

Global Trajectories of the Long-term Decline of Coral Reef Ecosystems

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Degradation of coral reef ecosystems began centuries ago but there is no global summary of the magnitude of change. We compiled records, extending back thousands of years, of the status and trends of seven major guilds of carnivores, herbivores, and architectural species from 14 regions. Large animals declined before small animals and architectural species, and Atlantic reefs declined before reefs in the Red Sea and Australia, but the trajectories of decline were strikingly similar worldwide. All reefs were substantially degraded long before outbreaks of coral disease and bleaching. Regardless of these new threats, reefs will not survive without immediate protection from human exploitation over large spatial scales.

Coral reefs and associated tropical nearshore ecosystems have suffered massive, long-term decline in abundance, diversity, and habitat structure due to overfishing and pollution (1-7). These losses were more recently compounded by substantial mortality due to disease and coral bleaching (8-12). Although much longer records exist for some coral (13) and commercially important fisheries species (2,3), detailed ecological descriptions of reef ecosystems are less than 50 years old (14, 15). The long-term historic sequence of ecosystem decline is unknown for any reef, thereby obscuring the potential linkage and interdependence of the different factors responsible that must be unraveled for successful restoration and management.

To this end, we reconstructed the ecological histories of 14 coral reef ecosystems worldwide (16) using consistent criteria throughout. We determined the ecological status of reefs ranging from pristine to globally extinct (Table 1) for seven general categories of biota (hereafter referred to as guilds) (17) for each of seven culturally defined periods

ranging from pre-human to the present (Table S1, 18). We used cultural periods rather than calendar years because the magnitude of human impacts depends primarily upon technological prowess and economic structures that were out of phase geographically until converging in the 20th century. Guilds and ecological status were broadly defined so that the same standards could be used for all periods and regions examined and to allow use of widely disparate paleontological, archeological, historical, fisheries, and ecological data in the same analysis (Tables S2 and S3, 17).

The average ecological status of each guild for all regions combined (17) declined sharply over time (Fig. 1). In general, large animals declined faster than small animals and free-living animals declined more rapidly than architectural builders such as seagrasses and corals. Large carnivores and herbivores were almost nowhere pristine by the beginning of the 20th century when these guilds were already depleted or rare in more than 80% of the 14 regions examined. The universal lag in decline of architectural guilds is consistent with earlier observations for Caribbean reefs (19).

We used principal components analysis (PCA) to ordinate the data and describe the historical trajectories of change within each region in terms of the ecological status of all seven guilds combined (17). Reef regions were defined as pristine for the initial (pre-human) period and we also included for purposes of comparison a hypothetical reef for which all seven guilds were ecologically extinct. Only the first principal component (PC1) was interpretable (17). The resulting trajectories (Fig. 2A) closely and consistently track PC1, which explains a remarkable 91% of the total variation in the data. The key structures in the dataset were thus effectively captured by a one-dimensional system, with

each region's time periods mostly sequentially ordered along PC1, which is described overwhelmingly by the status of large herbivores and carnivores (20).

Principal components analysis also provides a simple, objective index of present-day reef degradation as measured by the normalized scores for the end points of each regional trajectory along PC1 (Fig. 2B). As expected, reefs in the western Atlantic have declined more severely than in Australia or the Red Sea. The best-protected reefs in the world on the Great Barrier Reef are the closest to pristine. But these same reefs are also one-quarter to one-third of the way along PC1 to ecological extinction. Moreover, the reefs of Moreton Bay at the extreme southern end of the Great Barrier Reef are as close to ecological extinction for all seven guilds as the severely degraded reefs of eastern Panama and the Virgin Islands.

The overall historical trajectory of reef degradation across all cultural periods is strikingly linear, despite the wide range of values within any one cultural period (Fig. 3). Most importantly from the perspective of reef conservation and management, most of the reef ecosystems were substantially degraded before 1900. Recent widespread and catastrophic episodes of coral bleaching and disease have distracted attention from the chronic and severe historical decline of reef ecosystems (10, 21-23). However, all the reefs in our survey were significantly degraded long before the first observations of mass mortality due to bleaching and outbreaks of disease (10-11). The only reasonable explanation for this earlier decline is overfishing (3), though land-derived pollution could have acted synergistically with overfishing in some localities.

Historical trajectories of reef degradation provide a powerful tool to explain global patterns and causes of ecosystem collapse, as well as predict future ecosystem

states – allowing managers to anticipate ecosystem decline through an understanding of the sequence of species and habitat loss. Management options will vary among regions but there must be a common goal of reversing common trajectories of degradation. The maintenance of the status quo within partially protected areas such as the Great Barrier Reef is at best a weak goal for management that should strive instead for restoring the reefs that are clearly far from pristine. Regardless of the severity of increasing threats from pollution, disease, and coral bleaching, our results demonstrate that coral reef ecosystems will not survive for more than a few decades unless they are promptly and massively protected from human exploitation.

References and Notes

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16. The regions vary in size depending on the geographic detail of available information. Western Atlantic Ocean: Bahamas, Bermuda, Belize, Cayman Islands, Jamaica, U. S. Virgin Islands, western Panama, eastern Panama. Australia: inner Great Barrier Reef, outer Great Barrier Reef, Moreton Bay, Torres Straits. Red Sea: northern Red Sea, southern Red Sea.
17. Materials and methods are available as supporting material on *Science* Online.
18. The 7 cultural periods with their ranges of ages for the 14 regions studied are: pre-human (40,000bp-1609), hunter-gatherer (20,000bp-1824), agricultural (1400-1800), colonial occupation (1500-1800), colonial development (1800-1900), early modern (1900-1950), late modern (1950-present). Not all cultural periods existed for all sites. For example, Bermuda was unpopulated until 1609 when colonial occupation began and there was no agricultural stage in Australia prior to western colonization.
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20. Values of descriptors (guilds) along PC1 represent relative contribution to position of sites along PC1 and are as follows: large herbivores, 0.45; large carnivores, 0.43; corals, 0.38; seagrass, 0.37; suspension feeders, 0.34; small carnivores, 0.33; small herbivores, 0.33.

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Acknowledgments

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Supporting Online Material

www.sciencemag.org

Materials and Methods

Tables S1, S2, S3

Fig. 1. Ecological change in coral reef guilds through time. Time trajectories of ecological condition for each of 7 guilds of reef inhabitants (17) expressed as the percentage of regions in each state from 14 regions (16) in the tropical Western Atlantic, Red Sea, and northern Australia. Cultural periods (18): P, pre-human; H, hunter-gatherer; A, agricultural; CO, colonial occupation; CD, colonial development; M1, early modern; M2, late modern to present.

Fig. 2. Principal components analysis of ecosystem degradation based on the state of all 7 guilds of reef inhabitants at the 14 reef regions. Only PC1 was significant (17). **(A)** Time trajectories for each reef region over 7 cultural periods. Each reef started at a single point to the left in the PCA space that is the pristine ecosystem state (Table 1, 17). Trajectories are mostly monotonic through time, but minor reversals occur in four regions (denoted with an ‘x’ within the filled circle) . The hypothetical ecologically extinct state, on the right, is one where all 7 guilds are ecologically extinct. PC1 is interpreted as an axis of historical degradation over time measured in cultural periods. The most important guilds influencing the trajectories of decline are large herbivores and carnivores (20). **(B)** End-points (present ecosystem condition) of the 14 reef regions plotted along an axis of ecosystem degradation measured as the relative distance along PC1 between pristine and ecologically extinct. Oceanic regions color-coded: Australia, blue; Red Sea, green; Western Atlantic, purple. OGBR, outer Great Barrier Reef, IGBR, inner Great Barrier Reef; TORS, Torres Strait Islands; S.RED, southern Red Sea; N.RED, northern Red Sea; BELI, Belize; CAYM, Cayman Islands; BAHA, The Bahamas; BERM, Bermuda;

MORB, Moreton Bay; E.PAN, eastern Panamá; USVI, United States Virgin Islands;
W.PAN, western Panamá; JAMA, Jamaica.

Fig. 3. Percent degradation of 14 reef regions over time. Data for each cultural period are derived from the PCA analysis plotted in Fig. 2A as measured along PC1 as the axis of reef degradation. Each point represents percent degradation of a particular site at a particular time. Numbers in parentheses are numbers of reef regions recorded for each cultural period (17). Linear regression is plotted along with 95% confidence interval. Abbreviations for cultural periods as in Fig. 1.

Table 1. Ecological states and criteria used to assess the 14 tropical marine sites analyzed.

Ecological state	Criteria for classification
Pristine	Detailed historical record of marine resource lacks any evidence of human use or damage Example: Fossil coral assemblages
Abundant/Common	Human use with no evidence of reduction of marine resource Example: No reduction in size of fish vertebrae in middens or relative abundance of species
Depleted/Uncommon	Human use and evidence of reduced abundance (number, size, biomass, etc.) Example: Shift to smaller sized fish; decrease in abundance, size, or proportional representation of species
Rare	Evidence of severe human impact Examples: Truncated geographic ranges; greatly reduced population size; harvesting of pre-reproductive individuals
Ecologically extinct	Rarely observed and further reduction would have no further environmental effect Examples: Observation of individual sighting considered worthy of publication; local extinctions
Globally extinct	Gone forever Example: Caribbean monk seal

Figure 1

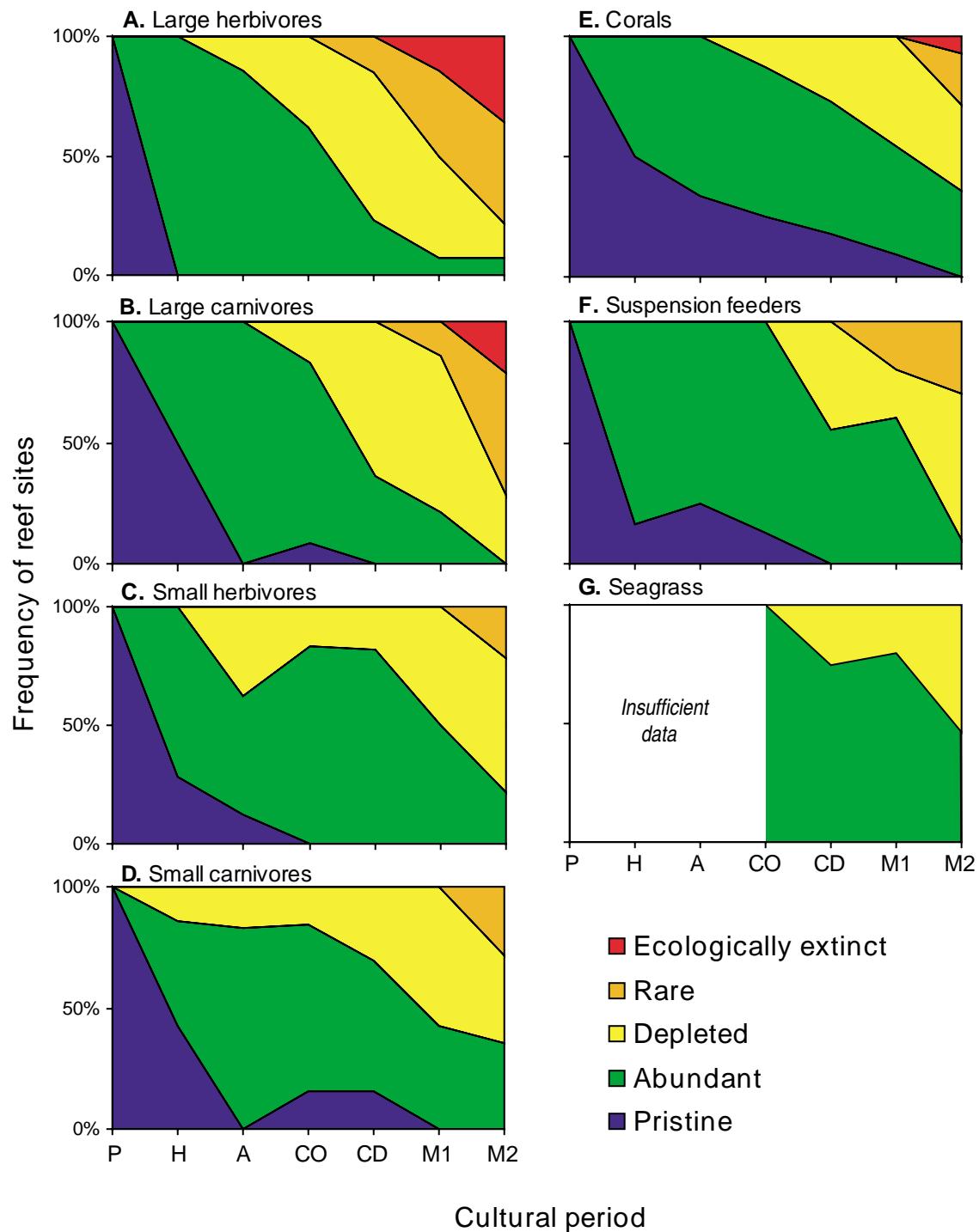


Figure 2

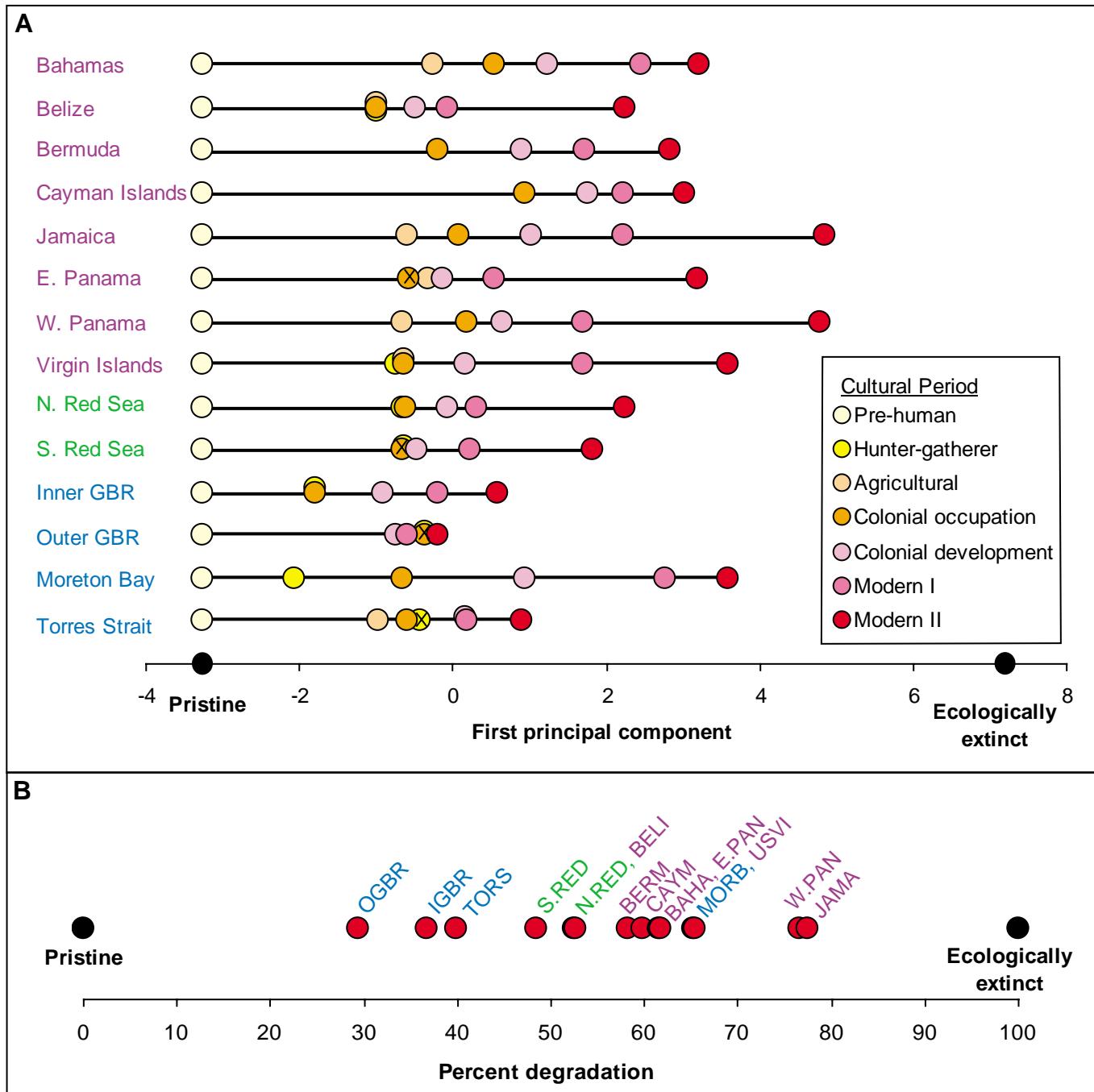
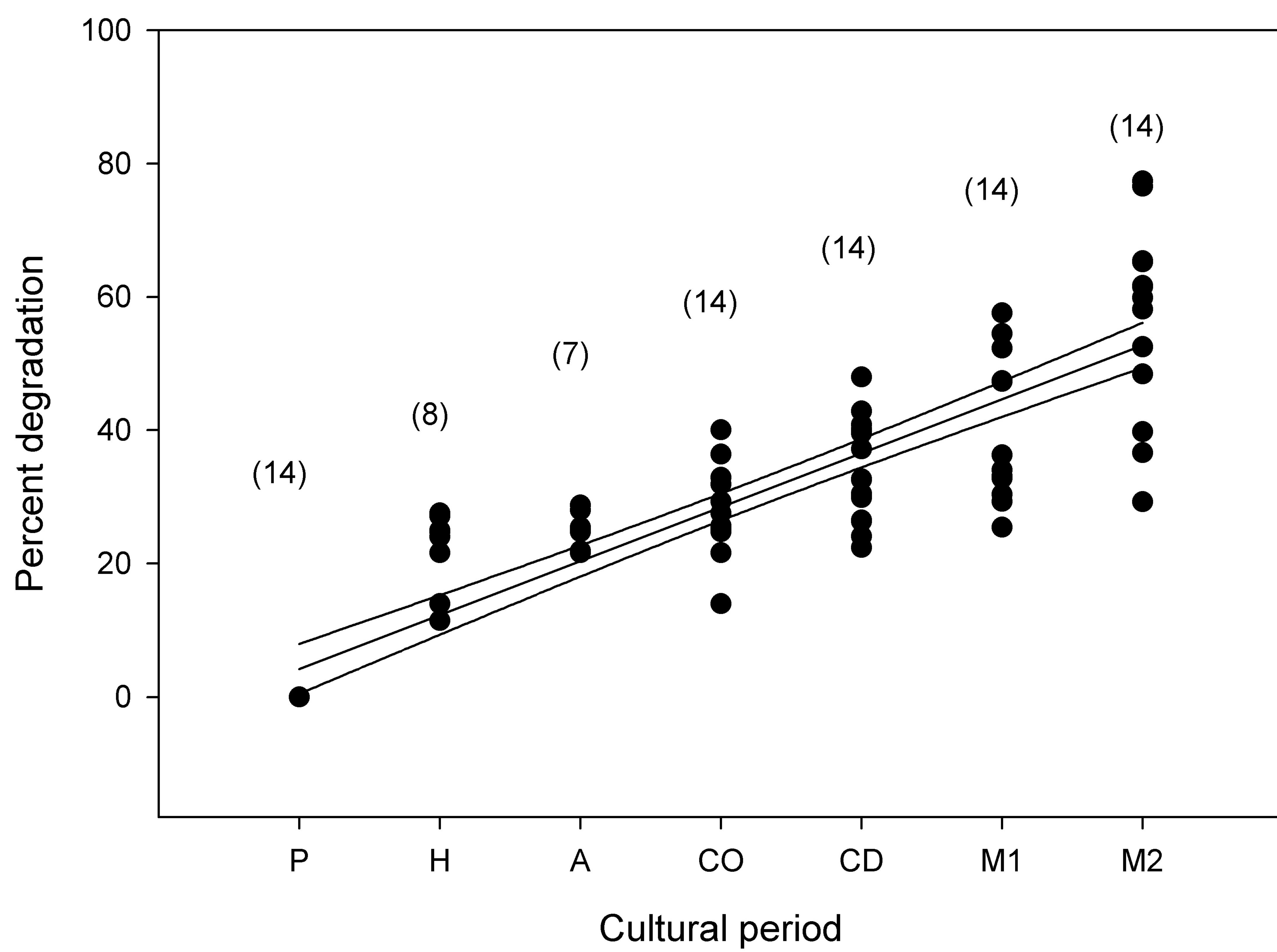


Figure 3



Supplemental Online Material

Materials and Methods

Guilds were defined on the basis of mode of nutrition (herbivore, carnivore), life habit (mobile free-living, sessile architectural), and size (for free living species, large > 1 m, small < 1 m). The 4 free-living guilds with common examples are: large herbivores (sea cows, green turtle, bump-head parrotfish), small herbivores (most parrotfish, sea urchins), large carnivores (sharks, crocodiles, monk seals, loggerhead and hawksbill turtles, barracuda, large groupers), small carnivores (most fish and invertebrates). The 3 sessile, architectural guilds are reef corals, seagrasses, and suspension feeders (sponges, oysters).

Cultural periods were defined in terms of how people obtained and used resources that were similar across regions but substantially different for the previous and following periods at any one region. To avoid circularity, the properties of cultural periods were chosen to be independent of the state of the marine resource (i.e., not derived from it) (Table S1). Earlier cultural periods were much longer than later periods.

Ecological status was scored on the basis of the most frequent status of species within each guild. Majority rule was essential because some resources were inevitably exploited well before others as fishers moved their focus from one species to another. All guilds were assumed pristine for the Pre-Human cultural period. Where ecological state for a cultural period was unknown, but the ecological states for the prior and following cultural periods were known and identical, the ecological state of the known cultural periods was used for the cultural period where ecological state was unknown.

Whenever possible, data were compiled for all 7 cultural periods for each of the 14 regions = 98 region-times. The ecosystem state was scored for all 7 guilds for all region-times, resulting in a data matrix of 686 cells (Table S2). The absence of some cultural periods at some regions, and of seagrasses not occurring on the outer Great Barrier Reef reduced the potential number of cells to 589. Of these there were 106 missing values (18%) due to inadequate data, though the majority of missing values (61) came from the seagrass and suspension feeder guilds. Each cell was converted to an ordered multistate ranging from 1 (pristine) to 6 (globally extinct). Each of the 483 scored cells had one or more literature references (Table S3).

We used standard principal components analysis (PCA). The multistate values were sufficiently like transformed quantitative measures (e.g., square root or log transformations) to justify use of PCA. For this analysis, we added a single depleted reef (region-time 99 in the analysis) with all 7 guilds classified as ecologically extinct. The pre-human cultural period was designated as pristine for all guilds at all sites. Missing values were well scattered among the reef regions and were not a problem for the analysis. We computed the analysis on those 85 region-times where cultural periods occurred at individual regions. We also retained all 14 present-day region-times. To focus on patterns among regions rather than among guilds, eigenvectors were normalized to 1 and the analysis was calculated on the variance-covariance matrix. Thus, we preserved the Euclidean distances among the region-times in the reduced space and the 7 guilds could then be used to help explain the patterns in the regions. A scree plot of eigenvalues versus PC showed that only PC1 was significant ($\lambda_1 = 6.31$, $\lambda_2 = 0.32$, $\lambda_3 = 0.25$).

We also plotted the percent degradation as a function of the PC1 axis normalized so that the pristine state was equal to 0% degradation and the ecologically extinct state was 100% degradation. All sites were represented in all cultural periods except two. The Hunter-gatherer cultural period was represented in the following 8 sites: Belize, inner and outer Great Barrier Reef, Moreton Bay, northern and southern Red Sea, Torres Strait, and U.S. Virgin Islands. The Agricultural cultural period was represented in the following 7 sites: The Bahamas, Belize, Jamaica, eastern and western Panamá, Torres Strait, and U.S. Virgin Islands. For the Outer Great Barrier Reef (OGBR), there were no seagrasses; hence assigning an ecological state was not applicable. Thus, values of PC1 loadings for the OGBR for the pre-human cultural period were slightly offset from ‘pristine’; however, for the purposes of clarity, plots (Fig. 2A and 3) were adjusted so that the OGBR plotted as pristine in the pre-human cultural period.

Table S1. Properties of Cultural Periods.

Cultural Period	Properties
Pre-human (40,000 bp – 1609)	No evidence of, or insignificant, human exploitation; pristine ecosystems with only natural perturbations.
Hunter-gatherer (20,000 bp – 1824)	No permanent settlements and no major surplus for trade; no major system for distribution and exchange over large areas.
Agricultural based (1400 – 1800)	People cultivated crops and raised livestock, so they could stay in one location. Agriculture enabled development of an economy, permanent settlements, and a culture.
Colonial occupation (1500 – 1800)	Spread of western values. Opening of sea-lanes and commencement of trade with the west. Catch more than needed for own consumption, develop techniques for storage and transport, ship surplus to neighbors (up country, next village, etc), exchange with barter.
Colonial development (1800 – 1900)	People become centralized into large, metropolitan cities. 'Development' is defined as developing the colonies' natural resources and mining sectors for use by their imperial 'owners.'
Modern I (1900 – 1950)	Distance no object; consumer preference starts to drive product development. Technological advances.
Modern II (1951 – 2002)	Globalization of markets. Establishment of free trade zones.

Table S2. Data matrix.

Site	Cultural Period Number	Large Carnivores	Small Carnivores	Large Herbivores	Small Herbivores	Corals	Seagrasses	Suspension Feeders
Bahamas	1	1	1	1	1	1	1	1
Bahamas	2	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Bahamas	3	2	3	3	3	2	1	1
Bahamas	4	3	3	3	3	2	2	1
Bahamas	5	3	3	3	3	2	2	3
Bahamas	6	4	3	4	3	2	2	4
Bahamas	7	4	3	4	3	3	3	4
Belize	1	1	1	1	1	1	1	1
Belize	2	2	2	2	2	1	no data	no data
Belize	3	2	2	2	2	1	no data	no data
Belize	4	2	2	2	2	1	no data	no data
Belize	5	2	2	3	no data	1	no data	no data
Belize	6	3	2	3	no data	1	no data	no data
Belize	7	5	2	4	3	3	2	2
Bermuda	1	1	1	1	1	1	1	1
Bermuda	2	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Bermuda	3	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Bermuda	4	2	2	3	2	no data	no data	2
Bermuda	5	3	3	3	2	2	no data	3
Bermuda	6	3	3	4	2	3	no data	3
Bermuda	7	4	3	4	3	3	2	4
Cayman Islands	1	1	1	1	1	1	1	1
Cayman Islands	2	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Cayman Islands	3	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Cayman Islands	4	3	3	3	3	2	2	no data
Cayman Islands	5	3	3	4	3	3	2	no data
Cayman Islands	6	3	3	5	3	3	2	no data
Cayman Islands	7	4	3	5	3	3	3	no data
GBR Inner	1	1	1	1	1	1	1	1
GBR Inner	2	1	1	2	2	1	no data	2
GBR Inner	3	N/A	N/A	N/A	N/A	N/A	N/A	N/A
GBR Inner	4	1	1	2	2	1	no data	2
GBR Inner	5	2	1	3	2	1	no data	2
GBR Inner	6	2	2	3	2	2	2	2
GBR Inner	7	3	2	3	2	2	2	3
GBR Outer	1	1	1	1	1	1	N/A	1
GBR Outer	2	no data	1	no data	no data	no data	N/A	no data
GBR Outer	3	N/A	N/A	N/A	N/A	N/A	N/A	N/A
GBR Outer	4	no data	1	no data	no data	no data	N/A	no data
GBR Outer	5	no data	1	2	2	no data	N/A	no data
GBR Outer	6	2	2	2	2	no data	N/A	no data
GBR Outer	7	3	2	2	2	2	N/A	no data
Jamaica	1	1	1	1	1	1	1	1
Jamaica	2	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Jamaica	3	2	2	2	2	no data	no data	no data
Jamaica	4	no data	no data	3	2	no data	no data	no data
Jamaica	5	3	3	4	2	2	2	2
Jamaica	6	4	3	5	3	no data	no data	2
Jamaica	7	5	4	5	4	5	3	no data

Site	Cultural Period Number	Large Carnivores	Small Carnivores	Large Herbivores	Small Herbivores	Corals	Seagrasses	Suspension Feeders
Moreton Bay	1	1	1	1	1	1	1	1
Moreton Bay	2	1	1	2	1	2	2	1
Moreton Bay	3	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Moreton Bay	4	2	2	2	2	2	2	2
Moreton Bay	5	3	2	3	2	2	3	3
Moreton Bay	6	3	3	4	3	3	3	4
Moreton Bay	7	4	3	4	3	4	3	4
Eastern Panama (San Blas)	1	1	1	1	1	1	1	1
Eastern Panama (San Blas)	2	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Eastern Panama (San Blas)	3	no data	no data	2	no data	no data	no data	no data
Eastern Panama (San Blas)	4	2	2	2	2	no data	2	no data
Eastern Panama (San Blas)	5	3	no data	2	2	no data	no data	no data
Eastern Panama (San Blas)	6	3	3	3	2	2	no data	2
Eastern Panama (San Blas)	7	4	4	4	3	3	3	3
Panama Western	1	1	1	1	1	1	1	1
Panama Western	2	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Panama Western	3	2	2	2	2	2	no data	2
Panama Western	4	2	2	3	2	3	2	2
Panama Western	5	3	2	3	no data	3	no data	2
Panama Western	6	3	3	4	3	3	no data	2
Panama Western	7	5	4	5	4	4	3	3
Red Sea, northern	1	1	1	1	1	1	1	1
Red Sea, northern	2	2	2	2	2	2	no data	2
Red Sea, northern	3	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Red Sea, northern	4	2	2	2	2	2	no data	no data
Red Sea, northern	5	no data	2	no data	no data	2	no data	no data
Red Sea, northern	6	3	2	3	no data	2	no data	no data
Red Sea, northern	7	4	2	5	3	2	2	3
Red Sea, southern	1	1	1	1	1	1	1	1
Red Sea, southern	2	2	2	2	2	no data	no data	2
Red Sea, southern	3	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Red Sea, southern	4	2	2	2	2	2	no data	2
Red Sea, southern	5	no data	2	2	2	2	no data	2
Red Sea, southern	6	3	2	3	2	2	no data	2
Red Sea, southern	7	3	2	5	3	2	2	3
Torres Strait	1	1	1	1	1	1	1	1
Torres Strait	2	no data	no data	no data	1	no data	no data	2
Torres Strait	3	2	2	2	1	no data	no data	2
Torres Strait	4	2	2	2	no data	no data	no data	2
Torres Strait	5	2	2	3	2	no data	no data	3
Torres Strait	6	2	2	3	2	no data	2	3
Torres Strait	7	3	3	3	2	2	2	3
Virgin Islands	1	1	1	1	1	1	1	1
Virgin Islands	2	1	3	2	2	no data	no data	2
Virgin Islands	3	2	2	2	2	no data	no data	2
Virgin Islands	4	2	2	2	2	no data	no data	2
Virgin Islands	5	2	2	3	2	3	no data	2
Virgin Islands	6	3	3	4	3	3	no data	2
Virgin Islands	7	4	4	4	4	4	3	no data

Legend:	Cultural Period		Ecological State
1	pre-human	1	pristine
2	hunter-gatherer	2	abundant/common
3	agricultural	3	depleted/uncommon
4	colonial occupation	4	rare
5	colonial development	5	ecologically extinct
6	early modern	6	globally extinct
7	late modern	N/A	cultural period or guild did not occur at that locality
		no data	no data exists to evaluate ecosystem state

Table S3. References for data matrix.

Data Matrix Cell Number Key:

Site	Cultural Period number	Large Carnivores	Small Carnivores	Large Herbivores	Small Herbivores	Corals	Seagrasses	Suspension Feeders
	1	8	15	22	29	36	43	
	2	9	16	23	30	37	44	
	3	10	17	24	31	38	45	
	4	11	18	25	32	39	46	
	5	12	19	26	33	40	47	
	6	13	20	27	34	41	48	
	7	14	21	28	35	42	49	

Definitions:

- Rule 1 – All guilds were assumed pristine for the Pre-Human cultural period.
- Rule 2 – Where ecological state for a cultural period was unknown, but the ecological states for the prior and following cultural periods were known and identical, the ecological state of the known cultural periods was used for the cultural period where ecological state was unknown.
- N/A – The cultural period did not exist at the site or the guild did not exist for the site at that time.
- No data – No data exists to evaluate ecosystem state.

BAHAMAS REFERENCE LIST

- 1) Rule 1
- 2) N/A
- 3) Carlson 1999, Keegan 1992, 1997, Keegan and DeNiro 1988, Wing 2001, Wing and Reitz 1982, Winter and Wing 1995
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- 8) Rule 1
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- 14) Burgess et al. 1994, Cayman Islands Conservation Association 1976, Giglioli 1994, Hess and Abbott 1994, Manfrino et al. 1999, Weidner et al. 2001, Wells 1988
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- 21) Aiken et al. 2001, Smith 2000, Wood and Wood 1994
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- 29) Rule 1
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- 10) N/A
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- 17) N/A
- 18) Jukes 1847, King 1827, Mack 1966
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- 22) Rule 1
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- 24) N/A
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- 35) Richmond 1993, Wollston 1995
- 36) Rule 1
- 37) no data
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- 8) Rule 1
- 9) Rule 2
- 10) N/A
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- 15) Rule 1
- 16) no data
- 17) N/A
- 18) no data
- 19) Benham 1951, Gill 1988
- 20) Anderson 1985, Musgrave and Whitley 1926, Paterson et al. 1994
- 21) Paterson et al. 1994
- 22) Rule 1
- 23) no data
- 24) N/A
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- 28) Ganter 1994, Wackenfeld et al. 1998
- 29) Rule 1
- 30) no data
- 31) N/A
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- 36) N/A
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- 43) Rule 1
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- 3) Carlson 2002a, b, De Wolf 1953, O'Day 2001, Scudder 1991
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- 5) Duerden 1901, Sloane 1707, 1725
- 6) Cundall 1928, Lewis 1949, Thompson 1945, Wells 1988
- 7) Hughes 1994, Koslow et al. 1988, 1994, Munro 1983, Underwood 1953
- 8) Rule 1
- 9) N/A
- 10) Carlson 2002a, b, O'Day 2001, Scudder 1991
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- 12) Duerden 1901, Gosse 1851, Sloane 1707
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- 22) Rule 1
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