Using Remote Sensing to Reassess the Mass Mortality of *Diadema antillarum* 1983–1984

JONATHAN T. PHINNEY,*§ FRANK MULLER-KARGER,† PHIL DUSTAN,‡ AND JACK SOBEL*

*Center for Marine Conservation, 1725 De Sales Street NW, Washington, D.C. 20036, U.S.A. †Department of Marine Science, University of South Florida, St. Petersburg, FL 33701–5016, U.S.A., carib@carbon.marine.usf.edu ‡Department of Biology, College of Charleston, Charleston, SC 29424, U.S.A.

Abstract: *The* 1983-1984 mass mortality of the sea urchin Diadema antillarum remains one of the most severe die-offs ever recorded in the Caribbean. Before 1983, the herbivore D. antillarum was pervasive on coral reefs in the region. Nine months after first detection of the mass mortality, 95% of the urchins had perished, and algal cover of coral increased between 100% and 250%. A water-borne pathogen was hypothesized as the causative agent, but it was never isolated. To date, surface current patterns have been used exclusively to explain both the cause and the distribution patterns of the mortality event. Using archived satellite images, we re-examined the water-borne pathogen hypothesis and investigated whether other mechanisms could also account for the dissemination pattern in some areas. In addition, archived satellite images were utilized to detect changes in coral reef reflectance. For infections in the Gulf of Mexico and Bermuda, satellite images confirm that surface currents are likely responsible for the distribution of the pathogen. For infections in the eastern Caribbean (Curacao, U.S. Virgin Islands, Barbados), however, another mechanism, possibly ballast water exchange, must be considered because the surface current and infection patterns do not coincide. Changes in coral reflectance were detectable from Landsat thermatic mapping data before and after the mass mortality and correspond to the change in algal cover. Results from our study demonstrate the potential of satellite images for use in determining connectivity between regions of the Caribbean and in detecting changes in coral reef cover.

Utilización de Percepción Remota para Reanalizar la Mortandad Masiva de Diadema antillarum de 1983-1984

Resumen: El evento de mortandad masiva de 1983-1984 del erizo de mar Diadema antillarum se mantiene como uno de los eventos de mortandad masiva más severos de que se tengan registros en el Caribe. Antes de 1983, el bervíboro D. antillarum, abundaba en los arrecifes de coral de la región. Nueve meses después de la detección de la mortandad masiva, 95% de los erizos fallecieron y la cobertura de algas sobre el coral se incrementó entre 100 y 250%. Se estableció la hipótesis de que el agente causante fue un patógeno de origen acuático, pero nunca fue aislado. A la fecha, los patrones de corrientes superficiales han sido usados exclusivamente para explicar tanto el agente causal como los patrones de distribución de la mortandad. Utilizando imágenes de archivo de satélite, re-examinamos la bipótesis del agente de origen acuático e investigamos si otros mecanismos podrían también ser considerados en los patrones de diseminación de algunas áreas. Para infecciones del Golfo de México y Bermudas, las imágenes de satélite confirman que las corrientes superficiales son los responsables más probables de la distribución del patógeno. Sin embargo, para infecciones en el Este del Caribe (Curacao, U.S., Islas Virginia, Barbados), otro mecanismo, posiblemente el cambio de agua de lastre, podría ser considerado debido a que las corrientes superficiales y los patrones de infección no coinciden. Se detectaron cambios en la reflectancia del coral por medio de datos del mapeador temático Landsat antes y después de la mortandad masiva, mismos que correspondieron con los cambios en la cobertura algal. Los resultados de nuestro estudio demuestran el potencial de usar imágenes de satélite para determinar la conectividad entre regiones del Caribe y para detectar cambios en la cobertura del arrecife coralino.

⁵*Current address: American Society of Limnology and Oceanography, 1444 Eye Street, Suite 200 NW, Washington, D.C. 20035, U.S.A., email jpbinney@aslo.org*

Paper submitted April 5, 2000; revised manuscript accepted February 7, 2001.

Introduction

Mass Mortality of Diadema antillarum

The 1983-1984 mass mortality of the sea urchin Diadema antillarum in the Caribbean remains one of the most severe marine mass mortality events ever recorded (Lessios 1995). Within 1 year, nearly 95% of the Caribbean urchins died. Mortality was first recorded in Galeta Point, Panama, near the entrance of the Panama Canal (Lessios et al. 1984); within 9 months it was reported throughout most of the Caribbean and as far north as Bermuda (Fig. 1). The trajectory of the die-off often coincided with surface-current patterns, suggesting that a water-borne pathogen was responsible for the mortality. The pathogen was specific to D. antillarum and did not affect other echinoid populations. Unfortunately, the mass mortality surprised the researchers in the area and urchin samples were never stored for pathology. The identity of the pathogen, whether virus, bacteria, or protozoa, remains unknown.

Prior to 1983, *D. antillarum* was pervasive on reefs, and it was an important herbivore of filamentous algae and a bioeroder of corals in the Caribbean (Carpenter 1981; Sammarco 1982). One year after the die-off, algal cover increased between 100% and 250% in some areas (de Ruyter van Steveninck & Bak 1986). Ten years after the mass mortality, urchin densities had not recovered



Figure 1. General circulation pattern for the Caribbean Sea from hydrographic and satellite data and the known chronology of the die-off of Diadema antillarum: (1) Panama, January 1983; (2) Jamaica, July 1983; (3a) Barbados, September 1983; (3b) Flower Garden Bank, September 1983; (4) Curaçao, October 1983; (5a) Tobago, December 1983; (5b) St. Thomas, December 1983; (6) St. Croix, January 1984 (Lessios et al., 1984). (Not included: Bermuda, September 1983.) Note the major eastward and northward surface-current pattern. The current is also from the east along the South American coast near the Gulf of Paria and Gulf of Venezuela.

significantly (Hughes 1994; Lessios 1995). The lack of recovery of *D. antillarum* is hypothesized to be due to low larval populations in the water column and not to lack of settlement cues or predation (Lessios 1995).

In light of the specificity of the die-off and the rapid infection rate throughout the Caribbean, the water-borne pathogen hypothesis remains the most viable, but neither the pathogen nor its dissemination by surface currents has ever been tested (Lessios et al. 1984; Lessios 1988). Because no urchin samples were preserved during the die-off, it is unlikely that the pathogen hypothesis can ever be tested fully. Alternative mechanisms of dissemination, however, can be reexamined with archived satellite data and include data on the transport and release of ballast water from commercial vessels. In addition, a second hypothesis for the die-off involving changes in the physical environment—for example, that temperature made *D. antillarum* susceptible to a local pathogen could also be tested with archived satellite imagery.

We used remote sensing to reexamine the 1983 *D. antillarum* outbreak and to determine whether a waterborne pathogen could transverse the Caribbean, move north through the Gulf of Mexico (from the first sighting near the Panama Canal) and eventually reach Bermuda, and spread eastward toward the Lesser Antilles. In addition, the dramatic increase in algal cover of coral after the mass mortality presents a unique opportunity to determine whether satellite images can detect changes in coral reef cover and thereby provide another analytical tool for coral reef scientists.

Overview of Remote-Sensing Imagery in Coral Reef Studies

Application of satellite imagery to coral reefs has been promoted widely, and its capabilities often oversold (Curry et al. 1987). Despite various workshops specifically addressing the use of remote sensing for coral reef ecosystems (e.g., three sponsored by the National Oceanic and Atmospheric Administration [NOAA] and one by the National Aeronautics and Space Administration [NASA] and the Center for Marine Conservation), there remains a paucity of published reports demonstrating the effectiveness of remote sensing in assessment of distributions and health (reviewed by Green et al. 1996).

Satellite remote sensing of coral reef ecosystems can be divided between sensors that provide direct data and those that provide indirect data. Direct information includes geomorphic features, such as reef configuration and zonation, whereas indirect information includes features such as sea-surface temperature and turbidity, which can affect coral reef health. Although a wide range of satellites is capable of mapping relevant coral reef features, most studies of direct information have focused on just four sensors from two satellites: Landsat multispectral scanner (MSS) and thematic mapper (TM) and SPOT high-resolution visible (HRV) and panchromatic (PAN). Indirect information such as sea-surface temperature comes primarily from advanced very-high-resolution radiometry (AVHRR) (Strong & Stowe 1993). Use of satellite images in coral reef ecosystems has been limited to discriminating reef geomorphology from other benthic substrates such as seagrass and sandy-bottom areas (reviewed by Green et al. 1996; Mumby et al. 1997). Success in discerning different reef habitats has been mixed and confounded by too few spectral bands within the visible region of the electromagnetic spectrum. SPOT and Landsat satellites are limited to two and four visible spectral bands, respectively. The most recent Landsat 7, launched in 1999, with its enhanced thematic mapper plus (ETM+) sensor has eight spectral bands, of which four are in the visible region. The advent of the SEAWiFS sensor in 1997 with eight spectral bands in the visible wavelength could help distinguish large-scale spectral signals for coral reefs. In addition to spectral considerations, spatial resolution has hampered the general use of satellites for coral reef studies. The spatial scale for SPOT and Landsat satellites ranges from 10 and 20 m to 30 and 80 m, respectively, whereas SEAWiFS has a resolution of approximately 1 km. Because many coral reefs are a conglomeration of live coral, sand, and hard substrate, it is difficult at a 1-km resolution to distinguish between different benthic habitats or small-scale changes in reef health.

Although there are limits to present satellite capabilities, several field studies have demonstrated a wide range of reflectance characteristics that could be utilized by satellite sensors. Laboratory and more recent in situ hyperspectral reflectance characteristics have been determined for healthy and bleached corals (Hardy et al. 1992; Holden & LeDrew 1998), which could help in the design of future satellite sensors.

Methods

Surface Current

Historical coastal-zone color scanner (CZCS) images of the Caribbean Sea were obtained from the Department of Marine Sciences at the University of South Florida. A time series from 1978-1985 was developed from the CZCS from over 3500 individual scenes. Nearly 60% of the images collected were from 1979-1980. For the 1983 data, the Caribbean Sea was divided into three sections—east, central, and west—and a ranking of image availability was given for each day (Fig. 2). Because of cloud cover or lack of program coverage (CZCS was an experimental sensor and was turned off for most of 1983), only 7% of the images from 1983 could be utilized.

Individual CZCS images were grouped into daily, weekly, and monthly mean compilations. All images were first mapped to congruent, cylindrical equidistant projections at a spatial resolution of 4×4 km² and 20×20 km², and

then the composite images were derived. We determined chlorophyll pigment concentrations for surface water at a spatial resolution of approximately 4 km by subsampling the original CZCS images to one-sixteenth of their original size (Feldman et al. 1989). Chlorophyll concentrations were derived from the ratio of the blue (443 nm) and blue-green (520 nm) radiance to green radiance (550 nm) (Gordon et al. 1983, 1988). We determined surface-current patterns by identifying specific chlorophyll patches (or coastal sediment plumes) and following them over time.

Sea-surface temperatures for the Caribbean Sea were obtained from the advanced very-high-resolution (AVHRR) sensor archived at the NASA Jet Propulsion Laboratory in Pasadena, California (Walton 1988). Data were sorted by time and grouped into 1-week segments for the period 1982–1986 and sorted geographically into pixels of a 2048×1024 matrix that covered the globe. A Laplacian interpolation was used to fill in data gaps with the condition that valid retrieval exists within nine of the pixels being evaluated. We derived sea-surface temperature for the Caribbean by binning the final data by month and across years.

Coral Reef Change

We conducted an initial survey of archived Landsat TM images from the EROS Data Center in Sioux Falls, South Dakota. Images from multiple sites were analyzed where the mass mortality was reported, including Discovery Bay (Jamaica), St. Croix (U.S. Virgin Islands), and Turneffe Reef (Belize). Early satellite images from the Caribbean generally were limited to U.S. waters, and no useable images prior to 1983 were found from the wider Caribbean outside U.S. waters. Landsat TM data at EROS Data Center are located in a "scrounge file" that is not completely indexed at present. Other TM images were collected from image archives at the NASA Jet Propulsion Laboratory and the Florida Marine Research Institute, St. Petersburg, Florida. All images were transferred into Erdas Image format and analyzed.

A time series of 22 cloud-free Landsat TM images was assembled from 1982 to 1996 out of 120 images available. The study area focused on Carysfort and Molasses reefs, the largest coral reefs in the Florida Keys, where extensive field studies have been conducted since 1975, including reporting of the *Daidema antillarum* mass mortality (Dustan 1985; Dustan et al. 1996).

The locations of Carysfort and Molasses reefs in the Landsat TM images were determined from an image of the Key Largo National Marine Sanctuary processed from a combination of SPOT, HRV, and PAN sensors. This image has been processed to show reef locations and assess the percent cover of benthic habitats in the sanctuary. The subsets from each image were carefully compared to ensure a "best-fit" image-to-image registration. Classes of images depicting shallow reef areas (1–2 m





Figure 2. Comparative coverage achieved over an area of interest with the coastal zone color scanner (CZCS) in 1979 and 1983. Ranking of availability (ordinate axis) was as follows: 2, good and useful coverage; 1, image present but of poor quality so only inferences can be made; 0, no coverage.

deep) were used in the analysis to eliminate significant light attenuation from the water column. Only cloudfree subsets were used to compile the statistics.

Mean pixel brightness values for all Landsat TM bands (blue, green, and red) were determined from the known reef areas at Carysfort and Molasses reefs. Mean brightness values (spectral reflectance) for each band and band-ratio changes were compared among TM images, and a time series was developed. Raw data in 1982 could not be corrected for atmospheric interference because the header for the image was not available. The other data have been corrected. There is a 5–15% decrease in reflectance values between raw and corrected images (P. Dustan, personal communication).

Results

Surface Currents and Temperature

Surface currents for the Caribbean have been well established from hydrographic data (Roemmich 1981; Morrison & Nowlin 1982) and confirmed by more recent Year of the Ocean buoy data (D. Wilson & R. Leben, personal communications). In general, surface water flows from the eastern Caribbean Sea to the west and northwest, with a well-defined cyclonic gyre (counterclockwise) in the Gulf of Darien near Panama (Fig. 1). Surface water originating in the Gulf of Darien is entrained in the cyclonic gyre and can flow northward along the coasts of Panama and Colombia. Surface currents from the east force water from the Gulf of Darian northward into the northwestern Caribbean Sea, where a portion heads to the Gulf of Mexico via the Yucatan Straits between Mexico and Cuba and another water parcel heads in an eastward direction to the Florida Keys. In the Gulf of Mexico, CZCS coverage was much more extensive than in the rest of the Caribbean region. Here, the loop current showed a pronounced northwestward angle and there was evidence that a portion of the current breaks off and heads toward the Flower Garden Bank region in the northwestern portion of the Gulf of Mexico. The main portion of the loop current flows south from the Gulf of Mexico through the Florida Straits where it is entrained in the Gulf Stream and flows northward past Bermuda.

The few 1983 CZCS images available for the Caribbean Sea confirm this general circulation pattern and suggest that there were no anomalous current patterns during the mass mortality (Fig. 3). In the eastern Caribbean, the flow of water from southeast to northwest is clearly traced by the Orinoco River Plume that flows out in the vicinity of the Gulf of Paria, near the Lesser Antilles. Another chlorophyll bloom associated with an upwelling shows a westward surface current flowing along the southern Caribbean between the Gulf of Venezuela and Gulf of Paria. A third plume from the Gulf of Venezuela and extending northward into the Caribbean Sea confirms that the chlorophyll bloom moves westward and northwestward from the eastern Caribbean into the Caribbean Sea.

The AVHRR data for sea-surface temperature in 1983 and 1985 also support the known surface circulation patterns of the Caribbean (data not presented). General patterns of sea-surface temperature suggest a cyclonicgyre surface current with an eastward and northward current path from coastal Colombia near Barranquilla and a western southwest component in the Gulf of Darien. For the first 10 weeks of 1983, sea-surface temperature was on average 2° C cooler for the Caribbean Sea than in other years, which may reflect reality or an artifact in processing of the data caused by the volcanic eruption of nearby El Chichon. Otherwise, sea-surface temperatures were normal for the remainder of 1983.

Coral Reef Change

Time-series data for Carysfort and Molasses reefs revealed a marked change in mean bright spectral reflectance for all three bands from 1982 to 1985, which coincides with the *D. antillarum* mass mortality and subsequent overgrowth of coral with filamentous algae (Table 1 & Fig. 4). The blue band decreased in brightness most markedly, approximately 75–80%, whereas the brightness of the green and red bands decreased approximately 25–30% and 40–70%, respectively. For subsequent years after 1982, brightness levels for the blue band remained >70% below the 1982 level. The brightness levels of the red and green bands for this period were in the ranges of 28-67% and 40-93% below the 1982 values, respectively.

Discussion

Three hypotheses have been proposed to account for the mass mortality in 1983: (1) a specific pathogen transported by surface current, (2) a specific pathogen transported by ballast water, and (3) changes in the environment such as water temperature that affected *Diadema antillarum*. Hypotheses 1 and 2 are discussed below; the third hypothesis is not discussed here because there is no evidence that the urchin is especially susceptible to temperature changes of 2° C.

The water-borne pathogen hypothesis set forth by Lessios et al. (1984) invokes surface currents as causing the spread of a pathogen throughout the Caribbean. This hypothesis is generally supported by satellite data. If the pathogen originated in the Gulf of Darien near Panama, the CZCS and AVHRR data show that the spread would be generally to the northwest Caribbean Sea and into the Gulf of Mexico. Within the Gulf of Mexico, other research (Muller-Karger et al. 1991) demonstrates a distinct loop current that flows northwestward around Flower Garden Bank and then south toward the Florida Straits and the Gulf Stream. Many field observations suggest that a water-borne pathogen likely affected D. antillarum populations in the following order: Discovery Bay, Jamaica; Flower Garden Bank, Gulf of Mexico; Florida Keys; Bahamas; and finally Bermuda (Lessios 1988).

In contrast, the proposed eastward flow of the pathogen from Panama along the coast of South America toward Curaçao, St. Thomas, and Barbados is not supported by satellite data (Fig. 1). Rather, coastal turbidity marked by sediment plumes or chlorophyll along the coast of South America shows a general westward current (Fig. 3) that is likely driven by the high trade winds in the area. Not resolved by the satellite data are possible small-scale westerly eddies that could form from the North Brazil Current and propagate along the northern South American coast. Such eddies have been proposed from models



Figure 3. Coastal-zone color scanner image showing the weekly mean pigment concentration for the second week of January 1983, which coincides with the first observations of the mass mortality of Diadema antillarum in Panama. Chlorophyll pigments are in micrograms per liter; $\mu g/L$. GP, Gulf of Paria; GV, Gulf of Venezuela.

 Table 1.
 Spectral reflectance values for Carysfort and Molasses

 Reefs from Landsat thematic mapper.

	Carysfort Reef			Molasses Reef		
Years	band 1	band 2	band 3	band 1	band 2	band 3
1982	107.4	41.9	30.1	112.4	41.7	28.8
1985	21.1	20.8	9.7	36.0	36.1	16.5
1986	10.2	22.8	6.6	22.9	32.6	7.8
1987	4.7	26.8	9.3	16.5	39.2	13.4
1988	1.0	29.1	12.0	33.6	35.3	10.0
1989	9.6	19.0	7.6	17.5	24.9	7.8
1990	9.7	13.4	2.2	20.9	25.1	6.5
1991	13.7	18.2	5.1	30.5	36.2	20.0
1992	14.2	20.5	12.3	14.5	22.0	11.6
1993	22.5	29.1	17.2	31.6	38.7	19.9
1996	1.0	13.5	3.6	9.7	31.8	11.5

(Chao & Carton 1998) but not measured in situ. Therefore, eastward transport along the coast cannot be completely ruled out by the satellite data. Nonetheless, given the general circulation patterns of the area, coastal eddies would be intermittent features if they indeed exist.

Therefore other mechanisms of transport are needed to resolve the dispersal pattern of the pathogen eastward from Panama to Curaçao and Barbados against the prevailing surface currents. One obvious mechanism is ballast-water exchange from large ships transiting from the Panama Canal to the island ports in the eastern Caribbean. Shipborne introduction of nonindigenous species is a well-established mechanism that is a worldwide problem (National Research Council 1996). Ballast water is also known to support viable microorganisms and viruses for weeks and months (McCarthy & Khambaty 1994; Ruiz et al. 2000). Ships potentially could load ballast water in an infected port and release it, along with the pathogen, in the eastern Caribbean ports of Colombia, Curaçao, and the Lesser Antilles. There is indirect evidence that ballast water may be responsible for certain infections during this period. Bak et al. (1984) traced the origin of the D. antillarum mass mortality in Curaçao to the mouth of the Willemstad Harbor, suggesting that the pathogen was introduced by ship activity in the port.

Landsat TM data that span the period of the mass mortality demonstrate a substantial decrease in reflectance in blue (74% average), green (32%), and red (56%) bands between 1982 and 1985 (Fig. 4). A likely mechanism to account for the decrease in reflectance is the overgrowth of filamentous algae on the coral and the corresponding decrease in albedo. Unfortunately, we found no useable TM images for the 1983-1984 period that could document the change more directly and corroborate this hypothesis.

Conclusions

Archived historical CZCS and AVHRR images demonstrate that currents in the Caribbean Sea were not anom-



Figure 4. Time series of spectral reflectance from Landsat TM images for Carysfort and Molasses reefs, Florida. Raw data in 1982 could not be corrected for atmospheric interference because the header for the image was not available; the other data has been corrected. There is approximately a 5-15% decrease in reflectance values between raw and corrected images (P. Dustan, personal communication). (Modified from Dustan et al. 2001, this issue.)

alous during the 1983–1984 mass mortality of the sea urchin, *D. antillarum*, and could have transported a water-borne pathogen from the region of the Panama Canal northward into the Gulf of Mexico and eventually the Gulf Stream. But surface currents cannot explain the eastward migration of the pathogen from the Panama Canal region toward the Lesser Antilles. Instead, other mechanisms of dispersal, notably ballast water, need to be considered. Archived Landsat TM images are also able to detect changes in coral-reef cover during this time period when algal cover of coral reefs increased 100–250% after the die-off of *D. antillarum*.

Unfortunately, there remains a paucity of satellite images from the early 1980s, and the mass mortality remains a lost opportunity for scientists. The CZCS sensor onboard the Nimbus 7 satellite was an experimental sensor that was not systematically turned on over the Caribbean, and the coral reef scientific community did not request such coverage during this period. Present satellite capabilities such as SEAWiFS and Landsat 7 have some spatial and spectral limitations in detecting small-scale changes in reef albedo. Nonetheless, large-scale (kilometer or larger) changes in reflectance from algal cover or coral bleaching might be detectable, and field researchers could utilize these techniques through better coordination with remote-sensing scientists.

The 1983 mass mortality of *D. antillarum* highlights the much-heralded need for better communication across scientific disciplines. On the one hand, remote-sensing scientists need to be informed of ecological calamities on the ground in order to direct satellite sensors and capture the event as it unfolds. On the other hand, satellite data is expensive to produce and needs a constituency as well as ideas from the research community. It is important for both fields that individuals be encouraged to work broadly between the interface of ecology and remote sensing.

Acknowledgments

This study was funded in part from the Research Division of the Office of Earth Science at the National Aeronautics and Space Administration (NASA) to the Center for Marine Conservation. The authors would like especially to thank W. Turner at NASA for his interest in and dedication to our project and for organizing this special section. This manuscript was greatly improved from comments of three reviewers.

Literature Cited

- Bak, R. P. M., M. J. E. Carpay, and E. D. de Ruyter van Steveninck. 1984. Densities of the sea urchin *Diadema antillarum* before and after mass mortalities on the coral reefs of Curaçao. Marine Ecology Progress Series 17:105-108.
- Carpenter, R. C. 1981. Grazing by *Diadema antillarum* and its effects on the benthic algal community. Journal Marine Research 39:749-765.
- Chao, Y., and J. Carton. 1998. Mesoscale eddies in the Caribbean Sea. Pages 8–11 in U.S. World Ocean Circulation Experiment (WOCE) Report. U.S. WOCE, Texas A&M, College Station.
- Curry, B., A. S. Fraser, and K. L. Bardsley. 1987. How useful is Landsat monitoring? Nature 328:587–589.
- de Ruyter van Steveninck, E. D., and R. P. M. Bak. 1986. Changes in abundance of coral-reef bottom components related to mass mortality of the sea urchin, *Diadema antillarum*. Marine Ecology Progress Series 34:87-94.
- Dustan, P. 1985. The bio-optics of coral reefs. Pages 189–197 in M. L. Reaka, editor. The ecology of coral reefs. Volume 3. National Oceanic and Atmospheric Association (NOAA) symposium series. NOAA Undersea Research Program, Rockville, Maryland.
- Dustan, P., W. Jaap, J. W. Porter, J. Wheaton, and O. Meier. 1996. Coral reef monitoring in the Florida Keys (abstract). Proceedings of the 8th International Coral Reef Symposium.
- Dustan, P., E. Dobson, and G. Nelson. 2001. Landsat thematic mapper: detection of shifts in community composition of coral reefs. Conservation Biology 15:892-902.

- Feldman, G., C. N. Kuring, W. E. Esaias, C. McClain, J. Elrod, N. Maynard, D. Endres, R. Evans, J. Brown, S. Walsh, M. Carle, and G. Podesta. 1989. Ocean color, availability of the global data set: the oceanography report. EOS, **70**:634.
- Gordon, H. R., D. K. Clark, J. W. Brown, O. B. Brown, R. H. Evans, and W. W. Broenkow. 1983. Phytoplankton pigment concentrations in the middle Atlantic Bight: comparison of ship determination and CZCS estimates. Applied Optics 22:20–35.
- Gordon, H. R., O. B. Brown, R. H. Evans, J. W. Brown, R. C. Smith, K. S. Baker, and D. K. Clark. 1988. A semi-analytic radiance model of ocean color. Journal of Geophysical Research 93(D9):10909-10924.
- Green, E. P., P. J. Mumby, A. L. Edwards, and C. D. Clark. 1996. A review of remote sensing for the application and management of tropical coastal resources. Coastal Management 24:1–40.
- Hardy, J. T., F. E. Hoge, J. K. Yungel, and R. E. Dodge. 1992. Remote detection of coral "bleaching" using pulsed-laser fluorescence spectroscopy. Marine Ecology Progress Series 88:247–255.
- Holden, H., and E. LeDrew. 1998. Spectral discrimination of healthy and non-healthy corals based on cluster analysis, principal components analysis and derivative spectroscopy. Remote Sensing of Environment 65:217–224.
- Hughes, T. P. 1994. Catastrophic, phases shifts, and large-scale degradation of a Caribbean coral reef. Science **265:**1547–1551.
- Lessios, H. A. 1988. Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? Annual Review of Ecological Systematics 19:371-393.
- Lessios, H. A. 1995. *Diadema antillarum* ten years after mass mortality: still rare, despite help from a competitor. Proceedings Royal Society Britain 259:331–337.
- Lessios, H. A., D. R. Robertson, and J. D. Cubit. 1984. Spread of mass *Diadema* mortality through the Caribbean. Science 226:335-337.
- McCarthy, S. A., and F. M. Khambaty 1994. International dissemination of the epic vibrio-Cholera by cargo ship ballast water. Applications in Environmental Microbiology 60:2597-2601
- Morrison, J. M., and W. D. Nowlin, Jr. 1982. General distributions of water masses within the eastern Caribbean sea during winter of 1972 and fall of 1983. Journal of Geophysical Research 87–C:4207-4229.
- Muller-Karger, F. E., J. J. Walsh, R. H. Evans, and M. B. Meyers. 1991. On the Seasonal phytoplankton concentration and sea surface temperature cycles of the Gulf of Mexico as determined by satellites. Journal of Geophysical Research 96–C:12645-12665.
- Mumby, P. J., E. P. Green, C. D. Clark, and A. J. Edwards. 1997. Coral reef habitat mapping: how much detail can remote sensing provide? Marine Biology 130:193–202.
- National Research Council. 1996. Stemming the tide. National Academy Press, Washington, D.C.
- Roemmich, D. 1981. Circulation of the Caribbean Sea: a well-resolved inverse problem. Journal of Geophysical Research 86–C:7993-8005.
- Ruiz, G. M., T. K. Rawlings, F. C. Dobbs, L. A. Drake, T. Mullady, A. Huq, and R. R. Colwell. 2000. Global spread of microorganisms by ships. Nature 408:49–50.
- Sammarco, P. W. 1982. Effects of Grazing by *Diadema antillarum* Phillipi on algal diversity and community structure. Journal of Experimental Marine Biology and Ecology 65:83–105.
- Strong, A. E., and L. L. Stowe. 1993. Comparing stratosphere aerosols from El Chichón and Mount Pinatubo using AVHRR data. Geophysical Research Letters 20:1183–1186.
- Walton, C. C. 1988. Nonlinear mutilchannel algorithms for estimating sea surface temperature with AVHRR satellite data. Journal of Applied Meteorology 27:115–127.



Conservation Biology Volume 15, No. 4, August 2001