Mapping and GIS analysis of the global distribution of coral reef fishes on an equal-area grid

Don E. McAllister, Frederick W. Schueler, Callum M. Roberts and Julie P. Hawkins

10.1 Introduction

10.1.1 Review of the diversity and status of coral reefs and fishes

Tropical coral reefs form the most diverse and productive ecosystems in the oceans (Dubinsky, 1990). At higher taxonomic levels (e.g. orders, classes and phyla) reefs are perhaps the most diverse ecosystems in the world and they

support a vast, morphologically diverse and colorful array of species. An estimated 4000 species of fishes, approximately 25% of the marine fish species, inhabit coral reefs (Mc-Allister, 1991a). Despite this high biodiversity, coral reefs cover only 0.18% of the world's oceans (Smith, 1978). The fish fauna of coral reefs is thus two orders of magnitude richer than the average of the fish diversity in the oceans. Coral reefs are important to people

Mapping the Diversity of Nature. Edited by Ronald I. Miller. Published in 1994 by Chapman & Hall, London. ISBN 0 412 45510 2.

since they provide more than half the animal protein in the diets of many tropical countries, considerable employment, and coastal protection against storm waves (McAllister, 1988).

If we are to effectively protect marine species along with the ecological benefits provided by these organisms, data about the geographic distribution of biodiversity hotspots is required to evaluate this most important resource. Such an evaluation is especially critical now, in order to best utilize the limited funds available from governments, NGOs, and international agencies for marine conservation. Current identification of megadiversity countries (McNeely et al., 1990) is largely based on terrestrial organisms (e.g. mammals, birds, reptiles, amphibians, butterflies and angiosperm plants). Increases in numbers of species toward the equator are firmly established in terrestrial ecosystems, but Clarke (1992) concluded that evidence for a latitudinal cline is lacking for the majority of marine taxa.

Coral reefs are found between 32°N and 32°S latitude in ocean waters of 20°C or warmer. The majority of reefs are shallower than 30 m depth and they border the coastlines of continents, islands and archipelagos, mostly within the waters of developing nations (UNEP/IUCN, 1988). This distribution, close to large, growing human populations (Harrison, 1992: 198), subjects many coral reefs to intense human impacts.

Coral reefs have formed and persisted only where they are able to recover from natural episodes of physical and biological stress phenomena such as storms, freshwater, cold and outbreaks of predators. Reefs have not formed or have died where natural stresses are chronic. Some anthropogenic stresses (e.g. oil spills and nuclear explosions) are episodic. Others (e.g. sedimentation and sewage) are typically chronic and they may co-occur with other stressors. Recovery under chronic stresses is usually unlikely. As a consequence, 70% or more of the reefs in Japan (Planck et al., 1988),

the Philippines (Gomez and Alcala, 1979), and in Costa Rica (Robinson, 1987) are in only poor or fair condition by the criteria of Gomez and Alcala (1979).

Anthropogenic stresses on coral reefs are summarized by UNEP/IUCN (1988), Smith and Buddemeier (1992), Wells and Hanna (1992) and Weber (1993). Sedimentation from inappropriate agricultural, development and forest management practices is one of the leading stressors in many countries (McManus, 1988; Planck et al., 1988; Samoilys, 1988). Destructive fishing techniques, including explosives, fish poisons and trawls, are degrading coral reefs in Southeast Asia, East Africa and the Caribbean (Rubec, 1986; Alcala and Gomez, 1987; Ansula and McAllister, 1992). Coral mining for landfill, building materials, and for the manufacture of lime removes the substance of reefs in many countries. Many other stressors are summarized in the cited reviews. Weber (1993) maps the degrees of threat to global reef areas.

It is thought that widespread coral bleaching (i.e. loss of colored symbiotic alga or their pigment from the coral polyps) in the Indo-Pacific and Caribbean reefs during the 1980s was caused by global warming (Goreau, 1990; Glynn, 1991; Smith and Buddemeier, 1992; but see D'Elia et al., 1991). Coral bleaching can result from a 1–2 day exposure to 3–4°C above the normal daily temperature maximum or exposure to several weeks of exposure to temperatures that are 1–2°C above the normal daily maximum (Smith and Buddemeier, 1992). Mortality is > 90% for temperature elevations of 4°C for even a few hours.

10.1.2 The information crisis

Compared with terrestrial ecosystems, marine conservation suffers from a lack of attention and resources (Norris, 1993), and although the decline of coral reef fishes and their habitat is apparent, documentation is scattered and

uneven. The establishment of underwater marine parks and reserves has been given a lower priority than those on land (reviewed by Randall, 1982), in part because of human bias in favor of land and in part because of greater human impacts on land. No coral reef fish species is classified as threatened or endangered throughout its range, principally, in our view, because scant attention has been devoted to the question (the jewfish, Epinephelus itajara, has been declared endangered in the US Virgin Islands). Declining numbers of large individuals and population sizes of certain species have been observed and documented in some areas, and of ca. 100 countries with coral reefs, 80 have reported overfishing (Wells and Hanna, 1992).

Economic overfishing is usually distinct from the danger of species-wide extinction. Indeed, some authorities (Randall, 1980) deny that coral reef fishes could become endangered, due to their wide geographic ranges (many species range from East Africa to the mid-Pacific, and some are pan-tropical). Even widespread and common species may become endangered or extinct if human impacts are widespread and chronic, and the total area of coral reef occupied within a range spanning several thousand kilometers may be quite small. This is especially true in archipelagos such as Micronesia and Polynesia. Furthermore, population densities of many species are low. Thus at Toliara, southwest Madagascar, only 25% (136) of the species were ranked as abundant (Groombridge, 1992). This pattern of species abundance is seen in most speciose communities (Magurran, 1991).

Until as little as 10 years ago, insufficient information was available for large-scale mapping of the distributions of coral reef fishes. There were few regional ichthyofaunal handbooks for identification and many groups were without monographic taxonomic treatments. Publication of increasing numbers of handbooks, many with photographs of live fishes,

and of revisions of genera and families, has produced an improvement in the accuracy of species lists published for reef areas. However, the taxonomic description of the world's ichthyofauna is incomplete and each year more than 100 new species, several genera, and the occasional family are described. Many of these newly described taxa are from coral reefs. Summaries of threatened coral reef species or of areas with high biodiversity and endemism are not currently available. There is only an estimate of the number of species of fishes regularly inhabiting coral reefs (McAllister, 1991a) and there is no published world list of fishes or coral reef fishes (DEM has a working manuscript list of fishes of the world). Environmental data, when available, are seldom assembled in ways that facilitate comparisons with biotic data. These problems are compounded by current reduced support for biosystematic research in the north, and the lack of funding for natural history museums and biosystematic research in the south.

10.1.3 The global perspective

All of the above concerns led the Species Survival Commission of IUCN to establish a Coral Reef Fish Specialist Group charged with promoting the conservation of coral reef fishes, obtaining sound information on the status of these fishes, evaluating human impacts and making recommendations for their conservation. Ocean Voice International, a non-profit marine environmental organization, was chosen to manage this project for the Coral Reef Fish Specialist Group. Challenged by the scale of the problem and a lack of information on coral fish biodiversity patterns, we developed and are enhancing a GIS that is similar to the GIS developed for the recent ICBP biodiversity mapping study (ICBP, 1992, ch. X).

Fish, like land birds, are better known taxonomically than invertebrates, non-vascular

plants, and microorganisms; they can therefore act as a provisional 'flagship' group for coral reefs. The coral reef fish GIS which we describe in this chapter is designed to provide information on where the biodiversity and threats to diversity are located, and so to focus efforts on fish habitat protection where it is most needed. We believe that fish are only a provisional flagship group, because coral reefs are such distinctive and important habitats that biosystematic studies, biological inventories, and biogeographic analyses should be carried out to evaluate the status of every major taxon.

Biogeographic hotspots are areas which support large numbers of species compared to the surrounding region. These are clusterings of species that create strong regional anomalies in the global increase in biodiversity toward the equator (e.g. Clarke, 1992; McAllister et al., 1986, North American freshwater fishes; Anderson, 1984a, b, North American amphibians, reptiles and birds). Hotspots may occur where several biogeographic zones abut (e.g. northwest Australia/southern Indonesia) and where several tectonic plates meet and biotas from adjacent plates come in contact or mix (Woodland, 1986; Springer, 1982; Planck et al., 1988). Hotspots also occur in areas where conditions favor rapid speciation or in areas with relatively stable conditions that reduce rates of extinction.

Hotspots for different taxa often do not coincide. The principal North American hotspot for freshwater fishes is in the Cumberland—Tennessee Plateau drainages of the eastern United States, while for birds it is in northern Mexico and the adjacent areas in the United States. This means that different protected areas may have to be chosen for the different taxa to maximize conservation of biodiversity. Establishing reserves for tigers may protect some of the less widely ranging species, but many species may be lost if these reserves do not fall in regional hotspots for the other taxa. Genera

of reef-forming (hermatypic) corals are mapped (Vernon, 1986, 1993), and the addition of maps for fish, perhaps the reef animals most unlike corals, should improve judgements about the total diversity of reefs. This will be an important step in selecting marine reserves or parks and for devising additional conservation strategies.

Fundamental changes are evolving in the philosophy of biodiversity conservation. Conventional conservation focuses on a few higher large-sized vertebrates and plants. Today a broader concept of biodiversity is becoming accepted. There are too many species at risk to classify as rare or endangered, let alone to prepare and carry out recovery programs for each species. One response to this problem is a call for the conservation of ecosystems, landscapes and seascapes, to protect numerous species and their habitats. This approach is valid, but it does not include a method to identify which ecosystem, landscape or seascape should be set aside as a protected area for optimal conservation.

Mapping and locating species hotspots offers a solution to this dilemma. But this approach ignores the phylogenetic differences between higher taxa, such as genera, families and orders (McAllister, 1991b). The species hotspot approach fails to distinguish between an area with three species of sparrows and another with a sparrow, an eagle and a swallow, despite the greater taxonomic, ecological and genetic diversity of the latter grouping. A resolution of the dilemma is simple. Compare the total number of taxa (species, genera, families, etc.) found in two prospective areas for conservation (or when cladistic analyses are available, total the number of cladogram nodes between species). This eco-taxa hotspot approach is discussed in more detail by Vane-Wright et al. (1991), Williams (1993), Williams and Humphries (1992), Williams and Gaston (in press) and McAllister (1993). The eco-taxa

approach is relatively simple and yet it is powerful in combining information from the two disciplines of biosystematics and ecology.

Except for a few widespread and conspicuous species which can be inventoried by remote sensing or repeated sampling schemes, knowledge of biotic distribution depends on analysis of individual records. A record, traditionally a museum specimen, is a documented verifiable encounter with a species at a particular place and time. Spot distribution maps represent each record with a symbol instead of using shading or encircling a presumed known range. Although such maps are available in some monographs for coral fishes (e.g. Allen, 1975), there are no published maps for most species.

We began our work by preparing spot distribution maps of >950 coral reef fishes, about a quarter of the known species (Roberts and Hawkins, 1992). Beginning with maps compiled by the late Sir Peter Scott, one of the founders of the IUCN's Species Survival Commission, records are assembled from taxonomic and regional publications and from museum specimens and they are plotted onto the equalarea basemaps described by Alfonso (1991).

The fish distribution maps show geographic patterns for individual species. McAllister et al. (1986) earlier used computers and software to assemble fish distributional and environmental data sets into grids and to carry out analyses within and among these data sets. This approach is now automated by the GIS and packages of programs, ranging in cost from a few hundred to many thousands of dollars, are now available commercially to handle data and cartographic manipulations. We use a GIS package (QUIKMap running in an inFocus module) in this study, but one of the several advantages of the equal-area grid GIS approach described here is that moderate-sized data sets can be compiled and manipulated manually.

10.1.4 GIS tools and conservation

(a) GIS parameters

Geographic units (e.g. countries) vary in size and shape and seldom coincide with trends or variables that one wishes to investigate. In addition, different sets of point data seldom coincide. The grid system is found to be advantageous in stabilizing the unevenness of sampling effort (McAllister et al., 1986) when trend surface analyses (from Schueler, 1982) are used to estimate environmental parameters between known data points. The establishment of a standard global grid would enable researchers to more easily exchange data sets, reduce duplication and labor, and facilitate comparison of results.

Quantitative biogeographic analysis, like all mapping, has always been hampered by the sphericity of the earth. McAllister *et al.* (1986) uses cells one degree of latitude by one degree of longitude that decrease in size and 'squareness' toward the pole. The usual method to produce a grid of 'square' cells for a local area (i.e. the Universal Transverse Mercator Grid) is based on a system of narrow longitudinal zones, each with its own grid system (Sebert, 1975; Weller and Oldham, 1988). This system, however, is awkward for global comparisons.

(b) Equal-area cell system

To create a global system of essentially square, equal-area cells, we sacrifice the requirement that the longitudinal bounds of the cells line up to produce a Cartesian grid. Therefore the system that we use to spatially define the cells does not provide a coordinate system for computations. Consequently we use the latitude and longitude at the center of each cell to locate it in spherical geometry or on a two-dimensional map projection. This equal-area cell system is based on the Sanson–Flamsteed map projection. In this projection longitude is collapsed onto a central meridian (i.e. east–

west distance from the meridian = longitude × cosine (longitude)) so that relative area is preserved and the parallels of latitude are straight lines perpendicular to the central meridian.

Research hypotheses and data impose restrictions on cell size for any project. A fine grid may be required to observe effects at a small geographic scale, but may not give better resolution than a coarser grid if sampling has been relatively sparse or uneven (McAllister et al., 1986). We selected the 2-degree cell system as the best compromise for obtaining locally useful results and for adequately spacing the records. A 2-degree cell has an area of about 50 000 km². The cell bands are bounded by even-numbered degrees of latitude and originate at the 0° meridian of longitude. Systems of cells are propagated east and west from this central meridian, and must meet somewhere, not necessarily at 180° (the last cell is usually smaller). We place this overlap zone in areas of minimal biogeographic and political interest (i.e. the tropical eastern Pacific, where there are no islands, and then west running northward through the Bering Strait). The overlap zone could be relocated for another study.

(c) GIS software and hardware used

We examined different moderately priced (under US\$1500) GIS packages for desktop microcomputers. This appraisal, based upon capability needs and user-friendliness, selected Earth and Ocean's inFOcus (Earth and Ocean Research Limited, 1991) that runs QUIKMap by Ayxs software (Environmental Sciences Limited, 1990) with FoxPro programs (Fox Software Inc., 1991). This GIS will run on a microcomputer with 525 kilobytes (kb) of random access memory (RAM), a VGAmonitor, and a 50 megabyte (Mb) hard disk. Memory above the DOS 640 kb limit will be utilized, if it is configured for EMS-memory. We ran it initially on a 386 20 MHz central processing unit (CPU) system with 8 Mb RAM, a 100 Mb hard disk and a VGA-monitor. We are now running it at 66 MHz internally and 33 MHz externally on an Intel 486 CPU with internal math coprocessor, a memory cache, 4 Mb RAM, a 200 Mb hard disk and a SVGA-monitor. The new system draws maps on the screen faster, saving time for the operator. The map can be saved for re-use, revision, zooming in on details, and printing or plotting. Maps can be labeled, printed or displayed on a variety of black or color printers and plotters.

Earth and Ocean prepared, on contract for Ocean Voice, a module incorporating Ocean Voice's equal-area grid. The world basemap provided by Earth and Ocean shows the location of most of the coral reefs of the world as a discrete colored map layer. The GIS can import other basemaps, switch between several map projections, zoom in on localities to provide more detail, and output on several printers and plotters. One can key information into the database, digitize localities from a map, create or edit records using a cursor on a map displayed on the computer screen, and transfer data between compatible databases. Although our initial goal was to study coral reef ecosystems in the tropics, the equal-area grid works equally well for most terrestrial areas.

The data are stored as latitude—longitude points in a generic FoxPro '.DBF' file and this allows the point locations to be used for other projects. Any data with either these or UTM coordinates can be imported into the system. Manipulation of the database then enables the number of species in a cell to be used for various analyses. This includes summation of any combination of species or families, counts of endemics and output of appropriate maps. These manipulations are done with FoxPro routines outside the inFOcus mapping module.

Table 10.1 lists the longitudinal width of 2degree cells for a range of latitudes. Mean latitudes in this table are lower than median cell band latitudes (odd-numbered degrees)

TABLE 10.1 A comparison of areas comprising 2-degree cells. These are calculated for a spherical model of the globe and then corrected for an oblate spheroid. Mean latitude is the latitude of the centroids of each cell band. Corrected longitudinal width is the width of cells adjacent to the Greenwich meridian, as calculated by Earth and Ocean on inFOcus. The relative area is the ratio corrected area/spherical area

Latitude		Longitude			
Cell band	Mean	Corrected area	Spherical area	Relative area	
1	1.00000	1.00015	1.00000	1.00015	
11	10.99865	1.01859	1.01856	1.00003	
21	20.99074	1.07962	1.07098	0.99966	
31	30.97112	1.16527	1.16646	0.99898	
41	40.93607	1.32189	1.32481	0.99780	
51	50.88377	1.58202	1.58877	0.99575	
61	60.81444	2.04589	2.06235	0.99202	
71	70.73032	3.02238	3.07109	0.98414	
81	80.63541	6.13179	6.39148	0.95937	

because cells bounded by meridians are wider toward the equator. The number of cells in a cell band ranges from 180 cells at the equator to 136 at 41° latitude and 30 at 81° latitude. Earth and Ocean calculates a system of 2degree cells designed to have equal areas on the 1927 North American Datum spheroid (a standard model of the flattened shape of the earth) used by QUIKMap. Table 10.1 compares the area of these cells to those based on a spherical earth. Up to a latitude of 61° the areas of cells agree within 1%, and even at 81° they agree within 5%. We use the corrected 2-degree cell system to obtain the results reported here but the simpler spherical model would have been sufficient.

There are about 5300 cells between 30°N and 30°S latitude but only about 700 contain coral reefs. Proportionally, about 64% of these are in the Pacific Ocean, 21% in the Indian Ocean and 15% in the Atlantic Ocean. The ratio of Indo-Pacific (85%) to Atlantic cells (15%) is close to the ratio for coral reef areas given by Newell (1971): 1 250 000 km² (83%) for the Indo-Pacific and 250 000 km² (17%) for the Caribbean. Fish data currently occupy 480 cells or about 68% of the known reef cells.

A few of the mapped fishes occur in cells having rock rather than coral reefs (e.g. Ascension and St Helena).

10.2 Methods

10.2.1 Map data collection, entry and processing

In this study about 950 species of coral reef fishes are mapped from eight families: surgeonfishes, Acanthuridae; butterflyfishes, Chaetodontidae; neon gobies, Gobiosoma, Gobiidae; wrasses, Labridae; angelfishes, Pomacanthidae; seabasses, Serranidae (sensu lato); pufferfishes, Tetraodontidae; and moorish idols, Zanclidae. For the study reported in this chapter, 8928 individual records were entered into the database for 799 of these species, including 12 Gobiidae, 264 Serranidae, 260 Labridae, 114 Chaetodontidae, 1 Zanclidae, 63 Acanthuridae and 85 Tetraodontidae. These 799 species comprise the all-family sample that includes about 20% of all coral reef species and 7 of the 46 primarily reef-associated families (Thresher, 1992). More than 110 fish families are found

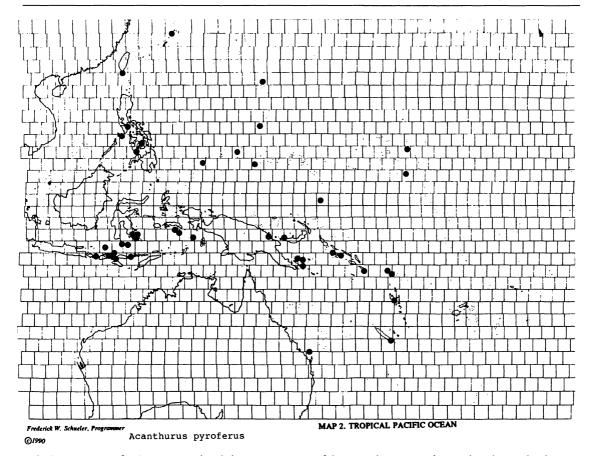


FIGURE 10.1 Pacific Ocean records of the mimic surgeonfish, *Acanthurus pyroferus*. This shows the form in which data were entered into the GIS database.

on coral reefs, but most have relatively few coral reef species. Figure 10.1 shows a sample spot distribution map for pacific records of the mimic surgeonfish *Acanthurus pyroferus*.

Distributional data for the maps are compiled from 66 sources. Sir Peter Scott's lists of species present at sites throughout the Indo-West Pacific during the 1970s and early 1980s are carefully checked using his detailed field descriptions and up-to-date taxonomic works (Roberts, 1987; Roberts and Hawkins, 1992). The map data are then transferred to the Ocean Voice equal-area grid maps, and records are added from other published and unpublished sources. A record or identity of a fish is not

used when the accuracy is in doubt. Map data for the 950 species are still being gathered, so future analyses will be based on more records.

Faunal studies are uneven and some are out of date. Recent faunal works or catalogues provide some degree of confidence for the Red Sea, southern Japan, the Bahamas, the Great Barrier Reef, and the Chagos Archipelago. On the other hand, studies in possibly important areas like Somalia, Mozambique, parts of Polynesia and the eastern tropical Pacific are either non-existent or focused upon only the commercial fishes.

A number of works (e.g. Myers, 1989) attribute records to island groups rather than

specific localities. Such records link with an arbitrary point in the center of the area and similar records for each species are plotted on this point. The maps thus represent a mix of very precise records and those which are more broadly defined. In these maps, species appear to be more widespread but this is probably attributable to lower species/cell totals that represent areas with records from individual collections rather than regional summaries.

The Chaetodontidae, for example, are well studied taxonomically, while there is no taxonomic monograph of the very diverse Gobiidae, although several of the genera are revised. Some areas (Japan, Israel, Natal, Florida, etc.) have high concentrations of ichthyologists or biological stations which have encouraged visits. All these factors augment or diminish the number of species known from an area and consequently distort the analysis results. Nevertheless, previous experience (McAllister et al., 1986) leads us to believe that grid-based species density maps are a robust method of locating hot spots. Subsamples of 311 and 501 of the 775 species of North American freshwater fishes and 125 endemic species all show the same major hotspots.

Map data (Figure 10.1) are entered into the computer using a mouse-driven cursor. The ability of QUIKMap to zoom in to any scale helps increase precision and about 80% of the points are entered from an enlarged basemap. For the western Pacific we enter records by stations since many of the records occupy the same locations. About 4% of the records are duplicates in the present data set.

(a) Hotspots and endemic species

Analyses are carried out for all species (Plates 7–8) and endemic species (Figure 10.3). ICBP (1992) defines endemic species as those with ranges of less than 50 000 km². Each of the grid cells on our maps correspond to this area. However, marine species with planktonic dispersal tend, on average, to have much larger

ranges than terrestrial species and so a range size of 50 000 km² would be inappropriate for fishes. For the purposes of this study we define endemics as those species restricted to an area with a diameter of 4 cells or fewer (i.e. an area of 12.5 cells or fewer).

We compile the number of species per cell for each family and for all families. To obtain a regional picture of species density, we prepare uniform maps in which each cell contains records of every species found in adjacent cells (calculated as cell centers within 3° of the center of the cell being summed). This helps compensate for the clumping of records at arbitrary archipelago centers.

We do not deal with patterns of similarity among cells or regions. Our hotspots are not biogeographical provinces but contiguous areas with fairly uniform high numbers of species. Likewise, our endemics are species with small ranges, not species with ranges limited to a geographic or biogeographic area.

(b) Latitude-longitude clines

We sum the species present in the 10° longitudinal bands (Figure 10.2) to test the hypothesis that species are evenly distributed around the tropics. We sum species in 4° latitudinal bands (Table 10.2) to test the hypothesis that the number of species increases toward the equator. Product-moment correlations test the relationship between the number of species and the latitude of the band. The tests are applied to several groupings of cell bands: (1) from the equator northward, (2) from the equator southward, (3) poleward from the equator (i.e. north and south latitudinal bands together), and (4) poleward from the equator excluding the bands immediately north or immediately south of the equator.

(c) Range sizes

To test the hypothesis that most coral fishes are widespread, and hence at little risk of extinc-

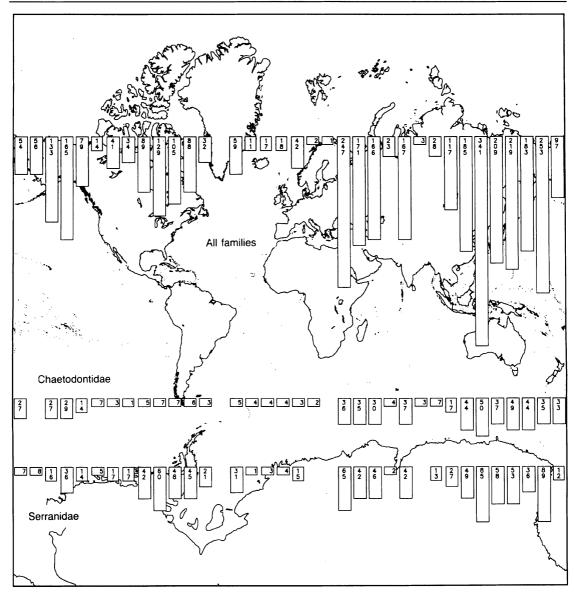


FIGURE 10.2 Histograms of the longitudinal species density (i.e. species numbers/10° longitudinal band) around the world for the butterflyfish and seabass families. The number of species is shown at the top of each bar of the histogram. Note that seabass (Serranidae) samples are relatively richer in species than butterflyfish (Chaetodontidae) samples in the western Atlantic.

tion, we measure the range span of each species as the angular distance between the centers of its most distant occupied cells. For species with ranges < 180°, this is calculated as the maximum angle (the great circle distance) between records. For species with larger ranges we use

TABLE 10.2 The occurrence of all families of coral reef fish species in latitudinal ranges across the globe

Latitude	Number of species	Latitude	Number of species
32–28°N	265	0-4°S	116
28-24°N	344	4–8°S	275
24-20°N	296	8-12°S	295
20–16°N	215	12-16°S	234
16-12°N	337	16-20°S	301
12-8°N	314	20-24°S	288
8-4°N	309	24–28°S	138
4-0°N	178	28-32°S	150

the shortest distance between records that crossed the greatest longitudinal gap in the range (Table 10.3).

(d) Differences in patterns between taxa

To test the 'tiger reserve hypothesis' that a reserve chosen for one species or taxonomic group effectively protects many others, we compare latitudinal and longitudinal trends for two family pairs. For latitude we compare the number of species of butterflyfishes, Chaetodontidae, and wrasses, Labridae, in 4° bands between 32°N and 32°S. For longitude, we compare the number of species of Chaetodontidae and seabasses, Serranidae, in 10° longitudinal bands around the globe (Figure 10.2).

(e) Higher taxon diversity

Using this same approach, we sum genera and families in each occupied cell and we calculate correlations between the number of species, genera, families and total taxa (i.e. species + genera + families).

10.2.2 Analysis

(a) Other data sets

The next stage in our project is to gather climatic, geologic, oceanographic and biologic information about the environment of coral reef fishes and to determine the location and severity of threats to fishes and reef habitats. To preserve biodiversity, we attach the highest conservation priority to areas where either reef fish diversity and/or endemism is high and human impacts are greatest.

(b) Statistical methods

Correlation coefficients were calculated between numbers of species in each family and total species, and latitude and longitude. Some data sets were compared using chi square tests. The shapes of latitude–longitude distributions were compared by 2-sample Kolmogorov–Smirnov tests (Sokal and Rohlf, 1981). A critical probability of p=0.05 was used. Figure 10.2 and Table 10.2 show latitudinal and longitudinal patterns of species richness, and the global species density maps, Plates 7–9 show the locations of hotspots.

10.3 Results and discussion

10.3.1 Species density: hotspots and clines

Plates 7–9 present the species density changes obtained in our analyses. The species densities on the maps in these plates reflect changes both in the level of sampling and in the biodiversity densities. The presented analyses of diversity clines are therefore performed at a level coarser than single cells to offset this sampling intensity bias. Further data will increase the accuracy of these mapped gradients.

(a) Hotspots

Inspection of the smoothed species density maps (Plates 7–9) and the latitudinal and longitudinal cline patterns (Table 10.2, Figure 10.2) reveal the locations of some global coral reef fish hotspots. The highest cell totals are found in the 'coral triangle' (cf. Briggs, 1974: 21) with cell counts well above 100 found from

TABLE 10.3 A comparison of coral reef fish species richness in relation to the species diverse range spans. The increasing number of coral reef fish species is shown in relation to the increase in the cumulative percentage. Range spans are defined as the angular distance between the most distant occurrence records

Geographic range		Species number		
Angle (degrees)	Range span (km)	Number of species	Cumulative number	Percent
0–2°	0–222	133	133	17%
<5°	223-555	12	145	18%
<10°	556-1 110	33	178	22%
<20°	1 111-2 220	86	264	33%
<40°	2 221-4 440	110	374	47%
<60°	4 441-6 660	100	474	59%
<90°	6 661-9 990	98	572	72%
<150°	9 991–16 650	112	684	86%
<180°	16 651-19 980	11	695	87%
<240°	19 981-26 640	13	708	89%
<300°	26 641-33 300	7	715	89%
≥300°	33 301-40 000	84	799	100%

the Ryukyu Islands of southern Japan, southeastern New Caledonia, in the eastern Indo-Australian Archipelago, and in Melanesia. The Rvukvu Islands have the highest smoothed cell count with 257 species, and Palau has the highest raw cell count with 183 species. Relatively better sampling in the Ryukyus and weaker sampling in the western Indo-Australian Archipelago is most probably reflected in the cell totals for these regions. Diversity decreases eastward through Polynesia, with regionally high smoothed cell values at Guam (151 species), Wake Island (140 species), Tahiti (148 species) and in the Tuamotu Archipelago (117 species). Nevertheless, only 87 species are recorded in Hawaii.

There are three hotspots in the Indian Ocean. The first is around Madagascar, on the islands to the east and north, and in East Africa. The maximum smoothed value of 168 species near Durban surely reflects intensive sampling in this area. The next most dense cells are 114 species on Zanzibar and 113 species in the Comores Archipelago. The second hotspot is the Red Sea with smoothed cells containing up to

102 species at the north end. The third hotspot spans the Laccadive–Maldive–Chagos–Sri Lankan regions and contains smoothed cell values up to 108 species in the northern Maldives. Perhaps due to weak sampling, the eastern shore of the Indian Ocean formed by Sumatra has low species cell values. Finally the Caribbean has moderate hotspots of 94 species in Florida and 84 in Jamaica.

(b) Latitudinal clines

Latitudinal gradients in diversity, noted in many other taxonomic groups, are relatively well defined for reef fishes in the western Pacific. The south end of the Great Barrier Reef has 800 species of fishes (69 in our smoothed data), while the north end, closer to the equator, has 2000 species (118 in our smoothed data; Sale, 1976). Emery (1978) points out that the latitudinal gradient in diversity is correlated with a host of parameters. These include increasing seasonality and frequency of winter storms, decreasing solar radiation, the geographic area, the continuity of productivity, and the long-term climatic stability

in high latitudes. In the Red Sea, on the other hand, peak fish diversity and the diversity of many other reef groups (e.g. corals and molluscs) is found in the central and northern region (Sheppard *et al.*, 1992). In the south, extreme environmental conditions and the amount of hard substrate restrict the growth of reef-building corals.

Correlations between the number of species in all families and the latitude were not significant for several partitions of the globe tested including: (1) north of the equator; (2) south of the equator; and (3) grouped poleward from the equator. Increases toward the equator are offset by a marked decrease in the bands immediately north and south of the equator. When the correlation is calculated without the two equatorial bands the correlation (-0.81) is significant (p=0.02). The reduced number of species near the equator is likely due to: (1) a reduction in coral reef habitat on the west coast of South America due to cool upwelling; (2) the large influx of fresh turbid water from the Amazon and Orinoco rivers on the east coast of South America: and (3) upwelling and influx of fresh turbid water from the Zaire river on the west coast of Africa. Parts of the coasts of Somalia in the Gulf of Aden and the Indian Ocean are exposed to seasonal monsoon-driven upwellings of cool water. There are coral reefs, untouched by upwelling on the Somali coast, but these are poorly sampled for coral fishes. The equatorial zone species counts are high only because of the species-rich 'coral triangle' around the East Indies.

(c) Longitudinal clines

Longitudinal clines in diversity are less well studied than latitudinal clines. However, Briggs (1986) analyzed sizable data sets on a number of biota that were grouped by biogeographic regions. We build on his approach and used the grid system to detect more precisely where

changes in diversity occur independent from biogeographic concepts. Figure 10.2 shows the changes in numbers of species around the tropics in the all-family sample. The results confirm that there are species-rich and species-poor zones and that the richest area is in the coral triangle from Sumatra east to the Marshall and Gilbert islands, with another moderately rich area in the West Indies. The GIS data enable us to quantitatively define the borders of these two areas and to define two more species-rich areas. The species-rich zones are:

- (1) the coral triangle from 100 to 170°E, with species counts per 10° band ranging from 117 to 341 species and a mean count of 215 species per band;
- (2) the Indian Ocean from East Africa to Sri Lanka (i.e. 30–80°E), with species counts ranging from 23 to 247, and a mean of 155 species per band;
- (3) eastern Polynesia from Samoa and Hawaii east to the Society Islands (i.e. 130–170°W), with counts ranging from 56 to 165 and averaging 108 species per band; and
- (4) the Caribbean Region including the West Indies, the Caribbean Sea and Gulf of Mexico (i.e. 60–100°W) with counts ranging from 88 to 129 with a mean count of 103 species per band.

The four species-rich zones have mean species counts of 103–205 species per band and are separated by species-poor bands of 3–59 species with an average of 24 species per 10° band. The species density maps in Plates 7–9 show the north-south limits as well as the east-west limits of these hotspots. We also note that bringing the north-south component into the analysis would more precisely align the eastern Polynesian hotspot with Victor G. Springer's (1982) Pacific Plate fauna.

10.3.2 Range sizes and taxonomic differences

(a) Range spans

The view has been expressed that most coral reef fish species are not threatened by human activities because populations are dispersed across wide ranges and this buffers the species against extinction from local impacts. We tested this hypothesis by calculating the frequency of range spans. Data in Table 10.3 show that 59% of the sample have range spans under 6660 km, 33% of the sample have range spans under 2220 km and 22% of the sample have range spans under 1110 km. That means that one-third of the species have range spans smaller than the length of the Great Barrier Reef (2300 km). Thus ranges of coral fishes fall into the same pattern found by McAllister et al. (1986) and Anderson (1984a, b), where North American freshwater fishes, amphibians, reptiles and birds are dominated by species with relatively small ranges. The hypothesis that a large range offers protection is not supported for the majority of coral reef fishes. Some of the species with small ranges will most probably be shown to have larger ranges in the future (e.g. deepwater coral fishes). These species are simply more poorly sampled than those from shallow water.

The GIS database cannot yet be used to measure the relationship between the number of species of corals and coral fishes. Harmelin-Vivien (1989) calculates this relationship for 14 Indo-Pacific sites varying from a small local reef to the Great Barrier Reef and the correlation is strong (r=0.94, p <0.001). A part of this correlation may reflect the species—area relationship due to the variation in the size of reefs. However, although this relationship holds true on the broad geographic scale, within reefs it is

less obvious and the two factors are not strongly correlated (Harmelin-Vivien, 1989).

(b) Taxonomic differences in patterns

A Kolmogorov–Smirnov test of the distribution of numbers of species of chaetodontids and labrids in the 4° latitudinal bands showed no significant differences between families (D = 0.0401, p = 0.4708). A similar comparison of chaetodontids and serranids in 10° longitudinal bands was significant (D = 0.1689, p < 0.0001). One can conclude that on a global scale optimal solutions for protection of biodiversity may differ among families. The tiger reserve hypothesis is thus not supported for the oceans, confirming results for freshwater and terrestrial vertebrates by Anderson (1984a, b) and McAllister *et al.* (1986).

(c) Taxonomic diversity

The finding that higher taxon richness predicts species richness in ferns, birds and bats (Williams and Gaston, 1993) is confirmed for coral fishes. The number of smoothed coral fish species is very strongly correlated with the number of genera (r=0.96), and less strongly related to the number of families (r=0.71). The weaker relationship with families may be an artifact of the small number of coral fish families. This may also reflect differences in the geographic coverages considered in studies that treat family-level taxa.

The correlations between species, genera and families demonstrate that the number of genera or even families in an area may reflect species diversity in coral fishes. This property could be used to advantage where decisions have to made quickly on whether to save a threatened area. For example, the RAP process could be modified to make a list and count the genera of several higher taxa rather than count the species of a few taxa. This would certainly increase the efficiency of the RAP and broaden its foundation.

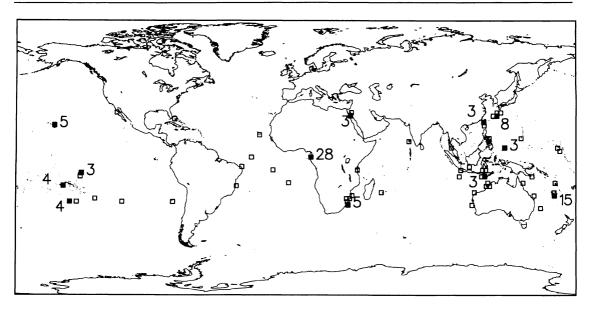


FIGURE 10.3 This is the world distribution of records of endemic species of coral fishes presented in the equidistant cylindrical projection. Open squares represent cells with one or two species and filled squares represent cells with three or more species (labeled with the species number). Endemism is defined here to include species with ranges that extend across a diameter of four cells or fewer. Approximately 92% of the coral fish endemics studied occupied a single cell. Symbols overlap since they are plotted in a slightly larger format than the 2-degree cells they represent.

10.3.3 Centers of endemism and extinction

Centers of endemism are areas where large proportions of localized endemic species are present. Our data show that 147 species or 18.4% of the 799 species in the all-family sample are endemics. Also 133 species or 16.7% occupy a single cell and 15% of the 114 chaetodontids occupy a single cell. These results indicate that one-sixth of coral fishes occupy very small ranges (i.e. on the order of 225 km wide).

Figure 10.3 shows areas of endemism world wide. A result that we did not expect is that the richest area in our database is the Gulf of Guinea on the Atlantic coast of Africa (28 species). Several other clusters of endemics in areas where there are relatively few total species include the Gulf of Guinea (28 endemics out of 42 species, 67%), New Caledonia (15

endemics out of 133 species, 11%) and Hawaii (5 endemics out of 87 species, 6%).

Many studies of endemism contain pseudoendemics. Pseudo-endemic species have known ranges that are geographically restricted but their actual ranges are considerably larger. Pseudo-endemics are more frequent in groups that are poorly studied taxonomically and have relatively high proportions of newly described species. Pseudo-endemic species also often are from habitats that are poorly sampled. For example, coral fishes with habitats in deep water and on rough bottoms are more poorly sampled. Therefore, it is expected that these ecotypes will contain more pseudo-endemics. Fifteen percent of the relatively well-studied butterflyfishes are endemic species while 18.4% of the species in the all-family sample are endemics. This suggests that the all-families species sample is reasonably good (has few pseudo-endemics) since it does not contain a significantly higher proportion of endemics than the well-studied butterflyfishes.

Centers of endemism are largely located around isolated islands or island groups and in marginal areas (e.g. the Red Sea). Briggs (1974) lists many such marine areas of endemism. For example, Lord Howe Island, about 300 miles east of Australia, has 390 species of inshore fishes (Allen et al., 1976). Of these species, 60% are wide-ranging tropical forms; 10% are endemic to Lord Howe Island, southern Australia and New Zealand; and less than 4% are endemic to Lord Howe and nearby Norfolk Island. Off Isla de Paques (Easter Island) in the eastern Pacific endemism reaches 26% (Randall and Cea Egaña, 1989). The Hawaiian Island shore fishes show 34% endemism, the eastern Pacific Cocos Island fishes show 7% endemism and 9-10% of the Revillagigedos Archipelago fish are endemic (Briggs, 1974). Approximately 10-15% of the 1000 fish species in the Red Sea are endemic (Botros, 1971).

However, these various percentages include a number of non-coral reef fish species and, thus, are not comparable with our data. In addition, our definitions of endemism are not the same. The *in situ* speciation associated with these islands is dependent upon the area, the degree of geographic isolation, the direction of the currents and the changes in climate over geological time. Centres of endemism for fishes also overlap with those for other taxa. Approximately 17% of reef fishes (by the criteria of Ormond and Edwards, 1986), 5.3% of the echinoderms and 6.3% of the corals are endemic in the Red Sea.

Centres of endemism are important for conservation because of the high proportion of unique species. The small ranges that endemics occupy make it more likely that human impacts could lead to extinction. That likelihood will vary according to the local human population size, its growth and the extent of its environment-disturbing activities. Those endemics occupying

a single cell are at high risk from human impacts. A crown-of-thorns plague, a spill of toxic chemicals, or sedimentation from deforestation or agriculture may push an endemic species toward extinction. Risks of extinction are higher when an individual threat is serious, when several threats are coincident and when the threats persist, as is the case with oil spills in the Arabian/Persian Gulf (Roberts *et al.*, 1993).

Global warming poses a number of threats to the survival of species. Insular endemics are especially at risk if no island or series of islands can act as stepping stones to suitable habitat when the current range becomes uninhabitable. If there are stepping stones in the right thermal direction, survival is still not guaranteed. All the requirements of the life cycle must be met; this includes adequate food, habitat, spawning grounds and currents to carry eggs and larvae to the new island. Migration of adult coral fishes to a new island is highly unlikely for most species. The hypothesis that climatic change is likely to cause extinctions is supported by Briggs' (1966) a posteriori analyses of endemism in isolated oceanic islands. He ascribes the low degree of endemism found on isolated north and middle Atlantic islands to a drop in sea surface temperature that occurred during Pleistocene glaciations. Thus risks of extinction in isolated oceanic island endemics are high, whether the climate warms or cools. Springer and Williams (1990) also argue that extinctions follow cold coastal upwelling during glacially lowered sea levels in the Indo-Australian region.

GIS can be used to model the likelihood of survival for insular endemic species. For example, suppose with Peters (1988) that a 3° warming shifts the isotherms 250 km toward the poles (cells in the current grid are about 220 km wide). It should be possible to model the chances of transport of spawn to a refuge given data regarding surface currents, temperatures and reproduction activity (e.g. time of spawning, duration of egg and larval stages). Similar

models calculated the likelihood of stormblown boats carrying human cultures in different directions in Polynesia.

10.4 Conclusions

Equal-area grids and GIS are shown to be useful manual or computerized tools for studying geographic patterns in biological diversity. Numbers of species, taxa, and endemic species per area or cell are relevant to conservation planners. Similarly, patterns of human activities that impact on the environment can be localized with data stored in equal-area grids and GIS data sets. Knowledge of those patterns is useful in prioritizing areas for protection, foreseeing impacts of pending threats, and planning other preventative or remedial conservation activities.

One of the advantages of grid GIS analysis is that concepts can be tested on quantified data. This is important for research on biodiversity, biogeography and ecology. It is also an important tool for establishing the wise use of the often limited resources available to conservationists. Hopefully the Global Environment Facility and other Earth Summit activity funders will provide significant new support for biosystematics, biological inventories and ecological studies to underpin GIS studies and conservation efforts.

10.5 Summary

Coral reefs in many areas of the world are degraded by human activities, but geographic information about the fishes (approximately 4000 species) on those reefs is unavailable or widely scattered. Based on an ongoing global study, this chapter describes the use of a GIS to assemble, analyze and present information to support the conservation of coral reef fishes. This includes the geographic occurrence, threat

status and areas of high diversity and endemism ('hotspots') for these species.

An equal-area grid is used to summarize the distribution patterns of species. The grid cells are 2° latitude wide and approximately 50 000 km² in area. Data about the geographic distribution of 799 coral reef species in the families Gobiidae (12 species), Serranidae (264), Labridae (260), Chaetodontidae (114), Zanclidae (1), Acanthuridae (63) and Tetraodontidae (85) are compiled and analyzed. Counts of species, species within each family, genera, and families are calculated for each cell and these same sums are also calculated from the records in contiguous cell groupings. The distributions of these sum totals are then mapped.

The number of coral reef fish species increases toward the equator, but there is a drop in the number of species within 4° of the equator. It is probable that this anomaly is due to either cool oceanic upwelling or high-volume turbid river discharges. These occur near the equator, on the east and west coasts of South America, and on the west coast of Africa. Latitudinal diversity peaks near the equator in the Indo-Australian Archipelago. If the anomalous belt is excluded, there is a significant negative correlation between latitude and the number of species.

A longitudinal summary of the distribution of coral reef fishes around the globe shows four peaks of diversity: the coral triangle around the East Indies; East Africa to Sri Lanka (with three clusters); Polynesia; and the Caribbean Sea–Gulf of Mexico area. These areas average 103–205 species per 10° longitudinal band compared to an average of 24 species per 10° longitudinal band elsewhere. This spatial analysis confirms the existence of these biodiversity hotspots and helps to define their boundaries.

The longitudinal distribution of species richness for the butterflyfishes (Chaetodontidae) and seabasses (Serranidae) are analyzed using the Kolmogorov–Smirnov test. The numbers of species in these two groups are very distinctive

(D=0.1689, p<0.0001) and this demonstrates that major taxa may differ in the geographic location of their hotspots.

Family and generic richness is strongly correlated with species richness and this suggests that the locales of higher taxa can be used to rapidly assess the importance of conserving a threatened seascape. The inclusion of counts for genera and families as well as for species in an area increases the comprehensiveness of the measured biodiversity.

Our data refute the view that most coral reef fishes are unlikely to be threatened by human activities because they are widespread geographically. In our sample 59% of the species ranges span less than 6660 km and 33% of the species ranges span less than 2220 km. Endemic species (i.e. most distant records less than 4 cells apart ca. 1000 km) comprise 18% of all the species studied. Almost 17% of the total and 15% of the butterflyfishes are only known from a single grid cell. This suggests that a number of coral fish species with small ranges may be threatened by human activities at regional and local scales. Pseudo-endemics (species whose real range is larger than their known range) may not confound this conclusion to any extent. This contention is tested in the butterflyfishes where pseudo-endemics are expected to be rare. The ratio of small-range to large-range butterflyfishes is not significantly different from that in the all-family sample.

A significant positive correlation between the number of coral species and the number of coral reef fish species in the Indo-Pacific sample lends credence to the view that the deteriorating condition of coral reef habitat poses a threat to the reef fishes. Data on anthropogenic threats will be added to the GIS data set to evaluate these impacts.

The equal-area grid technique is a useful tool for the compilation, analysis and presentation of data important to conservation assessment. It can be used to define and locate areas with high overall species richness, many endemic species, higher taxon richness, intense human environmental impacts, or with a need for increased biotic sampling. The accuracy of the results will be moderated by the level of taxonomic knowledge and the thoroughness of biological inventories. Thus taxonomic research, biological surveys, natural history museum collections and the resulting authoritative spot distribution maps are important resources for carefully planned conservation.

Acknowledgements

We gratefully acknowledge funding support for the GIS project from The Curtis and Edith Munson Foundation of Chicago, the Sir Peter Scott Trust for Education and Research in Conservation, the Sir Peter Scott IUCN/SSC Action Plan Fund, the British Ecological Society/Coalbourn Trust, The Norcross Wildlife Foundation and Ocean Voice International. Susan Tressler and Dr George Rabb of the Species Survival Commission provided invaluable assistance in finding support. The Canadian Museum of Nature provided computer time, office space, and library and other resources. The Department of Marine Sciences and Coastal Management of the University of Newcastle-on-Tyne, and the Eastern Caribbean Center of the University of the Virgin Islands, provided office and library facilities for compiling maps.

The late Sir Peter Scott, Gustavo Nunan, and the many other people who have generously donated their records of fish species distributions are gratefully acknowledged for the information that provided the kernel of our database. The second author's father, the late F. William Schueler III, helped develop the formula for the equal-area cells. Noel Alfonso and Ian Jones spent weeks drafting the original equal-area basemaps and compiling data on occurrence of genera of reef-building corals. Noel Alfonso also reviewed the manuscript.

Brian Eddy provided advice and training on use of the GIS package.

References

- Alcala, A.C. and Gomez, E.D. (1987) Dynamiting coral reefs for fish: A resource-destructive fishing method, in *Human Impacts on Coral Reefs: Facts and Recommendations* (ed. B. Salvat), Antenne Museum, E.P.H.E., Tahiti, pp. 51–60.
- Alfonso, N. (1991) An equal-area grid map for GIS: A tool for biodiversity conservation and biogeography. *Canadian Biodiversity*, 1(1), 30–2.
- Allen, G.R. (1975) Damselfishes of the South Seas, T.F.H. Publications, Inc., Neptune City, New Jersey, 240pp.
- Allen, G.R., Hoese, D.F., Paxton, J.R. et al., (1976) Annotated checklist of the fishes of Lord Howe Island. Records of the Australian Museum, 30, 365– 454.
- Anderson, S. (1984a) Geographic Ranges of North American Birds, American Museum Novitates (2785), pp. 1–17.
- Anderson S. (1984b) Areography of North American Fishes, amphibians and reptiles, American Museum Novitates (2802), pp. 1-16.
- Ansula, A.C. and McAllister, D.E. (1992) Fishing with explosives in the Philippines. Sea Wind, 6(2), 6-12.
- Botros, G.A. (1971) Fishes of the Red Sea. Oceanography and Marine Biology Annual Review, 9, 221-348.
- Briggs, J.C. (1966) Oceanic islands, endemism, and marine paleotemperatures. *Systematic Zoology*, 15(2), 153-63.
- Briggs, J.C. (1974) Marine Zoogeography, McGraw-Hill, New York, 475pp.
- Briggs, J.C. (1986) Species richness among the tropical shelf regions, in English translation of *Soviet Journal of Marine Biology*, Plenum Publishing Corporation, pp. 295–302.
- Clarke, A. (1992) Is there a latitudinal diversity cline in the sea? *Trends in Ecology and Evolution*, 7(9), 286–7.
- D'Elia, C.F. Buddemeier, R.W. and Smith, S.V. (1991) Workshop on Coral Bleaching, Coral Reef Ecosystems and Global Change: Report of the Proceedings, Maryland Sea Grant Publication UM-S4-TS-91-03. 49pp.
- Dubinsky, Z. (ed.) (1990) Coral reefs. Ecosystems of the World 25, Elsevier, Amsterdam, Oxford, 550pp.
- Earth and Ocean Research Limited (1991) in FOcus: A Geographic Information Management and Display System, Earth and Ocean Research Ltd, Dartmouth, Nova Scotia: users guide, complex pagination.

- Emery, A.R. (1978) The basis of fish community structure: Marine and freshwater comparisons. *Environmental Biology of Fishes*, 3, 33-47.
- Environmental Sciences Limited (1990) QUIKMap Version 2.50 Users Guide. Environmental Sciences Limited, Sidney, British Columbia: complex pagination.
- Fox Software, Inc. (1991) FoxPro, 3 vols, Fox Software, Perrysville, Ohio.
- Glynn, P.W. (1991) Coral reef bleaching in the 1980s and possible connections with global warming. Trends in Ecology and Evolution, (6), 175-9.
- Gomez, E.D. and Alcala, A.C. (1979). Status of Philippine coral reefs 1978. Proceedings of the International Symposium on Marine Biogeography and Evolution of the Southern Hemisphere, 2, 663– 9.
- Goreau, T.J. (1990) Coral bleaching in Jamaica. Nature, 343, 417.
- Groombridge, B. (1992). Global Biodiversity, Status of the Earth's Living Resources. A report compiled by the World Conservation Monitoring Centre. Chapman & Hall, London, 585pp.
- Harmelin-Vivien, M.L. (1989) Reef fish community structure: An Indo-Pacific comparison, in *Vertebrates in Complex Tropical Systems* (ed. M.L. Harmelin-Vivien and F. Bourlière), Springer-Verlag, New York, pp. 21-60.
- Harrison, P. (1992). The Third Revolution, Environment, Population and a Sustainable World, Tauris, London, New York, 359pp.
- ICBP (1992) Putting Biodiversity on the Map: Priority Areas for Global Conservation, International Council for Bird Preservation, Cambridge, UK.
- Magurran, A.E. (1991) Ecological Diversity and its Measurement, Chapman & Hall, London, 179pp.
- McAllister, D.E. (1988) Environmental, economic and social costs of coral reef destruction in the Philippines. *Galaxea*, 71, 161–78.
- McAllister, D.E. (1991a) What is the status of the world's coral reef fishes? Sea Wind, 5, 14-18.
- McAllister, D.E. (1991b) What is biodiversity? Canadian Biodiversity, Ottawa, 1(1), 4-6.
- McAllister, D.E. (1993). The eco-taxa hotspot approach to the conservation of biodiversity: Evolving tools. Association of Systematics Collections Newsletter, 21(4), 47–8.
- McAllister, D.E., Platania, S.P., Schueler, F.W. et al. (1986) Ichthyofaunal patterns on a geographic grid, in Zoogeography of North American Freshwater Fishes (ed. C.H. Hocutt and E.O. Wiley), Wiley, New York, pp. 18-51.
- New York, pp. 18-51. McManus, J.W. (1988) Coral reefs of the ASEAN region: Status and management. Ambio, 17, 189-93.
- McNeely, J.A., Miller, K.R., Reid, W.V. et al. (1990) Conserving the World's Biological Diversity, IUCN,

- WRI, CI, WWF-US and World Bank, Gland, Switzerland, 193pp.
- Myers, R.F. (1989) Micronesian Reef Fishes, Coral Graphics, Guam, 298pp.
- Newell, N.D. (1971) An Outline History of Tropical Organic Reefs, American Museum Novitates (2465), pp. 1–37.
- Norris, E.A. (ed.) (1993) Global Marine Biological Diversity. A Strategy for Building Conservation into Decision Making. Island Press, Washington, D.C., 383pp.
- Ormond, R.F.G. and Edwards, A.J. (1986) Red Sea fishes, in *Red Sea* (ed. A.J. Edwards and S.M. Head), Pergamon Press, Oxford, UK, pp. 251–87.
- Peters II, R.L. (1988) The effect of global climatic change on natural communities, in *Biodiversity* (ed. E.O. Wilson), National Academy Press, Washington, D.C., pp. 450–61.
- Planck, J., McAllister, D.E. and McAllister, A. (1988) Shiraho Coral Reef, and the Proposed New Ishigaki Island Airport, Japan, with a Review of the Status of Coral Reefs of the Ryukyu Archipelago, Japan. Species Survival Commission, International Union for the Conservation of Natural Resources, Switzerland, 232pp.
- Randall, J.E. (1980) Conserving marine fishes. Oryx, 15(3), 287-91.
- Randall, J.E. (1982) Tropical marine sanctuaries and their significance in reef fisheries research. Proceedings of a workshop held October 7–10, 1980 at St Thomas, Virgin Islands of the United States (ed. G.R. Huntsman, W.R. Nicholson and W.W. Fox, Jr). The Biological Bases for Reef Fishery Management. NOAA Technical Memorandum NMFS-SEFC-80, pp. 167–78.
- Randall, J.E. and Cea Egaña, A. (1989) Canthigaster cyanetron, a new toby (Teleostei; Tetraodontidae) from Easter Island. Revue francaise d'Aquariologie, 15(3), 93-6.
- Roberts, C.M. (1987) Report on the Distribution of Coral Reef Fish Species throughout the Indo-West Pacific Region using Data Collected by Sir Peter Scott, Tropical Marine Research Unit, York, UK.
- Roberts, C.M. and Hawkins, J.P. (1992), Mapping the distribution of coral reef fishes. *Sea Wind*, 5(4), 3–8.
- Roberts, C.M., Downing, M., and Price, A.R.G. (1993) on troubled waters: Effects of the Gulf War on coral reefs, in Proceedings of a meeting entitled 'Global Aspects of Coral Reefs: Health Hazards and History' held at the Rosentiel School of Marine and Atmospheric Sciences, Miami, Florida, USA, June 1993, pp. V35–V41.
- Robinson, S. (1987) The killing of Costa Rica's Caribbean coral reefs. Sea Wind, 1(2), 8-15.
- Rubec, P.J. (1986) The effects of sodium cyanide on coral reefs and marine fishes in the Philippines, in

- The First Asian Fisheries Forum (ed. J.L. Maclean, L.B. Dizon and L.V. Hosillos), Asian Fisheries Society, Manila, Philippines, pp. 297–302
- Sale, P. (1976) Reef fish lottery. Natural History, 85, 60-5.
- Sale, P. (ed.) (1991) The Ecology of Fishes on Coral Reefs, Academic Press, San Diego, 784pp.
- Samoilys, M.A. (1988) Abundance and species richness of coral reef fish on the Kenyan coast: The effects of protective management and fishing. Proceedings of the 6th International Coral Reef Symposium, Townsville, 2, 261–6.
- Schueler, F.W. (1982) Geographic Variation in Skin Pigmentation and Dermal Glands in the Northern Leopard Frog, Rana pipiens. Publications in Zoology, National Museum of Natural Sciences, National Museums of Canada 16, pp. 1–80.
- Sebert, L.M. (1975) The Mercator and Transverse Mercator Projections. Energy, Mines and Resources Canada, Technical Report No. 69-1, 12pp. Surveys and Mapping Branch.
- Sheppard, C.R.C., Price, A.R.G. and Roberts, C.M. (1992) Marine Ecology of the Arabian Region: Patterns and Processes in Extreme Tropical Environments, Academic Press, London, 359pp.
- Smith, S.V. (1978) Coral reef area and the contributions of reefs to processes and resources of the world's oceans. *Nature*, 273, 225–6.
- Smith, S.V. and Buddemeier, R.W. (1992) Global change and coral reef ecosystems. Annual Reviews in Ecology and Systematics, 23, 89-118.
- Sokal, R.R. and Rohlf, F.J. (1981) *Biometry*, Freeman, New York, 859pp.
- Springer, V.G. (1982) Pacific Plate Biogeography, with Special Reference to Shore Fishes, Smithsonian Contributions to Zoology (367), pp. 1–182.
- Springer, V.G. and Williams, J.T. (1990) Widely distributed Pacific Plate endemics and lowered sea-level. Bulletin of Marine Science, 47(3), 631–40.
- Thresher, R.E. (1992) Geographic variability in the ecology of coral reef fishes: Evidence, evolution, and possible implication, in *The Ecology of Fishes on Coral Reefs* (ed. P. Sale), Academic Press, San Diego, pp. 401–36.
- UNEP/IUCN (1988) Coral Reefs of the World. Hard-covers: Vol. 1, Atlantic and Eastern Pacific, 373 pp.; Vol. 2, Indian Ocean, Red Sea and Gulf, 389pp.; Vol. 3, Central and Western Pacific, 329pp. UNEP Regional Seas Directories and Bibliographies; IUCN, Gland, Switzerland and Cambridge, UK UNEP, Nairobi, Kenya.
- Vane-Wright, R.I., Humphries, C.J. and Williams, P.H. (1991) What to protect? Systematics and the agony of choice. *Biological Conservation*, 55, 235-54.

- Vernon, J.E.N. (1986) Corals of Australia and the Indo-Pacific, Angus and Robertson Publishers, London, 644pp.
- Vernon, J.E.N. (1993) A Biogeographic Database of Hermatypic Corals, Australian Institute of Marine Science Monograph Series 10, pp. 1–433.
- Weber, P. (1993) Reviving coral reefs, in *State of the World* 1993 (ed. Lester R. Brown), W.W. Norton, Washington, pp. 42-60.
- Weller, W.F. and Oldham, M.J. (1988) Ontario Herpetological Summary 1986, Ontario Field Herpetologists, Cambridge, Ontario, 221pp.
- Wells, S. and Hanna, N. (1992) The Greenpeace Book of Coral Reefs, Blandford, London, 160pp.
- Williams, P.H. (1993) Choosing conservation areas: Using taxonomy to measure more of biodiversity, in

- Biodiversity Conservation (ed. T.-Y. Moon), Korean Entomological Institute, Seoul, pp. 194–227.
- Williams, P.H. and Gaston, K.J. (in press) Measuring more of biodiversity. Can higher taxon-richness predict wholesale species richness? *Biological Conservation*.
- Williams, P.H. and Humphries, C. (1992) Biodiversity taxonomic relatedness and endemism in conservation, in *Systematics and Conservation Evaluation* (ed. P.L. Forey, C.J. Humphries and R.I. Vane-Wright), The Systematics Association, Oxford University Press, pp. 1–14.
- Woodland, D.J. (1986) Wallace's Line and the distribution of marine inshore fishes, in *Indo-Pacific Fish Biology*. Proceedings of the 2nd International Conference on Indo-Pacific Fishes (ed. T. Uyeno et al.), Ichthyological Society of Japan, Tokyo, pp. 453–60.