions, resulted in a comprehensive list (Online Annex)¹. Table 1 summarizes the number of species in each of the five groups of corals known to inhabit the seven geographic regions.

Stephen D.
Cairns^{1*},
Robert P.
Stone², Ewann
A. Berntson³,
and Shirley A.
Pomponi⁴

¹ National Museum of Natural History, Smithsonian Institution, Washington, DC * Corresponding Author: CairnsS@si.edu

² NOAA Auke Bay Laboratories, Alaska Fisheries Science Center, Juneau, AK

³NOAA Conservation Biology Division, Northwest Fisheries Science Center, Port Orchard, WA

⁴Marine Biomedical & Biotechnology Research Program, Harbor Branch Oceanographic Institute, Florida Atlantic University, Fort Pierce, FL

¹ Pacific Islands region is composed of the Hawaiian Islands, Guam, American Samoa, Northern Mariana Islands, and Pacific Remote Islands (Baker I., Howland I., Jarvis I., Johnston Atoll, Kingman Reef, Palmyra Atoll, and Wake I.); and the Caribbean region is composed only of Puerto Rico, the U.S. Virgin Islands, Navassa I., and Sarranilla Bank.

Number of Species of Deep Sea Corals

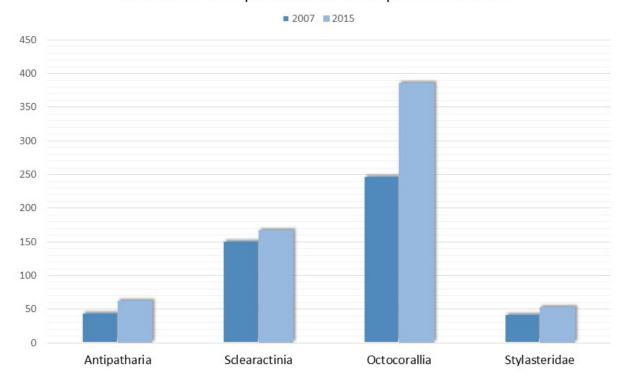


Figure 1. The number of deep coral species known from four taxonomic groups occurring in US waters as of 2007 (left bar, dark blue) and newly identified species as of 2016 (right bar, light blue).

	Antipatharia		Scleractinia		Zoanthidea		Octocorallia		Stylasteridae	
	2007	2016	2007	2016	2007	2016	2007	2016	2007	2016
Northeast U.S.	0	1	16	17	0	0	37	47	0	0
Southeast U.S.	2	14	57	77	0	0	42	92	7	15
Gulf of Mexico	17	28	47	72	0	0	44	118	8	9
U.S. Caribbean	9	13	42	45	0	0	23	43	14	14
U.S. West Coast	3	7	17	19	0	0	39	80	4	6
Alaska	10	8	8	9	0	0	45	58	12	23
Hawaii	20	21	53	54	0	1	93	104	4	4
Gross Totals	61	92	237	293	0	1	323	542	49	71
Corrected Totals	45	60	151	163	0	1	247	385	42	53
New taxa since 2007		15		12		1		138		11

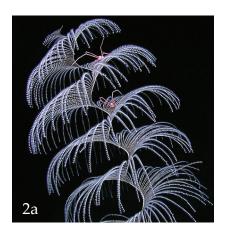
Table 1. Comparison of numbers of deep-water coral species by region between 2007 and 2016. Gross totals include species that overlap in two or more regions. Corrected totals eliminate the overlapping species. Taxa not identified to species level not included.

Among the 662 deep-water corals presently known from U.S. waters (Table 1, and comprehensive species list herein), Octocorallia have by far the highest species richness (58.2% of the grand total), followed by the azooxanthellate Scleractinia (24.6%), Antipatharia (9.1%), and the Stylasteridae (8.0%). The rank order of these four major groups is consistent with three other comprehensive lists of deep-water corals made for other oceanic regions, specifically the Gulf of Mexico (Cairns and Fautin 2009: 354 species), New Zealand (Cairns et al. 2009: 376 species), and European waters (Costello et al. 2001: 261 species). From this table one can also calculate that the most species-rich regions are the Gulf of Mexico (227 species), southeastern US (198 species), and Hawaii (184 species); the most depauperate regions being the northeastern U.S. (65 species) and Alaska (98 species). Table 1 can then form the basis for what progress has been made between mid-

2007 to 2016 in describing deep-water coral species richness of the seven U.S. regions.

Progress is inevitably a function of research effort. In the U.S., deep-water coral research is supported by the National Oceanic and Atmospheric Administration (NOAA), the Smithsonian, the U.S. Geological Survey (USGS), the Bureau of Ocean Energy Management (BOEM), the National Science Foundation (NSF), academia, and private industry, among others. These groups are all invested in the exploration, sampling, and systematics of deep-water corals and their habitats. Examples of new species discoveries are shown in Figures 2a, 2b, and 3.

A regional increase in species richness can occur in three ways: (1) by the description of new species, (2) by the discovery of a range extension into U.S. waters of a previously described species, and (3) by the addition of species previously overlooked. It is relatively





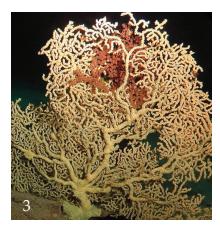


Figure 2a. Iridogorgia magnispiralis at 2200 m depth, a new record for the northern Gulf of Mexico, from NOAA's Okeanos Explorer expedition of 2012.

Figure 2b. Isidella tentaculum at 891 m depth, a new species in the Northeast Pacific described in 2008, from NOAA's Gulf of Alaska Seamount Expeditions aboard RV Atlantis in 2002 and 2004.

Figure 3. An in-situ image of a zoanthid gold coral from Hawaii called Kulamanamana haumeaae (Sinniger et al. 2013). The colony represents a new genus and species of gold coral, previously thought to be in a different genus, Salvia or Gerardia. Image credit: Public Library of Science One.

• •

easy to compile a list of the new species for a region but somewhat harder to ascertain if there has been a range extension, as evidence of the latter is often buried in the literature. After a thorough review of the scientific literature, we have determined that 62 new species and three new genera of deep-water corals had been newly described from U.S. waters between 2007 and 2016. In addition, numerous species had been reported as a result of range extensions, and as having been previously overlooked. The rate of 62 new species in ten years equates to 6.2 new species per year, or an annual worldwide increase in described species of 0.19% (6.2/3336 known deep-water coral species; Cairns 2007b). This is considerably lower than the annual increase in new species descriptions for Scleractinia over a 30-year period, as calculated by Cairns (1999) as 1.23%, although his rate applied to both deep- and shallow-water species around the world, and the 0.19% rate is limited to the deep-water species from U.S. waters. Table 1 and Figure 1 show that the most actively growing group was the Octocorallia, increasing by 138 names, or 55.9%, since 2007.

The relatively high number of new octocorals is due, at least in part, to the large size of the group, their poorly known taxonomy, and to the revisionary papers on the fauna of: (1) the New England Seamounts (Watling 2007, Simpson and Watling 2011, Watling and France 2011, Pante and Watling 2011, Cairns 2007c); (2) the Hawaiian Islands (Cairns and Bayer 2007, Cairns 2009, 2010); (3) the U.S. west coast (Cairns 2007c); and (4) the Alaskan waters (Cairns 2011, Cairns and Baco 2007). Most of those specimens have been collected by NOAA research vessels. Also, many new records of all taxonomic groups were based on as yet unpublished museum records and other gray literature reports. A revisionary work by Cairns and Lindner (2011) on the Alaskan stylasterids served to increase the number

of species in this deep-water coral group by 26.2%. Relatively few species were added to the U.S. antipatharian and scleractinian fauna, their components increasing by 33.3% and 7.9%, respectively. It is of interest to note that of the 62 new species described during this period, 16 (26%), were additionally characterized by molecular sequencing, usually of mitochondrial genes (Cairns and Baco 2007, Etnoyer 2008, Watling and France 2011, Pante and Watling 2011, Cairns and Lindner 2011, Opresko et al. 2012, and Tu et al. 2016).

Three faunistic lists were also published during this period, which helped to increase the number of species in U.S. waters: (1) Felder and Camp (2009), all taxa at all depths for the Gulf of Mexico; (2) DeVictor and Morton (2010), octocorals from the South Atlantic Bight from 0-200 m; and (3) Watling et al. (2011), octocorals at all depths and regions, the latter allowing for cross-checking of taxonomic names of the Atlantic regions, a guide to some of the range extensions for these regions, and the addition of some species that had been overlooked in the 2007 report. Based on Watling et al. (2011) eight species were added to the U.S. fauna (5 octocorals and 3 stylasterids), mainly from the southeastern region. The total number of deep-water corals now known from U.S. waters is 662 species, up 177 (36.5%) from the 485 species listed in 2007 (Table 1), representing 19.8% of the total known deep-water coral fauna (Cairns, 2007b). Sixty-two of the 177 new names were newly described (see the comprehensive species list) and 115 had been previously overlooked.

In summary, we believe that a significant amount of work is being done to discover new species, document range extensions, and to uncover previously overlooked records of deep-water corals in U.S. waters leading to numerous descriptions, especially in the group

Octocorallia. We expect that future increases in species descriptions will likely fall in that group. We also acknowledge that it is not the lack of collections that hinders advancement but the lack of manpower that limits progress and causes uneven growth (Cairns 2007b). A pertinent example of this is the dissertation by K. Muzik (1979), containing the description of 18 new species of Hawaiian deep-water octocorals, which remains unpublished.

II. Species Discovery of Deep-Water Sponges

Sponges are one of the simplest, oldest-living metazoan phyla and one of the most abundant groups of benthic marine organisms (Fig. 4). They are more diverse than corals, and single- or multi-species sponge aggregations may play a similarly important role in the ecology of deep-sea ecosystems (Maldonado et al. 2016). At present, there are approximately 8500 described species with perhaps as many yet to be discovered. Worldwide, about 50 new species are described each year (Cárdenas et al. 2012). The systematics of sponges are particularly challenging given their ancient origin, simple body organization, complex microbial associations and morphological plasticity. As a result, phylogenetic relationships within the Porifera remain mostly unresolved, and this hampers progress in basic studies of sponge biology and biodiversity, including comparative evolutionary studies that use sponge species as model organisms as well as efforts to conserve or economically exploit sponges.

The deep-water sponge fauna of the U.S. has not been inventoried as systematically as the deep-water coral fauna. There are important historical collections dating back decades or more for most regions but there have

been few dedicated efforts in recent years to collect sponges beyond those provided opportunistically. The 2006 Magnuson-Stevens Reauthorization Act established the Deep Sea Coral Research and Technology Program, but made no specific provision to consider deepwater sponges, and they were not included in the 2007 NOAA Report (Lumsden et al. 2007). Still, deep-water sponges are abundant in the same depth range as deep-water corals, have complex structure that provides habitat for other fauna, and face many of the same threats as deep-water corals (e.g. Hogg et al. 2010). Additionally, sponges and their associates produce a diverse array of chemicals that are of interest for biotechnology (Pomponi et al. 2007). Accordingly, the NOAA Strategic Plan for Deep-sea Coral and Sponge Ecosystems (2010) provides nearly equal emphasis on the deep-sea sponge and coral fauna, and clear guidance to include sponges in research and management efforts.

Whereas sponges have taken a back seat to their more charismatic deep-water counterparts, there is strong evidence that poriferans provide important habitat for fish and invertebrates. With that in mind, sponges were specifically collected during submersible cruises in the Aleutian Islands of Alaska in 2003–2004. This was done, in part, to construct a field guide (Stone et al. 2011) and to help establish a useful fisheries bycatch monitoring program. Ninety-four (94) sponge species were collected during this period, and 28 (30%) were new to science! This high rate of new species discovery, and many new range extensions, clearly indicated that the sponge fauna of the region is poorly documented. In response to these findings, NOAA scientists boarded regional groundfish survey vessels during the summer of 2012 and, with the new guide in hand, collected 118 unfamiliar bycatch specimens. These new collections



Figure 4. Sponge gardens (areas of particularly diverse and abundant sponge fauna) were discovered in the central Aleutian Islands in 2004. Seven species of sponges are visible in this photograph, including two new to science and recently described.

will undoubtedly yield many new discoveries and provide insight into the true species diversity of the region. Since 2004, more casual collections in other regions of Alaska (e.g., the Bering Sea and Gulf of Alaska) have yielded additional species that have either been recently described or are awaiting formal description.

More than 55 taxa, principally hexactinellids, have been opportunistically collected along the Pacific Coast as part of NOAA's Deep Sea Coral Research and Technology Program three-year research initiative in that region (Clarke et al., this report). Approximately 28 taxa (51%) are believed to be new to science and await formal identification. Thirty hexactinellid specimens were recently collected during an expedition to the Necker Ridge in the Northwest Hawaiian Islands and 19 taxa, or 72%, are believed to be new to science. Other collections in the Pacific Islands Region (principally funded by NOAA through the Hawaii Undersea Research Laboratory) included 10 new species, all believed to be new to science (Chris Kelley, University of Hawaii at Manoa, personal communication).

Together, these regional collections represent a new species discovery rate of about 60%. This rate could be somewhat inflated since researchers may preferentially collect forms that are unfamiliar to them. Regardless, these data support those from Alaska and clearly indicate that the deep-water sponge fauna of the Pacific Ocean is poorly documented and that a large percentage of the total fauna are yet to be discovered.

One particularly noteworthy example of unexplored and undocumented deepwater sponge fauna was the exciting discovery of the carnivorous harp sponge Chondrocladia lyra off the coast of California (Lee et al. 2012) (Figure 6). This unusual group of sponges, to date found only in the Class Demospongiae, Family Cladorhizidae, differs drastically in body plan and cellular organization from the rest of the Phylum Porifera, and was only recently discovered (Vacelet and Boury-Esnault 1995). Since that time, at least 133 (as of 2014) new species of carnivorous sponges have been described, primarily in deep water (Cristobo et al. 2015). Using MBARI ROVs Tiburon, Ventana and Doc Ricketts, four



Figure 5. Undescribed species of Geodia from 118 meters depth off the coast of Florida, collected by HBOI-FAU using the Johnson-Sea-Link submersibles in 2007.

new species were collected off the west coast of the U.S. (Lundsten et al. 2014) since 2007, increasing the total of U.S. Pacific carnivorous sponge species from 7 to 11 and several more are in the process of being described (Lundsten, MBARI, pers. comm.).

Many sponge collections have been made during the past decade in the South Atlantic Bight and Gulf of Mexico with funding from NOAA. Harbor Branch Oceanographic Institute-Florida Atlantic University has collected and archived more than 1200 deepwater sponges from U.S. waters using the Johnson-Sea-Link manned submersibles (Reed et al. 2005, 2006). Rützler et al. (2009) identified 339 sponge species in a checklist of the Gulf of Mexico, of which 66 (48 demosponges and 18 hexactinellids) were identified as deep-sea sponges. Species lists have been submitted to NOAA as part of the technical (cruise)

reports and several new species from these collections await formal identification (Fig.5). A new record of occurrence of the carnivorous sponge Chondrocladia verticillata was discovered in 2011 off the Florida Keys at a depth of 850 m by the Cooperative Institute for Ocean Exploration, Research, and Technology at HBOI-FAU, using the University of Connecticut ROV Kraken. Recent interest in resolving the phylogenetic relationships of the phylum Porifera has resulted in more detailed studies of these collections using molecular and morphological systematics (Dohrmann et al. 2012a, b; Hill et al. 2012). The increasing use of molecular techniques is facilitating species identification and discovery (Wörheide et al. 2007, Erpenbeck et al. 2015), and leading to significant revisions of sponge systematics (e.g., Morrow and Cardenas 2015).

There is a renewed interest in sponge taxonomy and systematics resulting from

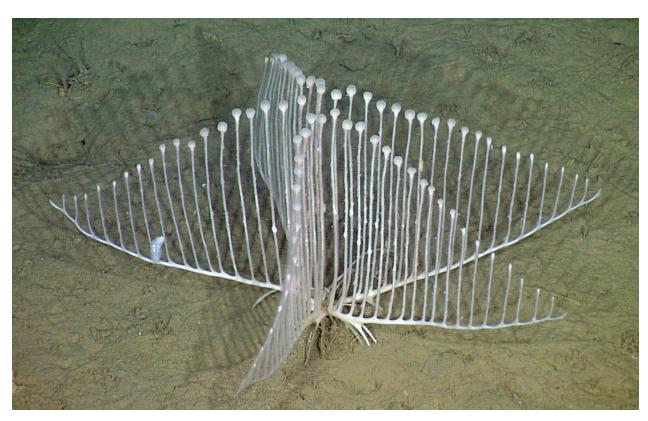


Figure 6. The carnivorous harp sponge Chondrocladia lyra with 5 vanes was collected with the ROV Doc Ricketts off California. This unusual group of sponges was discovered only a few decades ago and differs in body plan and cellular organization from all other sponges. © 2009 MBARI.

discoveries that continue to be made during exploration of poorly studied areas in U.S. waters. The discovery of sponge-associated microbial symbionts and natural products with pharmaceutical potential and the application of molecular systematics to resolve phylogenetic relationships have added to this interest. As with other deep-water fauna, there are already long queues in the laboratories of the few sponge taxonomists worldwide, suggesting that future collections should be carefully planned and coordinated with them if possible.

III. Genetic Identification of Deep-water Coral Species

An understanding of the population structure of deep-water coral species is critical to ascertaining gene flow within and among distant populations, in order to gauge the effects of habitat loss, and meet the directives of the 2006 Magnuson-Stevens Act and the National Marine Fisheries Service (NMFS) federal mandate. A species inventory of deep-water corals off U.S. coastlines is a necessary first step toward a comprehensive understanding of the ecology and distribution of this rich and diverse faunal assemblage. Fisheries bycatch data and benthic trawl surveys can help quantify species diversity and outline their biogeographical distributions, but such estimates require accurate and defensible species-level identifications; however, the taxonomic identification of deep-water corals to the species level can be problematic for both morphological and practical reasons (see McFadden et al. 2011); in some cases, species of octocorals that appear similar

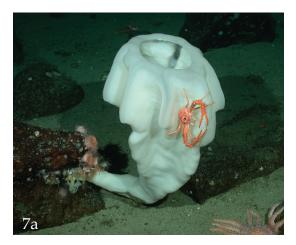




Figure7a. An unidentified sponge in the genus Aphrocallistes at 255 m depth on Kidney Bank in Southern California. Many unique taxa in the Pacific Region await formal description. Image credit: NOAA Southwest Fisheries Science Center, Advanced Survey Technologies Group, La Jolla CA.

Figure 7b. The recently described sponge Latrunculia austini occurs at depths between 30 - 384 m in the Northeast Pacific from the Olympic Coast off Washington State to the Gulf of Alaska. These sponges have unique compounds that offer biomedical potential to curing disease. Image credit: Bob Stone, NOAA Alaska Fisheries Science Center.

may only be distinguished from one another morphologically using scanning electron microscope (SEM) images of sclerites, minute skeletal structures embedded in the fleshy tissue of these corals. Some species of deep-water corals may be defined from a single known type specimen. In other cases, the known evolutionary relationships of some coral families are so inadequate that accurate species-level designations are currently impossible. Additionally, many deep-water coral specimens are collected in trawls or dredges, which may damage the specimen or yield partial colonies at best. These difficulties, combined with a scarcity of trained morphological taxonomists, make the expanded development of genetic techniques to aid in species identification a critical necessity. It is encouraging to see, and worth noting, that students are being trained in coral taxonomy in federal (e.g., S. Cairns, P. Etnoyer) and academic laboratories (e.g., S. France, P. López-González, and L. Watling). Nevertheless, the use of genetic information,

when combined with morphology, is currently the best approach to deciphering evolutionary patterns in these species.

Voucher collections are currently being compiled at NOAA's Northwest Fisheries Science Center (Seattle, WA) and NOAA's Center for Coastal Environmental Health and Biomolecular Research (Charleston, SC) to aid in a more rapid and accurate identification of coral specimens. Such collections include one or more specimens of each potential species, with taxonomic identifications to be confirmed by relevant experts. As part of this process, SEM images may be produced for the vouchers as necessary, to either allow the direct identification of some individuals or assist morphological taxonomists with their examinations and characterizations of unknown specimens. Genomic sequences are then generated for each voucher so that DNA from additional specimens can be used to ascertain their identity in the absence of labor intensive SEM imaging or the large sample sizes required for some morphological

analyses. Choosing which area of a coral's genome to investigate is, however, not immediately straightforward.

The selection of an appropriate genetic region or regions to uniquely identify individual species is critical, requiring a fast enough mutation rate to yield sufficient differences between species, but not so many differences that sequence alignment is difficult. Animals contain two types of genetic material in their cells, which have both similar and differing characteristics: nuclear DNA and mitochondrial DNA. In diploid organisms, nuclear DNA (nDNA) is inherited from both parents—one copy of each gene being contributed by each parent—and is present as a single set of chromosomes in each somatic cell. Mitochondrial DNA (mtDNA) is inherited from an organism's mother. Each cell also contains multiple copies mtDNA because there are numerous mitochondria whereas there is only a single nucleus. Mitochondrial genomes tend to evolve more quickly than nuclear genomes because, at least in higher vertebrates, mitochondria lack the ability to "repair" accidental mutations in their DNA that arise during cell division. This higher rate of evolution is useful when attempting to identify genetic regions - termed "markers" that exhibit sufficient diversity to distinguish individuals on a species level. As a result of these attributes, mtDNA sequencing has become the standard genetic tool for many species identifications. Recent reports, however, cite inherent problems with using mtDNA to investigate recent molecular evolution, and this must be considered when choosing an appropriate barcoding region (see Bazin et al. 2006, Galtier et al. 2009). Presently, the most concerted effort to generate a database of species-specific genetic sequences, i.e., genetic barcodes, is coordinated by the Barcode of Life (BOL) initiative

(www.barcodeoflife.org). The stated purpose for the BOL is to assist in situations where a specimen may be damaged, thereby making morphological identification difficult, or in cases where expert taxonomists are required to make a definitive identification. Barcoding would potentially solve the problem of species identification in both instances, as short DNA sequences can be generated from minimal amounts of tissue and used by non taxonomic experts to determine species designations. The genetic region targeted for most animal species is a 648 basepair region of the mitochondrial cytochrome c oxidase 1 gene (COI); however, this region is not sufficiently informative for species identification in octocorals because this subclass experiences a slower rate of evolution in their mtDNA than vertebrates (France and Hoover 2002). One reason cited for this stability is the presence of the mitochondrial MutS homolog, msh1 (mtMSH) gene, which has high similarity and homology to mismatch-repair genes found in bacterial genomes as well as eukaryotic nuclear genes (Culligan et al. 2000). If the MutS homolog is functional in octocorals, that could explain why the mitochondrial genomes of octocorals are often not sufficiently variable to distinguish among species.

Interestingly, the mtMSH gene itself appears to be highly variable and provides an alternative to the COI gene for species identification purposes (France and Hoover 2002). The mtMSH gene has been shown to be specific for many, but not all, coral species investigated (France and Hoover 2001). The addition of other gene regions, such as the "Folmer region" of COI and an adjacent intergenic area, have demonstrated good potential as a substitute to the COI when used in combination with *msh1* at the species level (McFadden et al. 2011). Despite this increased resolution, there remain limitations in

identification of certain deep-water coral taxa. Further investigations into using alternative genes must continue.

Examples of both the utility and limitations of combined genetic and morphological identifications are now appearing in the literature (e.g., Cairns and Baco 2007; Lapian et al. 2007; Wagner et al. 2010; Baco and Cairns 2012; Pante et al. 2012). Development of the Northwest Fisheries Science Center voucher collection exemplifies their utility; a number of octocorals frequently collected in trawl surveys in the Northeast Pacific are initially identified as Swiftia sp. (Family Plexauridae) based on overall similarities in appearance. These samples may also be assigned a shipboard species designation within the genus Swiftia based on general colony formation and color. Figure 4 depicts a group of such individuals, all of which were originally identified aboard trawling vessels as Swiftia sp., S. simplex, or S. pacifica. Identification by a taxonomist through a detailed morphological examination including SEM images of formations and arrangements of sclerites, revealed some of these individuals actually represent two additional genera plus one additional species of Swiftia, despite their superficial similarities (Fig. 8). A neighborjoining tree of pairwise differences of the mtDNA sequence data (including the Folmer region of COI plus the adjacent intergenic region, plus *msh1*) for these same specimens corroborated the taxonomic identities of these individuals (Fig. 8). On this phylogenetic tree, the horizontal branch lengths indicate the relative differences measured between individuals. Note that individuals of the same species group together in "clusters" and that the horizontal branch lengths among individuals within the same species are very short or even zero (e.g., the Swiftia simplex and Swiftia spauldingi clusters). Slightly longer branch lengths are found between

species within the same genus (e.g., the difference between *Swiftia simplex* and *Swiftia pacifica*), and the longest branch lengths are between different genera (e.g., *Leptogorgia* and *Eugorgia*). Additional specimens from this group can now be sequenced for the above genetic regions and compared to the vouchered sequences on this tree, yielding taxonomic identifications without requiring the consultation of a taxonomist for every new individual.

The use of molecular genetics in species identification alleviates pressure on the few, overworked coral taxonomists and can illuminate species distinctions when morphological distinctions are absent (as in the case of cryptic species). As previously mentioned, approximately 25% of newly described deep-water coral species included a molecular characterization of primarily mitochondrial markers. Further coordination of morphological taxonomists with genetic labs could readily contribute molecular information for the other 75% of newly described taxa. Many genetics labs across the country are now capable of generating and analyzing DNA sequence data, as is evidenced by the recent explosion in the number of institutions contributing to the BOL project.

In addition to barcode sequencing, recent advances in molecular genetic technologies are currently in use, or being developed, that may prove invaluable to the investigation of various aspects of deep-water coral species identification and genetics. Next-generation sequencing produces gigabases of data in mere days, enabling the assemblage and interrogation of entire genomes in a comparatively short amount of time. The generation of such massive amounts of molecular data also allows for the continued screening of additional genetic regions that might have utility for species-level

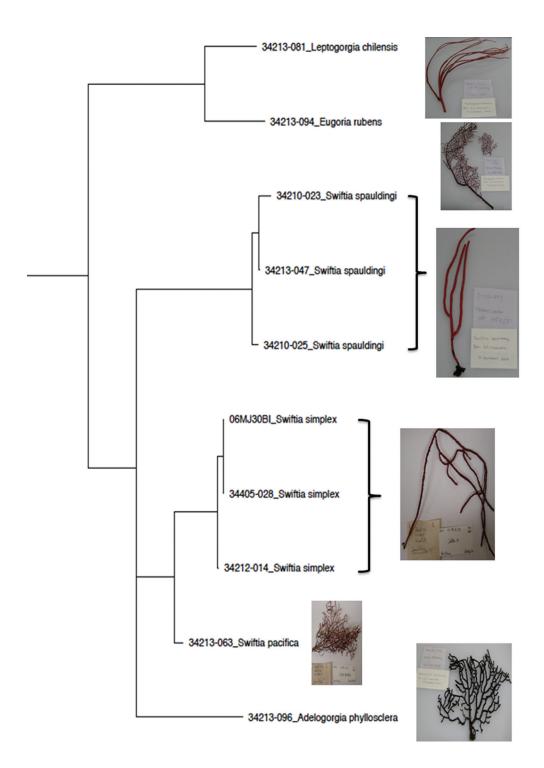


Figure 8. Phylogenetic comparison of the Fulmer region of COI plus adjacent intergenic region, plus msh1, of putative Swiftia spp. with other Plexauridae from the Northeast Pacific. The dendrogram shows three clusters of Swiftia specimens corresponding to three different species. Swiftia pacifica is more closely related to S. simplex than S. spauldingi. Adelogorgia phyllosclera is more closely related to Swiftia spp. than to two other genera - Leptogorgia and Eugorgia.

identification as well as population-level analyses. Other molecular genetic techniques that have relevant application in the genetic analysis of deep-water corals include, but are not limited to: (1) targeted amplicon sequencing (Bybee et al. 2011), which can use next-generation sequencing techniques (e.g., Roche 454, Illumina, and/or Ion Torrent platforms) and associated bioinformatics to generate large numbers of DNA barcodes simultaneously; (2) environmental DNA (eDNA), a relatively new technique that can identify the presence of species from ambient water samples, reducing the need to sample individual corals directly and increasing overall sampling opportunities; (3) microsatellites (msats), also known as simple short repeats (SSR), which are tandemly repeated stretches of 2-6 dinucleotides, and can be used to measure neutral variation among populations as well as help gauge the proportion of genetic variation among different groups within a single species; and (4) RAD sequencing (restriction site associated DNA sequencing), a genome reduction technique that is often employed to identify genetic markers—Single Nucleotide Polymorphisms (SNPs) and/or msats—that have the potential to distinguish among individuals, species, or even populations.

As we learn more about the genetic relationships among deep-water corals, we stand to gain a richer understanding of species diversity as well as ascertain the severity of pressing environmental disturbances on the health and vulnerability of habitat-forming anthozoans, a benefit that will guide the development of regulatory policies to protect these remote, productive, and fragile ecosystems.

IV. Acknowledgments

This manuscript was made more complete and more consistent in style by the reviews of Les Watling, Chris Kelley, Geoff Cook, Peter Etnoyer, Tom Hourigan, and Debe Tighe.

Online Annex - Comprehensive List of Deep-Sea Corals in the U.S. EEZ link: https://deepseacoraldata.noaa.gov/ library/2017-state-of-deep-sea-coralsreport

V. Literature Cited

Baco AB, Cairns SD (2012) Comparing molecular variation to morphological species designations in the deep-water coral *Narella* reveals new insights into seamount coral ranges. PLOS ONE 7(9):e45555

Bo M, Opresko DM (2015) Redescription of Stichopathes pourtalesi brook, 1889 (Cnidaria: Anthozoa: Anthipatharia: Antipathidae). Breviora 540: 1-18.

Bybee SM, Bracken-Grissom H, Haynes BD,
Hermansen RA, Byers RL, Clement MJ, Udall
JA, Wilcox ER, Crandall KA (2011). Targeted
amplicon sequencing (TAS): a scalable
next-gen approach to multilocus, Multitaxa
phylogenetics. Genome Biology and Evolution
3:1312-1323

Cairns SD (1999) Species richness in Recent Scleractinia. Atoll Research Bulletin 459: 1-12

Cairns SD (2007a) Studies on western Atlantic Octocorallia (Gorgonacea: Ellisellidae). Part 7: The genera *Riisea* Duchassaing & Michelotti, 1860 and *Nicella* Gray, 1870. Proceedings of the Biological Society of Washington 120(1): 1-38

- Cairns SD (2007b) Deep-water corals: an overview with special reference to diversity and distribution of deep-water scleractinian corals. Bulletin of Marine Science 81: 311-322
- Cairns SD (2007c) Studies on western Atlantic Octocorallia (Gorgonacea: Primnoidae). Part 8. New records of Primnoidae from the New England and Corner Rise Seamounts. Proceedings of the Biological Society of Washington 120: 243-263
- Cairns SD (2007d) Calcaxonian Octocorals (Cnidaria: Anthozoa) from the Eastern Pacific seamounts. Proceedings of the California Academy of Sciences 58: 511-541
- Cairns SD (2009) Review of Octocorallia (Cnidaria: Anthozoa) from Hawai'i and adjacent seamounts. Part 2. Genera *Paracalyptrophora* Kinoshita, 1908; *Candidella* Bayer, 1954; and *Calyptrophora* Gray, 1866. Pacific Science 63: 413-448
- Cairns SD (2010) A review of the Octocorallia (Cnidaria: Anthozoa) from Hawai'i and adjacent seamounts, Part 3: The genera *Thouarella, Plumarella, Callogorgia, Fanellia,* and *Parastenella*. Pacific Science 64: 413-440
- Cairns SD (2011) A revision of the Primnoidae (Octocorallia: Alcyonacea) from the Aleutian Islands and Bering Sea. Smithsonian Contributions to Zoology 634: 55 pp
- Cairns SD, Baco AB (2007) Review and five new Alaskan species of the deep-water octocoral *Narella* (Octocorallia: Primnoidae). Systematics and Biodiversity 5(4): 391-407
- Cairns SD, Bayer FM (2007) A review of the Octocorallia (Cnidaria: Anthozoa) from Hawai'i and adjacent seamounts: the genus *Narella* Gray, 1870. Pacific Science 62: 83-115

- Cairns SD, Fautin DF (2009) Cnidaria: Introduction.
 Pp 315-319 In: Felder DL, Camp DK (eds) Gulf
 of Mexico Origin, Waters, and Biota, Volume
 1, Biodiversity. Texas A&M University Press,
 College Station
- Cairns SD, Lindner A (2011) A revision of the Stylasteridae (Cnidaria, Hydrozoa, Filifera) from Alaska and adjacent waters. ZooKeys 158: 88 pp
- Cairns SD, Gershwin LA, Brook FJ, Pugh P,
 Dawson EW, Ocaña O, Vervoort W, Williams
 GC, Watson JE, Opresko D, Schuchert P,
 Hine PM, Gordon DP, Campbell HJ, Wright
 CA, Sánchez JA, Fautin DA (2009) Phylum
 Cnidaria: Corals, Medusae, Hydroids
 Myxozoans. Pp 59-101 In: Gordon DP (ed.)
 New Zealand Inventory of Biodiversity,
 Volume 1: Kingdom Animalia. Canterbury
 University Press, Canterbury
- Cárdenas P, Pérez T, Boury-Esnault N (2012) Sponge Systematics facing new challenges. Advances in Marine Biology 61: 79-209
- Clarke ME, Whitmire CE, Yoklavich MM
 (this volume) State of Deep-Sea Coral and
 Sponge Ecosystems of the U.S. West Coast.
 In: Hourigan TF, Etnoyer PJ, Cairns SD
 (eds.). State of Deep-Sea Coral and Sponge
 Ecosystems of the United States. NOAA Tech
 Memo NMFS-OHC-4, Silver Spring, MD
- Costello MJ, Emblow CS, White R (eds.) (2001) European Register of Marine Species. A checklist of the marine species in Europe and a bibliography of guides to their identification. Patrimoines Naturels 50: 463 pp
- Cristobo FJ, Ríos P, Pomponi SA, Xavier JR. (2015)
 A new carnivorous sponge, *Chondrocladia*robertballardi sp. nov. (Porifera: Cladorhizidae)
 from two north-east Atlantic seamounts. Journal
 of the Marine Biological Association of the United
 Kingdom, 95(7)

- Culligan KM, Meyer-Gauen G, Lyons-Weiler J, Hays JB (2000) Evolutionary origin, diversification and specialization of eukaryotic MutS homolog mismatch repair proteins.

 Nucleic Acids Research 28: 463–471
- DeVictor ST, Morton SL (2010) Identification guide to the shallow water (0-200 m) octocorals of the South Atlantic Bight. Zootaxa 2599: 1-62
- Dohrmann M, Göcke C, Reed J, Janussen D (2012a) Integrative taxonomy justifies a new genus, *Nodastrella* gen. nov., for North Atlantic "Rossella" species (Porifera: Hexactinellida: Rossellidae). Zootaxa 3383:1–13
- Dohrmann M, Haen KM, Lavrov DV, Wörheide, G (2012b) Molecular phylogeny of glass sponges (Porifera, Hexactinellida): increased taxon sampling and inclusion of the mitochondrial protein-coding gene, cytochrome oxidase subunit I. Hydrobiologia 687:11–20
- Erpenbeck D, Ekins M, Enghuber N, Hooper JNA, Lehnert H, Poliseno A, Schuster A, Setiawan E, De Voogd NJ, Wörheide G, Van Soest RWM (2015) Nothing in (sponge) biology makes sense – except when based on holotypes. Journal of the Marine Biological Association of the United Kingdom:1-7
- Etnoyer PJ (2008) A new species of *Isidella* bamboo coral (Octocorallia: Alcyonacea: Isididae) from northeast Pacific seamounts. Proceedings of the Biological Society of Washington 121(4): 541-553
- Felder DL, Camp DK (eds.) (2009) Gulf of Mexico Origin, Waters, and Biota. Vol. 1: Biodiversity. Texas A&M Press: College Station, 1393 pp
- France SC, Hoover LL (2001) Analysis of variation in mitochondrial DNA sequences (*ND3*, *ND4L*, *MSH*) among Octocorallia (=Alcyonaria) (Cnidaria: Anthozoa). Bulletin of the Biological Society of Washington 10:110–118

- France SC, Hoover LL (2002) DNA sequences of the mitochondrial *COI* gene have low levels of divergence among deep-water octocorals (Cnidaria: Anthozoa). Hydrobiologia 471:149-155
- Hill MS, Hill A, Lopez J, Peterson KJ, Pomponi S, Diaz MC, Thacker RW, Adamska M, Boury-Esnault N, Cárdenas P; Chaves-Fonnegra A, Danka E, De Laine B, Formica D, Hajdu E, Lobo-Hajdu G, Klontz S, Morrow CC, Patel J, Picton B, Pisani D, Pohlmann D, Redmond NE, Reed J, Richie S, Riesgo A, Rubin E, Russell Z, Rützler K, Sperling EA, di Stefano M, Tarver JD, Collins AD. (2013) Reconstruction of Family-level Phylogenetic Relationships within Demospongiae (Porifera) Using Nuclear Encoded Housekeeping Genes. PLoS ONE
- Hogg MM, Tendal OS, Conway KW, Pomponi SA, van Soest RWM, Gutt J, Krautter M, Roberts JM (2010) Deep-water sponge grounds: reservoirs of biodiversity. UNEP-WCMC Biodiversity Series No. 32. UNEP-WCMC, Cambridge, U.K., 84 p
- Horvath EA (2011) An unusual new "sea fan" from the northeastern Pacific Ocean (Cnidaria: Octocorallia: Gorgoniidae). Proceedings of the Biological Society of Washington 124(1): 45-52
- Lapian HFN, Barucca M, Bavestrello G, Biscotti MA, Bo M, Canapa A, Tazioli S, Olmo E (2007) A systematic study of some black corals species (Antipatharia, Hexacorallia) based on rDNA internal transcribed spacers sequences. Marine Biology 151:785-792
- Lee,WL, Reiswig HM, Austin,WC, Lundsten L. (2012), An extraordinary new carnivorous sponge, *Chondrocladia lyra*, in the new subgenus Symmetrocladia (Demospongiae, Cladorhizidae), from off of northern California, USA. Invertebrate Biology 131: 259-284
- Lindner & Cairns (2011) (see Cairns & Lindner (2011)

• •

- Lumsden S, Hourigan T, Bruckner A, Dorr G (eds.) (2007) The State of Deep Coral Ecosystems of the United States. CRCP-3: 365 pp
- Lundsten L, Reiswig HM, Austin WC (2014). Four new species of Cladorhizidae (Porifera, Demospongiae, Poecilosclerida) from the Northeast Pacific. Zootaxa, 3786(2), 101-123.
- Maldonado M, Aguilar R, Bannister RJ, Bell JJ,
 Conway KW, Dayton PK, Diaz C, Gutt J, Kelly M,
 Kenchington ELR, Leys SP, Pomponi SA, Rapp
 HT, Rutzler K, Tendal OS, Vacelet J, Young CM.
 2016. Sponge grounds as key marine habitats: a
 synthetic review of types, structure, functional
 roles, and conservation concerns. Pp. 1-39 in Rossi
 (ed) Marine Animal Forests. Springer International
 Publishing, Switzerland.
- McFadden CS, Benayahu Y., Pante E, Thoma JN, Nevarez PA, France SC (2011) Limitations of mitochondrial gene barcoding in Octocorallia. Molecular Ecology Resources 11:19-31
- Morrow C, Cardenas P (2015) Proposal for a revised classification of the Demospongiae (Porifera). Front Zool 12:7
- Muzik KM (1979) A systematic revision of the Hawaiian Paramuriceidae and Plexauridae (Coelenterata: Octocorallia). PhD dissertation, Coral Gables, Florida: Univ. of Miami, 227 pp
- National Oceanic and Atmospheric Administration (NOAA) 2010. NOAA Strategic Plan for Deep-water Coral and Sponge Ecosystems: Research, Management, and International Cooperation. Silver Spring, MD: NOAA Coral Reef Conservation Program. NOAA Technical Memorandum CRCP 11, 67 pp
- Opresko DM (2005) New genera and species of antipatharian corals (Cnidaria: Anthozoa) from the North pacific. Zool. Mededelingen Leiden 79(2): 129-165

- Opresko DM (2009) A new name for the Hawaiian antipatharian coral formerly known as *Antipathes dichotoma* (Cnidaria: Anthozoa: Antipatharia). Pacific Science 63(2): 277-291.
- Opresko DM & Loiola L (2008) Two new species of Chrysopathes (Cnidaria: Anthozoa: Antipathidae) from the western Atlantic. Zootaxa 1707: 49-59
- Opresko DM, Wagner D, Montgomery AD, Brugler MR (2012) Discovery of *Aphanipathes verticillata* (Cnidaria: Antipatharia) in the Hawaiian Islands. Zootaxa 3348: 24-39
- Pante E, Watling L (2011) *Chrysogorgia* from the New England and Corner Rise Seamounts: Atlantic-Pacific connections. Journal of the Marine Biological Association of the United Kingdom,92(5): 911-927
- Pante E, France SC, Couloux A, Cruaud C, McFadden CS, Samadi S, Watling L (2012) Deep-water origin and in-situ diversification of chrysogorgiid octocorals. PLOS ONE 7(6):e38357
- Pomponi SA, Baden DG, Zohar Y (2007) Marine Biotechnology: realizing the potential. Marine Technology Society Journal 41(3): 24-31
- Reed JK, Pomponi SA, Weaver D, Paull CK, Wright AE (2005) Deep-water sinkholes and bioherms of south Florida and the Pourtales Terrace habitat and fauna. Bulletin of Marine Science 77: 267-296
- Reed JK, Weaver DC, Pomponi SA (2006) Habitat and fauna of deep-water *Lophelia pertusa* coral reefs off the southeastern U.S.: Blake plateau, Straits of Florida, and Gulf of Mexico. Bulletin of Marine Science 78: 343-375

- Rützler K, Van Soest RW, Piantoni C (2009)

 Sponges (Porifera) of the Gulf of Mexico.

 Pp. 285–313 in: Felder DL, Camp DK (eds)
 Gulf of Mexico–Origins, Waters, and Biota
 Biodiversity, Book 1. Texas A&M University
 Press, College Station, Texas
- Simpson A, Watling L (2011) Precious corals (Coralliidae) from north-western Atlantic seamounts. Journal of the Marine Biological Association of the United Kingdom 91: 369-382
- Stone RP, Lehnert H, Reiswig H (2011) A guide to the deep-water sponges of the Aleutian island Archipelago. NOAA Professional paper NMFS 12, 187 pp
- Tu T-H, Dai C-F, Jeng M-S (2016) Taxonomic revision of Coralliidae with descriptions of new species from New Caledonia and the Hawaiian Archipelago. Mar Biol Res 12:1003-1038
- Vacelet J, Boury-Esnault N. (1995) Carnivorous sponges. Nature 373, 333-335.
- Viada ST, Cairns SD (2007) A new species of *Nicella* (Anthozoa: Octocorallia) from the western Atlantic. Proceedings of the Biological Society of Washington 120(2): 227-231
- Wagner D, Opresko DM (2015) description of a new species of *Leiopathes* (Antipatharia: Leiopathidae) from the Hawaiian Islands. Zootaxa 3974: 277-289.
- Wagner D, Brugler MR, Opresko DM, France SC, Montgomery AD, Toonen RJ (2010) Using morphometrics, *in situ* observations and genetic characters to distinguish among commercially valuable Hawaiian black coral species; a redescription of *Antipathes grandis* Verrill, 1928 (Antipatharia: Antipathidae). Invertebrate Systematics 24:271-290

- Watling L (2007) A review of the genus *Iridogorgia* (Octocorallia: Chrysogorgiidae) and its relatives, chiefly from the North Atlantic. Journal of the Marine Biological Association of the United Kingdom 87: 393-402
- Watling L, France SC (2011) A new genus and species of bamboo coral (Octocorallia: Isididae: Keratoisidinae) from the New England Seamounts. Bulletin of the Peabody Museum of Natural History 52: 209-220
- Watling L, France SC, Pante E, Simpson A (2011) Chapter 2: Biology of Deep-Water Octocorals. Advances in Marine Biology 60: 41-122
- Williams, CG & Alderslade P (2011) Three new species of pennatulacean octocorals with the ability to attach to rocky substrata (Cnidaria: Anthozoa: Pennatulacea). Zootaxa 3001: 33-48
- Williams GC, Lundsten L (2009) The nephtheid soft coral genus *Gersemia* Marenzeller, 1878, with the description of a new species from the northeast Pacific and a review of two additional species (Octocorallia: Alcyonacea) Zool. Med. Leiden 83 (34): 1067-1081
- Wörheide G, Erpenbeck D, Menke C (2007) The Sponge Barcoding Project: aiding in the identification and description of poriferan taxa. In: Custódio MR, Lôbo-Hajdu G, Hajdu E, Muricy G (eds) Porifera Research: Biodiversity, Innovation and Sustainability. Museu Nacional, Rio de Janeiro, Brazilet al.