

## NOTE

RECOVERY OF THE LONG-SPINED SEA URCHIN  
*DIADEMA ANTILLARUM* IN CURAÇAO (NETHERLANDS  
 ANTILLES) LINKED TO LAGOONAL AND WAVE  
 SHELTERED SHALLOW ROCKY HABITATS

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Prior to the 1983 Caribbean-wide mass mortality of the long-spined sea urchin *Diadema antillarum* Philippi, the urchin was a dominant herbivore on Curaçao's reefs (Bak et al., 1984). Teenstra (1836) first mentioned the existence of shallow subtidal aggregations of this species inside Schottegat Bay, Curaçao. Mean densities documented on the island at various shallow leeward, southwest coast sites during the 1960s to early 1980s ranged between 3 and 20 m<sup>-2</sup> (Smith, 1968; Juliana, 1974; Bak and van Eys, 1975; van Eys, 1976; Bauer, 1980; Geerlings, 1981; Bak et al., 1984; Carpay, 1985). In contrast, the species was almost completely lacking from the wave-exposed northeast coast of the island (Wanders, 1976). Van den Hoek et al. (1978) described the tendency of the species to aggregate into distinct depth-zones on the reefs of Curaçao, according to the availability of shelter. In the decade prior to the mass mortality event, the two study sites for which data are available had already begun to show significant declines in urchin density, which likely represented a natural fluctuation (Bak et al., 1984; Carpay, 1985). However, mass mortalities began abruptly in early October 1983 and by the end of that month, documented mortalities were 97.3%–100% and the urchin densities averaged only 0.01 m<sup>-2</sup> (Bak et al., 1984).

The demise of the urchin had major ecological consequences for reefs throughout the region, including increases in filamentous and fleshy algal cover, decreased crustose coralline algal cover and coral recruitment, and increased grazing activity by herbivorous fishes (Carpenter, 1985; Hay and Taylor, 1985; de Ruyter van Steveninck and Bak, 1986; Liddell and Ohlhorst, 1986; Carpenter, 1990a; Robertson, 1991). Detrimental effects of the removal of grazers, including *Diadema*, have been demonstrated using cage experiments by Wanders (1977), while results by Sammarco et al. (1974), Carpenter (1990b), and Hughes (1994) show that urchin grazing is particularly important in maintaining coral reef systems.

Barring some notable exceptions (e.g., Chiappone, 2002; Chiappone et al., 2002; Lessios, 2005), most recent studies suggest that *D. antillarum* may have started recovering throughout much of the greater Caribbean, including Barbados (Hunte and Younglao, 1988), Jamaica (Edmunds and Carpenter, 2001; Haley and Solandt, 2001; Moses and Bonem, 2001), Dry Tortugas (Chiappone et al., 2001), St. Croix (Miller et al., 2003), and Costa Rica (Alvarado et al., 2004). As the processes governing *Diadema* population dynamics are complex, involving both density dependence and interactions between biotic and abiotic factors (Levitan, 1988, 1989, 1991a, b; Rowley, 1990; McClanahan and Kurtis, 1991; Lemire and Himmelman, 1996), it is important to have data from the early stages of recovery, before critical patterns and processes become masked as recovery proceeds.

In the two decades since the mass mortality event occurred, *D. antillarum* has begun to recover in Curaçao, reaching fairly high densities in certain habitats on the

leeward coast of the island (A.O.D. pers. obs). The purpose of this study was to document *Diadema* densities and size structures in several different habitats for a better understanding of the extent of and any potential spatial patterns in the recovery of this keystone reef species. The results are compared to data from both prior to and immediately after the mass mortality of October 1983.

## METHODS

During September and October 2002, we conducted sea urchin surveys in four representative reef type categories distributed along the leeward fringing reef tract of Curaçao, Netherlands Antilles (Fig. 1), where water depths of 10 m usually are found within 100–150 m of the shore (Bak, 1975). The reef type categories were: (1) exposed fringing reefs (sites 3, 7, 11, 12, 20, 24, 27); (2) sheltered fringing reefs (sites 1, 2, 6, 8, 9, 10, 22); (3) fringing reefs with an adjacent natural/semi-natural lagoon (sites 4, 13, 21, 23, 25, 26, 28); and (4) fringing reefs with an adjacent manmade lagoon (sites 5, 14, 15, 16, 17, 18, 19).

The distribution of wave energy environments along the leeward reefs of Curaçao has been mapped by van Duyl (1985). Exposed reef sites, as defined in this study, were sites with shores facing SW–S, average wave heights of 0.50 m and generally classified by van Duyl (1985) as moderate to moderate–low wave energy environments (index levels 4 and 5). On land, these sites usually were bordered by *Acropora* spp. rubble beaches. The sites defined as sheltered reef sites in this study had shores facing W–WSW, average wave heights of 0–0.3 m, and were generally classified by van Duyl (1985) as low wave energy environments (index level 6). All except one of these sites (site 22) were on the western half of the island, to which level 6 wave-energy environments are practically limited (van Duyl, 1985). Most of such sites did not have rubble beaches but instead had vertical seaboard cliffs down to the sea surface with a distinctive intertidal notch (Loenhoud and van de Sande, 1977). Reefs with adjacent lagoons, both natural and manmade, are found at a variety of wave energy sites ranging up to index level 2 (waves 1.5–2 m in height). Manmade lagoons are made by breakwaters placed parallel to the shore for the purpose of boat mooring or artificial beaches.

Seven replicate sites distributed along the entire coast were selected for each of the four reef type categories, for a total of 28 sampling sites. All five sampling sites for which pre-mortality quantitative density estimates were available were incorporated in the 2002 survey (sites 12, 13, 16, 26, 28; van Eys, 1976; Bak et al., 1984; Bak, 1985; Carpay, 1985; Geerlings, 1981). At each sampling site, urchin densities were measured on hard substrate at stations in two or three depth zones (depending on reef type category) as follows: 8–12 m (the drop-off zone), 1–3 m (shallow reef) and, when present, 1–3 m in the entrances of adjacent (natural or manmade) lagoons. At each sampling station representing a particular depth zone at each site, two separate 20 × 4 m transects were laid out 25 m apart and parallel to the coast in pre-determined areas of hard substrate, and carefully searched by two SCUBA divers, during daytime (900–1500 hrs). At lagoon entrances, the transects were located on opposite sides of the entrance. As *Diadema* is largely nocturnal and typically seeks out shelter during daytime, a small number of animals were certainly missed. For each transect, test diameters of the first 25 urchins encountered were measured to the nearest 0.5 cm, using Vernier calipers with long jaws and without detaching the urchins. Urchins which could not be measured without significant risk of injury to the animal were visually estimated to the nearest 0.5 cm. All *Tri-pneustes ventricosus* (Lamarck) urchins encountered were likewise counted and measured. Density data were pooled for the two separate transects of each sampling station, and hence treated as a single sample. To calculate the mean size of urchins for the different depth zones, only stations harboring more than four urchins were used as replicates.

Urchin densities were log-transformed to improve homogeneity of variances and were compared among the three depth zones using a one-way ANOVA, followed by a Games-Howell post-hoc test, designed for cases with unequal variances (Field, 2000). The statistical results

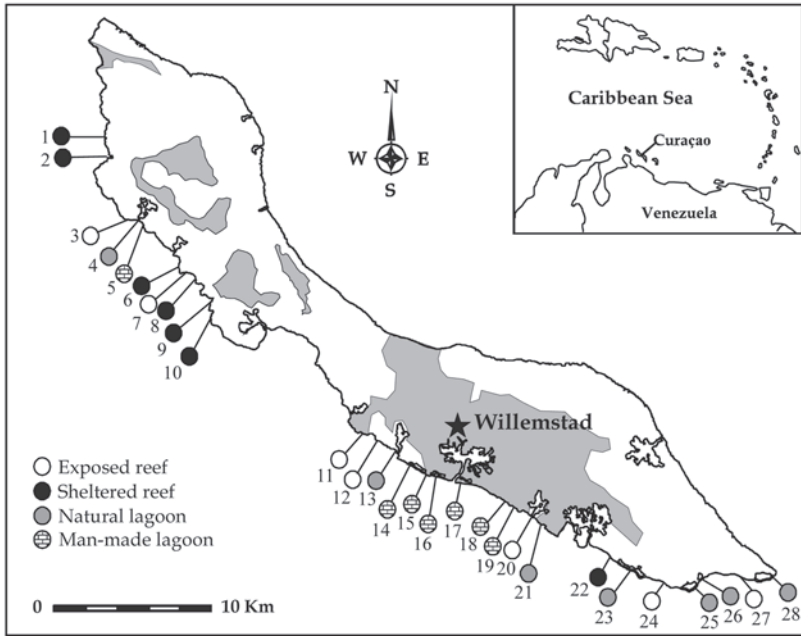


Figure 1. Map of Curaçao showing the 28 sampling sites (1 = Lagun, 2 = Sta. Cruz, 3 = West of Boka di Sta. Martha, 4 = Boka di Sta. Martha, 5 = Coral Cliff, 6 = Playa Shon Mosa, 7 = Playa Largu, 8 = Saliña di Cas Abao, 9 = Porto Marie, 10 = Daaibooi, 11 = Malmeeuw, 12 = Carmabi Boei 3, 13 = Carmabi Boei 1, 14 = Sonesta, 15 = KAE intake, 16 = Holiday Beach, 17 = Van der Valk, 18 = Princess Beach, 19 = Seaquarium, 20 = Boka di Sorsaka, 21 = West side of Janthiel Beach, 22 = Wela Bieuw, 23 = Fuikbaai, 24 = Saliña di Fuik, 25 = Lagun Blanku, 26 = Awa Blanku, 27 = Piedra Pretu, 28 = Awa di Kabes). Gray areas indicate major urban development.

presented are robust, as in all cases test results were similar when using the nonparametric Kruskal-Wallis test on untransformed data. As variances of urchin size data were homogeneous, mean urchin size was compared among the four reef types using untransformed data, testing the shallow reef and lagoonal depth zone separately, using a one-way ANOVA, followed by a Hochberg's GT2 post-hoc test (Field, 2000).

## RESULTS

**DIADEMA POPULATION DENSITIES.**—Urchins were encountered within 61 of the 140 transects and 38 of the 70 sampling stations. The three sites with highest densities per transect were from the lagoonal depth zone at sites 4 and 25 ( $3.1$  and  $2.7\text{ m}^{-2}$ , respectively), which are natural lagoons, and site 15 ( $2.7\text{ m}^{-2}$ ), a manmade lagoon. A comparison between habitat types (i.e. pooling depth strata) showed that overall densities (mean  $\pm$  1 SD) increased from exposed reefs ( $0.00 \pm 0.01\text{ m}^{-2}$ ) to sheltered reefs ( $0.04 \pm 0.05\text{ m}^{-2}$ ) to man-made ( $0.27 \pm 0.49\text{ m}^{-2}$ ) and natural ( $0.32 \pm 0.68\text{ m}^{-2}$ ) lagoonal habitat types (Fig. 2A). The presence of urchins was highest at the entrances of the lagoons where 93% of the sampling stations (13 out of 14) had urchins, intermediate at shallow reef stations where 71% of the stations (20 out of 28) had urchins, and lowest at the drop-off stations, where urchins were found at only 18% of the stations (5 out of 28). A comparison of densities between depth strata further showed mean densities to be significantly lower in the drop-off zone ( $0.00 \pm 0.003\text{ m}^{-2}$ ) as

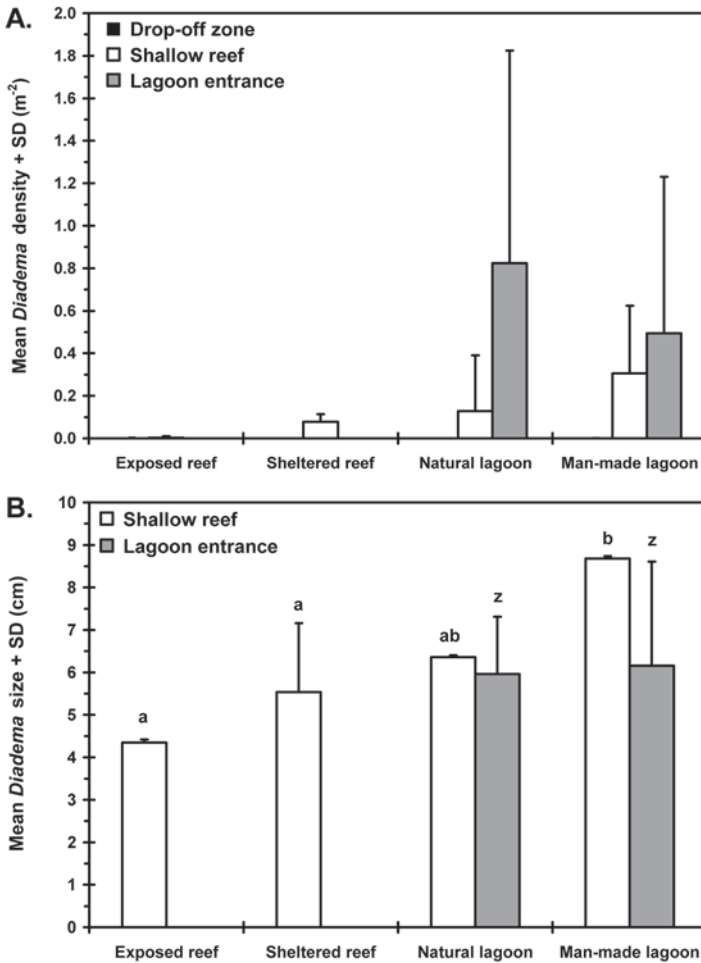


Figure 2. (A) Mean density and (B) mean size of *Diadema antillarum* at various depth zones of the four reef types (exposed and sheltered reef, natural, and man-made lagoon). Urchin sizes in the shallow depth zone or in the lagoon entrance depth zone differed significantly ( $P < 0.05$ ) between reef types when characters (a, b, or z) above the bars are different.

compared to the shallow reef ( $0.13 \pm 2.26 m^{-2}$ ) and significantly lower in the shallow reef as compared to lagoon entrances ( $0.66 \pm 8.61 m^{-2}$ ; One-way ANOVA,  $P < 0.039$ ). Even when comparing urchin densities separately for the four reef types, urchin densities also differed significantly among depth zones (One-way ANOVA,  $P \leq 0.013$ ), at all except exposed reef sites, where urchins were practically absent (Fig. 2A).

**DIADEMA SIZE-FREQUENCIES.**—Mean urchin test diameters varied as a function of reef type and depth zone (Fig. 2B). The largest mean ( $\pm$  SD) urchin test diameters were associated with the lagoonal sites, be they natural or manmade (mean diameters were  $6.3 \pm 2.2$  cm and  $7.5 \pm 2.4$  cm, respectively). An examination of size-structures in different depth zones and reef types further shows a tendency for higher densities of small urchins (sizes  $< 3$  cm) in the lagoon entrances as opposed to the adjacent shallow reefs (Fig. 3A).

Comparison of test diameters measured during our study with historical unpublished size-frequency data for *Diadema* from Curaçao shows that, allowing for vari-

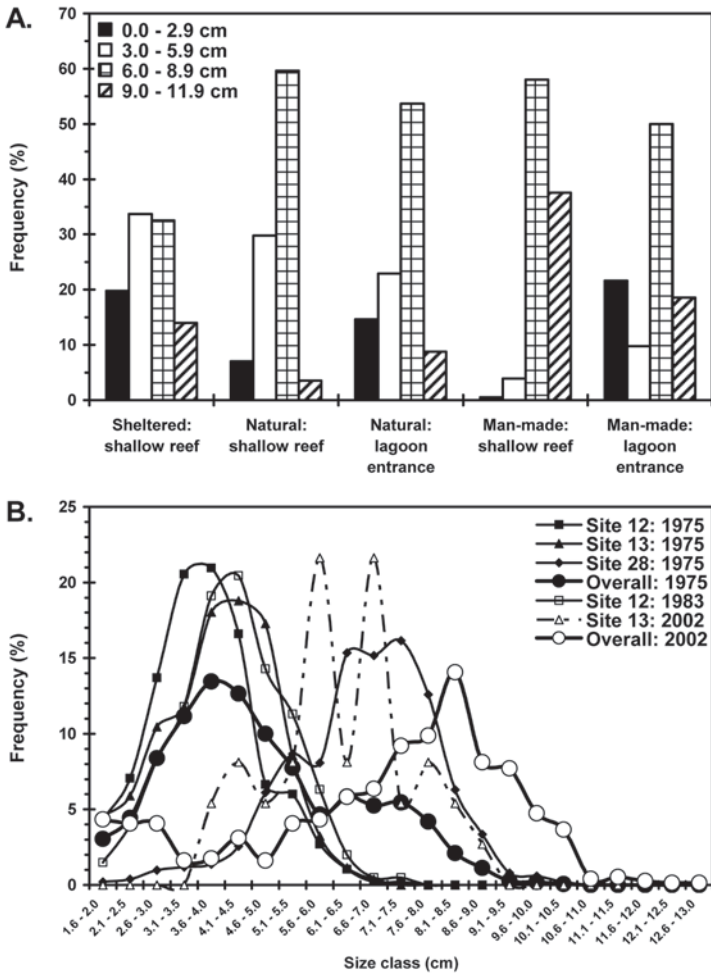


Figure 3. Size-frequency distribution (test size) of *Diadema antillarum*, (A) in two depth zones (shallow reef, lagoon entrance) of three habitat types (sheltered reef, natural lagoon, manmade lagoon), and, (B) based on both historical (van Eys, 1976; Carpay, 1985) and 2002 data.

ability between sites, present overall urchin test diameter (mean =  $6.8 \pm 2.5$  cm) is greater than in the past (1975 mean =  $4.8 \pm 1.7$  cm, van Eys, 1976). All of the size-structure data were generally unimodal with little in the way of pronounced cohorts, suggesting continuous or multiple recruitment events throughout the year, consistent with the findings of Bak (1985), or a merging of age groups. Animals larger than 8.0 cm in diameter historically constituted only a small fraction of the population at representative (high urchin density) reef sites, whereas at present, 39.0% of all urchins exceeded 8.0 cm. Only at site 28 did van Eys (1976) find a mean test diameter of  $6.4 \pm 1.3$  cm ( $n = 517$ , Fig. 3B) and a significant fraction (11.2%) of the population composed of animals greater than 8.0 cm. Due to the absence of urchins at sites 12 and 28 during our survey, the only site with both pre- and post mortality size-structure data was site 13. Results from this site are consistent with the overall pattern of increasing urchin test diameter over time in Curaçao (Fig. 3B).

*TRIPNEUSTES* POPULATION DENSITIES.—Mean densities ( $\pm$  SD) of *T. ventricosus* were  $0.0 \pm 0.0 \text{ m}^{-2}$  for exposed reefs,  $0.0 \pm 0.0 \text{ m}^{-2}$  for sheltered reefs,  $0.0 \pm 0.01 \text{ m}^{-2}$  for man-made lagoons, and  $0.08 \pm 0.3 \text{ m}^{-2}$  for natural lagoons, and these were not significantly different (One-way ANOVA,  $P > 0.50$ ). In our survey, *T. ventricosus* was encountered at only three sampling stations, two of which were in lagoon entrances (total of 263 specimens) and one of which was in the shallow depth zone at a sheltered reef site (one specimen).

## DISCUSSION

Various studies have suggested a preference of *D. antillarum* for shallow reef depths (Randall et al., 1964; van den Hoek et al., 1978; Bauer, 1980; Bak et al., 1984; de Ruyter van Steveninck and Bak, 1986; Moses and Bonem, 2001; Chiappone et al., 2002), whereas a number of studies further indicate that highest historical densities were from back-reef sites (e.g., Sammarco, 1980; Carpenter, 1990; Aronson, 1993; Moses and Bonem, 2001). Such observations suggest a special role for such shallow habitat in the population dynamics and eventual recovery of the species. Nevertheless, few workers have compared *Diadema* densities between habitats with replication on a broad scale. The fact that urchins are often subject to erratic population fluctuations, for instance due to variability in recruitment (Bak, 1985), and are susceptible to mortality and disease (Andrew, 1991; Forcucci, 1994; Hagen, 1995; Nagelkerken et al., 1999), indicates that replication and spatially-explicit sampling may be particularly important for discerning underlying patterns and processes. Our extensive replication, involving 70 sampling stations distributed among 28 sites and four habitat types, spread out along about 50 km of the coast of Curaçao was an attempt to thoroughly address population recovery questions for *Diadema*.

*Diadema* were recorded at 61 of 140 transects and 38 of 70 sampling stations, for a total of 2059 urchins. While recovery is clearly progressing in Curaçao as compared to post-mortality densities immediately after 1983–84 (Bak et al., 1984), recent (2002) densities nevertheless remain an order of magnitude or more lower than historical pre-mortality density estimates.

Our results further indicate that *Diadema* are preferentially found in shallow, wave-sheltered rocky habitat, and are significantly associated with coastal lagoons, whether natural or manmade. The highest densities were found particularly on rocky substrate at the entrances of such lagoonal habitat. Size-class distributions at such sites show the full range of urchin sizes, which indicate on-going recruitment and successful survival in recent years. These results contrast with 1999–2000 findings by Chiappone et al. (2002) for the Florida Keys, where recovery has been delayed and population size structure has been dominated by small urchins. Our results also suggest the preferential distribution of small individuals in wave-sheltered lagoonal habitat. However, the underlying reasons for higher densities in shallow, wave-sheltered rocky habitat remain unclear. Factors could include higher pre-settlement larval influx, settlement rates, or post-settlement survival, all potentially influenced by any of a number of biotic and abiotic factors. Further studies are needed to examine settlement, mortality, growth, as well as migration as a potential means of active post-settlement habitat selection in the different depth zones.

Predation, particularly by balistids (triggerfish), is believed to be an important determinant of urchin survival and ultimate urchin population density on the reef (Hay,



1984; Levitan, 1992). The reefs of Curaçao have been heavily overfished in recent decades (Van't Hof et al., 1995; Debrot and Sybesma, 2000; Debrot and Nagelkerken, 2000; Debrot and Criens, 2005) and densities of predatory fish are very low (Bruckner and Bruckner, 2003; Nagelkerken et al., 2005). Into the 1960s, triggerfishes still supported a small, directed sportfishery along the southwest coast of Curaçao, but the fishes have since disappeared (A. Debrot Sr., pers. comm.). Clearly, such general conditions of overfishing and concomitant low densities of *Diadema* predators, would seem to be favorable to potential *Diadema* recovery.

The fringing reef of Curaçao is quite narrow, generally spanning no more than 100–150 m from the drop-off to the shore (Bak, 1975). As a consequence, aside from lagoons opening out onto the reef, natural back-reef habitat is almost non-existent. Hence in Curaçao, the entrance areas of coastal lagoons may play a particularly important role in the gradual recovery of *Diadema*. The build-up of urchin densities at such sites may not only be critical to successful fertilization and reproductive output in this broadcast spawner (Levitan, 1991b), but may also help to trigger further settlement as evidence suggests that settlement may be positively density-dependent (Bak, 1985). In contrast to the areas surrounding the entrances of lagoons, the inner reaches of the larger natural lagoons (3–4 km<sup>2</sup> in surface area) are not likely to be important to *Diadema*. While the urchins have always occurred inside the natural lagoons of Curaçao (Teenstra, 1836), these sites have never had densities as high as on the reef (van Eys, 1976; Debrot et al., 1998).

At present, mean urchin size in Curaçao (6.8 cm) is large compared to the historical mean sizes for the island as well as elsewhere in the past, prior to the mass mortality (e.g. Randall et al., 1964, Florida: 4–6 cm; Levitan, 1988, St. John: 3–4 cm; Hunte and Younglao, 1988, Barbados: 4–5 cm). Both Carpenter (1990a) and Miller et al. (2003) further show that animals larger than 8.0 cm only rarely reached 18% of the sample population in St. Croix (as opposed to an average of 39% in our samples). Several workers have found inverse relationships between *Diadema* test diameter and population density (Levitan, 1988). In *Diadema* and other urchins, growth is known to be affected by food availability and food quality (Ebert, 1968; Levitan, 1988, 1991a; Dafni, 1992) and we surmise that the high observed test diameters in the present study may be related to the comparatively low population density.

Finally, in our survey, *T. ventricosus* was encountered in only three sampling stations. Therefore, contrary to findings by Moses and Bonem (2001) for Jamaica, our survey results provide no indication of niche expansion by *T. ventricosus* to fill the void left by *Diadema* roughly 20 yrs ago.

#### ACKNOWLEDGMENTS

We thank S. Stevens, P.-B. Broeckx, and C. Winterdaal for their generous assistance with field data collection, and L. Pors for preparing the map of Curaçao. We are grateful to the two anonymous reviewers for recommending many valuable improvements to the manuscript. This work was made possible by the Island Government of Curaçao and the Central Government of the Netherlands Antilles by means of their annual subsidy to the CARMABI Foundation.

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DATE SUBMITTED: 1 June, 2005.

DATE ACCEPTED: 23 March, 2006.

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