BULLETIN OF MARINE SCIENCE, 68(2): 163–179, 2001

MASS MORTALITY OF TROPICAL MARINE COMMUNITIES IN MORROCOY, VENEZUELA

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ABSTRACT

Over a period of several days, in January 1996, various shallow-water marine communities and populations sustained massive mortalities at the Morrocoy National Park, Venezuela. Sixty to ninety-eight percent of the corals, depending on the location, were annihilated. Holothurians disappeared from several sites. Other groups, including sand dollars, gastropods, sipunculans, polychaetes and sponges, were decimated. The marine vegetation, mainly composed of the seagrass *Thalassia testudinum* and macroalgae, however, did not show any signs of degradation; neither did the mangrove prop root adherent community. Abnormal levels in several physicochemical parameters were registered in the area, including average water temperatures 10°C lower than usual, reduced concentrations of dissolved oxygen, salinities nearing 5 psu at the bottom-water interface, and lower than normal surficial current speeds due to water slacking. Satellite images show that during the period under study unusual masses of cold water were near the area. The coverage of the affected area was estimated to extend for at least 160 km^2. Although various physicochemical and oceanographical parameters were involved, it is likely that low temperatures, probably spurred by a nearby upwelling of cold-water masses, coupled with punctual drops of salinity at some sites, converged to trigger the complex processes that included planktonic blooms and mucilaginous aggregates and finally induced widespread mortalities.

Massive mortalities are interesting events as they provide insight into the process of ecological disturbance and may reveal factors that structure communities and regulate populations. A number of factors have been linked to massive mortalities in marine environments. Physical stress is most pronounced in shallow waters, where several factors play a role in the regulation of communities. Extreme conditions seem to lead to the disruption of dampening mechanisms and subsequent blockage of energy transfer in marine ecosystems (Ott, 1981). The result may be the degradation of community structure to different extents or even mass mortality under exceptional circumstances (Stachowitsch, 1984).

In tropical areas, disturbances to three of the most common and highly productive shallow-water ecosystems, coral reefs, seagrass beds and mangroves, may arise from unpredictable factors or infrequent events. The stability of these circumtropical ecosystems is regulated by a number of agents, including salinity fluctuations, nutrient availability, species interactions, pathogens, currents, tidal patterns, and extreme temperatures and climatic events such as hurricanes and El Niño-Southern Oscillation (Lugo et al., 1987; Lessios, 1988; Brown and Suharsono, 1990; Warwick et al., 1990; Glynn and D'Croz, 1990; Glynn, 1991; Edmunds and Witman, 1991; Robblee et al., 1991; Mohammed and Johnstone, 1995; Laboy-Nieves, 1997). Hurricanes are critical elements in triggering widespread damage and massive mortalities (Glynn et al., 1964; Woodley et al., 1981; Rogers et al., 1991; Roth, 1992; McCoy et al., 1996). Just as important are stormy winds and heavy rains, which can spawn sudden salinity plunges and upsurges in resuspended sediments (Goodbody, 1961; Williams et al., 1987; Orihuela et al., 1991). In the Caribbean, mass mortality events have also been attributed to the occurrence of hyposaline conditions, due to mainland runoff or severe storms, including effects of siltation (Goodbody, 1961; Glynn, 1968; Woodley et al., 1981; Goenaga et al., 1989; Orihuela et al., 1991; Gosselin and Quian, 1997), or to ultraviolet radiation, which is known to cause bleaching in several groups (Williams et al., 1987). Even though a catalogue of critical effects is available, it is often difficult to blame any particular cause, since mortality is usually detected after it occurs and thus the relative importance of each factor is hard to assess.

In this paper, we report on a phenomenon recorded at the beginning of 1996 which resulted in widespread mortality within several groups of marine invertebrates in the Morrocoy National Park, Venezuela. We document changes in physicochemical parameters, nutrients, metals, oceanographic characteristics and the structure of some of the communities.

Study Area

Field work was carried out at the Morrocoy National Park (MNP). The MNP, a conservation unit located on the west-central coast of Venezuela (10°52′N, 68°16′W), covers an area of approximately 32,090 ha (Fig. 1). It is a system of semi-enclosed interconnected embayments, continuously fed by well-mixed oceanic water that is exchanged through several wide inlets (Fig. 1). The red mangrove, *Rhizophora mangle* L., dominates most of the coastline and is also the main vegetational element of the numerous islets interspersing the embayments (Conde and Alarcón, 1993). A highly diversified adherent community grows on the roots of *Rhizophora* (Díaz et al., 1992). Extensive meadows of the seagrass *Thalassia testudinum* Banks ex König are common in the embayments, and coral reefs abound in the external perimeter of the key belt and close to the inlets (Losada, 1988; Bone et al., 1998; Conde and Carmona-Suárez, 2000) (Fig. 1). Salinity under most conditions fluctuates slightly (36 ± 2‰) year-round (Díaz et al., 1985), although sustained brackish conditions can appear during the rainy season (Laboy-Nieves, 1997), or following large storms. Freshwater influx is restricted to several creeks that flow into the northwestern corner of the park and to seasonal rainfall, which averages 1213 mm yr^{-1} (Bone et al., 1998). Surficial water temperature in the area ranges from 26.0 to 29.0°C (Bone et al., 1998).

Materials and Methods

Within the framework of an ongoing project (March 1995–February 1997), distribution and abundance of two species of sea cucumbers*, Holothuria* (*Halodeima*) *mexicana* Ludwig and *Isostichopus badionotus* (Selenka), had been monitored in this area for 10 mo prior to massive mortalities (Laboy-Nieves, 1997). Accordingly, a set of physicochemical data recorded at the water-sediment interface (0.5–3.5 m) at 38 stations, belonging to a network deployed throughout the park, were available as a baseline for comparative purposes. Further information was secured within other two projects: CARICOMP (Caribbean Coastal Marine Productivity Program) (CARICOMP 1997a,b; Bone et al., 1998) and COF (Costa Oriental del Estado Falcón) (García et al., 1998), that started in 1992 and 1995, respectively, and were under way at the time of mass mortalities. Ad hoc visits were carried out in January–February 1999. Overall, 47 stations were sampled before, as well as after the die-offs.

At each station water temperature and dissolved oxygen at the water-sediment interface were determined by means of a YSI 50® instrument. Temperature was calibrated by means of a 0.5°C precision mercury thermometer. Bottom salinity was measured by means of a temperature-com-

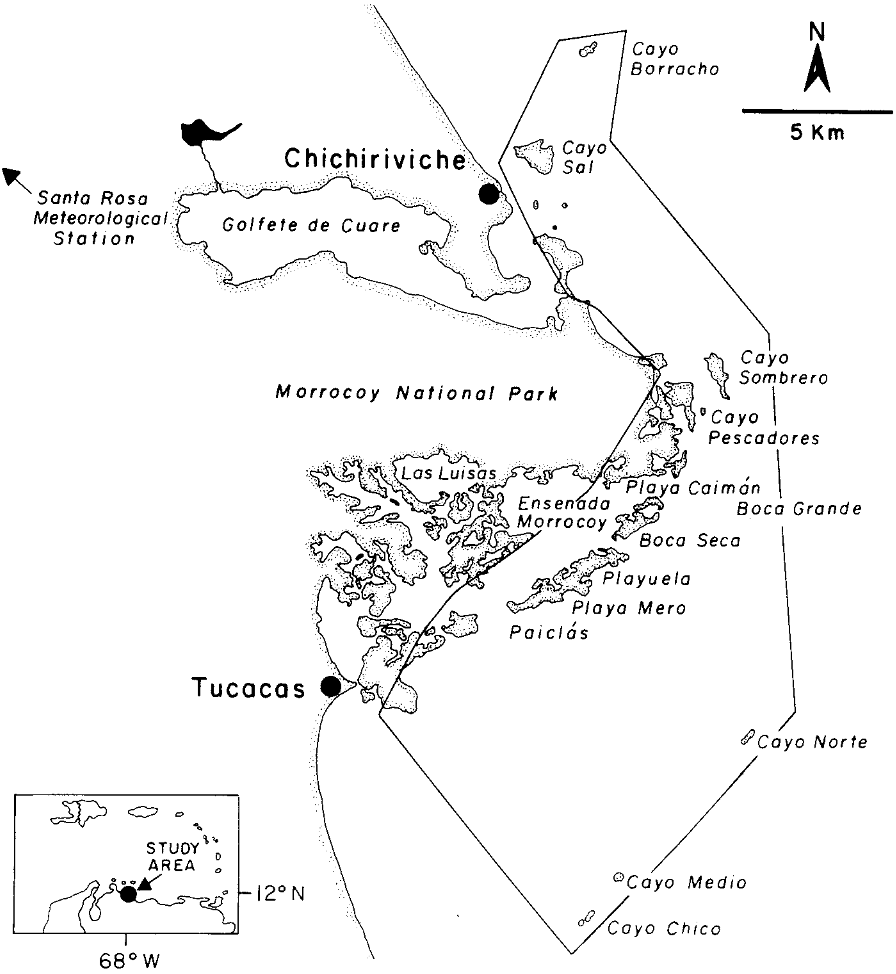

Figure 1. Map of Morrocoy National Park showing its relative location on the Venezuelan coast and the approximate area of mass mortality affectation (enclosed area).

pensated American Optical® hand refractometer. Transparency was determined with a Secchi disc as described in the CARICOMP protocol. A plastic, neutrally buoyant, sphere was employed to estimate currents, measuring their velocity along a submerged measuring tape. Sediment pH was determined using a HANNA HI-8424® apparatus on samples with a ratio of 1:2.5 sediment sample to deionized water.

Global sea surface temperature of the Venezuelan Caribbean was monitored using AVHRR data from the NOAA 12 satellite. Satellite image windows were provided by the CARIACO project (CArbon Retention In A Colored Ocean), an inter-institutional research initiative coordinated by F. Muller-Karger (University of South Florida), which deals with carbon balance in the Cariaco Basin, Southern Caribbean, Venezuela. The general oceanic wind patterns (3 m above the sea) observed with microwave satellite sensor (SSM/I) were provided by Remote Sensing Systems [www.ssmi.com]. This site is sponsored, in part, by NASA's Earth Science Information Partnerships (ESIP): a federation of information sites for Earth science and by the NOAA/NASA Pathfinder Program for early EOS products (Principal Investigator: Frank Wentz). Specific ground wind data for the Caribbean was obtained from NOAA's National Climate Data Center for selected stations [www.ncdc.noaa.gov]. Local rainfall data was provided by the Ministry of the Environment and Natural Resources and retrieved from a meterological station located about 10 km from the MNP (Fig. 1).

Coral and algae live cover at the Playa Caimán reef, which has been monitored since 1993, were estimated according to the CARICOMP protocol (CARICOMP, 1997a). Ten permanently marked chain transects, perpendicular to the slope, were randomly located within the coral reef, between 5 and 12 m of depth. On each transect, a reference line was secured tightly between two stakes. Beginning from one stake, lengths of chain (5–10 m), laid to follow the contour of the bottom, were deployed in a straight line towards the other, for a horizontal distance of 10 m. Intercepts of the line with corals were then examined to assess live coverage. Algae cover was concurrently accounted.

Holothurians were sampled at 28 stations located throughout the park. At each station, four permanent transects with a coverage of 40 m^2 each were set. Holothurians on the transects were identified at the species level and tallied to determine density (Laboy-Nieves, 1997).

RESULTS

CHRONOLOGY OF MAIN EVENTS.—On 20 January 1996, local fishermen reported large numbers of dead gastropods (*Astraea tecta*) near the shores of the most external keys of the Morrocoy National Park (MNP). On the following days (21–22 January), other dead organisms (mostly fishes) came ashore in most areas of the park. The sea water presented a red-brownish color and strings of white mucus-like matter floated in the water. During this week, abnormally low water temperatures and dissolved oxygen concentrations were recorded at 38 stations of the MNP. The atypical presence of vegetal terrestrial debris floating in the water and accumulating on the beaches was observed. In the same dates, the sea was exceptionally calm and winds, which usually are moderate steady northeasterly trades, had reversed their direction, blowing from the northwest with speeds nearing zero. After 30 January, the oceanographic and meteorological normal conditions of the MNP were regained. More detailed information on these events is presented subsequently.

Several physicochemical parameters recorded prior to (December 1995), during (January 1996) and after (February 1996) mass mortalities are presented in Table 1. Average values for the 38 stations are given, including those where holothurians were absent, as well as standard deviations and ranges for each parameter.

TEMPERATURE.—Temporal variations of bottom water temperature are presented in Figure 2. Monthly average values oscillated between 28 and 32.5°C, with the only exception of January 1996, when temperature at the water-sediment interface throughout the park averaged 19.3°C and reached a low of 18°C at one site (Table 1). This represented a difference of more than 10°C below mean temperatures on the previous month, and also a significant difference as compared to the preceding 10 mo (Grubbs Test: $z = 4.044$, $P = 0.005$) (Fig. 2). In January 1996, temperature readings were relatively uniform throughout the park; the range was only 2.3°C, a lower variability than the ones registered in December 1995 (3.4°C) and February 1996 (2.5°C). Similar temperature records were obtained independently (Alicia Villamizar, pers. comm.). The almost stagnant cold-water masses remained in the area for about 2 wks, but in February water temperatures resumed normal levels at an average of 28.8°C (Table 1).

Satellite images of the Venezuelan coast collected on January 1999, showing an invasion of cold-water masses, corroborate the aforementioned temperature readings (Fig. 3). The images depict the sea surface temperature (SST) and the typical seasonal upwelling

Table 1. Average, standard deviation (within parenthesis) and range [within brackets] of temperature, salinity, dissolved oxygen, current speed and transparency at the water-sediment interface at 38 stations in the Morrocoy National Park, Venezuela, from December 1995 to February 1996. Number of measurements of temperature, salinity and dissolved oxygen each was 152 every month. Number of measurements of current speed was 38 in December 1995, 30 in January 1996 and 32 in February 1996. Transparency was recorded 30 times in December 1995 and January 1996, and 32 times in February 1996.

	Month & Year		
Variables	December 1995	January 1996	February 1996
Temperature (° C)	29.5 (0.79) [27.6–31.0]	19.3 (0.70) [18.0–20.3]	28.8 (0.76) [27.7–30.2]
Salinity (psu)	39.0 (1.2) [33–40]	38.0 (5.1) [5–40]	36.0 (2.8) [19–37]
Dissolved oxygen (mg/L)	4.5 (1.8) [0.5–9.5]	2.3 (1.3) [0.0–4.1]	3.6 (1.5) [0.0–6.3]
Current speed (cm/min)	27.1 (5.8) [19.0–35.0]	11.1 (4.4) [4.0–20.0]	29.2 (6.6) [12.0–41.0]
Transparency (m)	6.3 (0.46)	5.7 (2.79)	4.8 (1.52)

areas for this time of the year, in which the oceanographic characteristics are controlled by the influence of northeast trade winds (Fig. 3A). Posteriorly, during the week of the mortality event, the normal structure of these upwelling loci was lost, particularly those of Cabo Codera and Puerto Cumarebo (Fig. 3B). The surface cold water mass expanded and reached the central-west coast of the country, including the semi-enclosed area of the MNP on 18 January (Fig. 3B). By 27 January, the discharge of the Tocuyo River (50 km northwest of the MNP) dispersed warm water both northward and southward, heating the coast of the MNP. The upwelling structure of the coast was not yet reestablished by this date (Fig. 3C). In the SST images from 1996 to 1999 that were examined, the coast near the MPN was always warmer than the surrounding ocean, except in the week of the mortality event.

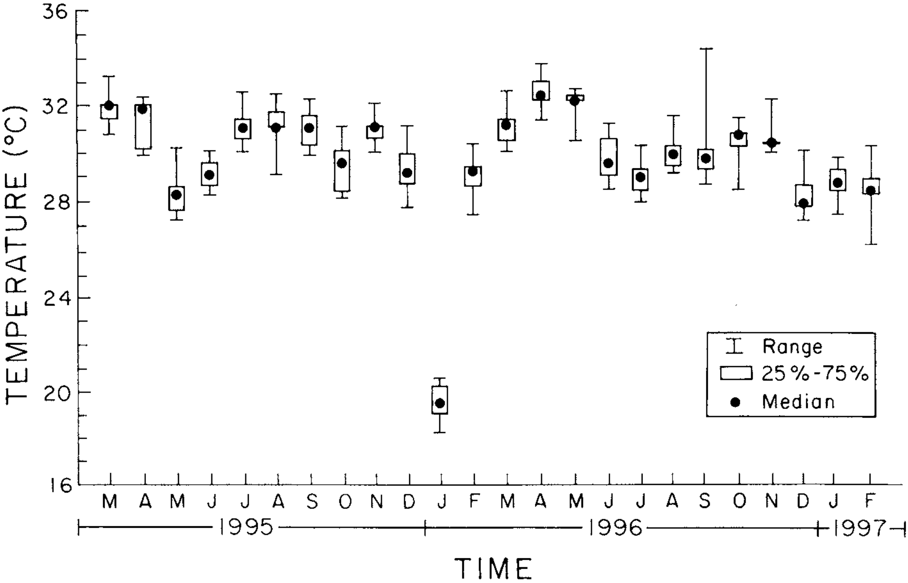

Figure 2. Monthly mean bottom water temperature at the Morrocoy National Park from March, 1995 to February, 1997 (38 stations).

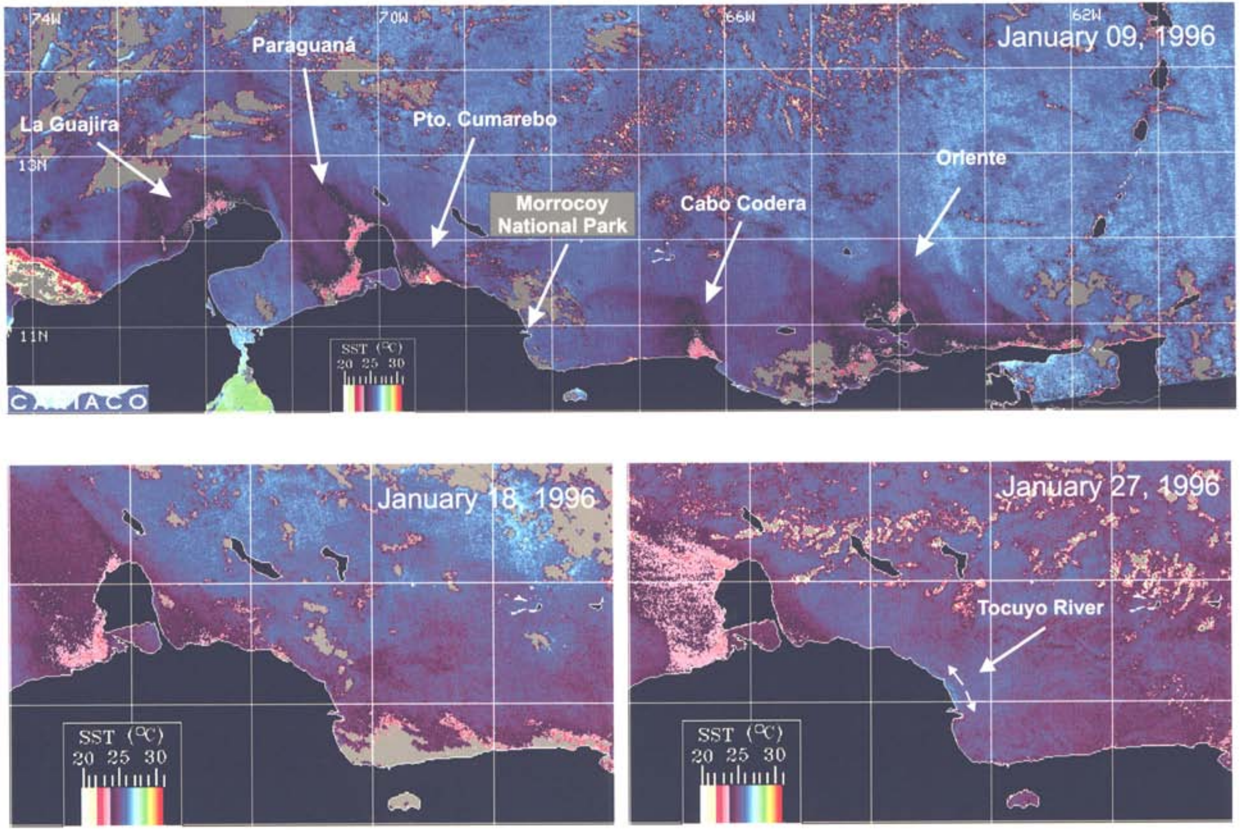

Figure 3. Sea surface temperature (from the Advanced Very High Resolution Radiometer, AVHRR sensor, on NOAA 12 satellite) of the Venezuelan coast on a: 9 January, showing the normal upwelling loci, and localized cold water areas adjacent to the coast. b: 18 January and c: 27 January, showing the direction of flow of the Tocuyo River discharge, a narrow, relatively warmer water to the north of the MNP. Images window courtesy of the CARIACO project (CArbon Retention In A Colored Ocean) and the Centro de Procesamiento Digital de Imágenes (CPDI) at the Fundación Instituto de Ingeniería (FII), Caracas, Venezuela.

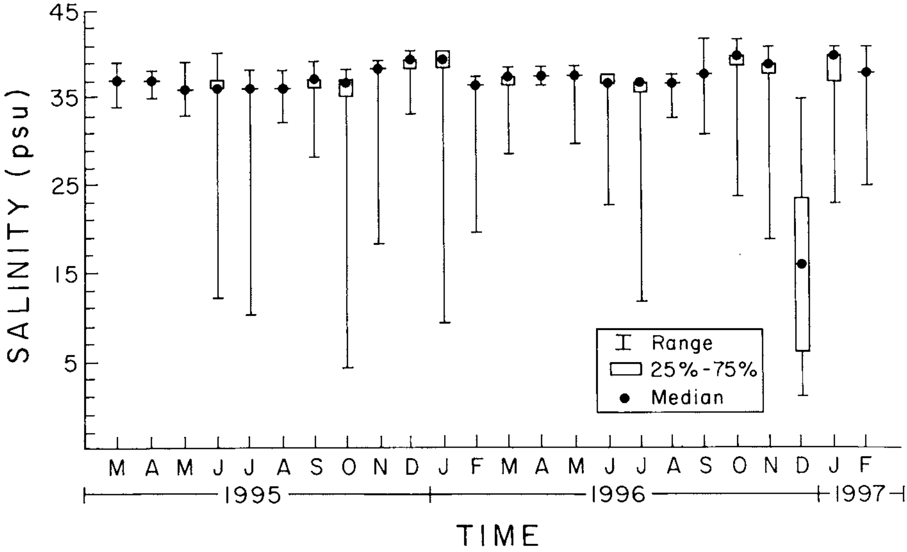

Figure 4. Bottom salinity fluctuations at the Morrocoy National Park from March 1995 to February 1997 (38 stations).

Salinity.—Prior to the mass mortality phenomenon, salinity at the MNP averaged 35.6 psu, although in several opportunities it exhibited substantial drops (Fig. 4). In December 1995, the average salinity was higher than the overall mean during the preeding months. However, during the mass mortality stint, in January 1996, salinity plummeted to 5 in several localities of the park, although the mean value did not differ from other months (Fig. 4, Table 1).

Current Speed.—Average surface current speed throughout the park in January 1996 (11.1 cm min^{-1}) was 59.0% lower than the mean value for the previous month (27.1 cm min^{-1}) and significantly lower than the series of former values averaged over the preceding 10 mo (Grubbs Test: z = 3.082, P = 0.05). Furthermore, most of the values registered at the 38 stations in January (4.0–20.0 cm min^{-1}) were below the minimum record for December 1995 (19.0 cm min^{-1}). In February, the mean current speed increased and reached previously observed values (29.2 cm min^{-1}).

Oxygen Concentration and Biochemical Oxygen Demand.—The average concentration of dissolved oxygen in January was 2.3 mg L^{-1}, almost 50% below readings from December (4.5 mg L^{-1}) ($t_s = 2.24$; P = 0.05) and higher, although not significantly, than the dissolved oxygen in February 1996 ($t_s = -1.29$; $0.10 > P > 0.05$) (Table 1). The Grubbs test also confirmed that oxygen concentration in December was lower than the average over the preceding 10 mo (z = 2.785; P = 0.05). With the exception of the oceanward stations, where oxygen concentrations were next to normal, anoxic levels were reached in December at all other stations. Thereafter, in February, dissolved oxygen returned to normal concentrations (3.6 mg L^{-1}). The mean biochemical oxygen demand did not vary between November 1995 (54.2 mg L^{-1}) and February 1996 (54.2 mg L^{-1}), although greater maximum values were recorded in February (494 vs 422.1 mg L^{-1}).

pH AND TRANSPARENCY.—In January 1996, the pH of the bottom sediments from Morrocoy averaged 8.3 (range: 6.3–9.1). This value was close to the averages recorded in October 1995, 8.2 (range: 6.9–8.8),and May 1996, 7.7 (6.3–8.4), although its range was greater.

The mean transparency value recorded in January 96 (5.7 ± 2.79) was significantly lower (Grubbs: $z = 3.446$, $0.05 > P > 0.01$) than the previous values in the park (Table 1). This value was also lower than the one recorded in December 1995 (6.3 ± 0.46), but transparency was even lesser in February 1996 (4.8 ± 1.52).

NUTRIENTS, HYDROCARBONS AND METALS.—No data are available for the concentrations of nitrogen and phosphorous for water samples in January 1996, when the events described took place. However, the information available prior to November 1995, and immediately after the mortalities in February 1996, shows that total nitrogen increased 236%; 0.25 ppm (range: 0.12–0.59) and 0.84 ppm (0.44–1.68), respectively. Total phosphorous concentrations did not vary over time, being 0.07 ppm in both cases.

Several oil-derived hydrocarbons, including xylene, methacresol and 2-chlorocyclohexanol, which can be very toxic to polychaetes and crustaceans, were found in water samples collected through 26–30 January 1996. However, there were only traces of them, far from toxic concentrations. Concentrations of these substances showed spatial trends, decreasing from north to south.

The concentrations of several metals (Al, As, Cd, Cr, Cu, Hg, Ni, Pb, V, Zn) were determined in the sediments and water column at nine stations in November 1995 and February 1996. Only two of them (Pb in the water and As in the sediment) showed substantial increases (108.0 and 417.9%, respectively), but their concentrations (122.3 and 640.1 ppb) did not surpass accepted normal values.

CORALS.—Among the most affected communities, if not the most affected, were coral reefs. Patches of coral reefs located in the embayments inside the park suffered mortalities that ranged from 60 to 98%. In some places coral die-offs were not so intense, being close to 30%. Live coverage of corals at Playa Caimán (Fig. 1), which had been estimated near 40% in September 1995, October 1995, and January 1996, had fallen to almost 0% in May 1996 and June 1996 (Fig. 5). Less affected were coral reefs at Cayo Sombrero and Cayo Pescadores (Fig. 1), at the northeastern tip of the park, and those located offshore at Cayo Norte and Cayo Chico (Fig. 1). Tracing these points, the area of impact can be estimated at no less than 160 km^2 (Fig. 1). *Acropora palmata* was the species most affected. This coral, as well as *Millepora* sp., presented evidence of bleaching. Some specimens of *Montrastea* were bleached at their distal part, while other individuals appeared completely untarnished or showed only some isolated bleached spots. Meanwhile, corals of the species *Siderastrea siderea*, *Porites asteroides* and *P. porites* did not suffer any obvious damage.

HOLOTHURIANS.—In December 1995, the average abundance of the holothurians *I. badionotus* and *H. mexicana* at 28 stations was 9.0 ($s = 10.54$) and 16.2 (10.54) individuals, respectively. In January 1996, a survey conducted along the park showed that the holothurian *I. badionotus* had dissappeared from three of the 13 stations where it used to be present. Three individuals of this species, harvested in other stations to extract fecal samples, had eviscerated (a reaction that occurs only under mechanical or chemical rebuking) and two of them showed evidence of abrasions or surficial necrosis on 20% of their dorsal skin. Posteriorly, in February 1996, abundances were slightly, although not significantly, lower than those observed in December 1995; 7.1 (7.29) for *I. badionotus* and 12.2 (15.29) for *H. mexicana*.

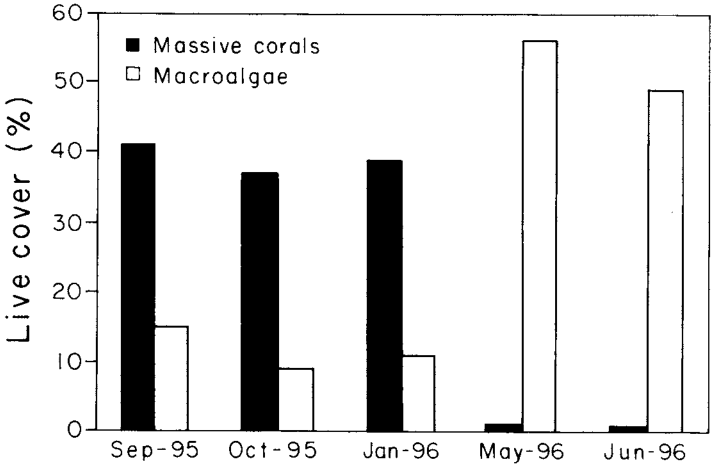

Figure 5. Live coverage of massive corals and macroalgae at Playa Caimán (Morrocoy National Park). Percent cover is the average of ten 10-m long transects. Samplings in January 1996 were carried out prior to mass mortality inception.

Other Groups.—Sipunculans, sand dollars and polychaetes were observed to leave their dwellings within the substrate and die thereafter. The response of sponges varied widely; some of them, mostly tubular, were eradicated, while others were decimated, and some were not affected at all. Many specimens of the gastropods *Astraea tecta* and *Voluta musica* were found dead, whereas other gastropods were not affected at all. Similarly, macroalgae and the seagrass *T. testudinum*, as well as their associated organisms, did not suffer obvious damage or mortality, neither did the mangrove prop root adherent community.

Debris and Amorphous Aggregates.—Many beaches on the keys were atypically covered by piles of terrestrial and freshwater vegetation allochthonous to the park, probably conveyed by the nearby rivers that discharge into the surroundings of the park. These materials comprised tree trunks, bamboo branches and remains of water hyacinths, as well as solid wastes. A few days before the mass mortalities, the sea was abnormally calm and winds, which usually are moderate steady northeasterly trades, had reversed their direction, blowing from the northwest.

Habitually, the water in the park is very translucent and exhibits low concentrations of suspended solids. Thus it was particularly noteworthy the presence of a whitish mucus-like matter floating in the water, forming lengthy gelatinous streamers and clouds or veils, that discontinuously spanned several hundred meters. These streamers were carried by the currents and coastal waves and in many cases were deposited on corals, sponges and bottom sediments at many sites in the park.

Also, brownish and reddish blots were observed in the water and on various beaches. The brownish sediment that covered dead corals contained a high diversity and abundance of diatoms. Several genera were identified: *Nitzschia*, *Licmophora*, *Cyclotella*, *Synedra*, *Thalassionema*, *Pleurosigma*, *Striatella*, among others, as well as ciguatoxic dinoflagellates, although in lesser concentrations. The water samples from several sites showed planktonic anomalies, such as a great abundance of filamentous cyanobacteria in one of the blots. Several days after the mass mortalities, a resinous substance was observed on several beaches. When dried, this resin formed a breakable crust.

DISCUSSION

The Morrocoy National Park (MNP) is a highly sensitive area, which has undergone environmental aggravations for decades (Conde and Carmona-Suárez, 2000). As early as 1974, anthropogenic impacts leading to degradation of coral reefs were catalogued (Weiss and Goddard, 1977). Within a radius of 50 km around the park, there is a pulp and paper mill, a petrochemical complex, and an electric power generation plant, whose outputs might be carried downstream to the MNP. The influx of three medium-sized rivers (Yaracuy, Boca de Aroa and Morón) probably conveys pesticides, fertilizers, soil amenders and herbicides to the park. Downcurrent lies the Tocuyo River, a larger river that could transport materials to the park during slack water and countercurrent episodes. Its detrimental effects on the coral reefs of Morrocoy have been documented (Bone et al., 1993) and several coral-bleaching episodes have been reported within the park (Losada, 1988; Lang et al., 1992; CARICOMP, 1997b). Furthermore, at the park's perimeter there are several marinas and boat-repairing facilities, where painting and metalworking are carried out, and several gas stations that supply leaded gasoline to the hundreds of boats that roam the park over the weekends and holidays. All these activities generate high metal concentrations, which in turn might be poured into aquatic environments. Currently, the marine sector of the park, which is of paramount economical importance to the residents of the surrounding areas, attracts some 3.5 million tourists every year (Lentino and Bruni, 1994). This spectrum of environmental pressures has yielded considerable debate over what is causing the deterioration of the region's marine ecosystems.

At the beginning of 1996, the MNP waters sustained a series of physical and chemical shifts that were at least partially documented and that led to the decimation of many invertebrates. Coral reefs were almost wiped out, and other groups, including holothurians, sand dollars, sipunculans, polychaetes, sponges and gastropods, were decimated. However, the marine vegetation, mainly composed of the seagrass *T. testudinum* and macroalgae, did not show any signs of degradation; neither did their associated organisms. In like manner, the mangrove prop root adherent community did not show any evident damage. Several of the elements, likely interconnected, that might have led to the destruction of the marine communities are discussed below, although the information available suggests that the entrance of cold water masses to the park, compunded with punctual plunges of salinity, was instrumental in causing widespread mortalities in marine organisms.

A gamut of hypothesis, not mutually exclusive, can be put forward to explain this phenomenon, including oil spills, metal concentration upsurges and other happenings related to anthropogenical activities. However, the information available does not support these potential explanations. Total nitrogen and phosphorous concentrations were within the levels considered normal for seawater. Metal concentrations were below the critical values regarded as hazardous for the aquatic biota (Clark, 1997). Oil tanker groundings, hull failures, collisions, fires or explosion that could have lead to oil spills were not reported in the area or acknowledged by the state-owned oil company PDVSA. Thus, it is more probable that the sharp decrease in water temperature throughout the park in January

1996, as well as the lowering of salinity at some locations, probably gave rise to a concatenation of events that ultimately led to widespread mortalities. Cold water upwellings reaching the park might be a recurrent phenomenon at that time, when phytoplanktonic blooms have been observed (MARNR, 1994), although they have not reached the intensity recorded in January 1996. Additionally, even though the setting of Morrocoy is undoubtedly tropical, the unusual distribution and abundance in the park of four macrophytes (*Halodule beaudettei, Syringodium filiforme, Penicillus capitatus* and *Sargassum filipendula*) suggests the influence of a nearby point-source of temperate waters (Steyermark, 1994). Also, a thermocline (13°C), ranging from 100 to 300 m, has been reported at a short distance offshore (40 km) in October 1973, August 1974 and February 1975 (Voltolina, 1975). It has been hypothesized that these cold waters may reach the surface due to the upwelling in the area (Voltolina, 1975).

As shown by satellite images of the Venezuelan coast collected on January 1999, an invasion of cold-water masses could indeed be held responsible for the mortalities. The images show the sea surface temperature (SST) and the typical seasonal upwelling areas at the beginning of the year. Posteriorly, during the week of the mortality event, the normal structure of several of these upwelling loci was lost and the surface cold water mass expanded and reached the central-west coast of the country, including the semi-enclosed area of the MNP on 18 January. Immediately after this large upwelling event, around 24–25 January, a very low wind speed cell developed in the east Atlantic (SSM/I microwave satellite wind speed images) and it moved towards the Caribbean, as confirmed by ground based meteorological stations (Fig. 6). The consequence was a reduced wind speed in the park's area for the last week of January. By 27 January, the discharge of the Tocuyo River dispersed warm water both northward and southward, heating the coast of the MNP. The upwelling structure of the coast was not yet reestablished by this date. Even though the extensive cooling of the sea surface in the Venezuelan coast due to the expansion of upwelling areas has been reported as a common phenomena in the first quarter of each year (Muller-Karger and Aparicio, 1994), in the SST images from 1996 to 1999 that were examined, the coast near the MPN was always warmer than the surrounding ocean, except in the week of the mortality event, a fact that suggests that this oceanographic episode reached exceptional levels.

In addition to the satellite images, calm seas and low wind speeds observed during that period suggest that the cold-water masses that invaded the reef and other ecosystems might have stayed there for several days, affecting tropical communities acclimatized to temperatures typically in the mid- to high 20s. Particularly coral reefs, one of the most affected communities, if not the most, are very sensitive to temperatures below 20°C and low oxygen concentrations (Barnes, 1987). On several previous occasions, coral die-offs have been observed in Morrocoy (Losada, 1988; Lang et al., 1992), suggesting that these corals, which have been deteriorating for more than two decades (Bone et al., 1998) and are regarded among the most debased coral reefs in the Caribbean (Woodley et al., 1997), probably were weakened. In late 1995, a widespread coral bleaching phenomena affected the Caribbean, including Morrocoy. In September 1995, more than 75% percent of the colonies (up to 90% in the dominant species in the park, *Montrastea annularis*) from the MNP were bleached, partially bleached, or pale. Although by mid-January 1996 the recovery of the normal visual appearance of the corals was observed in more than 90% of the colonies (CARICOMP, 1997b), they were probably already weakened and stressed for the date of the mortality event reported here. It has been shown that corals under stress

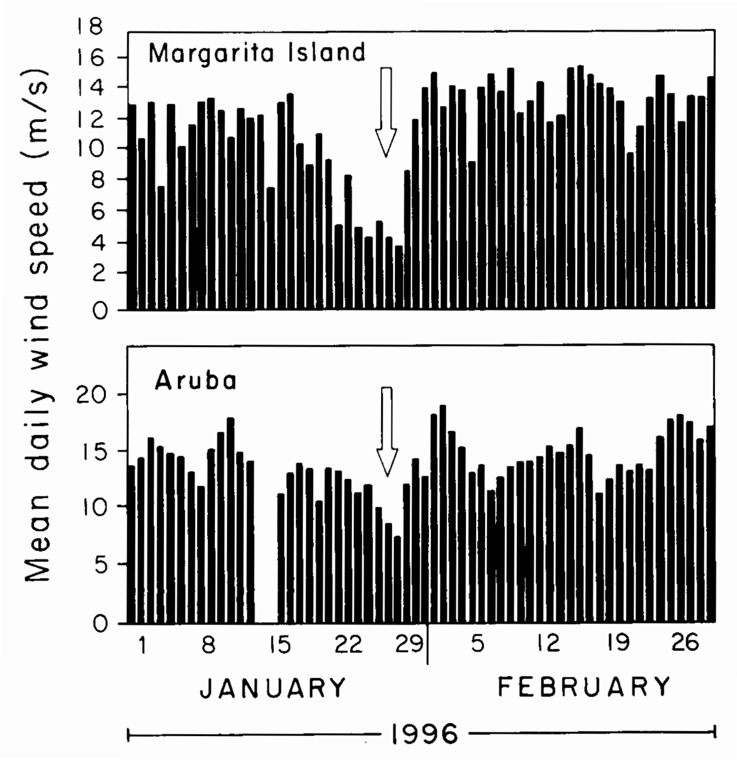

Figure 6. Mean daily wind speed (ms^{-1}) from meteorological ground stations at Margarita Island (Venezuela) and Aruba. Source: [*www.noaa.ncdc.gov*].

are particularly sensitive to shifts in environmental conditions (Meesters and Bak, 1993). With additional stresses, this sensitivity might have been the basis for compounded or synergistic responses in Morrocoy's corals.

As shown in Figure 3, substantial reductions of salinity were not uncommon in the park from March 1995 to February 1997. However, no massive mortalities were observed on those occasions, with the exception of the die-offs herein reported in January 1996, and again in January 1997 when the lowest salinity values for the period considered were recorded (Fig. 4). These results suggest that in the case of the mortalities that occurred in January 1996, salinity was not the crucial element in causing the phenomenon, although it probably contributed to the effect triggered by decreased temperatures. Since no heavy precipitations were observed in the area in December 1995 and January 1996, these low salinities probably were caused by the discharge of the downcurrent Tocuyo River, which could have intruded in the park, as a consequence of the calm seas and the switch of wind direction during that period. The intrusion of freshwater is also supported by the presence of heaps of allochthonous freshwater vegetation and remains covering the beaches in the park. Considering that this is a shallow-water area, the two masses of water probably intermingled in a brief lapse to produce a low temperature and reduced salinity body of water.

Mass mortalities probably were not only a straight consequence of low temperatures and salinities, but involved the interplay of several factors, as the outcomes imply. As suggested by the mucilaginous conglomerates floating in the water surface and covering corals and other dead organisms, the cold water surge, presumably nutrient-rich, might have brought about an extensive bloom of phytoplanktonic organisms. The subsequent decay of the bloom might have increased the biological oxygen demand, leading to oxygen depletion in the study area. Although hypoxia per se could have contributed to the the die-offs, the obstruction of respiratory mechanisms and structures due to clogging by planktonic organisms might have also caused mortalities in filtering organisms, as reported in similar events (Justic et al., 1987; Nilsson and Rosenberg, 1994; Gosselin and Qian, 1997; Sobral and Widdows, 1997; Stalder and Marcus, 1997). For instance, cyanobacteria, carried by the inflow of nearby rivers, have a sticky, mucilaginous sheath that in sufficient concentrations can clutter the internal canal system of sponges and hinder their functions (Butler et al., 1995). The differential mortalities observed in this group probably reflect their diverging internal architectures (Barnes, 1987). Additionally, the mucilage that ensues phytoplanktonic blooms forms a coating that could have covered coral reef colonies and other organisms, killing them by mechanical asphyxia. This mucus might have isolated the colonies from the environment, both reducing their possibilities of feeding, and curtailing respiratory and excretion processes, a phenomenon which has been described by Guzmán et al. (1990). Oxygen depletion has been associated with the amount of necroptic material in the water (Simpson et al., 1993; Díaz and Rosenberg, 1995; Pizzolon, 1996), creating a chain effect on mass mortality. This might have been exacerbated by the presence of biotoxins which follow cyanobacterial blooms (Pizzolon, 1996). In like manner, the respiration rate and the oxygen absorption efficiency of polyps, benthic invertebrates and fishes would be affected, eventually accelerating extinctions (Sobral and Widdows, 1997).

The sequence and factors just described for Morrocoy are not unique and share some points with catastrophic mortalities related by Stachowitsch (1984) at the Gulf of Trieste on the Adriatic Sea. Stachowitsch et al. (1990) have classified and systematized the progression of steps in mucus aggregation occurring in the Adriatic Sea and their range of effects on benthic communities. Stachowitsch (1984) identified five components that acted together to annihilate benthic communities at the Gulf of Trieste: a meteorological setting leading to the development of a strong thermocline; the confinement of the body of water, rendering it a hydrological trap; extremely high pelagic productivity conducting to long gelatinous streamers of living and dead plankton and bacteria; bottom currents influenced by storms and tidal patterns; and finally eutrophication and river discharge. Some of these factors were present in Morrocoy and the final outcome was similar to that in the Gulf of Trieste.

The mass mortalities substantiate the dramatic effects of mounting pressures on the ailing marine ecosystems of the Morrocoy National Park. In December 1996, another episode of die-offs was observed in the marine communities and populations of the park. In what was regarded as one the worst ecological disasters that has transpired on the Venezuelan seaboard, persistent rains—the heaviest in 28 yrs—lowered the salinity and hypoxic conditions were recorded throughout most of the park. Precipitation records show that just during the last quarter of 1996, 1086.9 mm of rain fell on the Morrocoy area; an amount comparable to the year-round average from 1968 to 1995 (1153.5 mm). As a consequence, massive mortalities of fishes, holothurians, sea urchins and sea stars were observed. *I. badionotus* vanished from most of the park, the exception being just one station at the fringe of the park; whereas *H. mexicana* disappeared from half the stations where it was present formerly. The density of the sea urchin *Lytechinus variegatus* from an internal seagrass bed was reduced from 30 ind m^{-2} to near zero. The recovery of the communities and populations impacted might be a prolonged and strenuous process, especially since habitats and ecosystems in Morrocoy have become unstable. Thus any new extreme episode of severe environmental fluctuations could lead to definitive sweeping mortalities. Finally, in a general framework, this is also a contribution to a further understanding of factors that shape coastal marine communities in the Caribbean.

Acknowledgments

This work was partially funded by the Decanato de Investigación y Desarrollo (Grant GID-003) and Instituto de Tecnología y Ciencias Marinas (Universidad Simón Bolívar) and Centro de Estudios Avanzados and Laboratorio de Biología Marina (Instituto Venezolano de Investigaciones Científicas). We thank P. Spiniello for identifying the microalgae, and the Laboratorio de Desechos Tóxicos (Universidad Simón Bolívar) and Laboratorio de Análisis Químicos (Universidad Nacional Experimental Francisco de Miranda) for chemical analysis. Satellite image processing was mainly undertaken by P. Castellanos and D. Stecconi, CARIACO Project (Carbon Retention In A Colored Ocean), at Centro de Procesamiento Digital de Imágenes, Fundación Instituto de Ingeniería (CPDI/FII - USB). Most of the field work on coral reefs was achieved thanks to the valuable help from M. Rada and C. Bastidas. We extend our gratitude to F. Muller-Karger, A. La Barbera , A. Boada and E. Guerra. We are indebted to D. Felder, C. Schubart, H. Guzmán, B. Kjerfve and two anonymous reviewers for making valuable comments on early drafts of the manuscript and to G. Rodríguez for enlightening discussions. J.E.C. gratefully acknowledges D. Felder (University of Louisiana at Lafayette) for providing space and facilities when writing preliminary versions of the manuscript. Thanks are extended to R. R. Twilley and C. Muñoz for furnishing printing facilities.

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DATE SUBMITTED: August 23, 1999. DATE ACCEPTED: July 21, 2000.

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