Anthropogenic Disturbance of Caribbean Mangrove Ecosystems: Past Impacts, Present Trends, and Future Predictions

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ABSTRACT

We review historical, current, and projected future impacts of four classes of anthropogenic disturbance—extraction, pollution, reclamation, and changing climate—on Caribbean mangrove ecosystems (mangal). These disturbances occur, respectively, at increasing spatial and temporal scales, and require increasing recovery time. Small-scale selective extraction has little system-wide effect, but regeneration is slow even on single hectare clear-cuts due to rapid soil acidification. Petroleum is the primary pollutant of Caribbean mangal, and results in tree defoliation, stand death, and loss of associated sessile and mobile animal species. Hydrocarbons persist in mangrove sediments for decades, and are correlated with increasing seedling mutation rates. Chemical, industrial, and urban wastes are associated with increased heavy metal content of seedlings, stand dic-back, reduced system-wide species richness, and higher incidence of Vibrio spp. (shellfish poisoning). Mangal has been reclaimed for urbanization, industrialization, and increasingly, for tourism. Overall, the region is losing mangrove forests at ≈1 percent per yr, although the rate is much faster on the Caribbean mainland (≈1.7% yr⁻¹) than it is on the islands (≈0.2% yr⁻¹). The region’s fisheries are declining at a similar rate, as most commercial shellfish and finfish use mangal for nurseries and/or refugia. Few Caribbean states have legislation or enforcement capabilities to protect or manage mangal, although at least 11 international treaties and conventions could be applied to conserve or sustainably use these forests. These treaties may protect riverine and basin mangal, but are likely to be moot with respect to fringing mangal, which may vanish as a consequence of global climate change. Growth enhancements of mangroves resulting from increasing atmospheric CO₂ probably will not compensate for negative effects of concomitant rises in regional sea level.

RESUMEN

Analizamos los impactos pasados, actuales y futuros de cuatro perturbaciones de origen humano: extracción, contaminación, reclamación, y cambio climático en los ecosistemas de manglares del Caribe. Estas perturbaciones ocurren, respectivamente, a escalas espaciales y temporales crecientes y requieren períodos de recuperación cada vez mayores. La extracción selectiva a pequeña escala tiene poco efecto a nivel del ecosistema, pero la generación es lenta debido a la rápida acidificación del suelo que ocurre inclusive en parcelas de una hectárea que han sido desforestadas. El petróleo es el contaminante principal de los manglares caribeños, produciendo defoliación, muerte en pie y pérdida de especies asociadas, sean fósiles o móviles. Los hidrocarburos persisten en los sedimentos de los manglares durante décadas y están correlacionados con el incremento en la tasa de mutación de las plantulas. Huy una clara asociación entre los desechos químicos, industriales y urbanos y el aumento del contenido de metales pesados en los plántones, muerte en pie, reducción del número de especies en el ecosistema y una mayor incidencia de Vibrio, que produce envenenamiento de los crustáceos. El manglar ha sido destruido debido a los procesos de urbanización, industrialización y, cada vez más, por el turismo. En total, la región está perdiendo el uno por ciento de los manglares anualmente, aunque la tasa es mucho mayor en tierra firme (≈1.7% anual) que en las islas (≈0.2% anual). La pesca regional está disminuyendo de manera similar, ya que la mayoría de los crustáceos y los peces de importancia comercial utilizan los manglares como criaderos y refugios. Pocos países caribeños poseen la legislación o la capacidad de implementación necesarias para proteger o gestionar los manglares, a pesar de que por lo menos once tratados internacionales y convenciones podrían ser aplicados para conservar o utilizar estos ecosistemas de manera sostenible. Estos tratados podrían proteger los manglares situados en cuencas y ribers, pero probablemente no sean efectivos con respecto a los manglares costeros, que podrían desaparecer como consecuencia de los cambios climáticos globales. Es probable que el crecimiento de los manglares debido a una mayor concentración de dióxido de carbono atmosférico no compense los efectos negativos del aumento simultáneo del nivel del mar.

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CARIBBEAN MANGAL NATURAL HISTORY


GEOGRAPHIC SETTING

WE CONSIDER DISTURBANCE OF MANGAL IN 32 COUNTRIES BORDERING THE CARIBBEAN LARGE MARINE ECOSYSTEM
### Table 1. Geographic information and extent of mangrove forests for insular and mainland Caribbean states.

<table>
<thead>
<tr>
<th>Country</th>
<th>Population* (× 10^3)</th>
<th>Pop. growth rate* (%)</th>
<th>Area (km²)*</th>
<th>Coastline (km)*</th>
<th>Mangrove area (km²); ca. 1980*</th>
<th>Mangrove area (km²); ca. 1990*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anguilla (U.K.)</td>
<td>7</td>
<td>0.67</td>
<td>91</td>
<td>60</td>
<td>1</td>
<td>0.3</td>
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<tr>
<td>Antigua &amp; Barbuda</td>
<td>65</td>
<td>0.59</td>
<td>440</td>
<td>152</td>
<td>9</td>
<td>1.5</td>
</tr>
<tr>
<td>Aruba (Netherlands)</td>
<td>66</td>
<td>0.65</td>
<td>193</td>
<td>69</td>
<td>NA</td>
<td>0.1</td>
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<tr>
<td>Bahamas</td>
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<td>1.57</td>
<td>13,940</td>
<td>3542</td>
<td>3086</td>
<td>1419</td>
</tr>
<tr>
<td>Barbados</td>
<td>256</td>
<td>0.21</td>
<td>430</td>
<td>97</td>
<td>NA</td>
<td>0.2</td>
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<tr>
<td>Belize</td>
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<td>2.42</td>
<td>22,960</td>
<td>386</td>
<td>730</td>
<td>783</td>
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<td>Cayman Islands (U.K.)</td>
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<td>4.33</td>
<td>260</td>
<td>160</td>
<td>114</td>
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<td>Colombia</td>
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<td>11,839,910</td>
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<td>821</td>
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<td>0.95</td>
<td>110,860</td>
<td>3735</td>
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<td>5,297</td>
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<td>750</td>
<td>148</td>
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<td>Dominican Republic</td>
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<td>1.80</td>
<td>48,730</td>
<td>1288</td>
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<td>90</td>
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<td>Grenada</td>
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<td>121</td>
<td>2</td>
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<tr>
<td>Guadeloupe (France)</td>
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<td>306</td>
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<td>Guatemala</td>
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<td>108,890</td>
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<td>27,750</td>
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<td>180</td>
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<td>112,090</td>
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<td>Jamaica</td>
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<td>10,990</td>
<td>1022</td>
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<td>106</td>
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<td>Martinique (France)</td>
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<td>1.20</td>
<td>1,100</td>
<td>290</td>
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<td>19</td>
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<tr>
<td>Montserrat (U.K.)</td>
<td>127</td>
<td>0.33</td>
<td>98</td>
<td>40</td>
<td>0.1</td>
<td>0.1</td>
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<tr>
<td>Netherlands Antilles (Neth.)</td>
<td>186</td>
<td>0.47</td>
<td>960</td>
<td>364</td>
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<td>22</td>
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<tr>
<td>Nicaragua</td>
<td>4,097</td>
<td>2.68</td>
<td>129,494</td>
<td>541</td>
<td>837</td>
<td>NA</td>
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<tr>
<td>Panamá</td>
<td>2,600</td>
<td>1.94</td>
<td>78,260</td>
<td>1160</td>
<td>204</td>
<td>59</td>
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<td>Puerto Rico (U.S.)</td>
<td>3,802</td>
<td>0.13</td>
<td>9104</td>
<td>501</td>
<td>80</td>
<td>65</td>
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<tr>
<td>St. Kitts &amp; Nevis</td>
<td>41</td>
<td>0.72</td>
<td>269</td>
<td>135</td>
<td>0.5</td>
<td>0.2</td>
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<tr>
<td>St. Lucia</td>
<td>145</td>
<td>0.52</td>
<td>620</td>
<td>158</td>
<td>3</td>
<td>1.8</td>
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<tr>
<td>St. Vincent &amp; Grenadines</td>
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<td>0.77</td>
<td>340</td>
<td>84</td>
<td>1</td>
<td>0.6</td>
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<tr>
<td>Trinidad and Tobago</td>
<td>1,328</td>
<td>1.40</td>
<td>5,130</td>
<td>362</td>
<td>40</td>
<td>71</td>
</tr>
<tr>
<td>Turks &amp; Caicos Islands (U.K.)</td>
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<td>2.69</td>
<td>430</td>
<td>389</td>
<td>NA</td>
<td>236</td>
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<tr>
<td>Virgin Islands (U.K.)</td>
<td>129</td>
<td>1.24</td>
<td>150</td>
<td>80</td>
<td>5</td>
<td>NA</td>
</tr>
<tr>
<td>Virgin Islands (U.S.)</td>
<td>98</td>
<td>-0.52</td>
<td>352</td>
<td>188</td>
<td>9.4</td>
<td>3.1</td>
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<tr>
<td>Venezuela</td>
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<td>2.16</td>
<td>912,050</td>
<td>2800</td>
<td>2500</td>
<td>NA</td>
</tr>
<tr>
<td>Subtotal: Insular</td>
<td>35,496</td>
<td>1.05</td>
<td>235,107</td>
<td>15,062</td>
<td>7798</td>
<td>762,5*</td>
</tr>
<tr>
<td>Subtotal: Mainland</td>
<td>82,424</td>
<td>2.32</td>
<td>2,553,754</td>
<td>7609</td>
<td>7046</td>
<td>5878.8*</td>
</tr>
<tr>
<td>Total: Caribbean</td>
<td>117,920</td>
<td>1.37</td>
<td>2,788,861</td>
<td>22,671</td>
<td>14,814</td>
<td>13,501.3*</td>
</tr>
</tbody>
</table>

* 1994 human population size and growth information from CIA (1995); area and coastline lengths from CIA (1995) and Ellison (in press).

* Coastline length and mangrove area data for Colombia, Costa Rica, Guatemala, Honduras, Nicaragua, and Panamá are lengths and area extent only for Caribbean coastlines.


* When 1990’s data were unavailable, 1980’s data were used to compute 1990’s regional totals of mangrove areas.

(LME: Richards & Bohnsack 1990) (Table 1). This group includes all Central American countries except El Salvador; two South American countries (Venezuela and Colombia); and 24 island states, eleven of which are still administered by colonial powers. The July 1994 regional human population was ≈ 118 × 10^6 and growing at 1.37 percent per yr (Table 1; CIA 1995). Only 30 percent of the region’s people live on the islands, but average insular population density is 6 times greater than mainland population density. Despite having < 10 percent of the region’s land area, the Caribbean islands have 66 percent of its coastline and 56 percent of its mangal (Table 1).

There are few estimates of past areal extent of Caribbean mangal. Palynological records indicate that current species composition and ranges were established by the mid-Pliocene (≈3.5 Ma: Graham 1995). Historical records rarely provide mangal area, but five estimates are available for the car-
ly- to mid-1900’s: 98 km² of mangal in Guadeloupe and 15 km² in Martinique ca. 1940 (Stehlé 1945); 243 km² in Puerto Rico prior to 1930 (Lugo & Cintrón 1975); 3,000 km² in Panamá (Caribbean and Pacific coasts combined) prior to 1960 (D’Croz 1993); and 10,000 km² in Venezuela ca. 1960 (Alarcón & Conde 1993).

Regional estimates of mangal area improved greatly between 1980 and the early 1990’s. While areal estimates of mangal ca. 1980 (Table 1) were incomplete (Saenger et al. 1983, Scott & Carbonell 1986), estimates ca. 1990 (Table 1) reflect a better combination of ground surveys and improved methods for interpreting aerial and satellite imagery (Lacerda et al. 1993). With the exceptions of Belize, Cuba, Jamaica, Netherlands Antilles, and Trinidad & Tobago, estimates ca. 1990 were lower than the ca. 1980 estimates (Table 1).

Reliable estimates of mangal loss are scant. Only ≈10 percent of Venezuelan mangal ca. 1960 remained by 1993 (Alarcón & Conde 1993). Panamá lost 41 percent of its mangrove cover between 1960 and 1988, although the majority of deforestation occurred on the Pacific coast (D’Croz 1993). Puerto Rico lost 25–33 percent of its original mangrove area between 1930 and 1960 (Heatwole 1985), and 85 percent by 1975 (Lugo & Cintrón 1975). Between 1976 and 1990, 65 percent (4,200 ha) of Grand Cayman’s mangal was reclaimed for development schemes (Bacon 1993a, Giglioli 1994). Based on the data presented in Table 1, overall mangal area in the Caribbean declined by ≈10 percent during the 1980’s. Mangal area declined by ≈17 percent on the mainland, but by only ≈2 percent on the islands. Although some of this decline may reflect significant overestimates ca. 1980 by the UNESCO and IUCN working groups (Lacerda et al. 1993), much of this decline is attributable to anthropogenic activities discussed below. The apparent rate of reduction in Caribbean mangal area throughout the 1980’s (≈1% yr⁻¹) is similar to conservative estimates of mangal loss rates due to human activities in southeast Asia (Ong 1995), as well as deforestation rates in upland tropical forests (e.g., FAO 1993a).

CLASSES OF ANTHROPOGENIC DISTURBANCE

We consider four classes of anthropogenic disturbance with respect to mangal: disturbance resulting from extractive uses of mangrove trees and mangal fauna; pollution of mangal; destruction of mangal associated with reclamation for non-extractive uses; and impacts of climate change on mangal expected to result from anthropogenically-driven increases in atmospheric CO₂ concentration and regional sea level. These four classes reflect a hierarchy of increasing spatial extent and temporal intensity of biological impacts on, and time to recovery of, disturbed mangal, although differences in frequency among disturbance classes can result in small spatial and temporal scale disturbances having larger cumulative environmental impacts (sense Preston & Bedford 1988). They also reflect a continuum of decreasing information concerning their regional extent and biological effects. These classes include four of the five disturbance categories identified by Bacon (1993b) as requiring management action in the insular Caribbean. We do not discuss separately disturbance to mangal resulting from changes in upland hydrology due to road construction, dyking, etc. Although upland hydrological changes can severely impact mangrove forests, existing data are rarely quantitative (Bacon 1975, 1993a, 1993b; Díaz & Zelwer 1985, UNEP 1994). Bacon (pers. comm.) suggests that the lack of attention to linkages between mangrove and upland forests may stem from the perception that the functional landward limit of a mangrove ecosystem is the high-water line.

EXTRACTION

WOOD AND WOOD PRODUCTS.—Caribbean mangroves have been harvested extensively for fuelwood and charcoal, poles, and saw timber (Hamilton & Snedaker 1984, Winograd 1987, Alarcón & Conde 1993, Bacon 1993a, Polanía & Mainardi 1993). Mangrove bark is now only a minor commercial source for tannins, although large expanses of Caribbean mangroves were cut over for tannin production from the early phases of European colonization until the middle of this century (Hamilton & Snedaker 1984, Alarcón & Conde 1993, Bacon 1993a). Early silvicultural trials were undertaken using L. racemosa in Puerto Rico (Wadsworth 1959), but only one commercial silvicultural operation was attempted, and subsequently failed (leaving a destroyed swamp) in Caribbean mangal: the Guarapiche Forest Reserve north of Venezuela’s Orinoco Delta (Alarcón & Conde 1993).

Small-scale, selective extraction of individual mangrove trees has little effect on mangal, but kills individual trees. Rhizophora spp. and P. rhizophorae do not resprout following cutting, while Avicennia spp., Conocarpus spp. and L. racemosa can resprout (Wadsworth 1959, Roth 1992). No data are avail-
able, however, on the relative contributions of each species to local extractive use. Clear-cutting mangroves, on scales as small as single hectares, results in rapid soil sulfide accumulation and subsequent soil acidification (Hamilton & Snedaker 1984). This can limit seeding regeneration on cleared sites and may explain declining yields of mangrove silvicultural operations in Venezuela (Alarcón & Conde 1993) and elsewhere in the world (Gong & Ong 1995), although local geomorphology can affect long-term success or failure of mangrove silvicultural operations (A. E. Lugo, pers. comm.).

Fisheries.—People have collected mangrove-associated shellfish and finfish for millennia (e.g., Sanoja 1989). Although there are few biological impacts to mangal associated with small-scale artisanal fisheries, larger commercial fisheries may disrupt mangrove-associated food webs. Conversely, large-scale extraction of mangroves for wood products or reclamation of mangroves for other purposes, including mariculture, may reduce fish yields by removing habitat for juveniles (see Reclamation, below). Documented declines in fish and prawn catches concurrent with loss of mangal have been observed in El Salvador (Daugherity 1975), India (Macintosh 1982), and throughout Asia (e.g., Martosubroto & Naamin 1977, Turner 1977), but there have been no attempts to correlate changes in fish yields with changes in mangrove cover in the Caribbean.

Paralleling the 10 percent decline in mangrove area from the early 1980’s to the early 1990’s (Table 1), the total marine fish catch also declined 10 percent in the Caribbean, exclusive of Venezuela (which accounts for 97 percent of the region’s catch and has a substantial mid-Atlantic fishery), and Guatemala, Costa Rica, and Colombia (whose fisheries are primarily Pacific) (FAO 1993b). Mangrove-associated fisheries in Venezuela are reported to be declining (Alarcón & Conde 1993), although precise figures are unavailable. This decline has occurred despite steady increases in fishing effort throughout the 1980’s (Richards & Bohnsack 1990). Between 1982 and 1991, penaeid shrimp catches in the insular Caribbean declined by 51 percent, and collection of mangrove oysters *Crassostrea rhizophorae* Guilding declined by 20 percent (FAO 1993b). There is also evidence that introduced species (e.g., *Tilapia mossambica* [Peters]) are displacing native, commercially important species in Puerto Rican mangrove estuaries (Burger et al. 1992). Without careful attention to declining habitat quality and enforcement of fishing quotas, the entire Caribbean LME fishery is expected to collapse within decades (Richards & Bohnsack 1990).

**POLLUTION**


Prior to the 1980’s, there were several notable spills that severely impacted mangroves (Lewis 1983). The *Ardea Prima* spilled ≈ 1 × 10^7 l of crude oil onto the southwest coast of Puerto Rico in July 1962. Diaz-Pferrer (1962) reported that oil accumulated among mangrove roots, killing large numbers of invertebrates, fish, and turtles. This same area was affected by the *Zoocrotonis* spill in August 1973 (7.4 × 10^3 l of crude oil). Hydrocarbon residues from both of these spills were still detectable at Bahía Suiyui in soil cores sampled in the late 1980’s (Corredor et al. 1990). Mutagenesis of *R. mangle* seedlings resulting from sediment hydrocarbons has been observed there and throughout the Caribbean (Klekowskii et al. 1994a). Rützler & Sterrer (1970) documented massive mortalities of mangrove trees, roots, and associated fauna following the *Wittwater* wreck in December 1968 (4 × 10^6 l of diesel oil and heavy crude oil) off Caleta Island, Panamá. This mangal again was affected severely by the 1986 spill of 1.5 × 10^7 l of medium-weight crude oil from Refinería Panamá (Keller & Jackson 1993). Five ha of mangroves on St. Croix, U.S. Virgin Islands were completely destroyed by the *Santa Augusta* spill in 1971 (1.3 × 10^7 l of crude oil). No recovery of the mangroves was observed there 7 yrs later (Getter et al. 1985).

There were 24–31 oil spills near Caribbean coastlines in the 1980’s (Burns et al. 1993, Lacerda et al. 1993). The best available data on effects of oil spills on mangrove flora, fauna, and ecosystem processes come from before-and-after studies conducted at the Smithsonian Tropical Research Institute following the 1986 spill at Caleta, Panamá (Keller & Jackson 1993). Consistent with previous spills, massive tree defoliation, followed by seedling, sapling, and tree death occurred rapidly (Garrity et al. 1994). Associated sessile marine fauna suffered more severe immediate and long-term effects than mobile species (Levings & Garrity 1994). Re-
duction of *R. mangle* prop root density by 33–74 percent (Garrity et al. 1994) dramatically reduced available habitat for sessile and motile invertebrates (Levings & Garrity 1994). Data from Puerto Rico dating from the 1970’s and 1980’s showed that oil persists for decades in mangrove sediments (Corredor et al. 1990). Similarly, there was continual release of toxic hydrocarbon residues from the sediment back into the water column and surrounding ecosystems at Galeta that continues to result in lethal and sub-lethal effects on marine flora and fauna (Burns et al. 1993, Burns & Yelle-Simmons 1994, Levings et al. 1994). The consensus of the Galeta study was that a minimum of 20 yrs is probably required for mangal to recover from catastrophic oil spills (Burns et al. 1993).

Restoration of oil-impacted mangal in the Caribbean has been rarely attempted and has succeeded only marginally (Getter et al. 1984). Long residence times of oil in mangrove sediments and attendant effects on transplanted seedlings, rapid erosion of deforested peat, rapid increases in soil sulfide levels, and lack of resources for long-term (> 10 yr) maintenance of restored areas all have contributed to failures of mangrove restoration projects (Getter et al. 1984). Use of mangroves as indicators of hydrocarbon pollutant levels (Klekowski et al. 1994b), and detection of these pollutants in mangrove estuaries far from refinery complexes (e.g., Bernard et al. 1995) indicate that the Caribbean may have higher overall levels of hydrocarbons than suspected previously (Atwood et al. 1987). These conditions will make mangal restoration more difficult.

Continued dependency of most Caribbean states on imported oil for energy needs (Hinrichsen 1981), the existence of large refinery and transshipment complexes throughout the region (Burns et al. 1993), and the approximately 7 × 10^7 tons of oil transported annually through the Panamá Canal (D’Croz 1993) strongly suggest that petroleum will continue to be the major pollutant impacting Caribbean mangal. Unfortunately, it is difficult to anticipate where future spills will occur. Maps of high risk zones for future spills produced in the early 1980’s (Rodriguez 1981) were poor predictors of locations and types of subsequent spills.

**Thermal pollution.**—Thermal pollution from power-plant cooling systems was identified as a hazard to mangal flora and fauna by Kolehmainen et al. (1974) and Canoy (1975). In the tropics, cooling towers are impractical, and condensers are cooled dissipatively using local water bodies (Kolehmainen et al. 1974). The biological effects of thermal pollution (water temperatures 35–40°C) on mangroves include: reductions in leaf area and leaf area index; achlorophyll; reduced net photosynthesis; and increased photospiration (Kolehmainen et al. 1974, Canoy 1975). High mortality of mangroves close to a power plant at Guaynilla, Puerto Rico, was caused by sediment erosion resulting from increased current flow associated with the outflow pipe. Water temperature increases alone (> 31°C) caused species richness of sessile and mobile marine invertebrates to decline by 50–90 percent and Shannon-Weiner diversity (*H*) to decline by 75 percent (Kolehmainen et al. 1974). Additional losses of marine invertebrate species can also occur due to habitat (tree) loss following bank erosion and collapse. There are no recent studies on thermal pollution impacts to mangal elsewhere in the Caribbean, despite repeated identification of this as a research priority (e.g., Linden & Jernelov 1980). Because thermal pollution is a continuous stress on mangal, it is difficult to imagine that such forests can recover from thermal effects until a power plant is decommissioned.

**Other pollutants.**—Little attention has been paid to other pollutants of Caribbean mangal (Odum & Johannes 1975). While stressing that petroleum was the primary pollutant throughout the Caribbean, Rodriguez (1981) identified four other locally or regionally important pollutants: mercury (Colombia, Cuba; see also Winograd [1987]); mine tailings and compounds (e.g., sodium hydroxide) associated with bauxite mines (Cuba, Jamaica, and the U.S. Virgin Islands; see also Odum & Johannes [1975]); sewage (Cuba, Haiti, Jamaica, Puerto Rico, Venezuela; see also Montgomery & Price [1979], Canestri & Ruiz [1973]); and urban runoff (Cuba, Dominican Republic). More recently, pesticide runoff, heavy metals from industrial activities, and domestic sewage in Belize, Colombia, Cuba, Jamaica, Nicaragua, Puerto Rico, and Trinidad & Tobago (Winograd 1987, Karz 1989, Alvarez-León 1993, Bacon 1993a, Goodbody 1993, Padrón et al. 1993, Polanía 1993, Polanía & Mainardi 1993); solid waste dumping throughout the Lesser Antilles, Jamaica, and Trinidad & Tobago (Bacon 1993a), and dredge spoil dumping in Antigua (Bacon 1993c) again have been identified as pollutant hazards in Caribbean mangal.

Low rates of primary production by Cuban mangroves have been attributed to pesticide contamination (Sansón & Rueda 1982). Mangrove ar-
Reclamation is defined as "mak[ing] (marshland, for example) suitable for cultivation or habitation, as by filling, irrigating, or fertilizing; or to procure (usable substances) from refuse or waste products" (American Heritage Dictionary of the English Language 1978). This definition implies that mangal, like other swamp lands, is without value, except as land to be converted to other uses. Despite apparent improvements in attitudes concerning wetlands observable in this hemisphere as early as 1850 (Miller 1989), contemporary recognition of the economic value of mangal for fisheries, coastal stabilization, and ecotourism (e.g., Bacon 1992, Lugo & Bayle 1992), and a panoply of legislation (e.g., Price et al. 1992, Alarcón & Conde 1993, Alvarez-León 1993, D’Croz 1993, Poliana & Mainardi 1993), Caribbean mangal continues to be reclaimed. There are few reliable estimates of reclaimed mangal area, other than those lumped within general loss of mangrove cover. Past reclamation efforts were observed but rarely catalogued (Canestri & Ruiz 1973, Bacon 1975, 1993b, Saenger et al. 1983, Winograd 1987), and current reclamation schemes often are based on piecemeal permits or poorly-regulated government concessions (e.g., Sebastiani et al. 1994).

Indigenous peoples reclaimed mangal for shifting agriculture (Bloom et al. 1983, Sanoja 1989), but these areas were small enough, and land-use brief enough, for mangrove vegetation to recover when environmental conditions were favorable (Sanoja 1989). Large areas of Caribbean mangroves were reclaimed to develop large cities and industrial complexes in Venezuela, Colombia, Puerto Rico, and Jamaica (Canestri & Ruiz 1973, Hudson 1983, Saenger et al. 1983, Winograd 1987, Alarcón & Conde 1993, Alvarez-León 1993, Bacon 1993a). Spectacular examples include the development of Cartagena, Colombia, on a reclaimed mangrove swamp (Alvarez-León 1993); the almost complete deforestation since 1950 of the mangroves surrounding Lake Maracaibo, Venezuela for tourism and oil refineries (Alarcón & Conde 1993); and the destruction of mangal in the Parque Nacional Laguna Tacarigua, Venezuela, through deforestation, dredging, urbanization, and changes in local and upland hydrology (Díaz & Zelwer 1985).

Tourism.—Reclamation efforts in the last two decades derive primarily from the burgeoning tourist industry (Beekhuis 1981, Hudson 1983, Wilson 1987, Alarcón & Conde 1993, Bacon 1993a). Mangal has been filled for resort and marina development, golf courses, road construction, airport expansion, insect control, and solid-waste disposal. Use of herbicides, such as 2,4-D, in such reclamation schemes has been shown to have persistent effects on mangrove growth and production (Teas 1976, Díaz & Zelwer 1985). Even where mangroves nominally are protected, it is relatively easy to obtain a permit to clear trees for development projects. Egregious examples include: the loss, between 1977 and 1990 of ≈97 percent of all wet-
lands on Grand Cayman for urban and tourist developments (Bacon 1993a); construction of tourist resorts and associated coastal developments on > 50 percent of the mangroves of Barbados (Bacon 1993a); and clearing and filling, for summer home construction, of a section of a 100 ha mangrove island in Belize that has been used for 20 yrs by the Smithsonian Institution as a field site for studies of mangrove ecology and systematics (A. M. Ellison & E. J. Farnsworth, pers. obs.). The permit for the latter was issued despite the Government’s stated intent to include the entire island within a proposed marine park.

Although mangal most often is cleared to construct tourist resorts, there are a few instances where mangroves themselves are promoted for tourism (Bacon 1987, Barzetti 1993). The Caroni swamp in Trinidad is known world-wide for its resident, accessible breeding colony of scarlet ibis (Eudocimus ruber L.) within a 37 km² mangal. Ecotourism at Caroni directly contributes ~U.S. $120,000 annually to the local economy (N. Gyan, Acting Director of Wildlife Section, Trinidad Government Forestry Division, pers. comm. to P. R. Bacon, 1995), although this may undervalue the overall contribution of this mangal to the local economy by ~50 percent (Bacon 1992, and pers. comm.). Visitors to Morrocoy National Park, Venezuela, can also view scarlet ibis on boat trips through mangrove channels (A. M. Ellison & E. J. Farnsworth, pers. obs.), and spend ~U.S. $7 million per yr there (Dugan 1990). Watching manatees (Trichechus manatus L.) and sport-fishing in mangal are promoted in Belize (A. M. Ellison & E. J. Farnsworth, pers. obs.), although there are no reliable data on either number of participants or income derived. While mangroves may provide some income to local tour operators, and they are viewed as a tourist resource ripe for development (Bacon 1987, Barzetti 1993), we have observed significant bank erosion and fringing tree collapse resulting from boat wakes (E. J. Farnsworth & A. M. Ellison, pers. obs.) that may limit the long-term sustainability of mangrove ecotourism. Similarly, demands by tourists for other amenities may increase their impact on surrounding wetlands. For example, tourists use at least seven times as much water and power per capita as residents in the insular Caribbean (Beekhuis 1981). Populations of bioluminescent dinoflagellates collapsed during construction (never completed) of a resort complex associated with promotion of the Phosphorescent Lagoon in Jamaica (Hudson 1983). The dinofla-
gellate population has not recovered, and the lagoon is no longer a major tourist attraction.

**AQUACULTURE.**—Although widespread in Asian and Ecuadorian mangal, construction of fish, shrimp, and salt ponds in mangal is relatively uncommon in the Caribbean. Relatively small areas of mangal (~2,054 ha between 1984 and 1991) have been converted to shrimp ponds adjacent to other reclamation projects in Colombia (Alvarez-León 1993). The governments of Belize and Venezuela have attempted to locate shrimp ponds outside of mangrove areas that have been recognized as key fishing grounds (Price et al. 1992, Sebastiáni et al. 1994). Fish and shrimp ponds have been constructed in or near Jamaican mangal, while salt ponds were constructed and subsequently abandoned in mangal on the Turks & Caicos Islands and St. Kitts (Bacon 1993a).

**EFFECTS OF CLIMATE CHANGE**

The rubric of ‘climate change’ encompasses a suite of climatic, atmospheric and sea-level changes, already underway and accelerating, that will alter dramatically Caribbean mangal. Several speculative reviews recently have discussed the implications of climate change for global mangrove productivity and persistence (Ellison 1994, UNEP 1994, Field 1995), prioritized research questions (Davis et al. 1994), and presented hypotheses regarding mangrove ecosystem response (UNEP 1994, Snedaker 1995).

Observed increases in mean atmospheric temperature are probably caused by rising levels of atmospheric CO₂ and CH₄ resulting from fossil fuel combustion and deforestation (Wigley & Raper 1992). However, predicting the magnitude of regional temperature change is complicated by interannual variability and interactions among climatic and anthropogenic forcing factors. Mean global air temperature at sea level has risen approximately 0.5°C since 1850 (0.003°C yr⁻¹; Houghton et al. 1990). In contrast, since 1941, mean annual temperature has increased twice as fast in the insular Caribbean (0.006–0.048°C yr⁻¹), but decreased 0.019–0.066°C per yr on the mainland (Granger 1991). Overall, mean monthly temperatures in the Caribbean region are expected to increase 1.0–2.3°C within the next 50 yrs from a current mean monthly temperature of ~25°C (Hanson & Maul 1989). Because mean air temperatures would have to exceed ~38°C before significant leaf drop or mass tree mortality ensues, and mangrove fauna
TABLE 2.  ESTIMATED sea level change, and mangrove forest types (sensu Lugo & Snedaker 1974) and areal extent associated with localities for which sea level change estimates are available. Mangrove areas (ha) are reported conservatively for known swamps occurring within a 30-km radius of the site for which sea level change was determined. Data on sea level change are estimates of rates inclusive of the past 4000 yr of relative Holocene stabilization only. Methods of estimating sea level change vary, and include $^{14}$C dating of mangrove peat samples (Maul & Martin 1993), >10 yr tide gauge readings (Aubrey et al. 1988, Granger 1991, Burton 1994), and studies of Holocene reef development in the Acropora palmata framework of the western Atlantic (Lighty et al. 1982).

<table>
<thead>
<tr>
<th>Country—Location</th>
<th>Riverine</th>
<th>Basin</th>
<th>Lagoon/fringe</th>
<th>Coral</th>
<th>sea level change (mm·yr$^{-1}$)</th>
</tr>
</thead>
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<td>$8^a$</td>
<td>$122^a$</td>
<td>0</td>
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<td>10$^a$</td>
<td>0</td>
<td>+3.9$^i$</td>
</tr>
</tbody>
</table>

$a$ Bacon (1993a); $b$ Granger (1991); $c$ Scott & Carbonell (1986); $d$ Aubrey et al. (1988); $e$ Alvarez-León (1993); $f$ Burton (1994); $g$ Lugo & Brown (1988); $h$ Digerfeldt & Hendry (1987); $i$ Lighty et al. (1982); $j$ Pirazzoli (1986); $k$ Garrity et al. (1994).

will not suffer until air or water temperatures exceed 31°C, atmospheric warming may not directly impact Caribbean mangal in the near future. However, other facets of climate change will have more significant effects on Caribbean mangal.

Higher atmospheric temperatures will be associated with soil warming, altered weather patterns, and sea level rise, all of which could profoundly influence mangrove growth and mortality. Implications of soil warming—increased soil respiration, peat decomposition, CH$_4$ or H$_2$S release, and root turnover—have not been explored hypothetically or experimentally for mangal. Predicting future trends in Caribbean weather patterns and hurricane dynamics is not yet possible; models disagree as to whether rainfall or storm frequency and intensity will increase or decrease (reviewed by Granger 1991). Improving such predictions is critical, as present-day mangal physiography may be controlled by frequency and intensity of hurricanes within the Caribbean hurricane belt (Brunt & Burton 1994; Smith et al. 1994).

In contrast, there has been much published discussion on sea level rise (SLR) in the Caribbean. Thermal expansion of oceans, and melting of ice caps and alpine glaciers, are predicted to contribute to a substantial global rise in sea level, although the magnitude of this increase will vary regionally. Estimates of recent relative SLR around the Caribbean basin (Table 2) range from −2.3 mm per yr at Barahona, Dominican Republic, to +9.3 mm per yr at Port-au-Prince, Haiti (Aubrey et al. 1988), with a mean region-wide increase of 2.3 ± 2.6 mm per yr (sd, $N = 22$). Such local variability may result from tectonic activity and subsidence near plate boundaries (Gornitz et al. 1982, Aubrey et al. 1988). Different estimation methods (e.g., $^{14}$C, $^{137}$Cs, or $^{210}$Pb-dating of peat cores; tide gauge readings) employ disparate assumptions and produce SLR curves for very different time scales.
(Lynch et al. 1989). Consistent, long-term monitoring must be applied systematically around the Caribbean to produce a coherent regional profile of ongoing SLR.

The ramifications of rising sea level for mangrove survival and community structure also are debated. Peat stratigraphy analyses from Bermuda (Ellison & Stoddart 1991, Ellison 1993) and Grand Cayman Island (Woodroffe 1982) indicate a landward migration or die-off of fringing mangroves during periods of Holocene transgression (= relative sea level rise) exceeding 0.8–0.9 mm per yr. Snedaker et al. (1994) and Maul & Martin (1993) contend that mangroves have expanded near Key West, Florida during transgression episodes of 2.3 mm per yr. Parkinson et al. (1994) project that mangroves on Caribbean carbonate platforms will be submerged if sea level rise exceeds 8 mm per yr. Regardless of their past or ideal physiological and ecological capacity to migrate as sea levels change, future mangal range shifts will be constrained severely by highways, urbanization, and other human impediments.

Local sedimentation regimes can offset some fraction of sea level rise (Pernetta 1993). Areas with high alluvial or carbonate inputs may accrete at rates matching transgressions for this time, while erosive and low-lying environments will be particularly vulnerable. Long-term studies of field mangrove populations support this conclusion. Stem growth, and leaf and meristem production of R. mangle saplings on a slowly accreting cay in Belize were significantly lower relative to populations at rapidly-accreting cays (Ellison & Farnsworth in press). Several species of mangrove seedlings grown in artificially flooded lab trials (Naidoo 1985, Farnsworth et al. 1995, Hovenden et al. 1995) show increased foliar sodium, and depressed water potentials, stomatal conductance, photosynthesis, oxygen transport through aerenchyma, and growth following prolonged inundation and soil anaerobiosis. Bacon (1994) reviewed methods for evaluating the risks of sea-level rise to different geomorphological types (sensu Lugo & Snedaker 1974) of Caribbean mangrove forests. Up to 54,900 ha (35%) of Caribbean fringe or island mangal in this sub-region may be affected imminently by rising sea level (Table 2), while riverine systems (= 90,000 ha or 57% of areal extent) may not shrink as quickly. Although total extent of mangal in the Caribbean is known better than ever before (Table 1), precise areal extents of different mangrove types throughout the Caribbean, their proximity to human settlements, and interspecific differences in flooding responses are needed to comprehend the magnitude of potential community change or loss.

Elevated concentrations of atmospheric CO₂ will influence mangrove growth in ways that may ameliorate or compound negative effects of rising tides. Physiological experiments predict that photosynthetic rates and water-use efficiency of paleotropical mangrove species will increase with increasing CO₂ (Ball & Munns 1992), a response typical of many carbon-limited C₃ species. *Rhizophora mangle* shows dramatic enhancement of stem elongation, meristem and leaf production, photosynthetic rates, stem lignification, and aerial root production when grown in twice-ambient CO₂ (Farnsworth et al. 1995). However, growth enhancements in elevated CO₂ rarely compensate for growth decreases observed under flooded conditions (Farnsworth et al. 1995). Additional long-term, controlled factorial studies of temperature, CO₂ and tidal interactions, interspecific comparisons across ontogeny, and field studies in a range of ecosystem types are needed to assess the potential effects of rising CO₂ and sea level on neotropical mangroves. Scaling up from responses of individual mangrove species to mangal-wide changes expected under climate change scenarios remains challenging. It is still impossible to predict if mangal will become a source or a sink for atmospheric CO₂ as air temperatures rise (Twilley et al. 1992, Ong 1993).

**CONSERVATION AND PROTECTION OF CARIBBEAN MANGAL**

In most insular Caribbean countries, there is no legislation specifically covering mangrove management (Bacon 1993a, Padrón et al. 1993), and we predict continued rapid loss of mangal. Because most mangal occurs on public (state-owned) lands, laws related to protection of wildlife (especially birds), forest management, and control of sewage disposal could be used in mangrove conservation programs. There has been some progress in creating protected areas that include mangrove stands (Barzetti 1993, IUCN 1993b, Giglioli 1994). Mainland countries nominally regulate mangrove cutting more strictly (Alarcón & Conde 1993, Ellison, in press). Government-issued permits are required to cut a single mangrove tree in Belize, Costa Rica, and Nicaragua (Price et al. 1992, Polanía 1993, Polanía & Mainardi 1993), although enforcement is virtually non-existent. Use of mangrove forest resources on the Caribbean coast of Colombia is completely prohibited (Alvarez-León 1993).
TABLE 3. CARIBBEAN states that have ratified (R) or signed but not yet ratified (S) international environmental agreements that could apply to conservation and management of mangroves. Signatory status from Sand (1992), CIA (1995), and D. Peck (Ramsar Bureau, pers. comm.). The signatory status of the Caribbean states that are not independent is governed by the signatory status of the colonial (administrative) power (see Table 1).

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<thead>
<tr>
<th>Country</th>
<th>NPWP</th>
<th>Ramsar</th>
<th>WCNH</th>
<th>MPD</th>
<th>CITES</th>
<th>MARPOL</th>
<th>LOS</th>
<th>ITTA</th>
<th>CAR</th>
<th>HAZ</th>
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There are at least 11 international treaties and conventions that could be used to protect or sustainably manage Caribbean mangal (see Table 3 for abbreviations and signatory status). Six international treaties could be used to protect mangal and maintain it for indigenous use and sensitive development of ecotourism if additional Caribbean nations would sign and ratify them: the NPWP, Ramsar, WCNH, CITES, Cartagena and Biodiversity Conventions. Four international agreements could be used to limit pollution in the Caribbean: MPD, MARPOL, LOS, and HAZ. The Cartagena Convention (CARE) has protocols both for protection of mangal and for cooperative responses to oil spills. Guidelines for oil exploration and production that explicitly account for the fragility of mangal have been promulgated recently (IUCN 1993a). The ITTA applies to mangrove forest resources, but few Caribbean countries are signatories, and application of Tropical Forestry Action Plans to Caribbean mangal is sparse (Lugo & Bayle 1992).

General principles derived from other Caribbean ecosystems, especially upland wet forests and coral reefs, are not strictly applicable to predicting mangrove resiliency to, and recovery from anthropogenic disturbance. Three ecological differences pertain. First, Caribbean mangal includes at most seven tree species, and in most areas, only four. These few ‘structural’ species (sensu Huston 1994) are the habitat for a far more diverse ‘interstitial’ species assemblage. Thus, loss of a single tree species reverberates through the system, but the ‘ecosystem functions’ of each mangrove species have not been quantified in ways that can inform management decisions about conserving forests or identifying ‘redundant’ species (Twilley et al., in press). Second, these intertidal systems are linked hydrodynamically to both upstream terrestrial ecosystems and downstream marine communities (e.g., Twilley et al. 1992, Wolanski 1992). Productivity and disturbance of upland communities strongly affect dynamics of downstream mangal, seagrass beds and coral reefs, while coral reefs and seagrass beds buffer mangrove forests from wave action (Ogden & Gladfelter 1983, Birkeland 1987). Finally, although recolonization of disturbed areas is limited in mangal, as in other ecosystems, by propagule availability, physiological tolerances, and seed predation (e.g., Smith et al. 1989, Ellison & Farnsworth 1993, McKee 1995, Farnsworth & Ellison, in press), the rapid deterioration and acidification of mangrove soils following disturbance constrains restoration efforts and demands rapid responses.

With the exception of projected climate change effects, the consequences to mangal of anthropogenic stressors are amply documented and well appreciated by biologists, managers, and local communities using mangrove resources. Amelioration of anthropogenic disturbances to Caribbean mangal requires a diversity of strategies that account for the different spatial and temporal scales on which different disturbance classes operate. Laws prohibiting extraction and cutting of small or declining mangrove stands must be enforced, while management plans that encourage participation of local residents and land managers must be simultaneously developed to prevent unsustainable exploitation of larger mangrove forests in the near term. Although mangal requires several decades to recover from oil spills, region-wide adoption of, and adherence to, international protocols for use and transport of petroleum and other hazardous materials can limit future chemical pollution of mangal in the region. Development of renewable energy sources (e.g., solar, wind, and tidal) could decrease regional dependence on fossil fuels and reduce the impact of energy-related pollutants on mangal within the next 50–100 yrs. Continued work on changing individual and cultural attitudes regarding the value of wetlands, and consistent regulation of the regional tourism industry may reduce future efforts to ‘reclaim’ mangal. In concert with actions to limit deforestation and pollution, restoration of areas where reclamation was unsuccessful could result in a long-term increase of mangal area throughout the Caribbean. Finally, the coming century will witness increasing atmospheric CO₂ concentration, air and water temperatures, and rapidly changing sea levels in the Caribbean region. Future distribution of mangrove ecosystems and their responses to these widespread, chronic environmental changes depend heavily on how well mangroves are managed today.

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