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Marine biodiversity of Guam and the Marianas: overview

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Abstract—The objective of this volume is to document the marine biodiversity of Guam, a small island at the southern end of the Mariana island arc. Guam has the best-documented marine biota in Micronesia, and affords a glimpse at the great biodiversity of Pacific island reefs. The papers that follow strive to provide a critical inventory of the marine biota of Guam, with less comprehensive coverage of other Mariana Islands. Diatoms are the only previously studied group not included. This paper serves to introduce and overview this effort, the Marine Biodiversity Survey of Guam. The environmental setting and marine habitats of the Marianas are briefly reviewed, followed by a description of the methods and resources used for the survey. A brief overview is presented of what we know and how much remains to be learned about species richness of major taxa in the region. Of the 6172 species listed in this volume, 5640 are recorded from marine habitats in the Marianas. This represents the greatest marine diversity recorded for any area of comparable size. Nevertheless most taxa remain poorly known, and the daily discovery of new records shows that even the most intensively surveyed groups remain incompletely studied and that the actual marine diversity of these islands is much greater.

Introduction

Knowing the organisms that live around us is perhaps the most fundamental of biological inquiries, dating back to before human origins. We draw many resources from the living world, and an ability to identify species and know their attributes is the first step in their utilization. Basic and applied research in most biological disciplines start with the identification of the organism(s) involved. This is especially true for fields that deal with diverse environments, such as tropical fisheries, conservation biology, rain forest ecology, or reef management. Despite the fundamental necessity for knowing the biota, we remain woefully ignorant of much of the diversity around us. How poorly known Earth's biodiversity is has become a cliché in recent years, especially with regards to the tropics (May 1990).

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The purpose of this volume is to bring together the records of marine species known from Guam, and to a lesser extent, all the Mariana Islands. That we know much, yet still little is amply demonstrated in the pages that follow. Over 5600 species are documented from marine habitats in the Marianas herein, yet this represents but a fraction of what lives in the sea around these islands. By documenting each species with vouchers, photographs, and literature records, this volume and associated photo-CD and web site strive to make identification of marine species accessible to everyone.

Our knowledge about the marine biodiversity of Guam and the Marianas goes back well over three millennia. The Marianas were among the first islands settled in Micronesia, with clear evidence for human occupation dating to 3500BP and indications of human presence to 4300BP (Kirch 2000). Human colonists introduced little in the way of terrestrial vertebrates, thus such Micronesian dietary mainstays as the jungle fowl, pig, and dog were prehistorically absent, and even rats were not establish in the archipelago until ca. AD 1000 (Steadman 1999). Thus the indigenous Chamorro society had to rely even more on the sea for its protein needs than inhabitants of most other high islands in Oceania. A vast knowledge about marine biodiversity must have existed prior to western contact, as evidenced by the wide range of marine resources utilized, and a highly efficient maritime culture that involved even a major pelagic fishery (Amesbury 1999, Kerr 1990). Much of this maritime lore was lost with the collapse of ancient Chamorro society during the Spanish colonial period, especially with the destruction of ocean-going canoes following the forced resettlement of most of the archipelago's population to Guam. Nevertheless indigenous taxonomy survives and has been supplanted with new and borrowed names (Kerr 1990). Much remains to be documented in marine ethnobiology and folk taxonomy in the Marianas, however. With the arrival of westerners, the focused scientific exploration and written documentation of the marine biota of the islands began. The early, largely expedition-based scientific exploration of Guam gave way to a more locally based effort following the establishment the University of Guam, especially after the establishment of the Marine Laboratory in 1970. The history of marine biological explorations on Guam is reviewed by Eldredge (2003) in the following paper.

This volume had its beginnings in a Technical Report published in 1981 by the University of Guam Marine Laboratory (UOGML), entitled "A working list of marine organisms from Guam". That report strived to bring together what was known about Guam's marine biota and documented 2009 species in checklist format. Coverage was uneven then as it remains today, with algae, corals, mollusks, echinoderms, and fishes comprising the bulk of the records. After I arrived at the UOGML in 1991 Chuck Birkeland suggested that it would be good to revise this checklist volume, as many additional species have been recorded informally and several additional, unpublished checklists have been put together since 1981. To enhance these we started to systematically document macroinvertebrates encountered, and sequentially focused more detailed study on one taxon after another. A series of biodiversity surveys funded by the Dept. of Defense, Sea Grant, and the Insular Pacific Marine Research Program in the late 1990's provided much needed resources for this endeavor and accelerated research on the biota, while my departure from UOGML in 2000 provided the impetus for publishing what was learned to date. This informal Marine Biodiversity Survey of Guam remains active, as a collaborative venture between the UOGML and the Florida Museum of Natural History at the University of Florida. Additional checklists and new records and species descriptions are planned for future issues of Micronesica, and the checklist of marine organisms will be actively maintained and updated at the project's web site (http://www.flmnh.ufl.edu: reefs). In this paper I review the geographic setting and habitats of the Marianas, the methods used in biodiversity compilations, and provide an overview of what we have learned about the biota to date.

Setting

The Marianas form a ca. 800 km long island arc system on the Philippine plate, just west of the northwestern, subducting margin of the Pacific plate. The Izu, Ogasawara (Bonin) and Kazan (Volcano) islands to the north are part of the same island arc system, while the Palau Islands to the south were formerly continuous but have since rifted. The archipelago is comprised of 15 high islands in two arcs, the young (max 1.3 Ma), volcanically-active, inner arc of the Northern Marianas and the older (max. 43 Ma), geologically-complex, and now volcanically-inactive, frontal arc of the Southern Marianas (Siegrist & Randall 1992).

This geographical/geological subdivision should not be confused with the political subdivision of the archipelago into the US Territory of Guam, the southernmost island, and the Commonwealth of the Northern Mariana Islands (CNMI), comprising all other islands in the chain. Thus Rota, Aguijan, Tinian, Saipan, and Farallon de Medinilla of the Southern Mariana frontal arc are part of the Commonwealth of the Northern Mariana Islands (Fig 1). All permanent habitations in the Marianas are on the southern islands. The northern islands have been periodically inhabited, but have been evacuated and remain largely uninhabited, partly because of the danger of active volcanism. Guam is the largest (541 km^2) and most populated (ca. 140,000) island in the Marianas and Micronesia, and the main economic and transportation hub of the region. In comparison the islands of the CNMI add up to ca. 475 km^2.

The Marianas were initiated about 43 Ma when the Pacific plate changed its direction of subduction from NW to WNW. The islands of the southern arc date back to this time, although they did not reach sea level for some time. They had a complex geological history since then, with periods of submarine and subaerial volcanism, uplift, subsidence, and rifting (see Tracey et al. 1964, Siegrist & Randall 1992). Their complex origins are manifested in heterogeneous surface

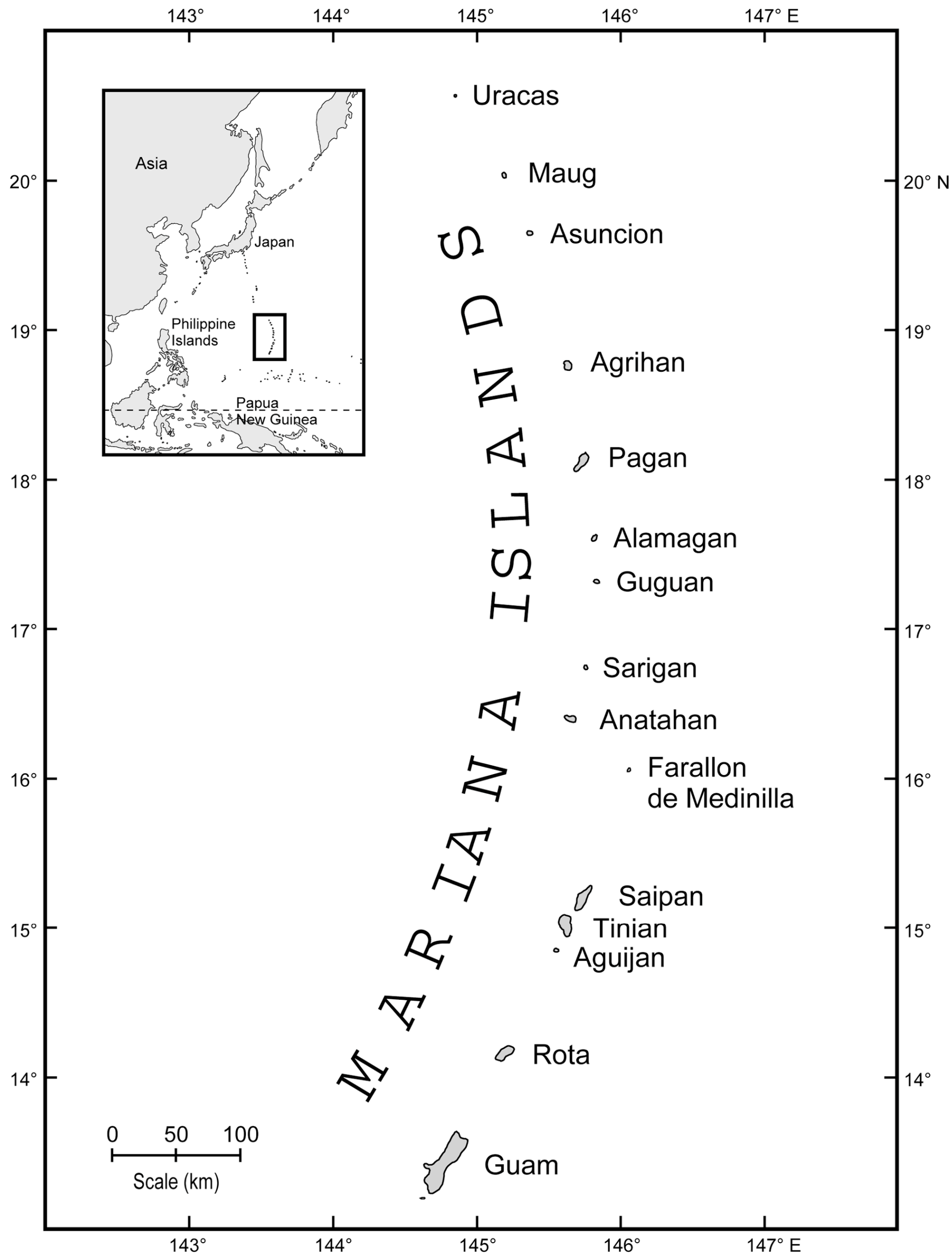

Figure 1. Map of the Mariana Islands

geology with varied igneous and sedimentary facies, with reefal and detrital limestones predominating. Guam has the most heterogeneous topography and geology. Northern Guam is a relatively flat, uplifted limestone plateau, bordered by karstic cliffs and limited reef development. In contrast southern Guam is dominated by volcanic hills, locally with limestone veneers, with same valleys terminating in protected embayments. Volcanic exposures are more limited in extent in the other southern islands, where karst predominates. In contrast, the islands of the Northern Mariana arc are all young, volcanically active, and comprised virtually exclusively of volcanic rocks.

The Southern Marianas are bathed by the westward flowing North Equatorial Current and thus lie upstream of Indo-Malayan archipelago. The narrow band of the eastward flowing Subtropical Countercurrent – Hawaiian Lee Countercurrent system however traverses the northern islands around 19^{o}N (Xie et al. 2001), although the nearest islands upstream are over 2000 km to the west. In contrast the Caroline Islands (Palau and Federated States of Micronesia) lie along the northern boundary of the eastward flowing Equatorial Countercurrent, and thus at times downstream of, and connected by numerous island stepping stones to, the megadiverse Indo-Malayan archipelago. This connection, termed the Caroline Conduit (Springer 1982) has facilitated dispersal into southern Micronesia, but is not available for the colonization of the Marianas.

Waters around Guam average 27^{o}C during the winter, warming to 30^{o}C during summer. Steady northeast tradewinds characterize the dry season from December to June, while winds are limited and variable during the rest of the year. Tidal range is less than 1 m, and rainfall at sea level averages 1.8 m per year on Guam.

Marine Habitats

The Northern Marianas have rocky and sandy littoral and sublittoral habitats with coral communities and incipient reefs growing on igneous outcrops and rubble. Consequently there are no fringing reefs or lagoonal habitats except for the protected crater of Maug. Although poorly known, the biota of the Northern Marianas appears to be largely a less diverse version of that of the Southern Marianas, although some species are clearly limited to the northern islands, likely specialized to uniquely northern habitats (Vermeij et al. 1983, Asakura & Furuki 1994). The remainder of this section on marine habitats focuses on the Southern Marianas.

The reefs and shallow marine habitats of Guam are reviewed by Emery (1962) and Randall & Eldredge (1976), while those of other Southern Marianas are reviewed by Cloud (1959) and Eldredge & Randall (1980). Numerous, more detailed studies of selected areas within several of the Mariana Islands have been published in the UOGML Technical Report series (see the UOGML website: http://www.uog.edu/marinelab/ for a listing). The composite volcanic and karstic nature of the Southern Marianas provides foundations for varied marine habitats. Coastal geology and physiography, level of uplift and groundwater discharge, and exposure to wind, wave and currents, all strongly influence the nature of marine habitats around each island. Volcanic shorelines are largely limited to southwestern Guam, while karstic shores of mostly Miocene to Pleistocene limestones predominate elsewhere in the Southern Marianas. Much of the shoreline is cliffed, with large sections lacking reef protection or fronted only by supratidal benches, often with rimmed pools. In such exposed areas huge boulders eroded from the cliff face often dot the fore reef slope, providing diverse microhabitats. While some cliffed coasts are fronted by narrow, intertidal reef flats, wider (>100 m) fringing reefs are largely restricted to less rugged shores. Large embayments created by faulting and groundwater discharge, such as Tumon, Hagåtña and Pago Bays on Guam, have wide fringing reefs, as do the gently sloping shores along southeastern Guam and southwestern Saipan. Fringing reefs in the Marianas generally have a well-developed reef crest. A gradient of southwardly increasing fringing reef development on Guam may partly be the result of greater tectonic uplift toward the north. Additional variation in reef habitats result from differences in wind, wave, and current exposure, with eastern reefs being more exposed than western reefs to both tradewinds and typhoons. Differences of exposure have a major impact not only on fringing reef but also on fore reef habitats.

As a result of uplift in the south and youth of volcanism in the north, barrier reef and lagoon development is limited in the Marianas, in striking contrast to other Micronesian island groups. The only significant lagoonal habitats in the Marianas are Apra Harbor and Cocos lagoon on Guam, and Tanapag-Garapan lagoon on Saipan. Only Apra Harbor has substantial lagoonal habitats >10 m deep. Mangals are thus poorly developed, and have also undergone considerable reduction since the arrival of humans (Amesbury 1999). The main remaining mangals on Guam are in inner Apra Harbor and along the SW shore (Wilder 1976). Seagrass beds are developed along the larger fringing reef and shallow lagoon systems.

Apra Harbor, the largest and busiest port in Micronesia, is the only deep (to 60 m) lagoon in the Marianas. Its unique habitats host many species not found elsewhere in the archipelago. The harbor is also the main entry point for species introduced by shipping traffic (Paulay et al. 2002). Apra Harbor has been substantially altered following World War II, as the Glass Breakwater, built over the barrier reef and bank that previously bound the lagoon along the north, has substantially reduced circulation with the surrounding ocean (see Fig. 2 in Paulay et al. 2002). Despite these major alterations, Apra Harbor has a vibrant and thriving marine biota, with well-developed reefs, some of the highest coral cover on Guam (albeit dominated by *Porites rus*), and a diverse biota. Physical, chemical, and biotic conditions all show pronounced east to west gradients in the harbor, related to the unidirectional exchange of water through the western entrance. Benthic habitats range from fairly exposed and oceanic reefs along the northwestern end of the Orote Peninsula, to silt-choked, lagoonal patch reefs and mangroves in Sasa Bay and the Inner Harbor, with corresponding variation in the biota.

Seaward of cliffed shores, benches, fringing and barrier reefs, the southern islands are encircled by a well-developed, oligotrophic fore reef, with small sand channels and pockets. The topography of this outer reef slope varies longshore, reflecting local conditions and physiography of the antecedent Plio-Pleistocene reef foundation. Fore reefs are moderately steep, with some terracing, and give way to a more gently-sloping, detrital slope with scattered patch reefs around 40-80 m depths along much of the island. Reef walls, the remnants of antecedent karst cliffs, are uncommon. On Guam they are best developed in deep water (>30 m) along strongly cliffed, exposed shores such as the south side of the Orote peninsula. The fore reef has rich coral communities with marked zonation with depth as well as variation longshore. As both prevailing winds and typhoons are from the east, habitats differ markedly between eastern, windward, and western, leeward exposures.

Typhoons are frequent as the Marianas lie in the western Pacific typhoon trough. In addition to their striking impact on algal and coral communities and reef geomorphology, immediately evident after the passage of major storms (e.g., Randall & Birkeland 1977), typhoons also have more subtle and long-term effects. For example, the cryptobiota of mobile rubble is heavily impacted by the grinding action of storm swells. Corals with delicate growth forms, such as the table *Acropora* that characterize most oceanic island reef slopes, are rare on fore reefs shallower than 30 m on Guam. *Acropora hyacinthus* and *A. cytherea*, two species that frequently dominate this biotope and range virtually throughout Oceania, are absent from the Marianas (Randall 2003). Several echinoderm species that live exposed on the reef, are virtually absent from windward exposures, apparently because they are injured and killed by wave surge during typhoons (Kerr et al. 1993). Reefs are also ravaged by crown of thorn sea stars and a variety of anthropogenic impacts, including overfishing, sedimentation, runoff, and other pollution, especially around Guam (Richmond & Davis 2002).

Both the environmental setting and impact from runoff make the southwest shores of Guam unusual. This area lies in the most-sheltered exposure on island. It also has the only substantial volcanic shoreline in the Southern Marianas, with interspersed valleys that open into soft-bottom bays. Soft-bottom habitats occupy larger tracks than elsewhere, sediments have a high terrigenous component, and the infauna is characterized by numerous species not known elsewhere. A number of epifaunal species, including several reef corals, are also largely or entirely restricted to this area. Unfortunately the luxurious coral communities that inhabited this area until the 1960's have been severely damaged by crown of thorns and sedimentation from ill-conceived road construction (Carlson & Hoff 2003, Richmond & Davis 2002)

The karstic limestones bordering and underlying reefs are riddled by caves and caverns above and below water (Taborosi 2000). Although marine caverns and crevices are fairly common, most are of limited horizontal extent. Caves and caverns are especially common in areas where cliffs meet the fore reef without intervening fringing reefs. The largest include the striking Grotto complex on

Saipan, a large cave in north Tinian, and the Blue Hole on Guam. Large blocks fallen from cliff faces provide additional cryptobiotic habitats. These latter are generally features of unprotected, cliffed coasts, and are especially common along the south face of the Orote Peninsula and the northern half of the east coast on Guam. Crevice and cave habitats have a rich sessile fauna dominated by forams, sponges, cnidarians, tubiculous polychaetes, bryozoans, brachiopods, and ascidians, as well as a rich mobile fauna that lives exposed on the walls as well as hidden in cracks and fissures.

Caverns appear to harbor largely the same biota as the reef's interior, but are more accessible to exploration because the large spaces allow ready human access. The same fauna is encountered deep in piles of reef rubble. Rubble fields are common on the fore reef as well as in deeper lagoons. The discovery of "rare" gastropods deep in rubble led to the exploration of this habitat by shell collectors on Guam, and numerous unusual species have been documented from this habitat (Smith 2003). This habitat was also explored for other invertebrates in the past decade, especially through the untiring efforts of the late Harry Conley, yielding numerous unusual and new mollusks, crustaceans, echinoderms, and other invertebrates.

Although zooxanthellate corals extend to remarkable depths in the Marianas (~150m; R.H. Randall pers. comm. 2002), in most areas they become uncommon around 60 m. Below this depth, the reef talus, or "twilight zone" hosts a diverse azooxanthellate cnidarian community of gorgonians, nephtheid soft corals, antipatharians, sponges, "giant" sessile foraminiferans, and other diverse epi- and infauna. There is a substantial turnover in species composition between the fore reef and the reef talus (Peshut 2000). The deep water biota has been explored with dredging, focused on the gently sloping detrital terrace developed at ca. 100-m depth around Guam. The biota below 150 m has received little attention as yet, although limited sampling through baited traps aimed at deep-water crustacean resources have revealed several interesting crustaceans, fishes, and a few echinoderms from greater depths.

The deep sea around the Mariana Islands harbors varied and unusual habitats as a result of the tectonic complexity of the area. The Mariana Trench to the east is the surface manifestation of the subduction zone responsible for the Mariana arc, and includes the deepest part of the world ocean, the 11,033 m Challenger Deep, ca. 350 km SW of Guam. Tectonic features associated with the subduction zone include mud volcanoes in the fore arc between the trench and the Marianas (Fryer 1992, 1996). The Mariana Trough to the west is the ca. 5 Ma spreading center of the Mariana back-arc, and has a well-developed hydrothermal vent system. The biota associated with these vents, explored in 1987 by the *Alvin* and subsequently by the *Shinkai*, has high endemism, a reflection of its isolation from other spreading centers (Hessler et al. 1988, Hessler & Lonsdale 1991, Hasegawa et al. 1997).

Methods and Volume

The objective of this volume is to review the marine biota of Guam, and to a more limited extent, of all the Mariana Islands. Papers cover virtually all groups that have been taxonomically studied on Guam. The main exception is diatoms, which have received some past attention (Zolan 1981), but are not reviewed herein. The volume is centered on critical checklists that list all species known in the groups covered, but provide little more than voucher information on individual species. It also includes papers that describe or review selected taxa and species in greater detail. Four of the latter (Sardá et al. 2002, McLaughlin 2002, Ng 2002a, 2002b), although part of this effort, were published in the previous issue (34:2) of Micronesia.

All the checklists are critical in the sense that authors were asked to evaluate and taxonomically update all previously published records, and to exclude or note questionable ones. The primary objective was biological accuracy rather than comprehensiveness of literature coverage. All too often checklists are uncritical compilations of species names from the literature, resulting in some species covered under multiple names (misidentifications or synonymies), while others are included erroneously (poor identifications or location records). The starting point for each checklist was authors' knowledge of the biota of Guam, and literature records were evaluated against this knowledge.

Several major groups (algae, corals, prosobranch and opisthobranch gastropods, fish and other marine vertebrates) have been intensively studied on Guam over the years by one or more dedicated taxonomists, who have assembled extensive, published or unpublished checklists, which were updated for this volume. Several other groups (forams, other anthozoans, crustaceans, echinoderms, and some minor phyla) have received considerable attention in the past, but also were the focus of recent survey efforts. Other taxa (sponges, hydrozoans, scyphozoans, flatworms, cephalopods, bivalves, and ascidians) were little studied previously, but received focused attention in recent biodiversity surveys or during the preparation of this volume. Finally numerous taxa remain virtually or entirely unstudied.

A focused effort was made in the past decade to record additional species encountered in previously studied taxa and to survey major groups not systematically examined in the past. This effort received a considerable boost between 1996-2000 through five major biodiversity surveys funded by COMNAVMARIANAS (U.S. Department of Defense), Sea Grant, and the Insular Pacific Marine Research Program. Two of these focused on Apra Harbor (Eldredge & Paulay 1996, Paulay et al. 1997), one on southern Orote – North Agat Bay area (Paulay et al. 2001), one on Pugua Patchreef – Haputo area (Amesbury et al. 2001), and one on non-indigenous species island-wide (Paulay et al. 2002). Taxonomic workshops held at the UOGML on sponges by Michelle Kelly, soft corals by Yehuda Benayahu, and ascidians by Gretchen Lambert, provided additional coverage. Benayahu (1998) and Lambert (2003) also pursued field and lab work on island.

Much of this recent effort combined field and lab taxonomy. We attempted to differentiate and provide temporary names for each recognizable morphospecies in the field. Each was then documented with field notes, *in situ* or lab photographs, preserved, and identified. Identification of species in some well-known groups were made by our team at UOGML, others were examined by specialists. Current taxonomic knowledge of the highly diverse biota of the tropical western Pacific remains limiting, as many commonly encountered species are either undescribed or belong to groups that have not been sufficiently studied to allow identification without a taxonomic revision. Furthermore, taxonomic studies have traditionally focused on preserved material, and although field data and photographs are increasingly making inroads into marine taxonomy, many taxonomists still work predominantly with fixed specimens. As a result museum-based specialists have not recognized some species that are readily identifiable in the field. Many characters apparent to a field worker and used in field identification are neither known to museum-based taxonomists nor described in the literature. Conversely some species that can be readily differentiated using laboratory techniques are impossible to differentiate in the field. A major task for field-based taxonomists is to denote characters useful in field identification for species that have been described based on museum specimens, i.e. to "translate" existing, traditional taxonomic knowledge for field use. This is ideally a two-way dialogue, as both field and museum taxonomists (if different) will benefit from the other's perspective. Field-based taxonomists also need to learn which species groups are difficult or impossible to differentiate in the field. Once field knowledge is developed for a group, taxonomic identifications can be effectively applied to field surveys. We have been developing such a field taxonomic knowledge base for Guam and neighboring islands. The results of this effort are partially presented in the photographic coverage presented on the web site and CD-ROM developed for this volume, covering 1283 species. Photographic coverage will be substantially expanded in a second edition of the CD-ROM, paralleled on the web-site, as well as in a field guide, all currently in preparation.

We used a field-based morphospecies concept for biodiversity surveys. Most species were first identified on the basis of field characters and assigned a name. This name was the species' scientific name if known, or a temporary field name coined for communication about that species. If unidentified, the species was photographed, fixed and identified using available taxonomic resources or given / sent to a specialist for identification. If there was one-to-one correspondence between the field and lab species concepts, then the identification work was considered complete. If two or more forms distinguished in the field were lumped by the specialist, then a discussion ensued about potential differences to resolve the conflict. Unresolved species limits were coded as forms of a species (e.g., *Didemnum ligulum* form A and form B). Unresolved species limits can be tested by additional study, often readily with molecular markers. If a single species identified in the field was identified as more than one species in the lab, then the field worker would attempt to find subtle characters differentiating these in the field. If such characters are difficult to find or apply under field conditions, such groups of species can be lumped under a single, wider category (e.g., *Porites* massive species) for the purposes of field surveys. The abundance of sibling species in the sea, resulting in part from the frequently non-visual species recognition signals utilized by marine species (Knowlton 1993), implies that a combination of field, museum-based, and genetic methods are often needed for effective species delineation.

Many species that can be reliably differentiated in the field nevertheless cannot be named immediately because they are undescribed or remain unidentified. Although authors were asked to be critical of literature records, they were encouraged to be comprehensive in recording all known species, including presently undescribed as well as unidentified taxa. Such species are identified in checklists to the lowest taxonomic level possible and given a numerical designation, with additional information added parenthetically if desired (e.g., *Dysidea* sp. 2 (n. sp.), *Chelonaplysilla* sp. 1 (gray)). Photographic and specimen vouchers allow for the eventual correlation of these names with future identifications or descriptions. A major advantage of the present inventory is that it creates a nomenclatural tag for all known marine morphospecies on Guam to which new records and future name changes can be compared, added, and applied. The modifiers '?', 'cf.", and 'aff.' are applied to species names to denote problems with identification. A '?' denotes uncertainty in identification because of lack of knowledge on the part of the identifier. The modifier 'cf.' denotes perceived differences from typical specimens of that species, but the species is still judged to be likely conspecific with the named form. The modifier 'aff.' is applied when the species is considered specifically distinct from, but similar to the named form.

Authors were asked to voucher all records by one or more of the following means: 1) reference to published record, 2) specimen in a permanent repository, 3) photographic record, 4) sight record by a reliable observer. In addition to voucher information, authors were encouraged to include information about depth range (<60 m, 60-200 m, >200 m), name of identifier, records from other islands in the Marianas, and brief notes about species when relevant. Notes could include additional observations or taxonomic information about the species, such as details of sight record or nomenclatural changes relative to published records from Guam.

A tabular summary of all records, together with copies of the 1283 cited voucher photographs will be available online at: http://www.flmnh.ufl.edu/reefs and on the Marine Biodiversity of Guam CD-ROM (see web site for ordering). Most of the cited photos show live or fresh specimens and document living colors and field appearance. Version 1 of both releases will cover exactly the records cited in this volume. Planned additions, corrections, and other improvements to the checklist and photographic database will be posted online as they become available, and released periodically as new, numbered versions on CD-ROM. A major photographic addition covering corals and fishes, two groups for which the checklists in this volume do not cite photographs, is planned in the immediate future. Future papers in Micronesica are planned to cover additions to and improvements in our knowledge of the marine biota.

Taxonomic Coverage

This volume documents 5728 species from the Marianas, including 5640 marine and 88 non-marine species (cnidarians, prosobranchs, crustaceans, and turtles), attesting to the biodiversity of the area. Nevertheless this represents but a fraction of the biota, much of which remains to be documented. An additional 446 species are recorded in two papers (Lobban & Tsuda 2003; Newman et al. 2003) from other areas of Micronesia, for a total of 6172 species documented. Here I review the current level of knowledge of each major group in the Marianas.

Prokaryotes and Eukaryotes Other than Animals

Except for algae and forams, virtually nothing is known about the non-metazoan marine biota of Guam. The megadiverse world of marine prokaryotes and protists remains largely undocumented. Macroscopic algae (multicellular cyanobacteria, as well as red, brown and green algae) and marine angiosperms have received considerable attention from Roy Tsuda and Chris Lobban, phycologists at the University of Guam. As a result the algal flora of the Marianas is fairly well characterized, and also vouchered in an extensive algal herbarium housed at the UOGML. Diatoms were briefly studied by Zolan (1981), who recorded 83 species from Pago Bay. Diatoms are the only marine taxon on Guam that was not restudied for the present volume. Foraminifera have received some attention over the years, and 303 species are now recorded (Richardson & Clayshulte 2003), although many more clearly remain to be documented.

Porifera

Much of what we know about the sponges of the Marianas was learned during the past decade, when macrosponges were collected for chemical, ecological, and biodiversity studies. The 128 species recorded to date are but a modest portion of even the macrosponge biota, and the fauna is estimated to consist of >500 species (Kelly et al. 2003).

Cnidaria

Cnidarians have received considerable but uneven attention in the Marianas. Hydrozoans (other than hydrocorals), scyphozoans, and cubozoans were virtually unstudied prior to this volume. These three classes remain but modestly worked, and a substantial diversity of especially hydrozoans awaits documentation.

Among anthozoans, scleractinians are best known, the result of Richard Randall's 35 year-effort: hard corals and vertebrates are the two best-documented groups in the Marianas. The numerous new records of corals listed in Randall (2003) are largely the result of new identification work (mostly of azooxanthellate taxa) on this previously extensively collected fauna. Soft corals have also received considerable attention, through Gawel's (1977) M.S. thesis and Benayahu's (1998) visit. In contrast other anthozoan groups have received limited attention, and numerous new records were just documented (Paulay et al. 2003b). A diverse, deep-water octocoral fauna has been collected but remains to be studied, and many species await documentation among hexacorals other than the Scleractinia.

MOLLUSCA

More species of mollusks than of any other phylum are documented in the Marianas. This is a reflection of both the size of the phylum and focused attention on major taxa. Thus opisthobranchs have been studied for over 30 years by Clay Carlson and Patty-Jo Hoff of the University of Guam. Their checklist, although previously unpublished, has been well known to opisthobranch workers. That Guam's documented opisthobranch diversity of 485 species is second only to Papua New Guinea's megadiverse fauna, from where 538 species have been documented, attest to their diligence (Carlson & Hoff 2003). Prosobranchs have received considerable attention over the past 25 years by Barry Smith of the UOGML, with 895 species currently recorded, albeit 46 of these are not marine. I gave considerable attention to the bivalve fauna of Guam in the 1990's, but much more remains to be documented. The 339 species recorded likely represent less than half of the fauna. Considerable effort has gone into documenting micromollusks among opisthobranchs and bivalves, but less so in prosobranchs. Cephalopods were virtually unstudied in the past, but received attention from Linda Ward, who focused on the group during her M.S. studies at the University of Guam. The numerous cephalopod species represented by singletons implies that the 22 species currently recorded are but a fraction of the total. Other molluscan classes are not very diverse, but also remain little studied.

ARTHROPODA

Marine arthropods and mollusks are comparable in diversity, but the former remain much more poorly documented in the Marianas. Decapods, stomatopods, and cirripeds have received the most attention, while microcrustaceans have been little studied. However even these macrocrustaceans remain undersampled. Crabs, with over 400 species recorded, are among the best known, but the rapid rate of new encounters and backlog of unidentified material implies that not more than half of even the crab diversity is currently recorded (Paulay et al. 2003a). Our knowledge of the crustacean fauna is the result of the combined efforts of several graduate students, faculty, and visiting investigators. Roy Kropp in particular sampled macrocrustaceans extensively. During the 1990's we reinvigorated crustacean collecting and doubled the known fauna. Pycnogonids are modestly known, while marine bugs and flies, but not other insects, are documented by Cheng & Mathis (2003).

ECHINODERMATA

Echinoderms have attracted attention in the Marianas for two centuries, and have been the focus of intensified effort since the crown-of-thorn sea star outbreaks of the 1960's. Despite this attention, 42% of the species recorded in this volume represent new records (Paulay 2003a). Although many of the new records are among small or cryptic ophiuroids and infaunal echinoids, many large and conspicuous species were also newly documented. Small and deep-water species remain substantially undersampled, implying that the group is considerably more diverse than the 202 species listed.

UROCHORDATA

Pelagic urochordates are common around Guam but remain undocumented. Ascidians are very diverse and were studied by Gretchen Lambert during two visits in the 1990's. She documented 117 species (Lambert 2003), but this diversity reflects more on the time she had available in Guam, than the total diversity of the fauna. Several hundred species likely occur on Guam.

VERTEBRATA

Fishes and other vertebrates are almost invariably the best-known part of any marine fauna, and Guam is no exception. However the rate of additions to the documented diversity of even this well-known group shows no sign of abating (Fig 1). 1106 fish species are now documented from the Marianas (Myers & Donaldson 2003). Marine reptiles, birds, and mammals are well documented around Guam, although additional records of pelagic species are likely.

OTHER METAZOAN PHYLA

The various worm phyla remain poorly documented in the Marianas. Most of what we know pertains to the larger-bodied worm groups, while the microfauna is unexplored. Thus polychaetes have received modest attention, mostly during visits by Alan Kohn and Julie Bailey-Brock (Bailey-Brock 2003), however many species remain to be documented even among large-bodied forms. Sipunculans and echiurans are moderately well known, but only a couple of nemerteans are documented (Paulay 2003b). Large, colorful polyclads received recent attention with Leslie Newman's (off-island) help. As a result more species of polyclads are presently documented from Guam than any other Pacific island (Newman et al. 2003). Nevertheless the rate of new species encounters suggests that less than half of the polyclad fauna has been documented. Other marine flatworms remain undocumented, as do other worm phyla. Bryozoans, diverse on Guam as elsewhere, remain virtually undocumented. A couple of brachiopods, ctenophores, and a placozoan have been recorded (Paulay 2003b). Only 16 of the 32 or so metazoan phyla are currently documented from Guam, even though all but three of these phyla are known from coral reefs (Paulay 1997) and most likely occur on island.

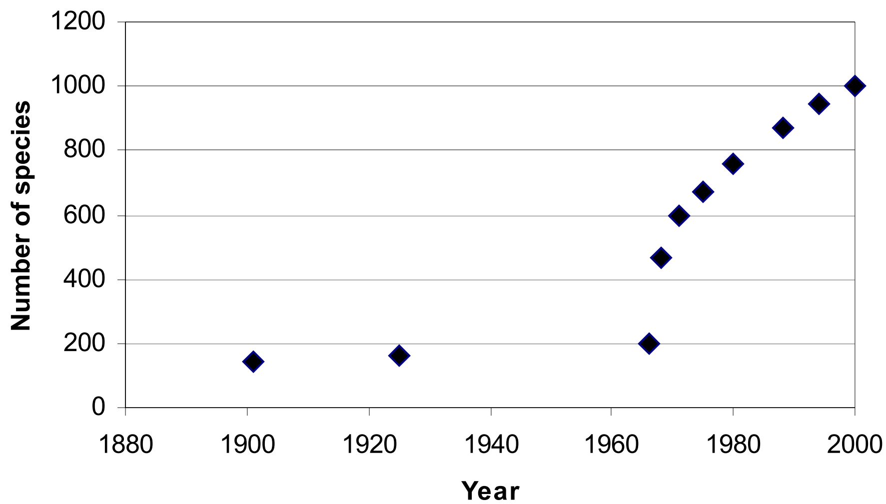

Figure 1. Fish species richness on Guam. Number of species recorded kindly provided by Rob Myers (pers. comm. 2000). Note that the change in the inflection of the curve corresponds to the arrival of the first resident fish taxonomist on island in the 1960's.

Biodiversity & Biogeography

Although more marine species are now known from the Marianas than from any comparable-sized area, the recorded species richness represent but a fraction of the actual diversity. Species richness of even the best known groups, such as fishes, keeps increasing with additional attention and has not plateaued (Fig 1). The megadiverse microbiota of small metazoans and algae, not to mention unicellular organisms, is essentially unsurveyed. A comparison between the last comprehensive survey (UOGML 1981) and the present effort reveals an overall 103% increase (4070 vs. 2009 species) in documented species richness for groups that were covered in the previous survey. Many groups covered in the present survey did not appear in the 1981 compilation. Taking all taxa into consideration, the present checklist includes a 181% increase in number of species over the 1981 study. There is considerable variation in the proportional increase among taxa (Fig 2), with little increase in documented diversity in some groups and huge increases in others. This variation is caused more by variation in taxonomic effort than by comprehensiveness of existing knowledge. For example, there have been substantial increases in the recorded diversity of some of the best-studied groups, like echinoderms, but little in others, like algae.

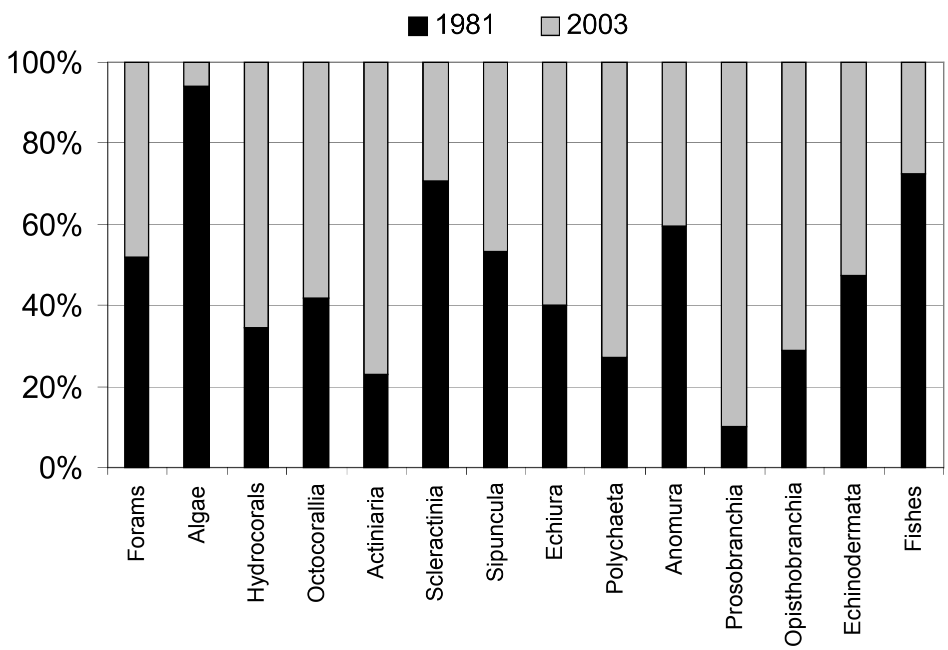

Figure 2. Change in documented species richness between 1981 and 2002. Comparison based on number of species documented in UOGML (1981) and this volume in all taxa that appeared in both studies. All taxa but diatoms that appeared in the 1981 have been restudied. Presently known species richness set as 100%.

The present volume includes up to 2619 new records for the fauna of the Marianas, which amounts to up to 46% of the recorded biota (Table 1). Unlike the comparison with UOGML (1981) above, this number takes into consideration taxonomic and nomenclatural changes and corrections, as well as records in the literature that were missed by, or appeared subsequent to the UOGML (1981) report. I have estimated our current level of knowledge of each major group covered in Table 1. Only vertebrates and placozoans (a monogeneric phylum) are considered well known, and most groups remain poorly known.

The number of species recorded from the Marianas is comparable to that recorded from Hawaii and French Polynesia (Table 2), the only other areas in Oceania for which biotic inventories are currently available. However the Marianas encompass a considerably smaller area than the other two island groups. Furthermore, not all of the checklists in the Hawaiian and French Polynesian inventories are critical, and the exceptions include numerous synonymous and erroneous records (pers. obs.). Substantially larger numbers of species have been recorded from Europe, Asia, Australia, and South Africa, areas that are of course much more intensively sampled and much larger, spanning multiple marine provinces (Table 2).

Table 1: Increasing knowledge of diversity

Species: Number of species recorded from the Marianas in this volume
New records: Number of taxa in this volume that were not previously recorded
Level of knowledge: estimate of proportion of actual diversity documented to date: 1) >67%; 2) 33-66%; 3) 10-33%; 4) <10%.

Taxon	Species	New records	Level of knowledge
Porifera	128	86	3
Placozoa	1	0	1
Cnidaria	587	202	2
Ctenophora	2	2	4
Platyhelminthes	60	58	3-4
Nemertea	8	8	3-4
Mollusca	1701	<1533[a]	2-3
Annelida	137	67	3
Sipuncula	15	0	2-3
Echiura	5	3	2
Arthropoda	849	340	3
Brachiopoda	1	1	3
Bryozoa	1	0	4
Hemichordata	1	1	2
Echinodermata	202	84	2
Urochordata	117	94	3
Vertebrata	1200	100	1
Other Metazoa	0	0	4
TOTAL METAZOA	5015	<2579 [a]	4
Unicellular algae	83	0	4
Multicellular algae & Chlorophyta	237	40	2
Ciliophora	2	0	4
Foraminifera	303	0	2-3
Other Eukaryota	0	0	4
SUBTOTAL	5640	<2619 [a]	4
Cnidaria non-marine	1	0	2
“Prosobranchia” non-marine	46	<34	2
Crustacea non-marine	34	0	3-4
Chelonia non-marine	7	4	1
TOTAL	5728	<2653 [a]	4

[a] The extent of published records of prosobranch gastropods is not fully documented; reported figure is based on records with literature citations reported in Smith (2003).

Although the number of species documented from the Marianas is high compared to inventories from comparable areas, taxon-based comparisons indicate that these islands have a substantially lower diversity than neighboring islands to the south. Thus the Palau Islands and the high islands and atolls of the Federated States of Micronesia clearly host a substantially more diverse biota in all groups that have been studied (e.g., Kelly et al. 2003, Myers 1999, Randall 1995). The high diversity on these islands is partly a result of the greater diversity of marine habitats provided by the large and complex lagoons of the Carolines compared with the limited lagoons of the Marianas. The eastward-flowing Equatorial Countercurrent also provides an express route for colonization of the Carolines from the Indo-West Pacific diversity center (Springer 1982), while the Marianas lie upstream, bathed by the westward-flowing North Equatorial Current. Thus the larger numbers of species recorded from the Marianas implies an even more diverse biota in the Carolines, not to mention in the Indo-Malaya.

Table 2: Documented marine species richness

Area	Coverage	Species	Reference
Galapagos	Marine invertebrates	2,000	Peck 1993
French Polynesia	Marine biota	3,776	Richard 1985
Bermuda	Marina biota	4,597	Sterrer 1998
British Columbia	Marine biota	4,703	Tunnicliffe 1992
Marianas	Marine biota	5,640	this volume
Hawaii	Marine biota	7,005	Eldredge & Miller 1995, Paulay 1997
South Africa	Marine fauna	11,130	Gibbons et al. 1999
China	Marine biota	19,537	Zongguo 2001
Europe	Marine biota	29,000	Costello et al. 2001
Australia	Marine fauna	~30,000	ABIF 2002*

* approximate, as based on taxon-by-taxon estimates, and because the inventory does not separate between marine and terrestrial species within higher taxa.

Four phyla, the Cnidaria, Mollusca, Arthropoda, and Chordata account for almost 80% of the documented marine species diversity in the Marianas (Fig 3). This is in part a reflection that these are major phyla, but also of our bias of emphasizing the macrofauna. The actual as well as proportional recorded diversity of major phyla are comparable between Hawaii and the Marianas. This again reflects similarity in taxonomic composition and research emphasis.

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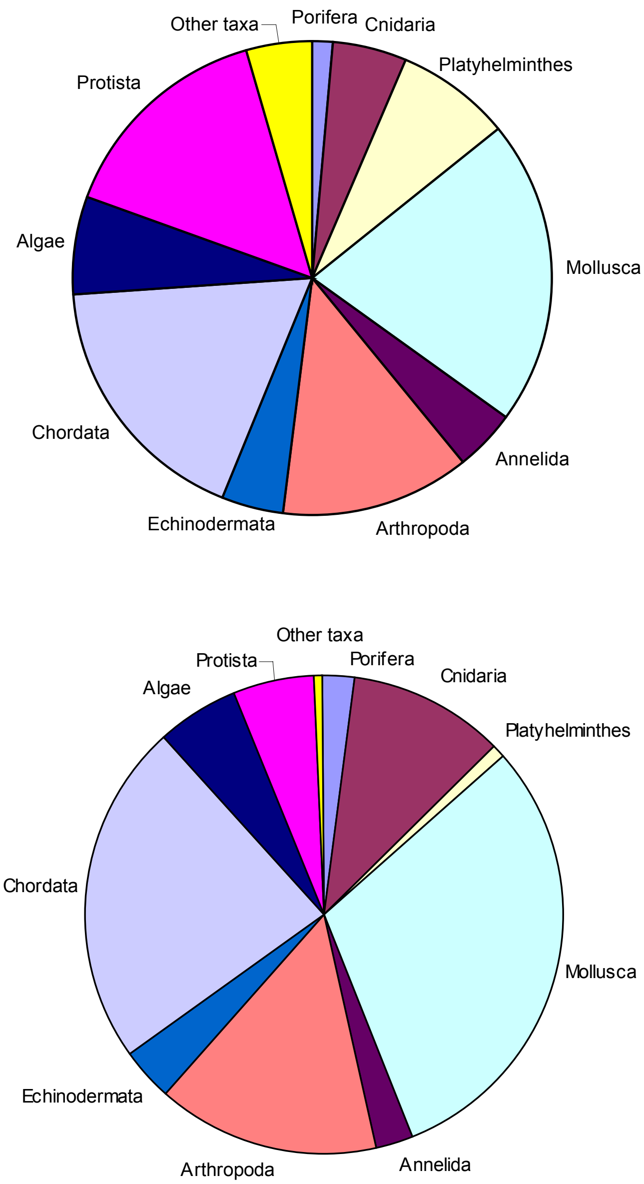

Figure 3. Diversity of major groups in the Hawaiian (top) and Mariana (bottom) Islands compared. Hawaiian data from Eldredge & Miller (1995) and Paulay (1997); Mariana data from Table 1.

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