

Disturbance and recovery of coral assemblages

J. H. Connell

Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, California 93106, USA
Tel.: (805) 893–2764, Fax: (805) 893–3777, e-mail: connell@lifesci.ucsb.edu

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Abstract. Trends in the health of coral reefs worldwide were examined by surveying the literature for quantitative studies of coral abundance that were at least four years long and contained data on variance among samples. Of the 65 examples in which sufficient data exist to make a judgment, coral cover did not decline in 29%, with fewer declines in the Indo-Pacific than in the W. Atlantic. Coral cover declined and recovered in 29% (all in the Indo-Pacific) and declined but did not recover in 42% of the examples (16% in the Indo-Pacific and 26% in the W. Atlantic). Thus, coral assemblages were relatively stable over ecological time scales in 58% of the examples surveyed. However, the W. Atlantic region was more unstable than the Indo-Pacific; declines without subsequent recovery occurred in 57% of W. Atlantic examples but in only 29% of those in the Indo-Pacific. The principal reason corals recovered in some local sites but not in others seems to be related to the type of disturbance that caused the decline. Coral cover recovered after 69% of the acute, short-term disturbances but after only 27% of the chronic, long-term ones.

Introduction

The effects of human disturbances on coral reefs have been a source of concern for some years (Ginsburg 1993). Since reefs are also disturbed by natural events, to assess and manage the impacts of human activities, the effects of natural disturbances need to be compared to those caused by people. Natural disturbances have been common events during the evolutionary history of all ecological assemblages, aquatic or terrestrial. In contrast, human activities, now widespread, may create qualitatively new kinds of disturbances.

Popular accounts of the effects of disturbances on coral reefs are often anecdotal, tending to emphasize the destructive aspects, with little attention to the process of recovery. To assess accurately the effects of disturbances, and the incidence of recovery thereafter, long-term quant-

itative measurements are clearly preferable to anecdotal observations. To make such assessments, the results of 23 long-term quantitative studies of coral abundance were analyzed.

Types and effects of disturbances

For the present purposes, I define a disturbance as an event that damages or kills residents (in this case, corals) on a given site. A disturbance can be classified as having either an acute or a chronic duration (Table 1). Acute disturbances are usually short-term, whereas chronic ones are longer-term, analogous to “pulse” and “press” experimental treatments, respectively (Bender et al. 1984). If a series of acute disturbances occurs so frequently that there is little time between them for recovery, this was regarded as a chronic disturbance.

Disturbances can also be classified as to the type of effect they have on the physical and biological environment within which corals live, i.e., whether they affect the environment directly or indirectly. These direct and indirect types of effects of disturbances are meant to apply only to the *environment* of the corals, not to the effects on the corals themselves. Disturbances can change the environment *directly* in many ways. Wave damage in storms sometimes alters the physical substrate, current patterns, and local topography. Disturbances can also directly change the biological environment, i.e., altering the abundance and distribution of associated species of animals and plants.

In contrast, a disturbance that has no direct effect on the environment, but only kills or removes corals, may *indirectly* affect the environment (Table 1). By removing the corals, such a disturbance will usually reduce the physical complexity of the substrate, increase water movement and incident light levels on the substrate, etc. By killing or removing the corals it also may indirectly affect the biological environment, by reducing refuges for mobile animals, increasing open space on which sessile species settle, altering the food supply of consumers, or concentrating the attacks of predators on the few survivors.

Table 1. Examples of the effects on the physical or biological environment of differences in the duration of disturbances

		Duration of disturbance Short: acute, "pulse"	Long: chronic, "press"
Effect on the physical and biological environment	Direct	A single disturbance that directly alters the environment temporarily, for example: (1) the physical environment: a storm alters the reef topography, or (2) the biological environment: a disease kills the predators or competitors of corals, or the grazers of algae.	Continuing disturbances that directly and continually alter the environment, for example: a series of storms that continually alters the reef topography, or chronic diseases that kill the predators or competitors of corals, or the grazers of algae.
	Indirect	A single disturbance, for example a disease outbreak or a storm that has no direct effect on the environment, but by simply killing or damaging corals, has an indirect effect on the environment.	Continuing disturbances, for example long-lasting diseases, or a series of storms, that have no direct effects on the environment, but, by continuing to kill or damage corals, have indirect effects on the environment.

Bleaching of corals, eruption of predator populations, storm effects, and disease often have such indirect effects on the physical and biological environment.

Recovery from disturbances

If the abundance of corals is reduced by a disturbance, it may subsequently increase, returning towards its former level. If there is a sufficient increase, we judge the assemblage to have recovered. Such a recovery in abundance (or constancy in abundance over time) does not necessarily imply that the assemblage has recovered in several other characteristics, such as its colony size structure, rates of reproduction and growth, species composition, and diversity. Thus recovery in abundance is only one aspect of recovery of a coral assemblage. However, since some of the long-term studies reviewed gave data only on abundance of all species combined, it was not possible to calculate these other aspects of recovery in all examples. Therefore, to allow comparison between as many examples as possible, I decided to use change in abundance alone as the index of decline and recovery.

In an attempt to see how well (or poorly) coral assemblages recover from disturbances, the literature of long-term studies of corals was surveyed to answer the following questions: (1) how frequently do the different sorts of disturbances affect coral assemblages? (2) What are the local and regional patterns of recovery or non-recovery of corals after disturbances? (3) What mechanisms or processes determine whether a coral assemblage recovers? (4) How does coral recovery from natural disturbances compare to that from human impacts?

Methods

To investigate the effects of, and recovery from, a disturbance, it is best to measure the abundance of corals both before and after the disturbance, and at sites with and without the disturbance (i.e., impact and control sites, respectively). Since natural disturbances are unpredictable, to ensure having data from both impact and

control sites requires that many sites be established ahead of time, a rarity in ecological studies. Also, since many studies are initiated in response to a disturbance, they have no quantitative observations, before which makes it impossible to accurately estimate the degree of decline or recovery. In such instances, I relied on the author's judgment that the disturbance had originally caused a significant decline in abundance and that the subsequent increase constituted a significant recovery. Last, since regrowth of survivors and recolonization by propagules takes time, fairly long-term observations are needed.

I surveyed the literature for quantitative long-term studies of coral abundances that (a) were carried on for at least 4 years and (b) provided either the original data, or summaries that included the number of samples, mean cover or change in cover, and some estimate of variation (SD, SE, etc.). Some studies without the requisite data were included if they included statistical tests of the changes in cover over time; in a few cases, the authors provided me with raw data. In studies without replicate samples at individual sites, variance was calculated from several sites or depths. I tested for statistical significance in the change in % coral cover between censuses with two-tailed *t*-tests. If a study included statistical tests, I usually used these instead of my own analyses.

In each study, I calculated the change in living coral cover for all intervals between censuses, and noted any cases of ecologically significant decline and recovery, which I defined with the following thresholds. An ecologically significant decline was defined as a decrease by at least 33% of the initial cover. For example, if coral cover fell from 70% to 40%, the decline was 43% (i.e., loss of 30% cover/70% original cover). The threshold of 33% was chosen, firstly, because no declines smaller than this were regarded as ecologically important by the authors (Appendix examples 13, 17, 18, 42, 45, 47, 50, 64, 73, 74, 75, 76). Secondly, several authors regarded declines between 33% and 39% as ecologically significant (Appendix examples 6, 8, 46, 55, and 71).

The degree of recovery after a decline was calculated as the ratio of the increase in coral cover to the amount that it had declined. For example, if cover fell from 75% to 25%, and subsequently rose to 55%, the degree of recovery was 60%, (i.e., a rise of 30%/fall of 50%). An ecologically significant recovery was defined as one in which the degree of recovery exceeded 50%. This threshold was chosen because in all of the examples that follow, it had much a lower degree of recovery, e.g., 37%, 30%, 29% and twelve others less than 15%.

Since two independent methods were used to judge whether declines or recoveries were ecologically significant, i.e., the thresholds and the *t*-tests, I compared the two judgements in each example (in addition, several examples had two comparisons, for both a decline and a recovery). In 85% of the 85 comparisons, the two judgements were in agreement. For the 15% of the comparisons

where they did not agree, I accepted the judgements based on the thresholds, rather than those from the *t*-tests, for the following reasons. In the examples where the change in cover did not exceed the threshold, but the *t* test indicated statistical significance, the variability in cover among samples was low relative to the average change so that even very small changes in cover became statistically significant (e.g., Appendix examples 9, 20, 64, 74 and 75). In contrast, in the examples where the *t*-test indicated a statistically non-significant result but the change exceeded the threshold (e.g., Appendix examples 5, 6, 7, 8, 12, 17, 46), the power of the test was low, either because the variability among samples was high, or the sample sizes were low. My rationale was that small absolute changes in abundance, however significant statistically, are probably of little ecological significance, whereas ones large enough to exceed the thresholds are likely to be important.

Each example of a decline caused by a disturbance at a particular site, with or without a subsequent recovery, as well as those with no decline, was identified and numbered, as shown in the Appendix. In some examples, declines occurred so near the end of the study period that it was not possible to document recovery. I found 23 long-term studies and identified 77 examples in which I could classify coral cover as having (a) declined and subsequently recovered, (b) declined but did not recover thereafter, (c) did not decline, or (d) declined, with too few further observations to judge recovery.

In a survey such as this, questions arise about how representative the examples are and whether they are biased toward a particular outcome. The examples in the present survey are geographically widespread, extending over much of the range of coral reefs, from the extreme western Indian Ocean (Gulf of Eilat, Red Sea) to the eastern Pacific in Panama, and from Bermuda to Costa Rica in the western Atlantic. Sample depths range from the intertidal to 35 m, and sites within reefs included sheltered versus wave-exposed margins, reef flats, reef crests, and outer slopes. However, since the survey includes only 62 different sites on 24 different reefs, many types of coral assemblages are probably not represented.

At least one source of bias may be inherent in these examples, as in many field studies, aquatic or terrestrial: sample locations are seldom placed in a purely random manner. Transects or quadrats are usually initially placed in sites where the habitat is deemed favorable because the study organisms are abundant, which also yields a large sample size (Hughes 1993). Therefore the estimates of initial abundances may tend to be higher than would be expected from randomly placed samples, and as a consequence, abundance is more likely to decline than to increase over time. This source of bias, if it exists in these examples, should not affect the results of the present study for the following reason. The main method in this study is a comparison between cases of recovery and non-recovery. Since it is reasonable to assume that the bias is as likely to apply to cases of recovery as to those of non-recovery, the comparisons themselves should not be biased.

The lack of decline in some studies could have been due to their observation periods being too short to include a major disturbance. However this seems unlikely, since the average period between 9 severe disturbances (mean 8.9 y, SE 2., Appendix, studies 1, 2, 3, 10 and 15) was shorter (though not significantly so), than the length of observation in the 19 examples in the group showing no decline (mean 12.2 y, SE 1.4, $t = 1.4$, $df = 26$, $P > 0.05$).

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Results

Cases of recovery after disturbances

Acute disturbances, indirect effects on the environment

In 8 of the long-term quantitative studies, there were 19 separate examples of declines with subsequent recovery (Table 2, Appendix). All were in the Indo-Pacific region, ranging from Eilat in the extreme northwestern Indian Ocean, to Hawaii; none were in the western Atlantic. Eleven of these examples resulted from acute disturbances that had indirect effects on the environment. For example, on the central Great Barrier Reef (GBR), a period of intense predation by *Acanthaster planci* in 1969–70 greatly reduced coral cover; corals recovered over the next seven years (Appendix example 1, Pearson 1974 1981). Likewise, on John Brewer reef 200 km to the south on the GBR, recovery probably occurred after similar *Acanthaster* attacks in the same period (Appendix example 2, Pearson 1981; Done 1985). Although there were no quantitative observations of coral abundance made at this site before

Table 2. Numbers of examples of the different types of disturbances that caused declines in corals, their duration and effects on the physical and biological environment, and the incidence of recovery thereafter

	Declines with subsequent recovery				Declines without subsequent recovery			
	Acute disturbances		Chronic disturbances		Acute disturbances		Chronic disturbances	
	Indo-Pacific	Western Atlantic	Indo-Pacific	Western Atlantic	Indo-Pacific	Western Atlantic	Indo-Pacific	Western Atlantic
Direct effects on physical and biological environment	0	0	Sewage: 8	0	Storm and air exposure: 1	0	Oil spills: 1 Sewage: 2	Coastal developments: 2 Storms + herbivore reductions: 12 Ship grounding: 1
Indirect effects on physical and biological environment	Storms: 4 Bleaching: 2 Predation: 3 Sediments: 1 Exposure: 1	0	0	0	Bleaching: 1 Storm: 1	Disease: 1 Storm: 1	Storms: 4	0

In addition, the survey found the following numbers of examples in two other categories:

1. Numbers of examples with percentage declines less than 33%: Indo-Pacific 6, Western Atlantic 13
2. Numbers of examples with too few observations after a decline to judge recovery: Indo-Pacific 6, Western Atlantic 6

the disturbance, anecdotal observations indicate that corals were common before the predation incident, so significant declines had probably occurred.

In three sites at Heron Island, GBR, coral cover experienced periods of sharp decline during four severe hurricanes. At the subtidal exposed pools site in two hurricanes, decline was followed by recovery in two and three years (Appendix examples 5 and 6, Connell et al. 1997). Similarly, the intertidal exposed crest site recovered most of the cover lost in a hurricane within the next five years, and the subtidal exposed slope site recovered within 14 years after a hurricane (Appendix examples 8 and 11, Connell et al. 1997).

At other locations in the Indo-Pacific, coral cover also declined and recovered. Coral cover recovered within two and five years of an acute bleaching event that reduced cover at two islands in Indonesia (Appendix examples 14 and 15, Brown and Suharsono 1990). Likewise at Phuket Island, Thailand, after an acute incidence of sedimentation from dredging had reduced coral cover, corals recovered quickly within 1 y (Appendix example 16, Brown et al. 1993). At Eilat, Red Sea, an unusually low tide killed much of the coral cover at one site; it recovered within 3 y (Appendix example 19, Loya 1990). Lastly, during an outbreak of *Acanthaster* in Guam, most of coral cover was killed. Recovery was slow over the next 4 y, but 11 y after the disturbance, coral cover had recovered (Appendix example 21, Randall 1973; Colgan 1987).

Chronic disturbances, direct effects on the environment

At sites in Kaneohe Bay, Hawaii, there were eight examples of recovery from the direct effects of chronic, long-term sewage discharges (Appendix examples 24, 25, 26, 28, 29, 31, 32, 34, Hunter and Evans 1995). Recovery occurred within six or 13 years after the discharges had been diverted. The sewage had directly affected the physical environment by increasing nutrient levels in the bay water. These apparently produced increases in phytoplankton density, turbidity, and benthic macroalgae that competed with the corals. Although there were no quantitative observations of coral abundance made at these sites before the disturbance, anecdotal observations indicate that corals were common before the discharges began, so significant declines at some sites had probably occurred as a result of the sewage.

Cases with no recovery after disturbances

Acute disturbances, indirect effects on the environment

At Heron Island, GBR, a hurricane in 1980 reduced coral cover at the protected crest site (Appendix example 10, Connell et al. 1997). Cover continued to decrease at this intertidal site over the next 12 y, because, as the colonies gradually grew up to a height sufficiently above low tide level, most of them died of exposure to air. As the dead corals were gradually eroded, the local topography of the substrate was altered, producing a smooth pavement with

few of the crevices in which newly-settled recruits survive well, and coral cover gradually diminished.

On Uva Island in the Gulf of Chiriqui, Panama, an acute bleaching event associated with the 1982–83 El Niño warming killed most corals; over the next 5 y, there was no recovery (Appendix example 41, Glynn 1990). Twelve years after the disturbance there has still been no recovery (personal communication P. Glynn), probably because of indirect effects on the biological environment. Because most corals have died, their crustacean “guards” have left or died, with the result that predation intensity on other species of corals has increased. Also, algae have colonized the dead coral surfaces, attracting sea urchin grazers. Both the predators and grazers probably reduce the survival of young coral recruits. Glynn (1990) and Glynn and Colgan (1992) suggest that recovery of these coral assemblages may take decades.

On the northern shallow foreereef on Buck Island, St. Croix, US Virgin Islands, white-band disease in the late 1970s and early 1980s killed corals, greatly reducing cover (Appendix example 42, Hubbard et al. 1993). There has been no recovery up to 1993; a hurricane in 1989 had no effect on coral cover at this site. In contrast, on the southern shallow foreereef, the 1989 storm reduced coral cover, which has continued to decline in the 4 y since (Appendix example 43, Hubbard et al. 1993). Reduction in cover of species of massive “head” corals accounts for most of the decline over the last 4 y. The reasons for non-recovery at both these sites are unknown.

Acute disturbances, direct effects on the environment

At Heron Island, GBR, a hurricane directly affected the physical environment, breaking away a portion of the reef crest about 100 m away from the exposed crest study site, reducing the water flow across the crest, and as a result, causing the substrate at this study site to dry out during most low tides, killing almost all corals. This substrate has been slowly eroded down, gradually reinstating the original pattern of water flow. As a result, the recruitment rates of corals have recently increased to their former levels. Coral cover has gradually risen, but in 23 years has not yet reached the recovery threshold of 50% of that lost in the storm (Appendix example 9, Connell et al. 1997).

Chronic disturbances, indirect effects on the environment

In two locations, frequent storms have interrupted the process of recovery. At Heron Island, GBR, a 1967 hurricane reduced coral cover almost to zero at the subtidal exposed pools site (Appendix example 4, Connell et al. 1997). Recolonization was slow, since it all came via propagules from elsewhere, none by regeneration of damaged survivors. Before recovery was achieved, a second hurricane struck in 1972, again reducing coral cover. At Kona, Hawaii, a severe storm in 1980 reduced coral cover at three depths. However, in the 13 y after this acute disturbance, there has been little recovery (Appendix

examples 37 to 39, Dollar and Tribble 1993). As in the previous example from Heron Island, the lack of recovery at Kona was probably not because of any direct effect on the environment, but because a series of recurrent severe storms in the 13 year period produced an overall chronic disturbance, which has continually set back recovery (Grigg 1983).

Chronic disturbances, direct effects on the environment

At the Nature Reserve site at Eilat, Red Sea, in the 12 y after an unusually low tide had caused high mortality, only 29% of the cover lost has been recovered (Appendix example 20, Loya 1990). The low level of recolonization (as compared to that at the nearby control site), is probably due to direct effects on the local environment from a chronic series of oil spills at a loading terminal near the site. Two sites in the southern part of Kaneohe Bay, Hawaii, have not increased beyond a cover of 3.5% in the 19 y since the sewage discharge was diverted (Appendix examples 22 and 23, Hunter and Evans 1995). Of the 15 sites in this study, these two are the closest to the concentration of urban development located in the southern part of the bay, which may account for their lack of recovery.

At 2 shallow depths on leeward reefs in Curacao and Bonaire, coral cover declined, with little sign of recovery within the study period of 19 y (Appendix examples 48 and 49, Bak and Nieuwland 1994). The non-recovery is apparently not due to storms, bleaching, disease, or algal blooms, but rather to effects of urbanization and development of the tourist industry, e.g., increasing coastal sewage discharges, construction on beaches, etc.

Several studies on the north coast of Jamaica document ten examples of declines without recovery after periods of 7–13 y (Appendix examples 53 to 62: Hughes 1993, 1994; Steneck 1993; Liddell and Ohlhorst 1994). The declines were due to acute disturbances in two hurricanes. Lack of recovery has been related to a reduction in rates of herbivory, resulting from intensive harvesting of fish with traps (Hughes 1994) and the devastating mortality in 1983–84 from disease of the common herbivorous echinoid *Diadema antillarum*, here as well as over the remainder of the Caribbean (Lessios et al. 1984; Lessios 1989). As a result of this reduction of herbivory, macroalgae have increased greatly (Hughes 1994). Likewise at Bellairs reef, Barbados, a hurricane in 1980 reduced coral cover, with no recovery over the next 12 y (Appendix example 52, Scoffin 1993). Lack of recovery here is also probably due to a reduction in herbivory as a consequence of the *Diadema* die-off.

At St. John, US Virgin Islands, a severe storm in 1989 reduced coral cover at Yawzi Point. After 6 y, cover has not recovered (Appendix example 66, Rogers 1993). The lack of recovery probably results from several factors. Most of the common corals at this site are massive, slow-growing ones such as *Montastraea*, which were damaged but rarely completely killed by the storm; these have been slow to regenerate and recruit. Also, perhaps due to chronic overfishing of herbivorous fish, strong blooms of macroalgae occur seasonally and chronically reduce coral

recruitment (personal communication C. Rogers, Rogers et al. in preparation). In Bermuda, a very large ship grounded on a reef in 1978, and there has been almost no recovery in 14 y since (Appendix example 68, Cook et al. 1993). Apparently the direct effects on the substrate were so intense that recruitment and/or survival of corals has been very slow.

Cases with no declines in coral abundance

In about 25% of the 77 examples of long-term records, coral abundance either increased or declined by less than one-third of the original cover (Table 2). In these examples, overall net changes in % cover were slight, e.g., Indo-Pacific, mean = 3.0, SD = 20.0, $n = 6$ examples from 4 studies; W. Atlantic, mean = 5.3, SD = 22.0, $n = 13$ examples from 7 studies. The proportion of examples of “no declines” was significantly greater in the W. Atlantic (WA) than in the Indo-Pacific (IP) (WA, 13 “no declines” out of 36 examples, IP, 6 out of 41 examples, contingency chi-square = 4.76, $df = 1$, $P < 0.05$).

Discussion

In this survey I analyzed the data on coral abundance in the same way for all studies surveyed, as well as applying standard definitions of decline and recovery. This made it possible to estimate the frequencies of different sorts of disturbances, to compare disturbance regimes in different regions, and to test hypotheses about the mechanisms and processes that determine why recovery occurred in some cases but not in others.

Reasons for declines in coral cover with or without subsequent recovery were sought at two spatial scales. At the small spatial scale of local sites, I formulated several possible hypotheses to answer this question and tested them with the data shown in the Appendix. First, in the instances when there was no recovery after a decline, the corals may not have been sampled long enough to witness recovery. I tested this hypothesis by calculating the length of time of observation after each disturbance and compared it between the set of examples that did or did not undergo recovery. I rejected this hypothesis because the period of observation was, on average, about 12 y at sites without recovery and about 5 y with recovery (Table 3, hypothesis 1). Second, perhaps having greater coral cover before the disturbance would predispose the site to much slower recovery. However, the examples with and without recovery had nearly the same average cover before the disturbance (Table 3, hypothesis 2). Third, if the disturbance causes greater loss of coral cover, this might take much longer to recover from, than if the loss were less. However, the examples with and without recovery had nearly the same average loss of cover during the disturbance (Table 3, hypothesis 3).

Fourth, corals at greater depths might recover more slowly, since rates of growth and recovery tend to be less at greater depths. However, the examples with and

Table 3. Hypotheses to explain why coral assemblages sometimes do not recover from disturbances

	Mean	SE	N	<i>t</i>	<i>P</i>
Hypothesis 1: period of observation too short to detect recovery					
	<u>Years observation after disturbance</u>				
No recovery	12.4	1.1	24	3.75	< 0.001
Recovery	5.2	1.3	10		
Hypothesis 2: greater coral cover before a disturbance led to poorer recovery					
	<u>% Cover before disturbance</u>				
No recovery	44.3	3.4	26	0.61	ns
Recovery	40.2	6.9	10		
Hypothesis 3: greater loss of cover in a disturbance led to poorer recovery					
	<u>% loss of cover</u>				
No recovery	72.5	3.9	26	0.32	ns
Recovery	70.2	6.3	10		
Hypothesis 4: corals at greater depths have slower recovery					
	<u>Depth of study site, m</u>				
No recovery	7.4	1.4	26	1.3	ns
Recovery	4.1	2.1	10		
Hypothesis 5: recovery is worse after human-caused disturbances than after natural ones					
	<u>Number of examples</u>				
	<u>Human-caused</u>	<u>Natural</u>			
No recovery	18	9	Chi-square	= 1.01	<i>P</i> > 0.05
Recovery	9	10			
Hypothesis 6: recovery is worse if disturbances directly affect the environment than if they affect it indirectly					
	<u>Number of examples</u>				
	<u>Direct</u>	<u>Indirect</u>			
No recovery	19	8	Chi-square	= 2.60	<i>P</i> > 0.05
Recovery	8	11			
Hypothesis 7: recovery is poorer after chronic disturbances than after acute ones					
	<u>Number of examples</u>				
	<u>Chronic</u>	<u>Acute</u>			
No recovery	22	5	Chi-square	= 5.99	<i>P</i> < 0.05
Recovery	8	11			

without recovery were not at significantly different average depths (Table 3, hypothesis 4). Fifth, after disturbances produced by human activities, recovery might be worse than after natural ones; this difference proved not to be significant (Table 3, hypothesis 5). Sixth, recovery might be worse after disturbances that had direct effects on the environment, than after those with indirect effects. However this difference again proved not to be significant (Table 3, hypothesis 6). Although all but one of the 27 human-caused disturbances had direct effects on the environment, and all but one of the 19 natural disturbances had indirect effects on the environment, by themselves none had a significant effect on the likelihood of recovery.

Lastly, corals reduced by acute, short-term disturbances might recover faster or more completely than those afflicted by chronic, long-term ones. The results of the analysis are consistent with this hypothesis (Table 3, hypothesis 7). Thus the only characteristic of disturbances in these seven tests that increased the chances of recovery was their duration. After an acute disturbance ends, recovery often follows. Similarly, the only examples of recovery from a chronic disturbance occurred after it was ended, i.e., when the chronic sewage at Kaneohe Bay, Hawaii was diverted.

At larger geographical scales, there are striking contrasts between the Indo-Pacific and the Western Atlantic regions. First, in the incidence of decline and recovery of coral assemblages within a single reef, there was greater spatial variation between local study sites in the Indo-Pacific than in the W. Atlantic. To estimate such spatial variation, I compared only those examples from different sites on the same reef that were sampled in the same time period and depth; 14 such comparisons were available in my survey. In the Indo-Pacific, from Heron Island, Australia, four such comparisons indicated that each differed in decline and/or recovery (Appendix examples 4 compared to 8, 5 to 9, 6 to 10, and 11 to 13). Likewise, at Eilat, Israel, examples 19 and 20 were different. At Kaneohe Bay, Hawaii, the 15 sites (Appendix examples 22 to 36) indicated considerable spatial variation, eight recovering, two not recovering, three showing no decline. The only study showing no spatial variation was in Indonesia, where Appendix examples 14 and 15 both recovered.

In contrast, in the Western Atlantic region, only one study, in the Virgin Islands, found local spatial variation (Appendix examples 14, 15). All seven other comparisons indicated no spatial variation among local sites. Thus all five comparisons from Jamaica indicated no local spatial

variation, since none recovered (Appendix examples 53, 54, compared to 57, 62, 55 compared to 58, 56 compared to 59 or 61, 57 to 62, and 58 to 60). Likewise neither of the two sites in Bermuda recovered (Appendix example 68), while neither of the sites in the Gulf of Mexico declined (Appendix examples 75 compared to 76). Overall, spatial variation occurred in 6 of 7 Indo-Pacific reefs, but in only 1 of 7 W. Atlantic reefs (contingency test, chi-square = 5.37, $df = 1$, $P < 0.05$).

Another contrast between the regions was the complete lack of recovery on any W. Atlantic reefs; some possible explanations for this are as follows. First, the type of disturbance, rather than any environmental characteristic of either region, may explain the difference. There were few recoveries from chronic disturbances anywhere, and the incidence of such disturbances was higher in the W. Atlantic than in the Indo-Pacific. Of 17 disturbances causing declines in the W. Atlantic, 88% were chronic, whereas of the 29 such disturbances in the Indo-Pacific, only 53% were chronic (chi-square = 4.79, $df = 1$, $P < 0.05$).

Second, recruitment rates may be lower and/or post-settlement mortality rates may be higher in the W. Atlantic than in the Indo-Pacific, contributing to slower rates of recolonization in the former. However, this seems unlikely based on a comparison of these rates for the two regions, using the summaries of data from several studies by Smith (1992, Tables 3, including only those studies using panels, and Table 4). It indicated that neither of these rates differed between the regions (t -tests, recruitment, $t = 1.21$, n for WA = 7, for IP = 19; mortality, $t = 0.92$, n for WA = 10, for IP = 8).

Lastly, the area occupied by coral reefs is much smaller and more compact in shape in the W. Atlantic than in the Indo-Pacific. The region of the W. Atlantic containing coral reefs has only about 15% of the world's reefs (Smith 1978), and extends over about one-seventh of the longitude of the Indo-Pacific, with most of the Western Atlantic reefs being in the northern hemisphere. As a consequence, single events in the W. Atlantic, such as the disease epidemic that caused the die-off of almost all of the herbivorous echinoids, *Diadema antillarum*, are able to spread over a high proportion of the entire region, an unlikely occurrence in the extensive Indo-Pacific. This situation probably also explains the lesser amount of local spatial variation on W. Atlantic reefs, as compared to Indo-Pacific ones. Thus, the effects of disturbances seems to be more homogeneous at small and large scales, both within individual reefs and among different reefs, in the compact W. Atlantic region than in the extensive Indo-Pacific.

Caveats and conclusions

A few caveats: first, the sites with quantitative long-term studies were distributed quite unevenly. Although W. Atlantic reefs comprise only 15% of the world's reefs, 47% of the examples in my survey came from this relatively small region. Likewise, a high proportion of the examples on which the statistics were based came from a very few reefs. For example, 61% of the Indo-Pacific

examples came from Heron Island and Kaneohe Bay, and of the 17 examples in the W. Atlantic where coral abundance declined but did not recover, over half came from two locations on the north shore of Jamaica. Whether this over-representation by a few heavily studied locations biased the results is unknown, but it would seem desirable to distribute future long-term studies more evenly.

Second, although corals either did not decline or recovered from declines in the majority of examples worldwide, the fact that there were no recoveries from declines in the W. Atlantic region is a cause for serious concern. The explanation for this situation probably lies in the interaction of several factors: the relatively small, compact nature of the region, which exacerbates the effects of intense human activities such as overfishing (Hughes 1994), together with high nutrient runoff and construction from increasing coastal development.

In summary, recovery of coral assemblages after disturbance seems to depend in large part on the type of disturbance causing the original decline. From the evidence assembled here, coral assemblages do not appear to be suffering worldwide degradation. Many assemblages had no declines, while others recovered from acute, short-term disturbances, such as widespread predator outbreaks or local episodes of bleaching, severe storms, sedimentation or air exposure, that do not directly affect the local environment. However, there was little recovery from chronic, continuing disturbances that directly alter the physical or biological environment.

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Appendix

Examples of changes in coral cover in studies at least 4 years long. Declines of less than 33%, or increases in cover, were labelled "no decline". If a % decline of at least 33% in coral cover occurred, recovery was judged only if % cover subsequently increased by at least 50% of the amount lost in the decline. "Further observation needed" indicates examples in which observations after a decline did not extend long enough to judge whether recovery occurred or not. See text for definitions of types of disturbances and effects on the environment

Type of disturbance and effect on environment	Type of change	Example No.	Period	Site	Depth m	Initial % cover Mean	Change in the absolute cover Mean Change	SE diff	df	P	t-test	% Change in cover Loss Gain	Study length Total (Y)	After decline or with no change	Recovery as % of loss	Probable causes of the changes
1. Pacific, central Great Barrier Reef (Pearson 1974, 1981), see footnote 1																
Acute, Indirect	Recovery	1	70-71 71-77	Innsfall reefs "	1-27 "	28.0 7.8	24.2 12.0	2.7 3.1	35 14	** **		-86 >100	7 7	7	50	Predation '69-'70 Recruitment and growth
2. Pacific, central Great Barrier Reef (Pearson 1981, Done 1985)																
Acute, Indirect	Recovery	2	74-78 78-83	John Brewer Reef "	3,6,12 "	6.0 35.3	29.3 21.3	7.9 11.5	4 4	* ns		>100 60	8 13	8 13	ND ND	Predation '69-'70 Recruitment and regrowth
Acute, Indirect	Further Observation needed	3	83-84	" "	" 3,6,12	56.7	-53.3	8.5	4	**		-94	10	1		predation '83-84
3. Pacific: southern Great Barrier Reef, Heron Is. (Connell et al 1997); see footnote 2																
Chronic Indirect	No recovery	4	65-67 67-71	Exposed pools "	1 "	57.6 0.1	-57.5 21.5	4.3 5.6	2 2	** ns		-100 >100		5	37	1967 Storm 1972 Storm interrupted recovery 1972 Storm Recruitment and re-growth
Acute, Indirect	Recovery	5	71-72 72-74	" "	" 1 "	21.5 6.2	-15.3 18.7	5.6 6.7	2 2	ns *		-71 >100		2	>100	1972 Storm Recruitment and re-growth
Acute, Indirect	Recovery	6	78-80 80-83	" "	" 1 "	78.8 47.7	-31.1 26.7	11.4 8.9	2 2	ns ns		-39 56		3	86	1980 Storm Recruitment and re-growth
Acute, Indirect	Further observation needed	7	91-92	" "	" 1 "	71.3	-60.7	15.3	2	ns		-85	30	1		1992 Storm
Acute, Indirect	Recovery	8	65-67 67-71	Exposed crest "	0 "	75.4 50.4	-25.1 20.1	9.9 9.1	8 8	* ns		-33 40		5	80	1967 Storm Recruitment and regrowth
Acute, Direct	No recovery	9	71-72 72-92	" "	" 0 "	70.4 0.0	-70.4 20.8	6.9 4.5	8 8	** **		-100 >100	29	20	30	1972 storm, air exposure Gradual erosion, slow recruitment
Acute Indirect	No recovery	10	78-80 80-92	Protected crest "	0 "	45.4 17.1	-28.3 -9.7	8.8 3.1	4 4	* *		-62 -56	29	12	0	1980 storm Air exposure
Acute, Indirect	Recovery	11	70-72 72-86	Exposed slope "	3-5 3-8	23.6 14.1	-9.5 42.8	2.3 6.8	4 4	* **		-44 >100		14	87	1972 storm Recruitment and re-growth
Acute, Indirect	Further observation needed	12	86-92	" "	" 3-8	56.9	-25.2	10.9	4	ns		-44	22	7		1992 storm
4. Pacific: Indonesia: S. Java Sea, Thousand Is. (Brown and Suharsono 1990, Fig. 4)																
Acute, Indirect	No decline	13	72-86 86-92	Protected slope "	1-10 "	61.3 55.4	-5.9 -5.4	14.7 17.0	12 10	ns ns		-10 -10	20	20		
Acute, Indirect	Recovery	14	81-83 83-88	Pari Is. "	0 "	22.0 3.5	-18.6 10.6	1.4 1.0	18 18	** **		-85 >100	7	5	57	Bleaching in 1983 Recruitment and re-growth
Acute, Indirect	Recovery	15	81-83 83-85	Tikus Is. "	0 "	26.0 2.1	-23.9 13.9	0.6 1.0	18 18	** **		-92 >100	7	2	58	Bleaching in 1983 Recruitment and regrowth

Type of disturbance and effect on environment	Type of change	Example No.	Period	Site	Depth m	Initial % cover Mean	Change in the absolute cover Mean Change	SE diff	df	P	t-test	% Change in cover Loss Gain	Study length Total (Y)	After decline or with no change	Recovery as % of loss	Probable causes of the changes
Chronic, Direct	Recovery	31	71–83	Site 10	"	3.7	28.5	–	"	**		>100	19	6		"
Chronic, Direct	Recovery	32	83–90	"	"	32.2	–2.7	–	"	ns		–9	13	6	ND	"
Chronic, Direct	Recovery	32	71–83	Site 11	"	15.3	23.2	–	"	**		>100	19	6		"
Chronic, Direct	Recovery	32	83–90	"	"	38.5	8.1	–	"	ns		21	19	13	ND	"
Chronic, Direct	Further observation	33	71–83	Site 12	"	34.1	13.6	–	"	ns		40	19	6		"
Chronic, Direct	Further observation	33	83–90	"	"	47.6	–21.8	–	"	ns		–46	19	13	ND	"
Chronic, Direct	Recovery	34	71–83	Site 13	"	2.6	31.0	–	"	*		>100	19	6		"
Chronic, Direct	Recovery	34	83–90	"	"	33.6	–10.9	–	"	*		–32	19	13	ND	"
Chronic, Direct	No decline	35	71–83	Site 14	"	41.0	8.5	–	"	ns		21	19	6		"
Chronic, Direct	No decline	35	83–90	"	"	49.5	–8.0	–	"	ns		–16	19	13	ND	"
Chronic, Direct	No decline	36	71–83	Site 15	"	34.8	–13.7	–	"	ns		–39	19	6		"
Chronic, Direct	No decline	36	83–90	"	"	21.1	12.3	–	"	ns		58	19	13	ND	"
10. Pacific: Hawaii, Hawaii Is. (Dollar and Tribble 1993, Fig. 5)																
Chronic, Indirect	No recovery	37	73–80	Boulder zone	3–5	30.2	–18.7	5.2	6	*		–62	20	13	0	1980 storm 2 severe storms '82,'92
Chronic, Indirect	No recovery	37	80–93	"	"	11.5	–5.1	3.7	6	ns		–44	20	13	0	1980 storm 2 severe storms '82,'92
Chronic, Indirect	No recovery	38	73–80	Bench zone	5–10	64.0	–43.6	4.5	6	**		–68	20	13	0	1980 storm 2 severe storms '82,'92
Chronic, Indirect	No recovery	38	80–93	"	"	20.4	–8.4	4.5	6	ns		–41	20	13	0	1980 storm 2 severe storms '82,'92
Chronic, Indirect	No recovery	39	73–80	Slope zone	10–35	75.4	–67.5	12.8	8	**		–90	20	13	15	1980 storm 2 severe storms '82,'92
Chronic, Indirect	No recovery	39	80–93	"	"	7.9	10.1	4.6	8	ns		>100	20	13	15	1980 storm 2 severe storms '82,'92
Chronic, Indirect	No decline	40	73–80	Rubble zone	35–40	3.0	2.4	4.4	2	ns		80	20	7		
Chronic, Indirect	No decline	40	80–93	"	"	5.4	–1.0	4.1	2	ns		–19	20	13		
11. Pacific: Panama (Glynn 1990, Fig. 26, and personal communication from P. Glynn)																
Acute, Indirect	No recovery	41	75–81	Gulf of Chiriqui	1–10	13.7	1.4	4.4	18	ns		10	13	5	14	Bleaching El Niño 82–83 Recruitment reduced by grazers, predators
Acute, Indirect	No recovery	41	81–84	"	"	15.1	–14.5	3.2	18	**		–96	13	5	14	White Band disease
Acute, Indirect	No recovery	41	84–88	"	"	0.6	2.1	1.1	18	ns		>100	13	5	14	1989 Storm Decline of massive spp
12. Atlantic: Virgin Is., St. Croix, Buck Is. (Hubbard et al. 1993, and personal communication from E. Gladfelter)																
Acute, Indirect	No recovery	42	76–88	N. shallow fore reef	2–5	52.3	–40.3	–	–	–		–77	17	13	3	
Acute, Indirect	No recovery	42	88–89	"	"	12.0	–0.6	–	–	–		–5	17	13	3	
Acute, Indirect	No recovery	42	89–93	"	"	11.4	1.2	3.9	27	ns		11	17	13	3	
Acute, Indirect	No recovery	43	88–89	S. shallow fore reef	2–5	25.7	–17.7	–	–	–		–69	5	4	0	
Acute, Indirect	No recovery	43	89–93	"	"	8.0	–7.0	2.5	25	**		–87	5	4	0	
Acute, Indirect	No decline	44	88–89	North, back reef	1–6	4.0	0.2	–	–	–		4	5	4		
Acute, Indirect	No decline	44	89–93	"	"	4.2	3.6	2.1	23	ns		86	5	4		
Acute, Indirect	No decline	45	88–89	N. lower fore reef	5–8	8.8	4.3	–	–	–		49	5	4		
Acute, Indirect	No decline	45	89–93	"	"	13.1	–2.2	3.7	33	ns		–17	5	4		
Acute, Indirect	Further observation	46	88–89	South, back reef	0.5–2	1.3	3.8	–	–	–		>100	5	4		
Acute, Indirect	Further observation	46	89–93	"	"	5.1	–1.9	2.1	23	ns		–37	5	4		
Acute, Indirect	Further observation	47	88–89	S. lower fore reef	5–10	45.4	–3.1	–	–	–		–7	5	4		
Acute, Indirect	Further observation	47	89–93	"	"	42.3	–20.2	6.8	32	**		–48	5	4		

13. Atlantic: Curacao and Bonaire (Bak and Nieuwland 1994, and personal communication from R. Bak)														
Chronic, Direct	No recovery	48	73-83	Leeward reef	10	54.1	-10.9	-20	10					Coastal development
			83-92	"	"	43.2	-12.2	-28	9					
Chronic, Direct	No recovery	49	73-92	"	"	54.1	-23.1	-43	19					"
			73-83	"	20	49.8	-7.8	-16	10					
Chronic, Direct	No recovery	50	83-92	"	"	42.0	-18.4	-44	9					"
			73-92	"	"	49.8	-26.2	-53	19					
Chronic, Direct	No decline	51	73-83	"	30	38.1	-2.6	-7	10					10
			83-92	"	"	35.5	-1.2	-3	9					
Chronic, Direct	No decline	52	73-92	"	"	38.1	-3.7	-10	19					1980 storm
			73-83	"	40	25.4	6.3		10					
Chronic, Direct	No decline	53	83-92	"	"	31.6	2.1		9					Herbivore reduction
			73-92	"	"	25.4	8.3		19					
14. Atlantic: Barbados (Scoffin 1993)														
Chronic, Direct	No recovery	54	74-81	Bellairs reef	0-3	36.7	-21.5	-59	12					1980 storm
			81-92	"	"	15.2	0.3		2					
15. Atlantic: Jamaica, Rio Bueno (Hughes 1993)														
Chronic, Direct	No recovery	55	77-81	Shallow platform	7	61.9	-40.9	-66	0					1980 storm
			81-85	"	"	21.0	-6.1	-29	0					
Chronic, Direct	No recovery	56	85-89	"	"	14.9	-11.0	-74	0					"
			89-93	"	"	3.9	-1.5	-38	13					
Chronic, Direct	No recovery	57	77-81	Vertical cliff	10	71.8	-34.4	-48	0					1980 storm
			81-85	"	"	37.4	-9.5	-25	0					
Chronic, Direct	No recovery	58	85-89	"	"	27.9	-19.8	-71	0					"
			89-93	"	"	8.1	-4.2	-52	0					
Chronic, Direct	No recovery	59	77-81	Vertical cliff	15-20	42.6	-15.6	-37	0					1980 storm
			81-85	"	"	27.0	1.0		6					
Chronic, Direct	No recovery	60	85-89	"	"	28.0	-19.1	-68	0					"
			89-93	"	"	8.9	-5.0	-56	0					
15. Atlantic: Jamaica, Discovery Bay (Hughes 1993)														
Chronic, Direct	No recovery	61	78-93	Foreereef, palmata	1	56.7	-56.5	-100	13					Same as Rio Bueno
			"	Foreereef,cervicornis	10	42.0	-39.2	-93	13					
Chronic, Direct	No recovery	62	"	Foreereef, 20 m	20	27.0	-25.2	-93	13					"
			75-93	Back reef	0-3	50.7	-47.2	-93	13					
16. Atlantic: Jamaica, Discovery Bay (Liddell and Ohlhorst 1994, Table 2, and personal communication from W. D. Liddell and S. Ohlhorst)														
Chronic, Direct	No recovery	63	80-84	Foreereef	15	33.2	-19.8	-60	9					1980 storm
			84-89	"	"	13.4	-11.1	-83	0					
17. Atlantic: Jamaica, Discovery Bay (Steneck 1993, and personal communication from R. Steneck)														
Chronic, Direct	No recovery	64	78-82	Foreereef	3	35.9	-21.5	-60	7					1980 storm
			82-87	"	"	14.5	-14.1	-97	0					
Chronic, Direct	No recovery	65	78-82	"	10	32.3	-23.6	-73	9					1980 storm
			82-87	"	"	8.7	2.2		9					
(continued)														

(continued)

Type of disturbance and effect on environment	Type of change	Example No.	Period	Site	Depth m	Initial % cover Mean	Change Mean	SE	df	Change in the absolute cover	% Change in cover	Study length Total (Y)	Recovery as % of loss	Probable causes of the changes
17. Atlantic: Chronic, Direct	Virgin Is., St. Croix, Teague Bay (Steneck 1993, and personal communication from R. Steneck)	63	82-88	North shore	3	33.6	-17.1	3.1	64	**	-51	6		Herbivore reduction
	observation needed													
	No decline	64	"	"	10	20.7	-6.2	0.7	77	**	-30	6		
	No decline	65	"	"	30	16.8	0.2	1.4	149	ns		6		
18. Atlantic: Chronic, Direct	Virgin Is., St. John (Rogers 1993, Fig. 1, ms in preparation and personal communication from C. Rogers and G. Garrison)	66	Ja-Nov89	Yawzi Point	12	22.6	-10.1	2.5	8	**	-45	6		Storm in Sept. 1989
	recovery		89-95	"	"	12.5	-1.8	2.3	8	ns	-14	6	0	Herbivore reduction
	No decline	67	90-95	Newfound Bay	5	21.9	3.8	2.3	8	ns		5		
19. Atlantic: Chronic, Direct	Bermuda (Cook et al. 1993, Fig. 3)	68	86-92	Site ED	7-9	0.7	2.6	0.6	28	**	>100	6		Ship grounding, 1978
	recovery		"	Site WD	"	1.0	2.4	0.5	28	**	>100	6		"
20. Atlantic: Chronic, Direct	Florida Keys, Carysfort Reef (Dustan and Halas 1987, Table 1, and personal communication P. Dustan)	69	75-83	Shallow sites	0.3-3.9	39.3	4.3	3.1	20	ns		8		
	decline		"	"	"	"	"	"	"	"	"	"		
	No decline	70	"	"	Deeper sites	4.7-21	-3.5	2.2	18	ns	-10	8		
21. Atlantic: Chronic, Direct	Florida Keys (Porter and Meier 1992, Table 2, and personal communication from J. Porter and O. Meier)	71	84-91	Carysfort Reef 1	4	16.6	-5.4	-	-	*	-33	7		Disease, bleaching
	observation needed													
	Further observation	72	"	"	Looe Reef 1	6	33.0	-14.5	-	-	**	7		"
	No decline	73	"	"	Carysfort Reef 2	15	33.2	-2.4	-	-	ns	7		"
	No decline	74	"	"	Looe Reef 2	8	30.7	-4.0	-	-	**	7		"
22. Atlantic: Chronic, Direct	Gulf of Mexico, Flower Gardens Reef (Gittings et al. 1993, and personal communication D. Hagman)	75	72-80	Site WFG	15 +	38.0	17.2	5.4	42	**	45	8		
	decline		80-90	"	"	55.2	-8.7	3.0	135	**	-16	18		
	No decline	76	79-90	Site EFG	"	50.4	-4.4	2.8	141	ns	-9	11		
23. Atlantic: Chronic, Direct	Costa Rica (Cortes 1993, and personal communication from J. Cortes)	77	80-93	Cahuita	3-4	40.4	-29.2	6.1	30	**	-72	13		Natural disturbances, human impacts

Notes: (1) Example 1: the change in coral cover between 1970 and 1971 was inferred from the average difference in cover in 1971 between reefs damaged by predation by *Acanthaster planci*, and those not so damaged; the changes between 1971 and 1977 were directly observed. (2) Example 11: depths and initial cover for 1970 from Table 1 in Pearson (1981). (3) Example 21: the changes in coral cover between 1969 and 1970 were observed at Tumon; those between 1970 and 1981 were observed at Tanguisson, near Tumon

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