Ecological Effects of a Major Oil Spill on Panamanian Coastal Marine Communities

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In 1986 more than 8 million liters of crude oil spilled into a complex region of mangroves, seagrasses, and coral reefs just east of the Caribbean entrance to the Panama Canal. This was the largest recorded spill into coastal habitats in the tropical Americas. Many populations of plants and animals in both oiled and unoiled sites had been studied previously, thereby providing an unprecedented measure of ecological variation before the spill. Documentation of the spread of oil and its biological effects begun immediately. Intertidal mangroves, seagrasses, algae, and associated invertebrates were covered by oil and died soon after. More surprisingly, there was also extensive mortality of shallow subtidal reef corals and infauna of seagrass beds. After 1.5 years only some organisms in areas exposed to the open sea have recovered.

OIL POLLUTION IN THE SEA HAS BEEN A MAJOR ENVIRONmental problem for several decades, but we know remarkably little about the effects of oil on natural populations and communities (*1*). Uptake of oil and physiological responses of organisms have been investigated in the laboratory or field, sometimes coupled with short-term monitoring of communities and of amounts of oil in water, sediments, and organisms (*2, 3*). Investigations of oil spills generally commence after any initial damage has occurred, and baseline ecological data are usually lacking. This approach precludes measurement of the effect of oil spills because there usually is no knowledge of natural ecological variation (*2*). Such was the case in 1968 following the release of 3.2 million liters of oil from the wreck of the *Witwater* near the Galeta Marine Laboratory (Smithsonian Tropical Research Institute) in Panama (*4, 5*). Another even larger spill occurred in the same region in 1986 (*6*) (Fig. 1). In this article, we describe the types and extent of damage to coastal populations and communities in the first 1.5 years after the 1986 spill, and contrast our findings with earlier work and widely held views regarding the effects of oil on tropical coastal communities.

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Our study is unique for two reasons. First, many of the habitats damaged by oil have been investigated since the *Witwater* spill 18 years before. Results of this research have been published in more than 130 articles, and the flora and fauna are well known taxonomically (*7*). Detailed time-series data on the physical environment and biota (*8, 9*) provide a measure of natural variation before the more recent oil spill against which subsequent events can be compared. Second, observations of the effects of the spill began as oil was coming ashore. Of additional importance, the coastal environments (including seagrass beds, mangroves, algal flats, and coral reefs) and most of the species affected are similar to those throughout the

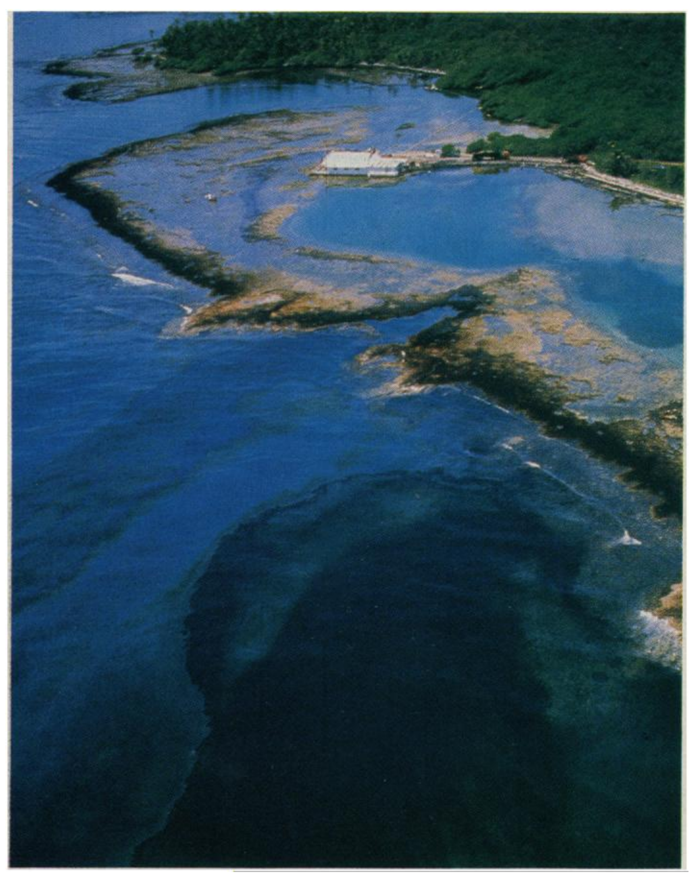

Fig. 1. Crude oil washing onto Galeta Reef on the Caribbean coast of Panama, site of a 15-year-old environmental monitoring program at the Galeta Marine Laboratory, Smithsonian Tropical Research Institute (white building on reef platform). [Photo by C. Hansen]

Caribbean, Gulf of Mexico, and southeastern United States (*10*). Thus our observations are relevant to assessment of potential biological effects of pollution in several areas where extraction or refining of oil is ongoing on planned (*11*).

On 27 April 1986 at least 8 million liters of medium-weight crude oil (*12*) spilled from a ruptured storage tank into the sea on the Caribbean coast of Panama (*6*) (Fig. 2). This is the greatest amount of oil spilled directly into a sheltered coastal habitat in the tropical Americas (*3, 13*). For 6 days, onshore winds held the oil within Bahia Cativa adjacent to the refinery (Fig. 2), but runoff from rains and shifting winds then flushed the oil out to sea. At this time dispersant was sprayed on slicks in the mouth of Bahia las Minas and offshore (*14*). By 15 May, the oil had swept across fringing reefs and entered mangrove forests, small estuaries, and sand beaches within 10 km of the refinery.

Table 1. Comparison of visual assessment of amount of oiling on four coral reefs [ranked heavy (H), moderate (M), and none (N)] with results of gas chromatographic (GC) analyses of saturated hydrocarbons in coral tissues and by ultraviolet fluorescence (UVF) analyses of aromatic hydrocarbon fractions. Oil content by GC was conservatively estimated as the unresolved hydrocarbons in the elution range for alkanes containing 12 to 36 carbon atoms. Oil units by UVF were determined by comparison with the spilled oil. Values are expressed as micrograms per milligram of coral tissue (lipid or protein) and are the mean and standard deviation of triplicate analyses. Reefs are listed from west to east (Fig. 2); Payardi West is adjacent to the refinery and Palina West is just west of Isla Grande.

Reef	Oil-ing	Petroleum hydrocarbons in coral tissue (μg) per milligram of		
		Protein by GC	Lipid by GC	Lipid by UVF
Galeta Channel	H	0.71 ± 0.11	2.7 ± 1.1	5.0 ± 3.4
Payardi West	H	0.78 ± 0.17	4.5 ± 0.8	25.5 ± 6.0
Naranjos South	M	0.32 ± 0.05	1.4 ± 0.1	1.3 ± 0.3
Palina West	N	0.22 ± 0.15	1.0 ± 0.6	0.1 ± 0.1

Plants and animals died wherever they came in contact with oil. However, the types and magnitude of effects varied greatly with coastal topography and location, and among habitats and taxa. Such complex effects are similar to those of powerful hurricanes on Jamaican and Australian coral reefs (*15*). We first consider the spatial pattern of the spill and its effects in different environments, including variations in effects on different taxa. We then describe the patterns of responses of different organisms that discuss prospects for recovery.

Spatial Distribution of Oil Among Habitats

The distribution of oil within 2 months of the spill was visually assessed by aerial surveys between Rio Chagres, 27 km west of the refinery, and Punta San Blas, 98 km to the east, and by boat and foot from Rio Chagres to Nombre de Dios (*16*) (Fig. 2). No oil was observed on shorelines east of Isla Grande, and only a few patches were observed east of Maria Chiquita and west of the Panama Canal entrance. Heavy oiling occurred along most of the coast between Isla Margarita and Islas Naranjos (Fig. 2). The straight-line distance between these two points is 11 km, but the labyrinthine shoreline is at least 82 km long and contains about 16 km^2 of mangroves and 8 km^2 of intertidal reef flats and subtidal reefs (*17*). Within this area, the only large unoiled areas 2 months after the spill were two mangrove lagoons that are isolated from open water by narrow channels (hatched areas in Fig. 2). Oil slicks ranging from a metallic sheen to brown patches are still common between Punta Muerto and Galeta, especially after heavy rains flush oil from mangroves and from the landfill beneath the refinery (*18*).

Within similar habitats, distance from the refinery, direction of oil movement, and water depth apparently caused considerable variation in the degree of oiling even in the most polluted region. Amounts of oil observed on or in sediments of seagrass beds, mangroves, and over reef flats were highest within a few kilometers of the refinery (Punta Muerto to Largo Remo and Punta Galeta)

Table 2. Population changes of gonoactylid stomatopods on four reef flats. Data for all years are from August to September. Densities and growth are given as the means ± SE.

Measure	Year	Location: Isla Margarita	Location: Largo Remo West	Location: Mina	Location: Largo Remo North
Oiling		Light*	Light*	Heavy†	Heavy‡
Density/m^2	1986	9.9 ± 1.5§	6.1 ± 1.5	4.9 ± 0.9	1.8 ± 0.4
Individuals ≥40 mm (%)	1986	9	20	3	4
Injured animals ≥35 mm (%)	1980	25			
	1981	31	36	35	20
	1982		21‖		
	1983			23	
	1986	38	38	11¶	10**
Growth†† (%)	1979–1983	6.3 ± 1.2		6.1 ± 1.1	
	1986	6.3 ± 1.2		9.4 ± 1.2	

*No oil evident on surface or in sediments and *Thalassia* appeared healthy. †Abundant oil on and in sediments and on adjacent mangroves. *Thalassia* leaves shed, but rhizomes appeared to be alive. ‡Entire *Thalassia* bed is gone, no leaves are present and the rhizomes are dead. §Mean density here prior to the spill was 9.6 ± 0.59; no comparable data on densities are available for the other sites. ‖Significantly different from 1981 to 1986, *G* test, $P < 0.01$. ¶Significantly different from previous years, *G* test, $P < 0.01$. **Significantly different from 1980, *G* test, $P < 0.05$. ††Values pooled for the two heavily oiled and lightly oiled sites. Analysis of covariance showed that slopes of percent growth against body length were not significantly different among the four groups of data ($P > 0.05$), but that mean growth adjusted for elevation did differ significantly ($P < 0.001$). There was a significant increase in adjusted mean growth at the heavily oiled sites after the spill compared to growth at these sites before the spill; there were no significant differences in adjusted mean growth at the lightly oiled sites before and after the spill, and between the lightly and heavily oiled sites prior to the spill.

and much less at Islas Naranjos and Isla Margarita (*19*). Moreover, similar differences occurred over just a few hundred meters between shores directly exposed to or sheltered from the wind-driven oil (*20*). On an even smaller scale, extreme low tides between 10 and 19 May (*6, 21*) caused oil to accumulate along the seaward borders of reef flats, whereas just shoreward much less oil contacted the substratum. In general, intertidal habitats just above mean low water were the most heavily oiled, including mangrove roots and sedi-

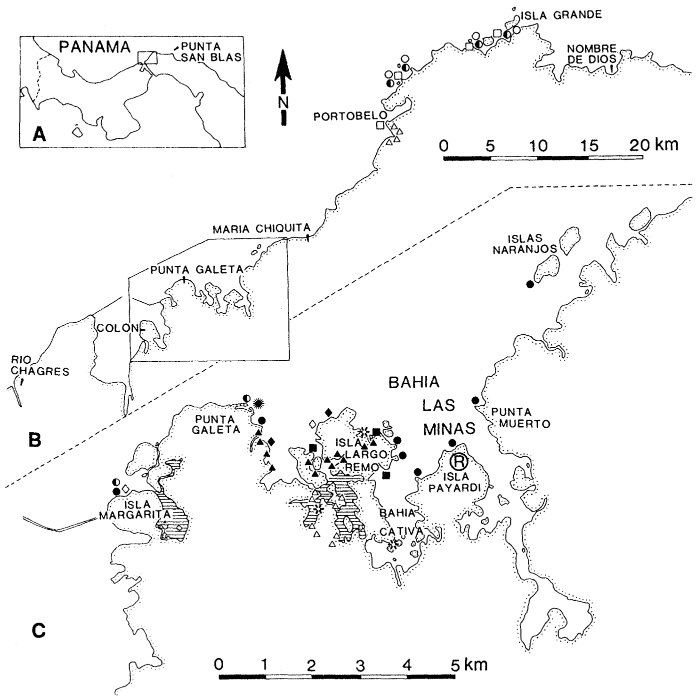

Fig. 2. Region of the Republic of Panama affected by the 27 April 1986 oil spill, shown as increasing enlargements (A to C). (**A**) Location within Panama, just east of the Caribbean entrance to the Panama Canal. (**B**) The boxed area includes the most heavily oiled coastal habitats. Punta Galeta, inside the boxed area, is 9°24′N, 79°52′W. Lightly oiled and unoiled study sites are east of Bahia las Minas, near Portobelo and Isla Grande. (**C**) Detail of the most heavily oiled area and location of study sites. Encircled "R" on Isla Payardi marks the refinery where the oil spill occurred. Horizontal hatching denotes embayments where little oil penetrated. Symbols for types of study sites (open symbols, unoiled or lightly oiled sites; filled symbols, oiled sites): △, mangrove root; □, seagrass bed; ○, subtidal coral reef, data collected only after the oil spill; ◐, subtidal coral reef, data collected both before and after the oil spill: the four sites near Portobelo and Isla Grande were not oiled, the site at Isla Margarita was moderately oiled, and the site at Punta Galeta was heavily oiled; ◇, reef-flat stomatopods; multirayed star, reef flat community, Punta Galeta; six-rayed symbol, mangrove forest.

Fig. 3. Organisms and habitats affected by the April 1986 oil spill at Bahia las Minas, Panama [all photographs by C. Hansen except (D) by S. D. Garrity]. (**A**) Oil accumulated along the seaward edge of the Galeta reef flat at low tide (seen as the dark border in the cover photo), directly coating and killing plants and animals, including the zoanthid *Palythoa* sp. (lighter patches in foreground) and the hydrocoral *Millepora* sp. (projecting through oil in background). (**B**) At high tide oil accumulated along sand beaches, where it soaked into the sand and settled onto the shoreward reef flat at low tide, killing seagrasses, algae, and invertebrates. The rectangular objects in the foreground are polyurethane mattresses used by cleanup crews to absorb oil. (**C**) Underwater view of the coral *S. siderea* partially killed by oil (horizontal length in the photograph, 12 cm). Live tissue forms the dark reddish area at the bottom. The central, light-colored area is skeleton showing through partially dead tissue, which is also being colonized by algae. The lightest area at the top is bare skeleton covered by a film of microalgae. (**D**) Oil-covered intertidal surfaces of prop roots of the red mangrove, *R. mangle*, killing oysters and other epibiota on the roots. Relieved of the weight of their leaves, defoliated branches flexed upward, lifting the roots out of the water and thus killing subtidal epibiota that previously escaped direct contact with floating oil. (**E**) Dead mangrove trees form a band about 8 to 100 m wide (February 1987), marking the area where oil accumulated as it entered the mangrove forests (horizontal distances: foreground ~0.4 km and background ~1.3 km). A band of defoliated trees was apparent within 2 months after the spill and widened thereafter.

ments, reef-flat seagrass beds, coral rock, and beaches. In contrast, higher than normal seas after the *Witwater* spill caused heaviest oiling in high intertidal and supertidal habitats, with much more transport of oil into mangroves far from shore (*4*). Much less oil was observed subtidally.

In addition to these qualitative observations, samples of water, substrata, and organisms were collected for analysis of hydrocarbons by means of gas chromatography and ultraviolet fluorescence analysis of aromatic hydrocarbon fractions (*22*). Preliminary results generally parallel classification of sites based on visual inspection, as shown here for the concentration of saturated hydrocarbons in tissues of the coral *Siderastrea sidera* (Table 1).

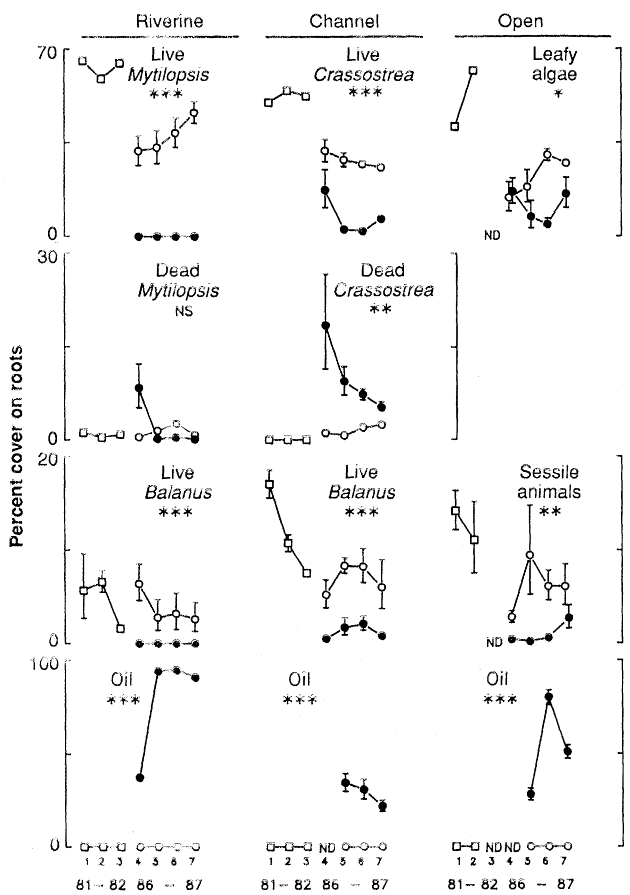

Fig. 4. Percent cover of formerly abundant taxa and oil on mangrove roots in riverine, channel, and open coast habitats before and after the oil spill. □, Prespill data; ○, unoiled sites; and ●, oiled sites. Means are plotted ±1 SE, converted from arcsine transformations. Some error bars lie within the plotting symbols, except for sampling time 3, when $n = 1$. ND, no data. "Leafy algae" include *Polysiphonia, Acanthophora*, and *Ceramium* as common genera; the most abundant "sessile animals" include hydroids and sponges. Sampling dates: 1 = September to October 1981; 2 = January 1982; 3 = June 1982; 4 = July to August 1986; 5 = October to November 1986; 6 = February 1987; and 7 = May 1987. Results of repeated measures analysis of variance for oiled and unoiled sites after the spill are shown on each graph. NS, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Biological Effects

Consequences of the spill were assessed differently, depending on the types of data available from before the oil spill (*23*). Ideally, biological parameters should have been measured at oiled and unoiled sites before and after the spill. This condition was satisfied for biota of mangrove roots and subtidal corals. Extensive prespill data are available for the reef flat at Galeta, but there are no control sites and effects must be inferred from temporal change and from the spatial distribution of oiling on the reef flat. In contrast, there are little or no appropriate prespill data for subtidal seagrass communities. In this case, comparisons were made between oiled and unoiled sites after the spill, confounding the treatment (oiling) and geography (Bahia las Minas verus the region between Portobelo and Isla Grande) (Fig. 2). The value of this approach is strengthened by information suggesting that faunas in seagrass beds were similar in the two regions before the spill (*24*), but confidence in assessment of oiling effects in this habitat is still more limited than in other habitats studied.

Mangrove communities. Red mangrove, *Rhizophora mangle*, forms nearly all of the fringing forest along this coast (*17*). By September 1986, a band of dead or dying trees marked the zone where oil washed ashore between Punta Galeta and Islas Naranjos (Fig. 3); no such band appears in photographs taken just as the oil was coming ashore. By November 1987 dead mangroves occurred along an estimated 27 km of the coast (*25*). Seedlings transplanted to heavily oiled sites did not produce new leaves, in contrast to transplants at an unoiled site (*26*).

The prop roots of *R. mangle* are overgrown by algae and invertebrates that vary in species composition with exposure to the sea (Fig. 3) (*6, 27*). The epibiota on roots in three different habitats were sampled before and after the spill (Fig. 2) (*28*). Before the spill (Fig. 4), roots of trees directly facing the open ocean were covered with foliose algae and sessile invertebrates such as sponges, hydroids, and ascidians. In mangrove channels, the edible oyster, *Crassostrea rhizophorae*, and a barnacle, *Balanus improvisus*, were most abundant on roots. Roots in small rivers were dominated by the false mussel *Mytilopsis domingensis* and *B. improvisus*. Certain groups were more abundant a few years before the oil spill (1981 to 1982) than in 1986 to 1987 at unoiled sites (Fig. 4), possibly because of natural fluctuations in abundance. After the spill, the cover of all major groups was very greatly reduced in each oiled habitat (Fig. 4). There has been patchy recovery in the open habitat of foliose algae and sessile invertebrates, although not of the same relative abundance of species. In the channels, cover of both the oyster and

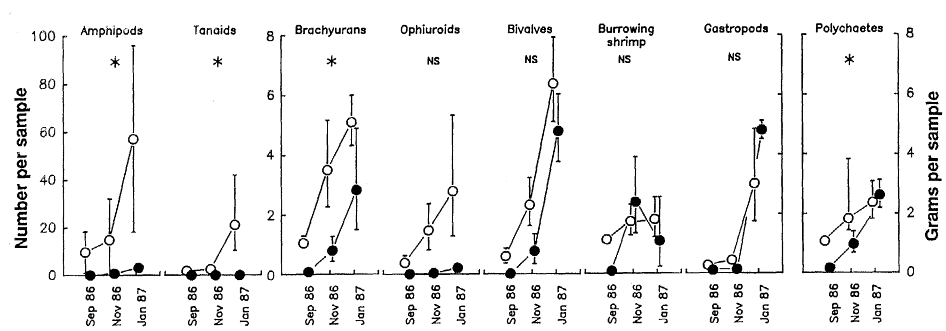

Fig. 5. Abundance or biomass per sample of eight major infaunal taxa in three oiled (●) and four control (○) seagrass beds 5, 7, and 9 months after the oil spill (*30*). Means are plotted ±1 SE, backtransformed from ln (x + 1); some error bars lie within the plotting symbols. "Burrowing shrimp" include alpheids (most abundant), processids, callianassids, and upogebids. NS, $P > 0.05$; *, $P < 0.05$ by repeated measures analysis of variance. Number per sample is shown at two scales. Data for polychaetes are shown as grams per sample.

barnacle dropped greatly and have since recovered little. False mussels and barnacles disappeared in oiled rivers and were not recorded again until 15 months after the spill.

The greatest cover on roots in all oiled habitats after the spill was oil (Fig. 4). In addition, most roots sampled for epibiota (*28*) were dead, broken, or rotting by August 1987 (54% on open coasts, 56% in channels, and 66% in rivers at oiled sites versus 8%, 1%, and 3%, respectively, at unoiled sites). Thus the mangrove-fringe root habitat has been largely destroyed at oiled sites and will not be restored unless new trees grow.

Seagrasses. Extensive meadows of the seagrass *Thalassia testudinum* cover much of the intertidal reef platforms and subtidal floors of shallow embayments and lagoons along this coast (*24*). Entire beds of intertidal *Thalassia* were killed on some heavily oiled reef flats, as shown by abundant oil-covered dead leaves washed ashore and dead but intact root-rhizome mats (for example, the site at Largo Remo North) (Table 2). In contrast, subtidal *Thalassia* survived everywhere after the spill, although leaves became brown and heavily fouled by algae for several months in heavily oiled areas.

Thalassia provides food, habitat, and refuge for dense populations of invertebrates and fishes (*24, 29*). Before the spill, amphipods, small decapods, ophiuroids and other echinoderms, bivalves, gastropods, polychaetes, and small fishes were all abundant in seagrass within the study area (*24*) and still are in unoiled beds (Fig. 5). Sampling of infauna began September 1986 at three oiled and four unoiled sites (*30*) (Fig. 2). Four taxa of invertebrates were significantly less abundant in oiled grassbeds after the spill, but four others showed no such difference (Fig. 5). Abundances of most taxa increased between September and January; preliminary analyses of body size indicate that recruitment caused these increases. Only the abundance of hermit crabs increased in oiled relative to unoiled areas (7.3 versus 3.4 crabs per sample, respectively, in January 1987, $P < 0.05$, repeated measures analysis of variance), perhaps because of a surplus of shells of recently dead snails (*31*).

Intertidal reef flats. Platforms of fringing reefs from extensive shallow to intertidal flats throughout the study region (Fig. 3) (*7, 9, 17, 32*). Populations on the reef flat at Punta Galeta have been monitored for up to 15 years (*9*) (Fig. 2). Damage was most extensive at the seaward border, where the oil accumulated at low tide. Immediately after the spill a bloom of microalgae covered recently vacated substratum (*33*) (Fig. 6). This area had been dominated by perennial macroalgae, particularly the fleshy red alga *Laurencia papillosa*, crustose corallines, and the articulated calcareous green alga *Halimeda opuntia*. Cover of all these plants was reduced to levels well below those observed previously, but had regained or exceeded typical abundance within 12 to 18 months, concurrent with a reduction of the microalgae. The most common sessile animals before the spill were zoanthids (*Zoanthus sociatus* and *Palythoa* spp.), hydrocorals (*Millepora* spp.), and scleractinian corals (*Porites* spp.). At the seaward border of the reef flat, populations of all these animals were severely reduced, and only *Zoanthus* had returned to typical abundance after 18 months (Fig. 6). Densities of sea urchins on the reef flat varied over three orders of magnitude before the spill (Fig. 6) (*9*). At the seaward edge, the most abundant

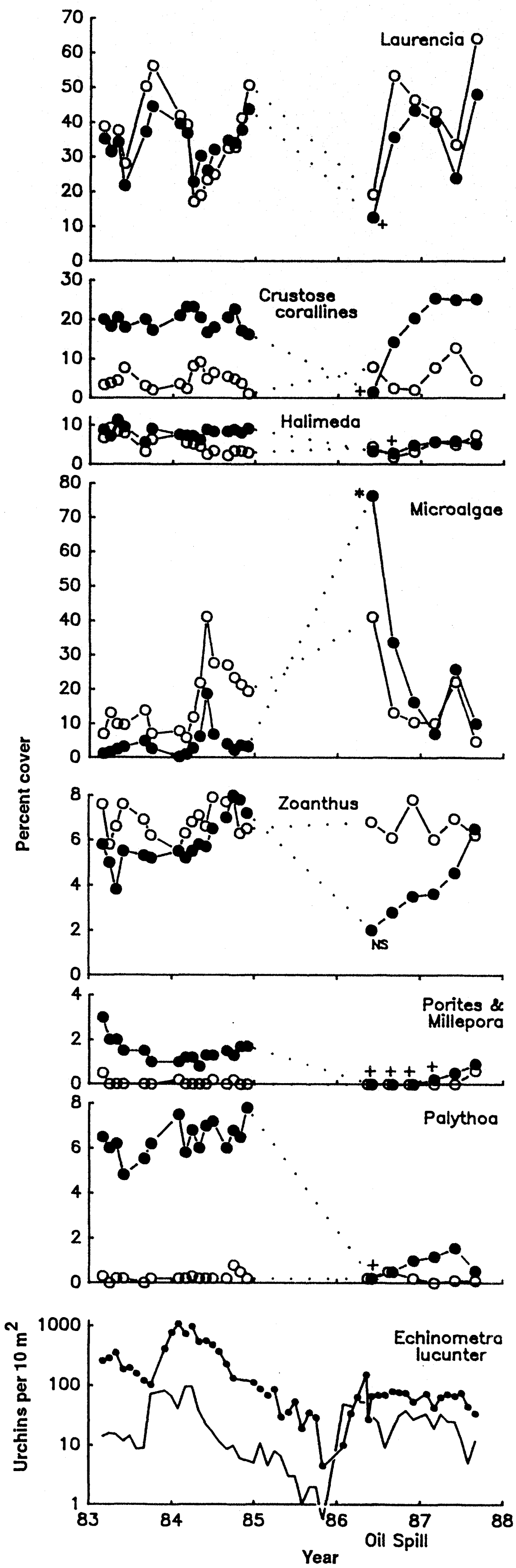

Fig. 6. Pre- and postspill comparisons of the abundance of algae and sessile animals (top seven panels) and the sea urchin *Echinometra lucunter* (bottom panel) on the seaward portion of the Galeta reef flat (*33*). Filled symbols denotes the heavily oiled zone closest to the water's edge at low tide (Fig. 3). Open symbols and the smooth line in the *E. lucunter* graph indicate less oiled (more landward) habitats; * and + mark postspill surveys of percent cover that were significantly higher or lower than any prespill survey at $P \leq 0.05$ and $P \leq 0.01$, respectively. In all cases, differences were significant only in the heavily oiled zone (●). Cover was compared survey by survey with the use of paired *t* tests matched by individual transects within surveys. Abundances of *E. lucunter* were compared with the use of residuals from regressions (*34*).

urchin *Echinometra lucunter* was reduced by about 80% within a few days of oiling, and the reef flat was littered with its skeletons. Although this decrease was small in an absolute sense relative to changes in abundance among years, it nevertheless departed significantly from the average trend in abundance between months of May and June over the last 8 years (*34*). Farther inshore, no such reductions occurred.

Gonodactylid stomatopods (mantis shrimp) are abundant in intertidal *Thalassia* beds from Isla Margarita to Isla Largo Remo, where they live in and aggressively defend cavities in coral rubble at densities up to 20 per square meter (*35*). They are prey for shorebirds, fish, and crabs, and in turn consume large numbers of hermit crabs, snails, and other animals (*36*). Population data are available for stomatopods from intertidal seagrass beds on four reef flats, including certain types of data collected at various times before the spill (Table 2 and Fig. 2). Two of the sites were heavily oiled, and large amounts of oil were still present on mangrove roots and in sandy sediment when sampling first began 3 months after the spill; the other two flats were at most lightly oiled. Densities of stomatopods were less on the heavily oiled flats, particularly for animals greater than 40 mm long (*37*). Loss of these large animals apparently made larger cavities available to the survivors, which consequently fought less and suffered fewer injuries (*38*) compared to the same sites before the spill and compared to lightly oiled flats afterwards (Table 2). Growth of larger survivors also increased on heavily oiled flats (*39*), probably because of decreased competition for cavities and an apparent population explosion of hermit crabs for food (*35, 40*). These effects have persisted in diminished form through our last census in September 1987.

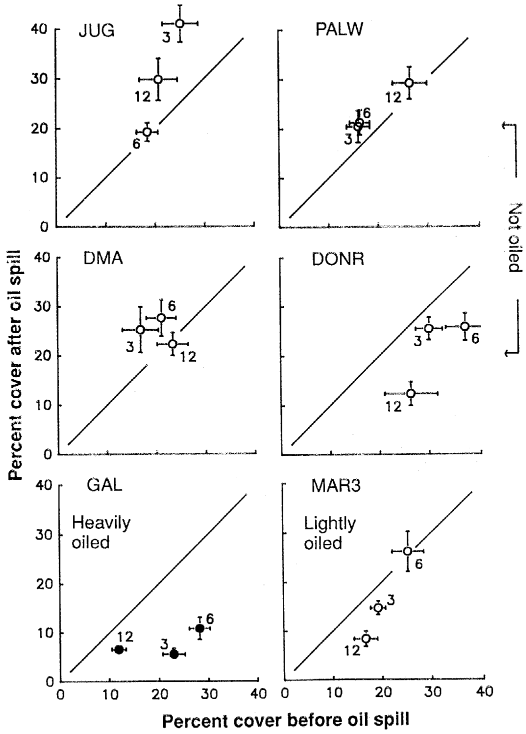

Fig. 7. Percent cover of corals before the oil spill plotted against their cover afterward. The diagonal lines represents no change in coral cover; points below this line indicate a decrease after the spill, and points above the line show an increase. The points are means ± 1 SE; some error bars lie within the plotting symbol. Oiling significantly affected coral cover only at the shallowest depth (*42*). Abbreviations: 3, 0- to 3-m depth; 6, 3- to 6-m depth; and 12, 6- to 12-m depth. JUG and PALW are located just west of Isla Grande, DMA and DONR are northeast of Portobelo, GAL is at Punta Galeta, and MAR3 is at Isla Margarita (Fig. 2, half-filled circles).

Subtidal reefs. Populations of subtidal sessile organisms were surveyed on six fringing reefs between Isla Margarita and Isla Grande within 1 year before and 4 months after the oil spill (Fig. 2) (*41*). These include the heavily oiled reef at Punta Galeta, a lightly oiled reef at Isla Margarita, and four unoiled reefs east of Portobelo. Abundance of most common scleractinian coral genera in depths ≤3 m decreased at Galeta by 51 to 96%, and total coral cover decreased by 76%; even at 9 to 12 m the drop was 45% (Fig. 7). Reductions were less at Isla Margarita and generally absent on the unoiled reefs, except at one site northeast of Portobelo (Fig. 2) for no apparent reason. This relation between amount of oiling on the six reefs and decrease in coral cover was significant for 0 to 3 m but not deeper (*42*).

Sublethal effects were also substantial. Within Bahia las Minas, most of the scleractinians still alive in depths less than 3 m showed signs of recent stress including bleaching or swelling of tissues, conspicuous production of mucus, recently dead areas devoid of coral tissue, and globules of oil (Fig. 3) (*43*). In some cases, bleached or dead areas were surrounded by a black halo characteristic of bacterial infection (*44*). Both the frequency and size of recently dead lesions on the commonest massive corals increased markedly with the amount of oiling at each reef and decreased with water depth (Fig. 8) (*45, 46*). These effects were also species specific. In the case of *S. siderea*, which suffered most, new partial mortality was still disproportionately common on heavily oiled reefs 1 year after the spill (*46*).

The oil spill also affected other organisms, including snails on the reef flat and intertidal zone at Punta Galeta and mobile epifauna, particularly shrimps above subtidal seagrasses. In summary, the spill harmed prominent organisms in all intertidal and subtidal environments examined, infauna and epifauna, and members of all trophic levels including primary producers, herbivores, carnivores, and detritivores.

Patterns of Responses and Their Significance

The severe damage to intertidal biotas and their response, such as the flush of ephemeral microalgae just after the spill, are similar to those documented previously for other oiled intertidal communities (*47–50*), including those inferred for Galeta after the *Witwater* spill (*4*). Likewise, biological effects of spills are usually greatest in low energy environments, where oil tends to accumulate and be retained in fine sediments, than in high energy environments where it is soon washed away (*50*). This pattern matches the greater and more persistent disturbance to riverine and channel mangrove root communities than to those along open coasts and the rapid recovery in abundance of many organisms at the seaward edge of the reef flat (Fig. 6).

In contrast, other results were not expected, and in some cases contradict widely held views about the effects of oil spills and the ways they are studied. First, extensive mortality of subtidal corals and infauna of seagrasses had not been demonstrated before (*1, 3*) and contradicts undocumented assertions that these organisms are not affected by oil spills. In part, subtidal effects may have been caused by the use of dispersant (*51*) but it seems unlikely that this was the only reason, given the regional breadth of the impact and the relatively small amount of dispersant employed (*14*).

Second, the magnitude of subtidal coral mortality and injury within Bahia las Minas is in striking contrast to findings of no lasting change in coral condition or growth after exposure to oil, with or without chemical dispersant, in small-scale experiments (*51, 52*). Such discrepancies underlie the importance of detailed long-term ecological studies, and the dangers inherent in extrapolation to

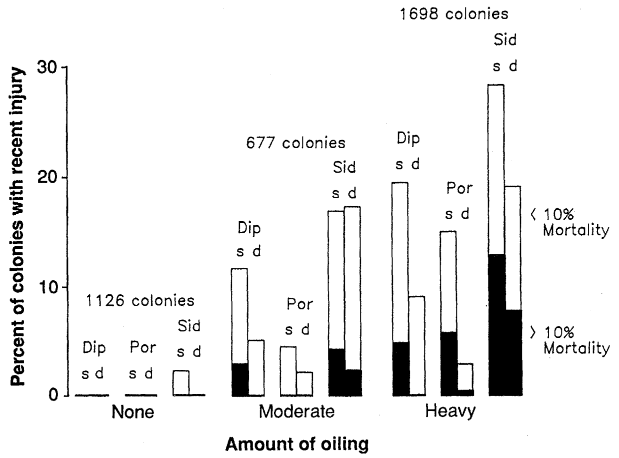

Fig. 8. Frequency of injury for the three most common species of massive corals in relation to the amount of oiling at 12 reefs (4 unoiled, 3 lightly to moderately oiled, and 5 heavily oiled). Open bars represent coral colonies with injuries that did not exceed 10% of the surface area of the coral; filled bars represent injuries greater than 10% (maximum observed, 100%). Sample sizes are shown above each category of oiling. Abbreviations; Dip, *Diploria clivosa*; Por, *Porites astreoides*; Sid, *Siderastrea siderea*; s, shallow (0 to 1 m); and d, deep (1 to 2 m).

natural populations from laboratory-based physiological data or small-scale, short-term press perturbation experiments in the field (*2, 3, 48, 52, 53*).

Third, sublethal effects are extensive and may be more important in the long term than initial mortality (*3, 48*). Changes in stomatopod behavior and population structure were more pronounced than might be expected from a simple reduction in numbers. Likewise, injury of corals has allowed colonization of their bare skeleton by algae and other sessile organisms that may overgrow parts of colonies that survived the initial effects of oil (*3, 54*). Corals stressed by oil are probably also more susceptible to epidemic disease and likely to grow and reproduce more slowly than unaffected colonies (*3, 5, 52*). Any combination of these effects may further reduce overall abundance of corals as much as the initial spill (*54*). Such a chain reaction could continue long after any petroleum hydrocarbons are present in the environment or coral tissues, just as staghorn coral continued to decline precipitously following a severe hurricane in Jamaica (*55*).

The response of organisms to an oil spill, or any other major disturbance, will depend on the conditions in which they normally live (*15, 48, 56*). Moreover, the suite of organisms able to survive under conditions of chronic pollution, and their resistance to further stress, is typically different from that in similar unpolluted habitats (*48, 57*). Much of Bahia las Minas has been subjected to human disturbance, beginning with decades of excavation, dredging, and landfilling for the construction of the Panama Canal and the City of Colon, drainage and spraying of mangroves for mosquito control, construction of the refinery and a large cement plant on landfill, a major oil spill in 1968, and unknown amounts of chronic oil pollution from the refinery and ships passing to and from the Canal (*4, 5, 17, 58*). It is a measure of the severity of the 1986 oil spill that the biological consequences were so detectable despite this history of environmental abuse.

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11. Ongoing drilling and refining off Yucatan and possible production along the west coast of Florida.
12. The oil type was 70% Venezuelan crude, 30% Mexican Isthmus crude, specific gravity 27° (American Petroleum Institute). Percent composition determined at the Bermuda Biological Station by column chromatography with the use of alumina and silica gels: 47.4% saturates (fraction 1, hexane); 6.4% light aromatics (fraction 2, 10% ether/90% hexane); 4.8% heavy aromatics (fraction 3, 20% methylene chloride/80% hexane); 18.9% polar fraction (fraction 4, methylene chloride); and 22.5% unrecovered.
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19. Within this area oil commonly escaped from sediments when we walked among mangroves or cored into shallow subtidal seagrass beds. Intertidal surfaces were heavily coated with oil.
20. Most of the oil that escaped from Bahia Cativa was driven west. Coasts facing north to northeast were heavily oiled, whereas adjacent areas facing west or south received little oil. The best studied example is at the northwestern side of Isla Largo Remo (Table 2).
21. These low tides occur annually at this time of year (*8, 9*). Sea levels during most of this time were as much as 10 cm below the 9-year average for this period of normally low sea level.
22. Corals were collected by divers on days when on surface slicks were visible, placed in solvent-rinsed aluminum foil, and frozen. Tissues were removed from skeletons with an air pick and homogenized with a tissue grinder. To minimize variations due to water or carbonate inclusions, standard Lowrey protein determinations were used as one measure of tissue mass. After solvent extraction, total lipid weights were determined microgravimetrically. Extracts were fractionated by adsorption chromatography. Hydrocarbons were analyzed with a capillary gas chromatograph equipped with a flame ionization detector and 25-m SE 52 fused silica columns.
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25. This estimate was extrapolated from aerial photographs of 36 km of the 82-km shoreline, of which 76 km contains mangroves. Of the photographed shoreline, 36% contained a band of dead mangroves.
26. Sprouting success was measured for seedlings collected from an unoiled site, and planted in one unoiled and two oiled sites. Of 25 seedlings transplanted into each site, 16 (64%) sprouted at the unoiled site and 1 (2%) sprouted at the oiled sites.
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28. Roots were sampled three times before the spill in rivers and channels (September to October 1981, January 1982, and June 1982) and twice in open habitats (September to October 1981 and January 1982). Several areas of shore within each habitat were chosen haphazardly. Fifteen to 25 intertidal roots ≥20 cm long that had not become firmly attached to the mud were lifted from the water, and cover of attached organisms was measured for each root by 100 random point counts after the oil spill or was estimated visually before the spill. Afte the spill, previously sampled riverine and channel habitats included both oiled and unoiled sites but all open sites were oiled. Thus it was necessary to choose sites near Portobelo (Fig. 2),

the nearest equivalent unoiled shoreline, for unoiled open habitat similar to oiled open habitat. One hundred roots were sampled in each oiled and unoiled habitat after the spill.

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30. All seagrass beds sampled lie adjacent to mangrove shoreline and are ≥1 m deep; unoiled beds meeting these criteria occur near Portobelo and Isla Grande (Fig. 2). Infauna were collected with 10.2-cm inside diameter polyvinyl chloride (PVC) tubes pushed into the sediment to a depth of at least 10 cm. Each sample consists of three pooled cores (240 cm^2). At each census eight samples were collected haphazardly at each site. Samples were sieved over 500-μm mesh and preserved in 10% formalin with rose bengal. Animals were sorted to major taxa and counted or weighed wet.
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33. Percent cover of sessile species attached to the substratum was estimated by point sampling along ten permanent transects 9 to 22 m long, perpendicular to the reef edge and spaced at random intervals within a 20-m strata. The number of points sampled per survey was between 1510 and 1560. The seaward 6 m of these transects were more directly exposed to oil than the landward portions. This 6-m band forms the "heavily oiled zone" of Fig. 6. Sea urchins were counted in two 1 × 20 m transects; one at the reef edge, the other 26 m farther landward.
34. For the reef edge transect only, residuals from regressions of changes in abundance from May to June were highly negative in 1986 compared with all other transects in all other years ($n = 41$, $r^2 = 0.88$, $P < 0.001$).
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37. The four collection sites ranged from 100 to 125 m × 25 to 40 m (all larger than 3000 m^2) and were selected before the spill to have intertidal *Thalassia* beds with firm, sandy substratum, and moderate amounts of rubble and coralline algal nodules. Densities of stomatopods were estimated from 30 quadrats (0.5 m^2) chosen at random within 400-m^2 plots at each site. All hard substrata were removed from each quadrat and broken, and all stomatopods were retained. A minimum of 300 individuals was collected, including ones from pieces of coral rubble collected haphazardly within each site, but outside the plot used for quadrats. These animals were included in the analysis of injuries and growth.
38. Cuticular injuries were recorded for all animals as described by I. K. Berzins and R. L. Caldwell [*Mar. Behav. Physiol.* **10**, 83 (1983)].
39. We estimated growth by comparing the length of the carapace of animals newly molted in the laboratory with its length before molting, using only animals that molted within 3 days of capture and were longer than 35 mm.
40. Almost every piece of rubble in the heavily oiled plots was covered by hundreds of hermit crabs. Such densities were not observed in unoiled plots or in any years previously.
41. See P. W. Glynn [*Bull. Biol. Soc. Wash.* **2**, 13 (1972)] and J. W. Porter (*ibid.*, p. 89) for general descriptions of Panamanian reefs. We selected fringing reefs that extended at least 100 m along the shoreline and to a depth of at least 12 m. At each reef four or five line transects were extended from haphazardly chosen points at the shoreward edge of the reef to the deepest point of the reef. Along each line, 1-m^2 quadrats were placed contiguously or up to 3 m apart, depending on transect length (8 to 81 quadrats per transect). Quadrats were divided into 100-cm^2 cells, and total cover was estimated by eye within each cell.
42. We determined differences in coral cover before and after the spill (July to October 1985 and July to August 1986) by combining all quadrats at each of three depths (0 to 3, 3 to 6, and 6 to 12 m; prespill $n = 306$, 219, and 135 quadrats, respectively; postspill $n = 294$, 200, and 187) at each site and then calculating ln (mean cover before the spill/mean cover afterward). The effect of oil was examined by one-way analysis of variance of these values for one heavily oiled, one lightly oiled, and four unoiled reefs; df = 2. For 0 to 3 m depth, $F = 13.3$, $P = 0.032$; 3 to 6 m, $F = 4.48$; $P = 0.13$; 6 to 12 m, $F = 0.90$, $P = 0.49$.
43. Dead areas were bare or colonized by thin growth of filamentous algae. Ten such colonies of *S. sidera* were sealed in plastic bags underwater, brought to the laboratory, and placed in clean tanks and seawater. A film of oil appeared on the surface of each tank when the filamentous algae growing over the recently dead areas were squeezed by hand.
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45. Recent injuries were counted on 12 reefs for all corals in 2 × 50 m transects haphazardly located at 0 to 1 m and 1 to 2 m depth. Injuries were counted only when the exposed skeleton was bare or only lightly overgrown by filamentous algae. Size of injury was visually estimated as percent of the total surface area of each coral.
46. Significance was tested with hierarchical log-linear models (SPSS/PC+, 1987) with the following variables: coral species (three levels), water depth (two levels), amount of injury (three levels), and amount of oiling (three levels). Injuries were not distributed equally as a function of amount of oiling for any of the three coral species ($P < 0.001$); injuries increased in frequency and severity as amount of oiling increased among sites. The effect of oiling on coral injuries was not independent of depth ($P < 0.001$); injuries were more frequent at shallower depths. The three coral species differed in frequency of injuries ($P < 0.001$), with *S. sidera* > *Porites astreoides* > *Diploria clivosa*. In April 1987, about 1 year after the oil spill, coral injuries were still not distributed equally as a function of amount of oiling among sites ($P < 0.001$).
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