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# 2000-2002 Rapid Ecological Assessment of Corals (Anthozoa) on Shallow Reefs of the Northwestern Hawaiian Islands. Part 1: Species and Distribution

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# 2000–2002 Rapid Ecological Assessment of Corals (Anthozoa) on Shallow Reefs of the Northwestern Hawaiian Islands. Part 1: Species and Distribution[1]

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**Abstract:** Rapid Ecological Assessment (REA) surveys at 465 sites on 11 reefs in the Northwestern Hawaiian Islands (NWHI) inventoried coral species, their relative abundances, and their distributions during 2000–2002. Surveys (462) around the 10 islands were in depths of ≤20 m, and three surveys on the submerged Raita Bank were in depths of 30–35 m. Data from 401 REA sites met criteria for quantitative analysis. Results include 11 first records for stony coral species in the Hawaiian Archipelago and 29 range extensions to the NWHI. Several species may be new to science. There are now 57 stony coral species known in the shallow subtropical waters of the NWHI, similar to the 59 shallow and deep-water species known in the better-studied and more tropical main Hawaiian Islands. Coral endemism is high in the NWHI: 17 endemic species (30%) account for 37–53% of the abundance of stony corals on each reef of the NWHI. Three genera (*Montipora, Porites, Pocillopora*) contain 15 of the 17 endemic species and most of the endemic abundance. Seven *Acropora* species are now known from the central NWHI despite their near absence from the main Hawaiian Islands. Coral abundance and diversity are highest at the large, open atolls of the central NWHI (French Frigate, Maro, Lisianski) and decline gradually through the remaining atolls to the northwest (Pearl and Hermes, Midway, and Kure). Stony corals are also less abundant and less diverse off the exposed basalt islands to the southeast (Nihoa, Necker, La Pérouse, Gardner), where soft corals (*Sinularia, Palythoa*) are more abundant. Exposure to severe wave action appears to limit coral development off these small islands and surrounding deep platforms. Temperature extremes and natural accumulation of lagoon sediments may contribute to decline of coral species and abundance at the northwestern end of the chain.

[1] The Northwestern Hawaiian Islands Reef Assessment and Monitoring Program (NOWRAMP) was funded mainly by the University of Hawai'i Coral Reef Initiative Research Program (HCRI) and the National Oceanic and Atmospheric Administration (NOAA) in 2000 and 2001. The U.S. Fish and Wildlife Service (USFWS) co-funded the 2000 cruise and provided matching support during all 3 yr. The NOAA Northwestern Hawaiian Islands Coral Reef Ecosystem Reserve (NWHICRER) and NOAA Fisheries Pacific Islands Fisheries Science Center (PIFSC) provided most of the financial and administrative support in 2002. PIFSC's Coral Reef Ecosystems Investigation (CREI) provided technical support and funds for four cruises from 2000 to 2002. Manuscript accepted 27 May 2003.

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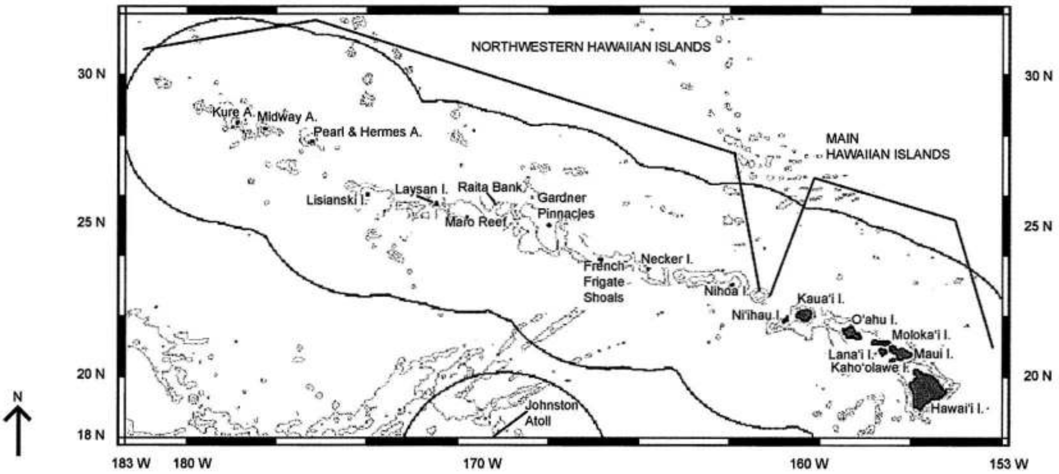


FIGURE 1. Map of the Northwestern Hawaiian Islands and main Hawaiian Islands.

IN THIS PAPER WE describe Rapid Ecological Assessment (REA) surveys of stony corals (Hexacorallia: Scleractinia), nonstony corals (Octocorallia: Alcyonacea), whip corals (Hexacorallia: Antipatharia), zoanthids (Hexacorallia: Zoanthidea), and conspicuous anemones (Hexacorallia: Actiniaria) conducted between 2000 and 2002 at 462 shallow reef sites around the 10 Northwestern Hawaiian Islands (NWHI). From southeast to northwest the NWHI are Nihoa Island, Necker Island, French Frigate Shoals, Gardner Pinnacles, Maro Reef, Laysan Island, Lisianski Island, Pearl and Hermes Atoll, Midway Atoll, and Kure Atoll (Figure 1). Three additional deep REA sites were surveyed in 2001 on the submerged Raita Bank (between Maro and Gardner).

Their remoteness and protected status has spared the NWHI reefs from much of the degradation experienced by most other coral reef systems, especially during the last half century. Protection began in 1909 when President Theodore Roosevelt designated nine "islets and reefs" (excluding Midway) as part of what became the Hawaiian Islands National Wildlife Refuge, administered by the U.S. Fish and Wildlife Service (USFWS). Shortly afterward, jurisdiction over Kure was transferred to the Territory of Hawai'i, and terrestrial parts of the atoll later became a State Wildlife Sanctuary. The tenth reef, Midway, remains a U.S. Federal Territory that was administered by the U.S. Navy until 1996, when it was designated a National Wildlife Refuge (NWR) under the USFWS. All NWHI reef environments and submerged banks seaward of the jurisdictions of the State of Hawai'i and USFWS (except Midway) were afforded additional protection by the Northwestern Hawaiian Islands Coral Reef Ecosystem Reserve (NWHICRER) designated by President William Clinton in 2000. Some NWHI land areas were severely degraded by logging, alien species, mining, agriculture, and military use since the late nineteenth century, but the islands today support millions of seabirds and migratory shorebirds; endangered land and water birds; terrestrial plants; and nesting and feeding grounds of threatened sea turtles and endangered Hawaiian monk seals. By contrast, the adjacent reef and shore areas have been relatively unaffected by human activity, although parts of some reefs have been exposed to marine debris (especially trawl and drift nets), invasive species (especially at harbors and on marine debris), chemical contaminants, fisheries, bioprospecting, coral bleaching, and ship groundings.

Most knowledge of Hawaiian corals is restricted to reefs around the eight inhabited main Hawaiian Islands (from Ni'ihau to Hawai'i) and is still based largely on the studies of Dana (1846) and Vaughan (1907). Major compilations of corals from the main Hawaiian Islands since then include Edmondson (1933, 1946), Maragos (1977, 1995), and Veron (2000), who included descriptions and photographs of endemic Hawaiian species. Knowledge of corals from the much more extensive reefs of the NWHI is far more limited. Since Vaughan (1907), who included descriptions of 21 nominal species from Laysan and four from French Frigate Shoals in his monographic treatment of Hawaiian corals, only six contributions to NWHI coral diversity have been published, all since 1970. These are a limited shallow-water survey and list of 18 coral species at Kure (Dana 1971), a broader ecological survey involving 22 coral species over the entire NWHI (Grigg and Dollar 1980), the first report of three *Acropora* species in Hawai'i (Grigg 1981, Grigg et al. 1981), the first record of *Montipora turgescens* (Coles 1998), and a recent educational publication (Maragos and Gulko 2002).

Reefs surrounding the NWHI (total land area <10 $km^2$) have submerged areas to depths of 30 m and 100 m that total 10,603 $km^2$ and 11,554 $km^2$, respectively (Hunter 1995, National Oceanic and Atmospheric Administration 2003). Until recently, scientific surveys of these reefs have been severely constrained by distance, hazardous seas, inaccurate charts, and the high cost of ship-based expeditions (the only means of access to most of these reefs and islands). Beginning in 2000, six large ship-based expeditions and several smaller efforts have conducted several kinds of surveys on both the reefs and the terrestrial environments of the NWHI under auspices of the Northwestern Hawaiian Islands Reef Assessment and Monitoring Program (NOWRAMP), a consortium of government agencies and research institutions. NOWRAMP projects took advantage of recent advances in satellite technology that permitted accurate positioning, mapping, and assessment of both reef habitats and associated temperatures, wave regimes, and other oceanographic parameters to address the initial NOWRAMP goal to "map and rapidly assess the shallow reefs of the NWHI for their biodiversity, status, and management needs." The initial NOWRAMP projects were designed mainly to collect comparable information on the abundance and distribution of major reef organisms and habitats over as broad an area as possible. Two broad-scale approaches were used to study benthic organisms: towed divers who videotaped and estimated characteristics of long transects (≥2 km by 30 m), and teams of five to eight taxonomic specialists who worked simultaneously at the same finite sites (~100 by 50 m) to conduct intensive REAs. The REA teams focused on recording the presence, abundance, and population characteristics of all observable (i.e., larger) species in four main groups (corals, fishes, algae, other invertebrates).

This report is limited to describing the occurrences and relative abundances of species of stony corals, nonstony corals, and sea anemones recorded by the REA coral specialists from all 10 of the NWHI reefs. Companion reports will address quantitative estimates of coral abundance, population size distributions, and incidence of diseased, bleached, and predated corals (G.A., J.K., and D.C.P., unpubl. data; J.K., G.A., R. E. Brainard, J. D. Chojnacki, M. Dunlap, and C. Wilkinson, unpubl. data).

## MATERIALS AND METHODS

### *Coral Survey Constraints and REA Rationale*

Working in the remote expanses and hazardous waters of the NWHI is very costly, and severe constraints were imposed on the design and execution of surveys to enumerate the species, relative abundance, and distribution of corals: (1) large-scale expeditions were limited to two per year; (2) expeditions were scheduled only in the "calm" season (August–October); (3) spatially extensive, rather than locally intensive surveys were emphasized; (4) numbers of specialists for each discipline (i.e., corals, fishes, algae, invertebrates) were limited by bunk space, and only one specialist could be assigned to study corals; (5) numbers of teams were limited by numbers of skiffs (two to five skiffs per ship); (6) because each scientist worked in a multitaxon team, various

TABLE 1

Locations of Surveyed Reefs of the 10 NWHI and One Submerged Bank (Raita) and Summary of REA Surveys 2000–2002

| NWHI Reefs | | | | | REA Sites | | REA Survey |
|---|---|---|---|---|---|---|---|
| Name | Code | Lat. (N) | Long. (W) | Area ≤20 m Deep (km²) | Total | Analyzed | Density (sites km⁻²) |
| Nihoa | NIH | 23° 03′ | 161° 55′ | 1 | 12 | 12 | 12.00 |
| Necker | NEC | 23° 34′ | 164° 42′ | 2 | 22 | 19 | 9.50 |
| French Frigate Shoals | FFS | 23° 52′ | 166° 16′ | 510 | 99 | 85 | 0.17 |
| Gardner Pinnacles | GAR | 25° 00′ | 168° 00′ | 3 | 13 | 13 | 4.30 |
| Raita Bank | RAI | 25° 26′ | 169° 33′ | 0 | 3 | 0 | ~0.01 |
| Maro | MAR | 25° 25′ | 170° 50′ | 431 | 50 | 39 | 0.09 |
| Laysan | LAY | 25° 46′ | 171° 45′ | 57 | 26 | 22 | 0.39 |
| Lisianski/Neva Shoal | LIS | 26° 00′ | 173° 55′ | 325 | 45 | 37 | 0.11 |
| Pearl and Hermes | P&H | 27° 50′ | 175° 50′ | 359 | 81 | 69 | 0.19 |
| Midway | MID | 28° 14′ | 177° 35′ | 101 | 51 | 51 | 0.50 |
| Kure | KUR | 28° 30′ | 178° 20′ | 55 | 63 | 54 | 0.98 |
| Totals | | | | 1,844 | 465 | 401 | 0.22 |

*Note:* Reefs arranged from southeast to northwest. Estimates of reef area to depths of 20 m from Grigg and Dollar (1980) and Hunter (1995).

compromises were imposed on site selection and activities at each site; (7) conservative diving practices limited work to a maximum of three dives to <20 m per day; (8) bottom time for each dive was limited to about 1 hr.

As a consequence, complete reliance on traditional transect and quadrat methods was not feasible because the limited dive time was insufficient for one person to survey more than about 25 $m^2$ during each dive using such techniques (Grigg and Dollar 1980). Although these traditional methods adequately quantify population characteristics of common corals, sampling such a limited area cannot include many of the rare species nor describe their distributions relative to the broad reef area of the NWHI. Even within the shallow depths of our surveys (to 20 m), the NWHI reefs total 1844 $km^2$ (Grigg and Dollar 1980, Hunter 1995). Past transect surveys in the NWHI (Grigg and Dollar 1980) had "2 to 8 stations" per reef and, at best, covered only a fraction of 1 $km^2$ (80 dives $\times$ 25 $m^2 = 2000$ $m^2 = 0.002$ $km^2$). In contrast, by relying on a combination of transect and REA techniques to collect species richness, distribution, and relative abundance data on corals in much broader reef areas during 2000–2002, we covered from 1000 to 5000 $m^2$ per REA dive at over 400 sites (5000 $m^2 \times 400 = 2$ $km^2$), a 200- to 1000-fold increase in coverage compared with that of Grigg and Dollar (1980).

### *Scope and REA Protocols during NOWRAMP Expeditions*

A total of 465 REA sites was surveyed from 2000 to 2002: 462 from shallow sites (≤20 m) around the 10 NWHI and three much deeper sites (30–35 m) on the completely submerged Raita Bank (Table 1). Each survey was conducted by a team of four to eight divers using small skiffs that were deployed daily from large vessels.

Protocols for the 2000 and 2001 REA coral surveys followed previously developed and tested methods (Maragos and Elliott 1985, Maragos 1994, Maragos and Cook 1995, AGRA Organizing Committee 1999, Miller et al. 2000) with some adjustments for the constraints listed earlier. Initial field identification of stony coral species was based mainly on Vaughan (1907), Maragos (1977, 1995), and Veron (1986, 2000). Vaughan's type specimens at the Bishop Museum in Honolulu and additional sources were consulted after fieldwork ended (Cairns 2001; D.

Fenner, unpubl. data). J.E.M. oversaw the coral identification process and instituted several checks to ensure consistency: he prepared color digital photos of NWHI corals as a reference source and standard for the other coral specialists; he briefed all but one of the less-experienced coral specialists personally before each cruise; he consulted frequently with the others during the surveys, making some taxonomic reassignments in the field; and after the REA surveys, he examined representative specimens to confirm assignments used by each person. All stony coral species reported to date (from all sources) from the NWHI are listed. Because none of the specialists had much experience with the nonstony alcyonarian and other anthozoans, all teams relied on Hoover (1998) for identifying these species.

A separate report will provide an updated checklist of the stony coral species of Hawai'i including taxonomic notes and photographs of unidentified species and new records (J.E.M., S. Cairns, D.G., D.C.P., and D.S., unpubl. data). Consequently, descriptions of individual coral species are not covered in this report. Color photographs of 15 corals, including several unidentified species and new records for the NWHI, are provided in Maragos and Gulko (2002). A worldwide web version of this report will include photos of selected corals and maps of all 10 reefs showing the locations of the REA sites (http://pacificislands.fws.gov).

During 2000 and 2001, each coral specialist also collected downward-pointing digital video imagery along two 25-m transects laid end-on-end and separated by a distance of about 5 m. The specialist then recorded (on waterproof paper on a clipboard) every species and its relative abundance within a larger area, extending up to 25 m beyond each side and ends of the transects. Because analysis of the videotapes was delayed by lack of funds and personnel, the coral REA protocols were revised for 2002 to include quantitative counts of corals. However, approximately half the REA sites were also videotaped in 2002. These revisions provided in situ quantitative estimates of coral size distributions, recruitment, density, percentage live cover, diversity, and various stresses affecting corals within a total area of 100 $m^2$ at each REA site in 2002.

### *Field Data Collection and Tabulation Procedures*

Before each day's diving, the full REA teams (all taxa) decided on the general location of sites to achieve representative coverage of as many major habitats to a 20-m depth as conditions and time allowed. At each site, the fish observers entered the water first, selected the site, and laid out, surveyed, and eventually retrieved the 25-m tapes used as transect lines. To avoid disturbing the fishes, the benthic observers (corals, invertebrates, algae) entered the water 15 to 20 min later and went to the start of the first 25-m transect.

During 2001–2002 surveys, the coral specialist videotaped the two 25-m transect lines and then, starting in 2002, returned along the line recording the genus (some to species) of each coral whose center fell within 1 m of the line and assigning it to one of seven size classes (based on longest diameter): 1–5, 6–10, 11–20, 21–40, 41–80, 81–160, >160 cm. These size classes and protocols were adapted from Mundy (1996), who used them successfully for broad-scale surveys in American Samoa.

Corals showing signs of disease, predation, abnormal growth, or a bleached appearance were tallied, described, and representative specimens were photographed or collected. Rare corals or unusual colonies that could not be identified in situ were also collected. The total length and width of the transect area surveyed during the census was recorded if there was insufficient time to complete both transects during the dive.

Finally, the relative abundance of species in the 25-m wider zone around the transect lines (a total maximum area of $\leq 5000$ $m^2$) was estimated by assigning a "DACOR" relative abundance value to each species: D, dominant; A, abundant; C, common; O, occasional; and R, rare. The DACOR is a robust five-point scale used for nearly 20 yr in previous REA surveys in the Pacific (Maragos and Elliott 1985, Maragos 1994, Maragos and Cook 1995). Definitions of the five classes were based on Appendix B of Maragos (1994) with slight modifications: D (dominant): coral contributes substantial abundance or coverage (25% or more of total or conspicuous in all habitats); A (abundant): coral conspicuous in most habitats or dominant in a single habitat; C (common): coral conspicuous in only one (or a few) habitats or locally substantial in a single habitat; O (occasional): coral present more than once but not substantial within any habitat; R (rare): coral reported only once during the survey.

### *Data Analysis*

A total of 465 REA sites was surveyed around the 10 NWHI and on one submerged bank from 2000 to 2002, but only 401 sites had data suitable for analysis and presentation in this report (Table 1). REA surveys at 61 sites from 2000 were excluded because they did not record soft corals and underreported the rarer species of *Montipora*, *Pocillopora*, and *Porites*. The three REA sites for Raita Bank were also excluded because they were in substantially different habitats, at considerably greater depth (30–35 m), and three sites were too few for useful comparisons with the more numerous sites on the other reefs.

An occurrence index (OI) was calculated to summarize qualitatively the presence/absence of each species at all sites on each reef (with "reef" defined as any one of the 10 NWHI):

$$\text{occurrence index \%} = \frac{\text{number of REA sites where present}}{\text{total number of REA sites}} \times 100$$

$$\text{OI} = \text{\% of REA sites with that species present (for that reef)}$$

Next, a quantitative abundance index (AI) was calculated for each species on each reef after converting the DACOR relative abundance estimates to numerical abundance scores: D = 5, A = 4, C = 3, O = 2, R = 1; species absent from a site were assigned a value of zero. Assuming "*n*" sites on a particular reef, the abundance index for each species was calculated for each reef by entering these numerical scores into the following equation:

$$\text{abundance index \%} = \frac{\Sigma\,\text{DACOR scores (across } n \text{ REA sites)}}{\text{maximum DACOR total}} \times 100 = \frac{\Sigma\,\text{DACOR scores}}{5 \times n} \times 100$$

$$\text{AI} = \text{\% of maximum possible DACOR score (for that reef)}$$

(where D = dominant = 5 is the maximum score for one species at one site). Occurrence and abundance indices for all stony coral species are tabulated in Appendix 1, and those for nonstony corals and anemone species are in Appendix 2.

Finally, each species was assigned to one of 12 groups that share common or similar taxonomic characteristics: *Acropora*, *Montipora*. *Pocillopora*, *Porites*, *Pavona/Gardineroseris/Leptoseris*, *Balanophyllia/Cladopsammia/Tubastraea*, *Cyphastrea/Leptastrea*, *Cycloseris/Fungia*, *Psammocora*, *Sinularia*, *Palythoa/Zoanthus*, and remaining species. Group occurrence and abundance indices were then calculated for these groups.

The group occurrence index (GOI) for each reef is the sum of the occurrence indices for all species in a group divided by 100; it also represents the average number of species in that group per REA site:

$$\text{GOI} = \frac{\Sigma\,\text{OI (for species assigned to that group) (for that reef)}}{100}$$

The group abundance index (GAI) for a reef is the sum of the abundance indices for all species in a group:

$$\text{GAI} = \Sigma\,\text{AI (for species assigned to a group) (for that reef)}$$

## RESULTS

### *Species and Generic Diversity*

During the 2000–2002 surveys of the NWHI, a total of 57 stony coral species in 15 genera (Tables 2, 3, Appendix 1) and at least

TABLE 2

Checklist of All Stony Corals (Anthozoa: Scleractinia) Reported from the NWHI, Including 2000–2002 REA Surveys

| | |
|---|---|
| | ACROPORIDAE |
| ++j | *Acropora cerealis* (Dana, 1846) |
| j | *A. cytherea* (Dana, 1846) |
| ++j | *A. gemmifera* (Brook, 1892) |
| j | *A. humilis* (Dana, 1846) |
| ++j | *A. nasuta* (Dana, 1846) |
| +j | *A. paniculata* Verrill, 1902 |
| j | *A. valida* (Dana, 1846) |
| *?j | *Montipora capitata* (Dana, 1846) |
| *v | *M. dilatata* Studer, 1901 |
| *++ | *M.* cf *dilatata* Studer, 1901 |
| * | *M. flabellata* Studer, 1901 |
| *j | *M. patula* Verrill, 1864 |
| *+j | *M.* cf *incrassata* (Dana, 1846) |
| ++j | *M. tuberculosa* Lamarck, 1816 |
| | *M. turgescens* Bernard, 1897 |
| *+ | *M. verrilli* Vaughan, 1907 |
| | AGARICIIDAE |
| | *Pavona clavus* (Dana, 1846) |
| *?j | *P. duerdeni* Vaughan, 1907 |
| j | *P. maldivensis* (Gardiner, 1905) |
| j | *P. varians* Verrill, 1864 |
| vj | *Leptoseris hawaiiensis* Vaughan, 1907 |
| j | *L. incrustans* (Quelch, 1886) |
| +j | *L. scabra* Vaughan, 1907 |
| + | *Gardineroseris planulata* (Dana, 1846) |
| | BALANOPHYLLIIDAE |
| + | *Balanophyllia* sp. |
| + | *Cladopsammia* cf. *eguchii* (Wells, 1982) |
| | DENDROPHYLLIIDAE |
| + | *Tubastraea coccinea* Lesson, 1829 |
| | FAVIIDAE |
| + | *Leptastrea agassizi* Vaughan, 1907 |
| ++ | *L. bewickensis* Veron & Pichon, 1977 |
| *++ | *L.* cf *Favia hawaiiensis* (Vaughan, 1907) |
| ++ | *L.* cf *pruinosa* Crossland, 1952 |
| j | *L. purpurea* (Dana, 1846) |
| j | *Cyphastrea ocellina* (Dana, 1846) |
| | FUNGIIDAE |
| j | *Fungia scutaria* Lamarck, 1801 |
| ++ | *F. granulosa* Klunzinger, 1879 |
| +j | *Cycloseris vaughani* (Boschma, 1923) |
| | POCILLOPORIDAE |
| *r | *Pocillopora* cf. *cespitosa* var. *laysanensis* Vaughan, 1907 |
| j | *P. damicornis* (Linnaeus, 1758) |
| j | *P. eydouxi* Edwards & Haime, 1860 |
| | *P. ligulata* Dana, 1846 |
| j | *P. meandrina* Dana, 1846 |
| *+ | *P. molokensis* Vaughan, 1907 |
| *++ | *P.* cf *capitata* Verrill, 1864 |
| | PORITIDAE |
| * | *Porites brighami* Vaughan, 1907 |
| * | *P. compressa* Dana, 1846 |
| *+ | *P. duerdeni* Vaughan, 1907 |
| *+ | *P. evermanni* Vaughan, 1907 |
| j | *P. lobata* Dana, 1846 |
| | *P. rus* (Forskål, 1775) |
| * | *P. hawaiiensis* (Vaughan, 1907) |
| *++ | *P.* cf *annae* Crossland, 1952 |
| + | *P.* cf *solida* (Forskål, 1775) |
| | SIDERASTREIDAE |
| + | *Psammocora explanulata* Horst, 1921 |
| +j | *P. nierstraszi* Horst, 1921 |
| +j | *P. stellata* Verrill, 1864 |
| *+ | *P. verrilli* Vaughan, 1907 |

*Note:* Older sources are Dana (1846), Vaughan (1907), Dana (1971), Grigg and Dollar (1980), Grigg (1981), Grigg et al. (1981), Coles (1998), and Cairns (2001). Johnston Atoll records from Maragos and Jokiel (1986).

+, New range record for the NWHI (previously known in main Hawaiian Islands).

++, New range record for Hawai'i as a whole.

j, Hawaiian species also reported at Johnston Atoll.

r, Reported only at Raita Bank and now considered endemic at the species level.

v, Reported by Vaughan (1907) at Laysan but not during current study.

*, Species endemic to Hawai'i and northern Line Islands (including Johnston).

*?, Considered endemic to Hawai'i and Line Islands here and by Maragos (1995) but not by Veron (2000).

12 nonstony coral and anemone species (Appendix 2) was recorded from the 465 REA sites. Previous accounts included only 24 stony coral species (Vaughan 1907, Dana 1971, Grigg and Dollar 1980, Grigg et al. 1981, Coles 1998), less than half the current total. The total is comparable to the 59 species now known from the main Hawaiian Islands including unpublished new records (Maragos 1995, Cairns 2001; D. Fenner, unpubl. data), based on many, much more intensive surveys over the past half century. Stony corals now known from the NWHI include eight species each for *Montipora* and

TABLE 3

Species Occurrence Indices and Diversity Patterns for Major Coral Groups

| | NWHI Reef and REA Sites per Reef | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | NIH 12 | NEC 19 | FFS 85 | GAR 13 | MAR 39 | LAY 22 | LIS 37 | P&H 69 | MID 51 | KUR 54 | |
| Coral Group | Group Occurrence Index for Each Reef | | | | | | | | | | Sums |
| *Acropora* | | 0.05 | 1.3 | 0.8 | 0.5 | 0.1 | | | | | 143 |
| *Montipora* | 1.3 | 1.5 | 2.0 | 1.5 | 3.3 | 2.5 | 2.5 | 1.0 | 0.9 | 1.0 | 682 |
| *Pavona* and other agariciids | 0.6 | 0.8 | 1.0 | 1.2 | 1.0 | 0.7 | 1.0 | 0.6 | 0.3 | 0.5 | 295 |
| *Balanophyllia, Cladopsammia,* and *Tubastraea* | 0.1 | | 0.06 | 0.5 | 0.1 | 0.1 | | 0.01 | 0.04 | 0.1 | 30 |
| *Cyphastrea* and *Leptastrea* | 1.3 | 1.2 | 1.3 | 1.5 | 1.8 | 1.2 | 1.3 | 1.3 | 0.8 | 1.3 | 510 |
| *Cycloseris* and *Fungia* | 0.1 | | 0.2 | 0.3 | 0.5 | 0.2 | 0.5 | 0.6 | 0.1 | 0.1 | 108 |
| *Pocillopora* | 2.4 | 2.2 | 2.7 | 2.2 | 3.1 | 3.2 | 2.3 | 2.6 | 2.4 | 3.2 | 1,083 |
| *Porites* | 2.0 | 2.8 | 2.9 | 3.0 | 3.2 | 3.3 | 3.0 | 2.0 | 1.6 | 2.1 | 1,007 |
| *Psammocora* | 0.2 | | 0.3 | 0.9 | 0.4 | 0.1 | 0.4 | 0.5 | 0.2 | 0.7 | 149 |
| *Palythoa* and *Zoanthus* | 1.1 | 1.0 | 0.7 | 0.8 | 0.5 | 0.6 | 0.1 | 0.5 | 0.3 | 0.7 | 229 |
| *Sinularia* | 0.4 | 0.05 | 0.04 | 0.8 | | | | | | | 20 |
| Other anthozoans | 0.1 | | 0.1 | 0.1 | 0.03 | | | 0.04 | | 0.1 | 20 |
| Mean spp. per REA site | 9.6 | 9.6 | 12.6 | 13.6 | 14.4 | 12.1 | 11.1 | 9.2 | 6.6 | 9.8 | |
| % Endemic stony coral spp. | 47 | 60 | 38 | 36 | 42 | 41 | 50 | 44 | 39 | 50 | |
| Total spp. per reef | 21 | 23 | 49 | 32 | 40 | 32 | 28 | 34 | 29 | 37 | |

*Note:* From 401 analyzed REA sites 2000–2002. Reefs arranged from southeast to northwest. Reef codes from Table 1. The group occurrence index for each reef is the average number of species in that group per site and is also the sum of the occurrence indices for all species in the group divided by 100. Sums = sum of occurrences for all species within a group for all 401 sites.

*Porites;* seven species each for *Acropora* and *Pocillopora;* five species for *Leptastrea;* four species each for *Pavona* and *Psammocora;* two species each for *Leptoseris* and *Fungia;* and one species each for *Balanophyllia*, *Cladopsammia*, *Cycloseris*, *Cyphastrea*, *Gardinoseris*, and *Tubastraea.* The stony coral species include 29 new records for the NWHI and 11 new records for Hawai'i as a whole (Table 2).

At least 17 species (30%) in five genera (Table 2) are likely to be endemic to the Hawaiian chain and nearby islands (J.E.M., S. Cairns, D.G., D.C.P., and D.S., unpubl. data). Some may also be endemic to the NWHI, and a few may be new to science. All but two of the endemic species belong to three genera (*Montipora*, *Pocillopora*, *Porites*) that are well represented on all NWHI reefs and contain nine of the 10 most frequently occurring and most abundant species (Appendix 1). Only one nonstony species, *Palythoa tuberculosa*, was among the top 10 most abundant corals. Two otherwise common genera had more restricted distributions: *Psammocora* (not reported from Necker); and *Acropora* (not reported from Nihoa, Lisianski, Pearl and Hermes, Midway, or Kure).

### *Distribution Patterns*

The distributions and abundances of coral species and genera (Tables 3, 4, Appendix 1) are closely associated with variation in the geomorphology, size, and age of the 10 NWHI reefs over their 2000-km extent (Grigg and Dollar 1980, Grigg 1988). Reefs near the southeastern end of the chain (Nihoa at 23° N, 162° W; Necker; Gardner Pinnacles) are poorly developed with small, basalt islands or pinnacles. The middle reefs are mainly large, open atolls (French Frigate Shoals, Maro, Neva Shoal) or shallow reef platforms around low coral islands (Laysan, Lisianski). Toward the northwestern end (Kure at 29° N, 178° W; Pearl and Hermes; Midway), the reefs become "classical atolls"

TABLE 4

Summary of Relative Abundance Patterns for Major Coral Groups

| | NWHI Reef and REA Sites per Reef | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | NIH 12 | NEC 19 | FFS 85 | GAR 13 | MAR 39 | LAY 22 | LIS 37 | P&H 69 | MID 51 | KUR 54 | |
| Coral Group | Group Abundance Index for Each Reef | | | | | | | | | | Sums |
| *Acropora* | | 1 | 59 | 31 | 26 | 4 | | | | | 121 |
| *Montipora* | 60 | 70 | 88 | 58 | 195 | 107 | 150 | 41 | 55 | 47 | 871 |
| *Pavona* and other agariciids | 21 | 26 | 43 | 42 | 56 | 29 | 47 | 27 | 9 | 22 | 322 |
| *Balanophyllia*, *Cladopsammia*, and *Tubastraea* | 3 | | 1 | 18 | 3 | 2 | | <1 | 2 | 3 | 32 |
| *Cyphastrea* and *Leptastrea* | 59 | 43 | 52 | 60 | 82 | 52 | 67 | 57 | 30 | 54 | 556 |
| *Cycloseris* and *Fungia* | 2 | | 4 | 8 | 22 | 7 | 25 | 21 | 3 | 2 | 94 |
| *Pocillopora* | 128 | 137 | 132 | 107 | 150 | 150 | 100 | 134 | 121 | 173 | 1,332 |
| *Porites* | 112 | 175 | 180 | 161 | 214 | 189 | 210 | 105 | 92 | 107 | 1,545 |
| *Psammocora* | 3 | | 11 | 26 | 18 | 3 | 16 | 17 | 6 | 24 | 124 |
| *Palythoa* and *Zoanthus* | 59 | 42 | 32 | 38 | 24 | 27 | 6 | 22 | 13 | 30 | 293 |
| *Sinularia* | 18 | 2 | <1 | 52 | | | | | | | 72 |
| Other corals and anemones | 2 | | 3 | 2 | 1 | | | 2 | | 2 | 12 |
| Total abundance/reef | 467 | 496 | 605 | 603 | 791 | 569 | 621 | 426 | 331 | 464 | |

*Note:* From 401 analyzed REA sites in 2000–2002. Reefs arranged from southeast to northwest. Reef codes from Table 1. Group abundance index for a reef is the sum of the abundance indices for all species in that group. Sums = sum of abundance indices for each group for all 401 sites.

with nearly complete protective perimeter reefs (Kure and Midway are also the two smallest platforms in the chain). The lagoons of the middle and northern reefs are being filled with extensive areas of calcareous sediments especially toward the windward sides (north to east) facing into the prevailing trade winds and trade-wind-driven swells.

The small islands at the southeastern end of the NWHI provide little protection from wave action, and distributions, sizes, and abundances of most common (*Montipora*, *Porites*, *Psammocora*, *Pavona*) and delicate *Pocillopora* stony corals are limited, although a few robust species of *Pocillopora* and *Porites* and some nonstony species (*Sinularia*, *Palythoa*) appear to thrive. The large middle atolls have a wide variety of habitats, including large, sheltered lagoons where many stony species (of the genera just mentioned) flourish, and where the mushroom (*Fungia*) and table corals (*Acropora*) reach their maximum abundance in the NWHI. Toward the northwestern end of the chain, some stony species decline in abundance and others drop out, a few species of *Pocillopora* and *Montipora* increase in abundance, and the extensive sand shallows toward the eastern sides of the atoll lagoons have limited coral development. Only the common but usually small, encrusting faviids (*Cyphastrea*, *Leptastrea*) are relatively common throughout the entire NWHI.

The occurrence index (OI) patterns across the NWHI, calculated for the 13 most frequently encountered species (Appendixes 1, 2), corroborate most of these generalizations. Five species decrease (occur at a lower proportion of sites on a reef) toward the northwestern (NW) end of the chain (*Montipora capitata*, *M. patula*, *Pavona duerdeni*, *Porites evermanni*, *P. lobata*), two increase (occur at a higher proportion of sites) along the NW half of the chain (*M. turgescens*, *Pocillopora damicornis*), and six have no obvious trends in their occurrences (*Cyphastrea ocellina*, *Leptastrea purpurea*, *Pocillopora ligulata*, *P. meandrina*, *Porites compressa*, *Palythoa tuberculosa*).

Frequency of occurrence of a species on a reef is likely to be correlated with its relative abundance on that reef, and the abundance indices (AI) for the first seven species just mentioned (Figure 2*A–D*) do parallel their

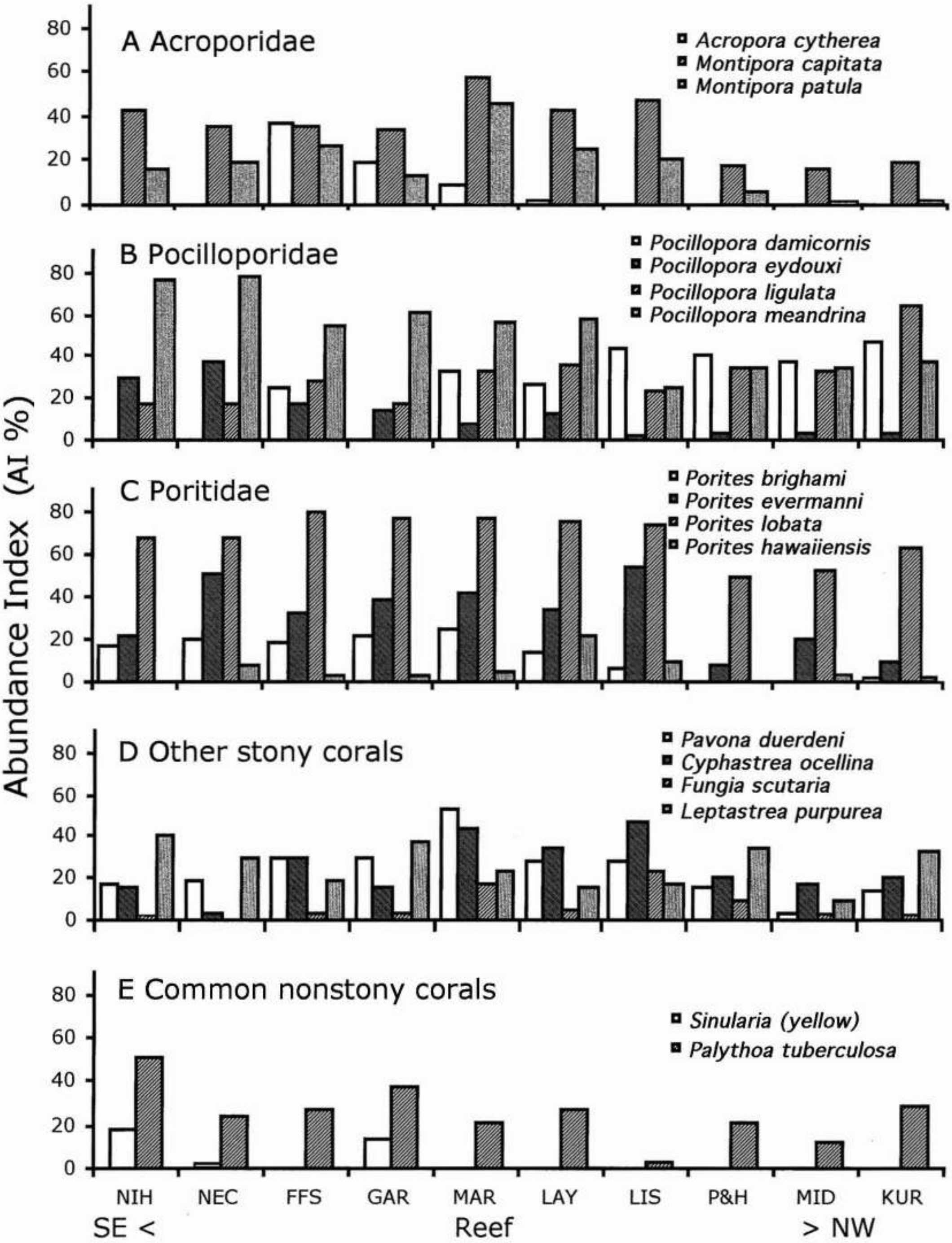


FIGURE 2. Abundance indices for common corals, based on sums of abundance indices for each species on each reef in Appendixes 1 and 2. Reefs arranged from southeast (SE) to northwest (NW). Reef codes from Table 1.

occurrence index trends. Also three of the species with no occurrence trends did have abundance trends: *Pocillopora ligulata* increased to the northwest (Figure 2*B*), and *Pocillopora meandrina* and *Palythoa tuberculosa* declined (Figure 2*B,E*). Only two of the top 10 widely distributed (high OI) species had no obvious trends in abundance (*Leptastrea purpurea, Porites compressa*); a third (*Cyphastrea ocellina*) was common throughout the NWHI, with a slight peak in the middle (Figure 2*C,D*, Appendix 1). Less widely distributed genera and species followed similar trends: (1) higher abundance and/or occurrence indices in the center of the NWHI: all species of *Acropora, Sinularia, Fungia; Montipora flabellata; Porites hawaiiensis* (Figure 2*A,C–E*); (2) higher abundance indices toward the northwest: *Pocillopora* cf. *capitata, Montipora turgescens* (Figure 2*A,B*); (3) declining abundance indices toward the northwest: *Pocillopora eydouxi, Porites brighami* (Figure 2*B,C*); (4) no obvious trend: *Montipora verrilli, Psammocora stellata.*

When species and genera were grouped on the basis of taxonomic similarity, the groups maintained similar trends (Tables 3, 4): (1) six groups peaked in the center of the NWHI: table corals (*Acropora*), mushroom corals (*Fungia/Cycloseris*), tube corals (*Balanophyllia/Cladopsammia/Tubastraea*), *Pavona*/other agariciids, *Montipora, Porites;* (2) two groups declined toward the northwest: soft corals (*Sinularia, Palythoa/Zoanthus*); (3) four groups had no obvious trend: *Pocillopora, Cyphastrea/Leptastrea, Psammocora*, other corals.

### *Raita Bank*

The three REA coral surveys in 2001 on Raita Bank, 73 km west of Maro Reef, were at 30–35 m on a submerged reef with its shallowest crest at about 25 m. Due to the depth and strong currents, the three dives were short and concentrated on photography and inventory of species, rather than gathering any quantitative data. Most surfaces were scoured, had low profiles, and were covered with a mat of the green alga *Microdictyon.* Only eight coral species were seen across the three sites. The main corals were evenly spaced, erect colonies of several species of *Pocillopora* (*P.* cf. *cespitosa* var. *laysanensis, P.* cf. *capitata, P. ligulata, P. meandrina, P. molokensis*) covering about 5% of the bottom, and the first species has unusual forms not encountered elsewhere during the REA surveys. Both live and dead standing colonies of *Pocillopora* were occupied by many small fish and invertebrates. Other stony corals were minor contributors: *Montipora capitata* and single colonies of *Psammocora stellata* and *Porites compressa.* Seven of the eight were endemic; *Pocillopora meandrina* was the only nonendemic. Physically, geomorphologically, and biologically, the three deeper sites at Raita were atypical of all the shallower REA sites in the NWHI.

### *Coral Bleaching*

During mid-September 2002, populations of several species of *Pocillopora, Montipora*, and *Porites* on the four most northwesterly reefs (Lisianski to Kure) were experiencing bleaching. More than 20% of all coral colonies at Kure, Midway, and Pearl and Hermes were affected, but the levels varied with habitat. Bleaching percentages were higher in shallow, especially back reef, habitats and lower on deeper, ocean-facing reef fronts. The bleaching event coincided with high seawater temperatures that were predicted in advance by the National Oceanic and Atmospheric Administration (NOAA) from satellite data and publicized on NOAA web sites (www.coris.noaa.gov). At Midway, water temperatures reached nearly 29°C by early August and remained elevated throughout the month: this is 2°C higher than usual summer maximum water temperature (27°C) at Midway. The September 2002 bleaching is described in Aeby et al. (2003), and the subsequent course of the bleaching event is being monitored (J.K., G.A., R. E. Brainard, J. D. Chojnacki, M. Dunlap, and C. W. Wilkinson, unpubl. data).

## DISCUSSION

### *Diversity and Distribution Patterns*

The REA surveys conducted in 2000–2002 as one component of NOWRAMP added many species records to previous reports from the NWHI and greatly extended knowledge of abundance and distribution patterns for more than 70 stony coral and other anthozoan species (57 scleractinians, 4 alcyonaceans, 6 zoanthideans, 1 antipatharian, and 1 actiniarian [anemone]) throughout an extremely large ecosystem (>2000 km long).

The REA data reported here more than double the number of stony coral species previously known from the NWHI and increase the total number of species reported from Hawai'i as a whole to about 70 species, including approximately 20 endemic species. The new Hawaiian totals are lower than those from other large tropical Pacific island groups that have been surveyed, but the endemism levels are much higher. In the central Pacific, only some small, isolated, single atolls and islands such as Johnston Atoll (35 species) and Wake Atoll (41 species) are known to have fewer stony coral species (Maragos and Jokiel 1986, U.S. Fish and Wildlife Service, Pacific Islands Ecoregion, and National Marine Fisheries Service, Pacific Islands Area Office 1999).

Many species fit into one of several common trends of abundance (AI) and occurrence (OI) indices across the NWHI chain. Species richness per reef, number of species per REA site, and coral abundance all reached maximum values on the central NWHI atolls (French Frigate Shoals, Maro Reef). These indices declined noticeably toward the northwestern end of the chain (from Pearl and Hermes out to smaller Midway and Kure Atolls) and also toward the southeast on the deep platforms with small basalt islands (Gardner, Necker, Nihoa). These patterns are comparable with those of Grigg and Dollar (1980). Some of the high species richness on the central atolls is attributable to the presence of one to seven species of *Acropora* that are absent at both ends of the NWHI chain. The lower diversity and abundance of corals toward the ends of the chain seem to be associated with different environmental stresses. Toward the southeast, the limited reef development results in severe exposure to waves, and the general lack of sheltered habitats probably restricts coral recruitment, subsequent survival, and ultimately reef development. In contrast, the bleaching of corals that we observed on the northwestern reefs in mid- to late September 2002 may be a periodic event, and this suggests that periodic high summer and low winter temperatures may be two mechanisms restricting coral abundance at high latitudes toward the northwest. Lagoon sediment accumulations and movement during winter storms may also adversely affect coral development on the northwestern reefs.

### *Affinities of NWHI and Johnston Atoll Coral Faunas*

The species-level similarities between the stony coral faunas of Johnston Atoll and the NWHI, reviewed previously by Grigg (1981), Grigg et al. (1981), and Maragos and Jokiel (1986), are further strengthened by our REA data. There are now 35 stony coral species recorded from Johnston Atoll and 57 from the NWHI. These totals include 26 species common to both localities (Table 2); 31 species in the NWHI are not known from Johnston (Table 2). Nine species are known from Johnston but not the NWHI: six scleractinian corals (3 *Acropora*, 1 *Montipora*, 1 *Oulangia*, 1 *Porites*) and three hydrozoan corals (1 *Distichopora*, 1 *Stylaster*, 1 *Millepora*). All seven species of *Acropora* in the NWHI are now known from Johnston, but three Johnston species (*A. elseyi*, *A. selago*, *A. yongei*) are not reported from the NWHI. In the NWHI, the genus *Acropora* is limited to the five central islands and atolls (from Necker to Laysan), with the most species and the highest abundances at French Frigate Shoals (Tables 3, 4; Appendix 1; Figure 2*A*). French Frigate Shoals is also the closest NWHI reef to Johnston Atoll (800 km) although the other NWHI reefs with *Acropora* are not much farther away (Figure 1).

Earlier investigators concluded that *Acropora* probably reached the NWHI from Johnston Atoll via the Subtropical Countercurrent or by wake eddies forming to leeward of Johnston and then spinning off to the north (Grigg 1981, Grigg et al. 1981, Maragos and Jokiel 1986). Another widely distributed Pacific species, *Montipora tuberculosa* (common at Johnston but absent from the main Hawaiian Islands), is restricted to the central and northern NWHI (Appendix 1); it also may have colonized the NWHI in a similar fashion. Populations of the more common *Acropora* species at French Frigate Shoals include large mature colonies that reproduce sexually, and Kenyon (1992) suggested that this reef may serve as the main source of recruits that settle and colonize adjacent islands and atolls (Figure 1). The coral species found at Johnston that have not been reported in the NWHI may be excluded by distances too great for successful larval transport and colonization (Maragos and Jokiel 1986) or by unfavorable temperature regimes.

### *Endemism in NWHI Stony Corals*

Endemism is extremely high in the NWHI, both throughout the chain and on each reef. Endemic species account for at least 30% of all NWHI stony coral species, and they range from 36 to 60% of the species at individual REA reef sites (Table 3, Appendix 1). There are no obvious patterns of decline or increase in endemism across the NWHI. Endemic species are also extremely important in terms of their abundances in the NWHI: they average about 45% of summed abundance indices, ranging from 37 to 53% among the 10 NWHI reefs (Table 4, Appendix 1).

When records are combined for the entire Hawaiian Archipelago, including both the NWHI and the main Hawaiian Islands, overall stony coral endemism is 29% (20 of 70% species), an increase over previous estimates of 20 to 25% (Grigg 1988, Maragos 1995). Twelve nonendemic stony coral species in the main Hawaiian Islands have not been reported from the NWHI: eight (3 *Leptoseris* spp., 2 *Diaseris* spp., *Coscinaraea wellsi*, *Tethocyathus minor*, *Rhizopsammia verrilli*) typically live at >30 m depths, considerably deeper than sites sampled during the REA surveys (<20 m); the remaining four (*Culicia* cf. *tenella*, 2 *Tubastraea* spp., *Madracis pharensis*) are small, cryptic, ahermatypic, and rarely encountered in the main Hawaiian Islands. Only three rare Hawaiian endemics (*Eguchipsammia serpentina*, *Porites studeri*, *P. pukoensis*) have not been reported from the NWHI. Of the three species, the first two are deep-water species and the two *Porites* spp. are difficult to distinguish in the field from more common species of *Porites*. Additional surveys to greater depth and in cryptic habitats in the NWHI may yield some of the species now reported only from the main Hawaiian Islands.

The total number of stony coral species in the Hawaiian Islands remains unknown. Our NWHI surveys revealed several unrecognized, unidentified, and probably undescribed species (*Leptastrea* cf. *Favia hawaiiensis*, *Montipora* cf. *incrassata*, *Pocillopora* cf. *capitata*, *P.* cf. *cespitosa* var. *laysanensis*, *Porites* cf. *annae*, *Montipora* cf. *dilatata*), all of which are presumed to be endemic because none resembles forms reported elsewhere in Hawai'i or neighboring island groups.

There also may be other potential endemic species in Hawai'i (Maragos 1995) that are currently assigned by Veron (2000) to more widely distributed species (e.g., *Pocillopora ligulata*, *Porites evermanni*, *Pavona duerdeni*, *Montipora capitata*, *Cyphastrea ocellina*, *Montipora turgescens*, and some varieties of *Porites lobata* and *P. compressa*). The Hawaiian forms of all of these species have not been observed outside Hawai'i and the adjacent northern Line Islands, nor do they conform to published photographs of accepted species. In one relevant NWHI example, it is very difficult to distinguish the morphologically similar *Montipora flabellata* and *M. turgescens* using skeletal characteristics, yet living colonies have differences in growth form, tissue appearance, and color. During the September 2002 bleaching on some NWHI reefs (Aeby et al. 2003), most *M. turgescens* colonies in affected back reef environments bleached, but few *M. flabellata* colonies in the same habitats bleached.

Grigg (1988) stated that the Hawaiian Archipelago has existed for at least 69 million yr and that scleractinian corals have been present for at least 34 million yr. During this long period, ancestors of extant Hawaiian endemic species must have successfully colonized some reefs and may have persisted by "island hopping" from older to younger reefs, as volcanic islands emerged and later subsided to form the Hawaiian and Emperor Seamounts. These early colonizers could have evolved into "new" (endemic) species via genetic drift, genetic bottlenecks, and founder effects. Most of the current Hawaiian endemic species have evolved from ancestral species in only three genera, *Porites*, *Montipora*, and *Pocillopora*. These genera are among the most widespread of Pacific scleractinians and have highly adapted and successful larval recruitment and adult survival strategies.

Before our 2000–2002 surveys, the NWHI coral faunas were assumed to have low species diversity and sparse ecological abundances and to make limited contributions to reef development (Grigg and Dollar 1980, Grigg 1982). Instead, our data demonstrate that the 10 NWHI reefs collectively support as many stony species as the main Hawaiian Islands and have higher endemism. Most endemic and many of the more widely distributed Hawaiian coral species probably occupied older NWHI reefs before successfully establishing on the younger main Hawaiian Islands. Today the NWHI reefs account for nearly 80% of coral reef habitat in the archipelago, and they have a greater variety of habitats, especially the larger open (e.g., French Frigate, Maro, Lisianski/Neva Shoal) and more classical, closed atolls (e.g., Pearl and Hermes, Midway, Kure) with their diverse lagoon habitats favoring coral diversity and abundance.

Some coral taxonomists and geneticists have suggested that many coral species remain undescribed and that endemism levels are underestimated, partly because so many tropical reefs and, especially, deeper habitats have not been explored by experienced coral biologists, and partly because the traditional taxonomic approaches relying on skeletal morphology are unable to distinguish many closely related species (e.g., Knowlton 1993, Potts et al. 1993). Future coral systematics will increasingly use characteristics of soft tissues, including polyp morphology and coloration, physiological and behavioral responses to environmental stimuli, ecological interactions (e.g., with competitors, predators, borers, symbionts), and biochemical and genetic analyses. Geographically extensive REA surveys and species inventories will be necessary as early steps in the process of collecting the kinds of field observations, samples, and photographs that may detect relevant variation in soft tissue characters.

### *REA Methodology: Limitations*

Although our REA methods allowed collection of extensive and comparable diversity and quantitative information on corals over broad areas, we also learned ways to improve REA surveys. For example:

(1) The need for standardizing and coordinating training was demonstrated by the unavoidable absence of one coral specialist from the 2000 training; this led to incomplete species counts and ultimately to elimination of 61 REA sites from the analysis. The other two coral specialists in 2000 consistently averaged much higher species counts per dive and still had sufficient time to inventory species and assign DACOR relative abundance values.

(2) In 2001, a single coral team of two specialists worked together, dividing time between REA and non-REA tasks (e.g., coral coring, remote sensing verification, etc.), but the presence of the second specialist largely compensated for less time per diver devoted to the REA.

(3) In 2002, three REA coral specialists worked alone and found that their dive times were often insufficient to complete the REA in accordance with the revised procedures that included addition of in situ censuses of coral colonies, plus responsibilities for other specialized tasks (collecting coral samples; tallying data on coral disease, bleaching, predation, or mortality). Often neither species inventory nor colony census was completed to the specialist's satisfaction, but there was no opportunity to finish them during subsequent dives.

(4) Because levels of expertise in field identification varied, there was a tendency to underestimate rare and cryptic species, which affected species totals, occurrences, and abundance scores. Abundance indices for common

species were much less affected. Each specialist in 2002 conducted similar numbers of REA surveys (about 60), and potential biases in the data for any one reef were avoided by having all specialists doing similar numbers of sites on each reef.

Although DACOR relative abundance estimates have been collected in previous REAs, this is one of the first situations where the data have been converted to numerical estimates of abundance (abundance index values) and used to demonstrate abundance trends for corals across a large reef ecosystem. Visually assigning relative abundance values for corals is inherently subjective and will lead to discrepancies among various observers assigning such values for the same corals at the same sites. In contrast, occurrence values (presence or absence data) are more objective and have been more widely used in other REAs.

However, occurrence values have less information content and are not very useful for defining distributional patterns for corals unless a large number of sites are surveyed. This was an especially important issue at the smaller basalt NWHI where there was little justification for more than 10 to 15 total REA sites at each, given the limited ship time and the thousands of square kilometers of reefs at the other islands and atolls needing surveys (see Table 1 for the sampling frequencies per NWHI). The added task of estimating the DACOR relative abundance values for each site took only a few minutes but substantially increased the information content for each coral. As a consequence, plots of the abundance values for common corals across the NWHI showed clearer and better-defined trends than those for occurrence values (Appendixes 1,2; Figure 2). Not much is lost and much is gained by adding visual abundance estimates for corals where survey time and site totals are limited. It will be instructive to compare the abundance values expressed in this report with those that will be estimated quantitatively on the two transects at the same REA sites using colony counts (G.A., J.K., and D.C.P., unpubl. data) and image analysis of videotapes and photoquadrats (J.K., P. Vroom, K. Page, and G.A., unpubl. data).

*REA Methodology: Recommendations*

Future REA surveys should plan for two coral specialists on each team to reduce or eliminate most of the concerns just mentioned. The less-experienced specialist should concentrate on the census tasks, with the more-experienced specialist inventorying species, assigning DACOR relative abundance values, and handling special tasks (collections, examination of diseased corals, etc.).

Although REA approaches have been used extensively for conservation and management (e.g., Allen et al. 2003), they have not been adopted widely by many field biologists who advocate more conventional, more quantitative approaches (e.g., multiple replicated transects and quadrats per site). However, the many practical constraints imposed on ship-based surveys at remote localities severely limit numbers of personnel and especially time at a site (e.g., about 1 hr for most NOWRAMP sites). Nor would the sampling area likely be sufficient to document the status of more than a fraction of the total species and their habitats. With time and experience, the objectivity, consistency, and acceptability of spatially extensive REA approaches should improve as more specialists are trained, gain experience, and appreciate the increased value they provide. Reef surveys involving species inventories are essential for many marine protected areas where adequate knowledge on diversity, endemism, and rare, endangered, depleted, and alien species is needed for proper management, monitoring, and restoration. Such information is especially important in remote areas that are relatively free of anthropogenic disturbance, where local levels of species recruitment are limited, and where valued species and habitats are more vulnerable to unauthorized harvesting, ship groundings, bleaching events, marine debris, and other stresses. The improved REA procedures developed over 3 yr for the NWHI provide a balance that includes quantitative and diversity information on corals over broad areas that can be collected rapidly by one or two well-trained specialists. The findings of our REA surveys differ in some ways from the conclusions of earlier surveys

(Grigg and Dollar 1980) and raise alternative hypotheses on the functioning, future, and importance of the NWHI, alternatives that would not be apparent without extensive surveys including species inventories.

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**Appendix 1**

Compilation of All Occurrence and Abundance Indices for Each Species of Stony Coral (Scleractinia) for 401 Analyzed REA Sites on 10 NWHI Reefs

| | NWHI Reef and REA Sites per Reef | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Stony Coral Species | NIH 12 | NEC 19 | FFS 85 | GAR 13 | MAR 39 | LAY 22 | LIS 37 | P&H 69 | MID 51 | KUR 54 | *O* | **A** |
| *Acropora cerealis* | | | *8* **4** | *8* **2** | *21* **9** | | | | | | *16* | **15** |
| *A. cytherea* | | *5* **1** | *67* **38** | *54* **20** | *18* **9** | *9* **2** | | | | | *74* | **70** |
| *A. gemmifera* | | | *1* **5** | *8* **6** | | | | | | | *16* | **11** |
| *A. humilis* | | | *15* **5** | *8* **3** | *5* **2** | | | | | | *16* | **10** |
| *A. nasuta* | | | *4* **1** | | | *5* **2** | | | | | *4* | **3** |
| *A. paniculata* | | | *5* **2** | | | | | | | | *4* | **2** |
| *A. valida* | | | *12* **4** | | *8* **6** | | | | | | *13* | **10** |
| *Montipora capitata**? | *83* **43** | *74* **36** | *76* **36** | *92* **35** | *87* **58** | *91* **44** | *73* **48** | *41* **18** | *31* **17** | *40* **19** | *247* | **354** |
| *M. flabellata** | | *26* **11** | *28* **10** | *23* **9** | *59* **31** | *59* **24** | *57* **31** | *19* **7** | *25* **19** | *28* **12** | *134* | **154** |
| *M. patula** | *50* **17** | *42* **20** | *53* **27** | *38* **14** | *72* **46** | *64* **26** | *35* **21** | *12* **6** | *6* **2** | *4* **2** | *132* | **181** |
| *M.* cf. *dilatata** | | | | | *3* **1** | | | | | | *1* | **1** |
| *M.* cf. *incrassata** | | | *21* **8** | | *23* **9** | | | | | *2* **1** | *28* | **18** |
| *M. tuberculosa* | | | *13* **5** | | *41* **25** | *9* **5** | *24* **16** | *1* **<1** | *2* **<1** | *9* **3** | *45* | **55** |
| *M. turgescens* | | | | | *33* **17** | *18* **6** | *41* **26** | *19* **7** | *27* **17** | *11* **6** | *65* | **79** |
| *M. verrilli** | | *11* **3** | *5* **2** | | *15* **8** | *9* **2** | *19* **8** | *4* **2** | | *11* **4** | *30* | **29** |
| *Gardineroseris planulata* | | | | | | | | | *2* **<1** | | *1* | **<1** |
| *Leptoseris incrustans* | | | *2* **1** | | | | | | | | *2* | **1** |
| *L. scabra* | | | *1* **<1** | | | | | | | | *1* | **<1** |
| *Pavona clavus* | | | | | | | | *1* **<1** | | *X* **X** | *1* | **<1** |
| *P. duerdeni**? | *50* **18** | *58* **20** | *61* **30** | *77* **31** | *90* **54** | *68* **29** | *65* **29** | *3* **17** | *10* **4** | *30* **15** | *199* | **247** |
| *P. maldivensis* | | | *2* **1** | | | | *24* **11** | *6* **3** | | *2* **1** | *16* | **16** |
| *P. varians* | *8* **3** | *21* **6** | *33* **11** | *38* **11** | *8* **2** | *X* **X** | *14* **7** | *19* **7** | *14* **5** | *17* **6** | *75* | **58** |
| *Balanophyllia* sp. | | | *X* **X** | | | | | | | | | |
| *Cladopsammia eguchii* | | | *2* **<1** | *23* **9** | *5* **1** | *5* **1** | | *1* **<1** | *2* **<1** | *7* **2** | *16* | **14** |
| *Tubastraea coccinea* | *8* **3** | | *4* **1** | *31* **9** | *8* **2** | *5* **1** | | *X* **X** | *2* **1** | *2* **1** | *14* | **18** |
| *Cyphastrea ocellina* | *42* **17** | *21* **4** | *67* **30** | *54* **17** | *87* **44** | *73* **35** | *86* **48** | *48* **21** | *45* **18** | *59* **21** | *243* | **255** |
| *Leptastrea agassizi* | | | | | *X* **X** | | | | *8* **2** | | *4* | **2** |
| *L.* cf. *pruinosa* | | *5* **2** | *5* **1** | *8* **5** | *15* **8** | | | | | | *12* | **16** |
| *L. purpurea/bewickensis* | *92* **42** | *79* **31** | *5* **20** | *85* **38** | *62* **25** | *50* **17** | *41* **18** | *81* **36** | *31* **10** | *70* **33** | *242* | **270** |
| *L.* sp. | | | *X* **X** | | | | | | | | | |
| *L.* cf. *hawaiiensis** | | *11* **6** | *1* **<1** | | *13* **5** | | *3* **1** | | | | *9* | **13** |
| *Cycloseris vaughani* | | | | *8* **3** | | | | *12* **4** | *2* **<1** | | *11* | **8** |
| *Fungia granulosa* | | | | | *5* **3** | *5* **1** | | *14* **6** | | | *13* | **10** |
| *F. scutaria* | *8* **2** | | *15* **4** | *23* **5** | *44* **19** | *14* **6** | *54* **25** | *28* **11** | *8* **3** | *9* **2** | *85* | **77** |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pocillopora damicornis* | | | *59* **26** | | *79* **34** | *59* **27** | *92* **44** | *83* **41** | *70* **38** | *93* **47** | | *274* **257** |
| *P. eydouxi* | *83* **30** | *74* **39** | *52* **18** | *4* **15** | *31* **9** | *36* **13** | *8* **3** | *12* **4** | *18* **4** | *13* **4** | | *127* **139** |
| *P. ligulata* | *42* **18** | *47* **18** | *61* **29** | *54* **18** | *69* **34** | *77* **37** | *54* **24** | *51* **35** | *61* **33** | *85* **65** | | *249* **311** |
| *P. meandrina* | *100* **77** | *100* **80** | *88* **55** | *9* **62** | *90* **57** | *100* **59** | *59* **26** | *70* **35** | *67* **36** | *74* **38** | | *319* **525** |
| *P. molokensis** | *17* **3** | | *4* **1** | *23* **12** | *15* **8** | *18* **6** | *11* **2** | *16* **6** | | *4* **2** | | *35* **40** |
| *P.* cf. *capitata** | | | *8* **3** | | *23* **8** | *27* **8** | *3* **1** | *28* **13** | *22* **10** | *48* **17** | | *79* **60** |
| *Porites brighami** | *42* **18** | *58* **21** | *51* **19** | *62* **23** | *51* **25** | *36* **15** | *16* **7** | *3* **1** | | *4* **2** | | *106* **131** |
| *P. compressa** | *8* **3** | *42* **21** | *67* **40** | *38* **17** | *90* **63** | *64* **38** | *92* **63** | *74* **41** | *35* **15** | *61* **26** | | *256* **327** |
| *P. duerdeni** | | *11* **5** | *4* **2** | | | | | *7* **3** | *2* **1** | *7* **2** | | *15* **13** |
| *P. evermanni**? | | *50* **23** | *79* **51** | *62* **33** | *85* **40** | *77* **42** | *77* **35** | *76* **54** | *22* **9** | *43* **21** | *28* **10** | *212* **318** |
| *P. lobata* | | *100* **68** | *79* **68** | *99* **83** | *100* **78** | *87* **78** | *100* **76** | *92* **75** | *83* **50** | *80* **53** | *96* **64** | *364* **693** |
| *P. rus* | | | | | | *X* **X** | | | | | | |
| *P.* cf. *solida* | | | | | | | *5* **1** | | | | | *1* **1** |
| *P. hawaiiensis** | | | *16* **9** | *12* **3** | *15* **3** | *15* **6** | *50* **23** | *24* **11** | *6* **1** | *4* **2** | *7* **2** | *51* **60** |
| *P.* cf. *annae** | | | | | | | | | | | *2* **1** | *1* **1** |
| *Psammocora explanulata* | | | | | *8* **2** | | | | | | | *1* **2** |
| *P. nierstraszi* | | | | *13* **6** | *23* **6** | *8* **4** | | *3* **1** | *4* **2** | *4* **1** | | *20* **20** |
| *P. stellata* | | *17* **3** | | *1* **5** | *6* **18** | *3* **14** | *9* **3** | *38* **15** | *39* **14** | *6* **3** | *59* **21** | *117* **96** |
| *P. verrilli** | | | | | | | | | *3* **1** | *10* **2** | *7* **3** | *11* **6** |
| Total abundance/reef | 388 | 452 | 570 | 511 | 766 | 542 | 615 | 402 | 318 | 432 | | |
| % Endemic abundance | 37 | 42 | 43 | 41 | 52 | 53 | 49 | 41 | 40 | 43 | | |
| % Endemic stony spp. | 47 | 60 | 38 | 36 | 42 | 41 | 50 | 44 | 39 | 50 | | |

*Note:* From 401 analyzed REA sites 2000–2002; excludes data from Raita Bank. Reefs arranged from southeast to northwest. Reef codes from Table 1. Species data are occurrence indices (*italics*) and abundance indices (**bold**). *O*, the sum of all occurrences per species; **A**, sum of all abundance scores per species. *, endemic to Hawai'i and the northern Line Islands. *?, considered endemic in this report and by Maragos (1995), but not by Veron (2000). *X*, **X**, observed on reef but outside REA sites.

**Appendix 2**

Compilation of All Occurrence and Abundance Indices for Each Species of Nonstony Coral and Other Anthozoans for 401 Analyzed REA Sites on 10 NWHI Reefs

| Other Anthozoans | NWHI Reef and REA Sites per Reef | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | NIH 12 | NEC 19 | FFS 85 | GAR 13 | MAR 39 | LAY 22 | LIS 37 | P&H 69 | MID 51 | KUR 54 | *O* | **A** |
| Subclass Octocorallia | | | | | | | | | | | | |
| Order Alcyonacea | | | | | | | | | | | | |
| *Acabaria bicolor* | | | *6* **1** | | | | | | | *4* **1** | *7* | **2** |
| *Sinularia* sp. (brown) | | | *1* **<1** | | | | | | | | *1* | **<1** |
| *S.* sp. (purple) | | | | *62* **38** | | | | | | | *8* | **38** |
| *S.* sp. (yellow) | *42* **18** | *5* **2** | *2* **<1** | *23* **14** | | | | | | | *11* | **35** |
| Subclass Hexacorallia | | | | | | | | | | | | |
| Order Antipatharia | | | | | | | | | | | | |
| *Cirrhipathes* sp. | *8* **2** | | *2* **1** | | | | | | | | *3* | **3** |
| Order Actiniaria | | | | | | | | | | | | |
| *Heteractis malu* | | | *1* **<1** | *8* **2** | *5* **1** | *X* X | | | | *6* **1** | *7* | **5** |
| Order Zoanthidea | | | | | | | | | | | | |
| *Palythoa* sp. | | | *2* **1** | | | | | | | | *2* | **1** |
| *P. tuberculosa* | *83* **52** | *58* **24** | *5* **28** | *77* **38** | *41* **21** | *64* **27** | *5* **3** | *52* **21** | *33* **13** | *6* **29** | *198* | **256** |
| *Zoanthus pacifica* | | | *5* **2** | | *8* **2** | | | *1* **1** | | *X* **X** | *8* | **5** |
| *Z.* sp. (A) | | | | | *5* **1** | *X* **X** | *5* **3** | | | | *4* | **4** |
| *Z.* sp. (B) | *25* **7** | *42* **18** | *4* **1** | | | | | | | | *14* | **26** |
| *Z.* sp. (Kure) | | | | | | | | | | *6* **1** | *3* | **1** |
| Unidentified anthozoans | | | | | | | | *4* **2** | | | *3* | **2** |
| Total abundance/reef | 79 | 44 | 35 | 92 | 25 | 27 | 6 | 24 | 13 | 32 | | |

*Note:* From 401 analyzed REA sites 2000–2002; excludes data from Raita Bank. Reefs arranged from southeast to northwest. Reef codes from Table 1. Species data are occurrence indices (*italics*) and abundance indices (**bold**). *O*, the sum of all occurrences per species; **A**, sum of all abundance scores per species. *X*, **X**, observed on reef but outside REA sites.