EFFECTS OF OIL SPILLS ON FRINGING RED MANGROVES (*RHIZOPHORA MANGLE*): LOSSES OF MOBILE SPECIES ASSOCIATED WITH SUBMERGED PROP ROOTS

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**ABSTRACT**

Extrapolation of results from empirical studies of natural or anthropogenic perturbations are a useful tool in estimating potential effects of future impacts. For 5 years we studied the direct effects of a major oil spill on fringing red mangroves (*Rhizophora mangle*) and the organisms that live attached to their submerged prop roots. Based on these data, we here estimate the effects of this oil spill on associated mobile species using (1) direct measures of the abundance of wood-boring isopods and (2) losses of epibiota used as shelter, settlement and juvenile habitat by non-boring species associated with submerged prop roots. Using a descending hierarchical analysis, we examined losses (a) in the density of submerged prop roots per unit shoreline fringed with red mangroves, (b) in the suitability of submerged prop roots, and (c) in the amount of settlement substrate available on roots. For boring isopods in sheltered channels and lagoons, there was no significant difference in isopod abundance on suitable (live) roots at oiled and unoiled sites. However, suitable (live) submerged prop roots were less abundant at oiled sites, leading to a reduction of over 60% in the number of submerged prop roots containing isopods at oiled as compared to unoiled sites 5 years after the oil spill. We estimated effects on non-boring species using two groups of epibiota (foliose red algae and arborescent hydroids and bryozoans) utilized as juvenile habitat by spiny lobsters (*Panulirus argus*). Changes in two mangrove habitats, the exposed open coast and sheltered channels and lagoons, reduced the estimated amount of juvenile habitat by ~40-50% for at least 5 years after oiling. In channels and lagoons, losses were directly proportional to reductions in the number of submerged prop roots-unit$^{-1}$ of shoreline, because average root size did not change after oiling and approximately the same area on root surfaces was covered with foliose red algae and arborescent hydroids and bryozoans. On the open coast, there were additional losses in juvenile habitat, because roots were significantly shorter at oiled than unoiled sites in years 2-4 post-spill. For arborescent hydroids and bryozoans (but not foliose red algae), reductions in cover were greater than reductions in the amount of potential habitat, indicating further negative effects of oiling. These additional reductions may have been caused by toxic hydrocarbons or further physical changes related to oiling.

The effects of natural or anthropogenic perturbations depend on the type of habitat affected. Habitats created at least in part by their constituent plants or animals are especially vulnerable to negative impacts; such biogenically-structured habitats include salt marshes, seagrass beds, coral reefs and mangrove forests. Damage to the structuring organism(s) can cause loss of the habitat (i.e., erosion of the salt marsh), with cascading effects on the suite of associated species (loss of salt marsh crab, snail, fish and bird populations). If a perturbation is also accompanied by persistent toxic compounds, then negative effects may be prolonged due to the action of the toxins. Interactions between physical damage, toxic compounds and the process of recovery are complex and largely unknown (Teal et al., 1992).

Studies of natural or anthropogenic perturbations are most important when results can be extrapolated to other studies or used as part of planning for future impacts. For 5 years, we studied the effects of an oil spill on fringing red mangroves (*Rhizophora mangle*) and the plants and animals that live attached to submerged mangrove roots (Burns et al. (1993) and included references). Thickets of submerged red mangrove prop roots provide hard substrata in areas of soft
sediments, and they and their attached epibiota form a major component of coastal nursery grounds (Odum et al., 1982; Rützler and Feller, 1987).

In 1986, the rupture of an oil storage tank spilled an estimated 75,000–100,000 barrels of medium weight crude oil into Bahia las Minas on the Caribbean coast of Panamá (Cubit et al., 1987). We documented alterations in the physical structure of the mangrove fringe caused by oiling and monitored the percent cover of epibiotic plants and animals in oiled and unoiled areas over time. Structural alterations included reductions in the amount of shoreline fringed with red mangroves and decreases in the density and size of submerged roots within surviving fringe (Garrity et al., 1994). Independent of structural alterations, there were long-term reductions (at least 5 year) in the abundance of epibiota on roots after the oil spill (Levings et al., 1994). Given the strength and persistence of the effects identified, it is clear that oil spills have the potential to cause severe and long-lasting damage to the mangrove fringe and to its associated species.

Our studies of the effects of this spill included observations and limited collections of the suite of mobile species living on submerged prop roots. Crustacea were especially abundant, with at least 18 species present. These included spiny lobsters, amphipods, isopods, mysids, penaeid and caridid shrimp, and xanthid, grapsid, portunid, decorator and porcellanid crabs. Crustaceans are sensitive to petroleum hydrocarbons, with effects ranging from behavioral alterations to acute toxicity (Krebs and Burns, 1977; NRC, 1985; Capuzzo, 1987). For associated mobile species like crustaceans, negative effects of oiling could have two pathways: direct reductions in populations caused by contact with oil and indirect reductions caused by habitat destruction or alteration.

We approached the question of direct negative effects on associated mobile crustaceans by monitoring the presence of a representative group, wood-boring isopods, on submerged prop roots at oiled and unoiled sites over time. Wood-boring isopods were chosen because their presence or absence on roots could be measured by the presence or absence of characteristic holes in the root tip’s surface (Ellison and Farnsworth, 1990). We estimated possible indirect effects of this oil spill on other mobile crustaceans by examining changes in the abundance of epibiota used as shelter, settlement substrate and juvenile habitat by non-boring species associated with submerged prop roots. We present a hierarchical analysis of characteristics of the mangrove fringe important for associated mobile species documenting (1) the amount of shoreline fringed with mangroves, (2) the density of submerged prop roots within the mangrove fringe, (3) the suitability of submerged roots as habitat for associated mobile species, and (4) the abundance of groups of epibiota used by associated mobile species.

**Materials and Methods**

*Oil Spill and Sampling Methods.*—Initial effects of the spill were reported in Cubit et al. (1987), Burns and Knap (1989), Jackson et al. (1989) and Garrity and Levings (1993a). For the mangrove fringe, a series of detailed papers describe the spill, changes in the habitat and patterns of epibiotic cover for major groups, and hydrocarbons of the sediments and bivalves (Burns et al., 1994; Burns and Yellesimmons, 1994; Garrity et al., 1994; Levings et al., 1994).

Four or five replicate study sites each were examined in oiled and unoiled areas in two habitats on the gradient between the open coast and inner drainages of mangrove swamps. Open coast sites fronted the ocean along the inner margins of reef flats; the most abundant epibiota on roots were foliose algae and sessile invertebrates. Physical conditions on the open coast were primarily controlled by the movement of oceanic waters across reef flats (Cubit et al., 1986, 1988, 1989). Further into the estuary, channels led inward from the sea and into sheltered lagoons. Roots in channels and lagoons were encrusted with bivalves, other sessile invertebrates and foliose algae. Physical conditions changed seasonally, with fluctuations in salinity related to patterns of tidal changes, winds, rainfall and runoff (Cubit and Levings, 1993; Garrity and Levings, 1993b).
Mangrove roots were sampled along the mangrove fringe at each site by randomly selecting 20 roots submerged at least 20 cm but not yet attached to bottom sediments. Root length was measured as the distance between mean high water and the longest root tip; the diameter of each root was recorded at the waterline. We also recorded if the root was live or dead. The abundance of epiibionts was measured as the percent of space between mean high water and the longest root tip occupied by individual species (e.g., Laurencia papillosa), mixed species groups (diatoms, blue-green algae), oil, or bare space (methods detailed in Garrity and Levings, 1993b). Vertical distribution on roots was estimated by recording data individually with depth, allowing us to assign locations (depths) to categories. We sampled every 3 months between August 1986 and May 1991.

Estimation of Habitat Losses: Density and Size of Submerged Roots.—Data on habitat losses are presented in detail in Garrity et al., 1994. Briefly, in May 1991, each site was visited and the physical condition of the mangrove fringe was measured for each meter of the shore along the fringe. We determined whether areas without festivities mangroves in 1991 had been previously occupied by red mangroves by looking for physical evidence that mangroves had been present before the spill (i.e., decaying root channels or stumps) and verifying our findings with photo transects and field notes from each site beginning 3 months after the spill. At each site the density of roots in the remaining fringe was calculated by counting the number of roots that met our monitoring criteria (above) in 10 randomly-selected 0.25 m² quadrats positioned where mangrove fringe survived (intact, damaged and new fringe included). We assumed that the percent of shoreline fringed with red mangroves at unoiled sites was the approximate amount of shore expected to be fringed with mangroves at oiled sites, and calculated the difference as the ratio of observed to expected meters of shoreline fringed with mangroves. We then estimated how many submerged prop roots that met our monitoring criteria (above) were found within the fringe at oiled as compared to unoiled sites. These values were combined and standardized to a 100 m length of shoreline (units of number of submerged roots·100 m⁻¹ shoreline in 1991). This was our first, and largest scale, estimate of habitat loss. Second, we estimated root surface area from root length and diameter, assuming that roots were approximately cylindrical in shape (estimates not adjusted for the presence of multiple root tips). These data were available for years 2–5 post-spill, providing a long-term estimate of changes at the level of individual roots. Third, we generated an overall estimate of the percent of the mangrove fringe habitat remaining 5 years after the spill by combining our first two estimates. Average surface area/root was multiplied by the number of roots·100 m⁻¹ shoreline, yielding an estimate of the number of square meters of submerged root surface at oiled as compared to unoiled sites (m² submerged root surface·100 m⁻¹ shoreline). This was an underestimate of the actual amount of habitat along the fringe (because not all roots met our monitoring criteria), but was not differentially biased among sites or habitats.

Isopod Abundance.—From August 1988 until May 1991 (years 3–5 post-spill), the presence of isopod holes on submerged prop roots was recorded as the percent of the root surface bored by isopods for each root sampled (see description above). Because isopod holes were rare to absent on the open coast, we analyzed data from channels only. First, the presence of isopods was quantified as the percent of (a) all censused roots with at least one isopod bore hole containing isopods and (b) live censused roots with at least one isopod bore hole containing isopods. Second, we examined the average percent of root surface bored by isopods for roots with at least one isopod hole. We assumed that the amount of root surface occupied by isopod bore holes containing isopods was an unbiased estimate of isopod abundance on submerged prop roots at oiled and unoiled sites.

Calculations of Shelter, Settlement and Juvenile Habitats.—There are little data on detailed habitat requirements of mobile species associated with submerged prop roots. We therefore examined two groups of epibionts used by juvenile spiny lobsters (Panulirus argus), which have been well-studied compared to other groups recorded in our study. Spiny lobsters settle in reefs, seagrasses, algal beds, clumps of arborescent hydroids and bryozoans, and among the epibionts on submerged prop roots of Rhizophora mangle (Witham et al., 1964; Marx and Herrnkind, 1983a, 1985b; Marx, 1986; Herrnkind and Butler, 1986; Herrnkind et al., 1988; Butler and Herrnkind, 1991). Clumps of foliose red algae and arborescent hydroids and bryozoans are preferred habitats for juveniles, providing both shelter from predators and food in the form of small invertebrates that live and feed within them (Marx and Herrnkind, 1983a, 1985b; Herrnkind et al., 1988). Both foliose red algae and arborescent hydroids and bryozoans (hereafter called red algae and AHB) were present on submerged prop roots. We assumed the abundance (percent cover) of red algae and AHB roughly estimated the amount of juvenile habitat on submerged prop roots. We analyzed percent cover data for these two groups, examining the open coast and channels and lagoons separately for each group.

All red algae found on submerged prop roots were included except articulated coralline species (Table 1; to our knowledge articulated coralline algae have not been recorded as juvenile lobster habitat). Since red algae occurred both subtidally and intertidally (Garrity and Levings, 1993b), we defined suitable habitat for red algae as the entire wetted root surface (units of cm² red algae·cm⁻²
Table 1. Foliose red algae from mangrove roots on the Caribbean coast of Panama*

<table>
<thead>
<tr>
<th>Algae Name</th>
<th>Species Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthophora spicifera</td>
<td>Gelidiella acerosa</td>
</tr>
<tr>
<td>Bostrychia binderi</td>
<td>Gelidium americanum</td>
</tr>
<tr>
<td>Bostrychia montagnei</td>
<td>Gracilaria mammillaris</td>
</tr>
<tr>
<td>Bostrychia tenella</td>
<td>?Griffiethia sp.</td>
</tr>
<tr>
<td>Caloglossa leprieuiri</td>
<td>Herposiphonia tenella</td>
</tr>
<tr>
<td>Catanella repens</td>
<td>Heterosiphonia sp.</td>
</tr>
<tr>
<td>Centroceras clavulatum</td>
<td>Hypnea cervicornis</td>
</tr>
<tr>
<td>Ceramium fastigatum</td>
<td>Laurencia obtusa</td>
</tr>
<tr>
<td>Ceramium rubrum</td>
<td>Laurencia papillosa</td>
</tr>
<tr>
<td>?Champia parvula</td>
<td>Murrayella pericladios</td>
</tr>
<tr>
<td>Coelothrix irregularis</td>
<td>Polysiphonia subtilissima</td>
</tr>
<tr>
<td>Eucheuma sp.</td>
<td>Spyridia hypnoides</td>
</tr>
<tr>
<td>Galaxaura comans</td>
<td>Wrangelia argus</td>
</tr>
<tr>
<td>Galaxaura oblongata</td>
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root surface between MHW and the longest root tip). The use of red algae by crustaceans at all depths is possible and is likely to vary with changing water levels.

All AHB were combined for analysis since they generally occurred in mixed species groups on roots. AHB primarily occurred deeper than ~40 cm below MHW (approximately the upper limit of the subtidal zone in this region, Garrity and Levings, unpubl.). Their contribution to potential habitat was thus calculated based on the amount of root surface that was deeper than 40 cm based on root length (units of cm² AHB·cm⁻² root surface >40 cm in depth).

Our analyses gave an estimate of the area (number of square centimeters) of potential juvenile habitat·root⁻¹ at oiled and unoiled sites for each type of cover. This estimate was then compared with the total surface area/root to examine what fraction of available area on root surfaces was actually occupied for years 2–5 post-spill, and whether that differed between oiled and unoiled sites. To yield a total estimate of potential juvenile habitat per 100 m shoreline 5 years after the oil spill the number of roots·100 m⁻¹ shoreline in 1991 was multiplied by surface area·root⁻¹ (units of m² of habitat·100 m⁻¹ shoreline) for both AHB and red algae at oiled and unoiled sites.

Statistical Analyses.—Repeated measures analysis of variance (ANOVAR) was applied to arcsine-transformed percent cover data and to presence/absence data for isopods (Green, 1979; SAS, 1988). Annual means·site⁻¹ were used to eliminate effects of seasonal fluctuations; probability levels were adjusted by the Huynh-Feldt procedure if data failed to pass sphericity tests. Among-year comparisons were calculated using Fisher’s least significant difference (LSD) methods (Milliken and Johnson, 1984). These conservative tests indicated if there were significant differences in (1) the presence of isopods or (2) the amount of red algae or AHB within surviving fringe at oiled vs. unoiled sites. Because of changes in site locations a year after the spill, analyses were restricted to years 2–5 post-spill (August 1987–May 1991); two overlapping analyses for red algae and AHB are presented for channels because an additional unoiled site was added in year 3 post-spill (see Levings et al., 1994 for discussion of statistical methods).

Results

Estimation of Habitat Losses: Density and Size of Submerged Roots.—Open Coast. Less of the shoreline was fringed by red mangroves at oiled than unoiled sites in 1991 (see Garrity et al., 1994, for details). At unoiled sites, an average of ~98% of the shore was fringed with red mangroves, while only ~85% was fringed with red mangroves at oiled sites (range 77–97%, n = 4 sites). Thus we estimated there had been a loss of ~13% of the shoreline that had once been fringed with mangroves at oiled sites. Within the surviving fringe at oiled sites, there were 10–51% fewer submerged prop roots than at unoiled sites (mean percent remaining = 76%, n = 4). Combining these estimates, we would expect to find ~1,534 submerged roots·100 m⁻¹ shoreline at unoiled sites and ~1,075 roots·100 m⁻¹ shoreline at oiled sites.

Roots were significantly shorter at oiled than unoiled sites, but the mean dif-
Figure 1 (left). Estimated surface area on submerged mangrove roots suitable for growth of red algae (circles) and AHB (squares). Open symbols = unoiled sites, filled symbols = oiled sites. Among site means and associated standard errors. $N = 4$ oiled, 4 unoiled sites on the open coast; $N = 5$ oiled sites, 4 unoiled sites in channels. Standard error may be smaller than the symbol plotted.

Figure 2 (right). Percent of roots (among site mean ± 1 standard error) containing isopod bore holes for all roots (bottom, left panel) and for live roots only (top left panel). Percent of root surface (among site mean ± 1 standard error) bored by isopods for roots containing at least one isopod bore hole (bottom right panel). Sample size as in caption to Figure 1.

ference in root length declined over time (Garrity et al., 1994, table 5). In year 2 post-spill (August 1987–May 1988), roots at oiled sites were ~11% shorter than at unoiled sites; in year 5 post-spill, the difference was only ~5%. Thus one effect of oiling was a change in the average depth to which roots were submerged on the open coast.

The estimated surface area on roots suitable for red algae at unoiled sites ranged from 433–495 cm$^2$·root$^{-1}$ from 1987–1991 (Fig. 1). Area suitable for AHB was lower, 158–222 cm$^2$·root$^{-1}$ (estimated surface area·root$^{-1}$ >40 cm deep). After oiling, root length declined and, correspondingly, surface area·root$^{-1}$ declined. As roots grew back into the water with time after oiling, surface area·root$^{-1}$ increased at oiled sites, and began to converge with that at unoiled sites. There was 16% less surface area·root$^{-1}$ for red algae at oiled sites in 1987, while by 1991 the difference was 6%. For AHB, differences were stronger: in 1987 there was 29% less surface area·root$^{-1}$ and in 1991 there was 15% less surface area·root$^{-1}$ suitable for AHB.

Oiling changed the amount of potential habitat for red algae and AHB on the open coast, but the strength of the effect declined over time. There were disproportionately large declines in the amount of potential habitat for AHB at depth, with ~2.5 times the reduction in surface area·root$^{-1}$ calculated for red algae.

Overall estimates of habitat loss in May 1991 were generated by multiplying surface area·root$^{-1}$ by the number of roots·100 m$^{-1}$ shoreline. At unoiled sites, roots had an estimated surface area of ~65.8 m$^2$·100 m$^{-1}$ shoreline suitable for
red algae and 24.2 m²·100 m⁻¹ shoreline suitable for growth of AHB. At oiled sites, there was an estimated ~43.8 m²·100 m⁻¹ shoreline suitable for red algae and 14.5 m²·100 m⁻¹ shoreline suitable for AHB.

**CHANNELS AND LAGOONS.** At unoiled sites, the mangrove fringe remained, with 100% of the shoreline fringed with red mangroves between 1986 and 1991. Five years after oiling, 22–94% of the fringe remained at oiled sites (mean = 77%, n = 5). Within surviving fringe, there were ~20% fewer roots at oiled than unoiled sites. Combining these estimates, we would expect to find ~1,840 roots in a 100 m section of shoreline in an unoiled channel compared to ~1,132 roots in 100 m of shoreline in an oiled channel.

There was no significant effect of oiling on root length in channels, but there was a significant effect of year (Garrity et al., 1994, table 5). This effect was small, with annual grand means ranging from 57.2–61.5 cm.

Surface area-root⁻¹ suitable for red algae or AHB was somewhat less in oiled than unoiled channels, especially in the first few years after the oil spill (Fig. 1). However, this difference was not significant based on ANOVAR results (Garrity et al., 1994, table 5). Oiling did not change the overall depth distribution of roots or the surface area-root⁻¹ for red algae or AHB.

At unoiled sites, we estimated that submerged prop roots had a surface area of 67.7 m²·100 m⁻¹ shoreline suitable for red algae and 19.9 m²·100 m⁻¹ shoreline suitable for AHB. At oiled sites, we estimated that there was ~42.1 m²·100 m⁻¹ shoreline suitable for red algae and 13 m²·100 m⁻¹ shoreline for AHB.

**Changes in Isopod Abundance.**—**CHANNELS AND LAGOONS.** Significantly more roots were bored by isopods in unoiled than oiled channels between August 1988 and May 1991 (Fig. 2, Table 2). The average percent of submerged prop roots that were bored was 72.7% of all sampled roots at unoiled sites as compared with 37.3% at oiled sites. There was a significant main effect of year with a significant increase in percent bored each year (year 3 < year 4 < year 5, Fisher LSD tests, $P < 0.05$). However, the percent of root surface bored by isopods did not differ
between bored roots at oiled and unoiled sites (Fig. 2, Table 2). That is, if an isopod was present in a root, it was likely to bore the same amount of the root surface at both oiled and unoiled sites. There was a significant effect of year, with a significant increase only between year 3 and year 5 post-spill (Fisher LSD tests, $P < 0.05$). When the percent of roots containing isopods was examined for live roots only, there was no significant effect of oil (Fig. 2, Table 2). Instead, there was an effect of year, with significantly fewer roots bored in year 3 post-spill, as compared with years 4 and 5 (Fisher LSD tests, $P < 0.05$).

When structural changes in the mangrove fringe were combined with percent of submerged prop roots containing isopods, reductions in isopod abundance at oiled sites were strong. In May 1991, we estimated an average of 1,132 roots·100 m$^{-1}$ shoreline at oiled sites and 1,840 roots·100 m$^{-1}$ shoreline at unoiled sites. At oiled sites, 56% of roots contained isopods and we estimated that there were 634 roots·100 m$^{-1}$ shoreline containing isopods. In contrast, at unoiled sites, 87.5% of roots had at least one isopod hole. We estimated that there were 1,610 roots·100 m$^{-1}$ shoreline with at least one isopod hole at unoiled sites, more than 2.5 times as many bored roots than at oiled sites.

**Changes in Epibiotic Cover.**—**OPEN COAST.** On the open coast, red algae occurred regularly on roots, but mean percent cover was rarely greater than 10% at any one monitoring. There was high variability among roots (range 0–87% of root surfaces over all roots sampled). There were also differences among unoiled sites that persisted throughout our sampling. For example, the annual mean percent cover of red algae at one site (coded OU3) was <1% between 1987–1991; during the same period at another site (OU1), mean cover ranged from 4.1–6.1%.

There was a significant year-oil interaction in ANOVAR for differences between oiled and unoiled sites in percent cover of red algae on roots on the open coast (Table 2, analyses for years 2–5 post-spill). Fisher's LSD tests were not significant at $P < 0.05$ when oiled and unoiled sites were compared for each year, but oiled and unoiled sites in year 2 post-spill differed at $P < 0.10$. When the data were examined over time, there were no significant differences among years at unoiled sites (Fisher LSD tests, $P > 0.05$) while cover of red algae increased significantly at oiled sites each year (Fisher LSD tests, $P < 0.05$, all inter-year comparisons). It appeared that red algae were rare at oiled sites in the second year after the spill (mean cover 0.4% at oiled sites vs. 2.4% at unoiled sites in year 2 post-spill), rebounding to levels like those at unoiled sites in year 5 post-spill (mean cover 3.8% vs. 2.7% at unoiled sites in year 5 post-spill).

AHB were common on the open coast, ranging up to 10% cover on roots. There was a significant negative effect of oil on the open coast (Table 2). Differences between oiled and unoiled sites were significant for years 2–4 post-spill, but not in year 5 post-spill (Fisher LSD tests, $P < 0.05$).

**CHANNELS AND LAGOONS.** In channels and lagoons, red algae covered >1.5% of root surfaces at all unoiled sites in all monitorings; average cover was usually >5%. There were no significant differences between oiled and unoiled sites in percent cover of red algae on roots (Table 2, analyses for years 2–5 and 3–5 post-spill). There was a significant main effect of year on cover of red algae in channels in the year 3–5-analysis only. Cover was lowest in year 3 post-spill at oiled sites. Based on both analyses, we interpret this as random variation among years that was unrelated to oiling.

Results were similar for AHB in channels, but there was a significant effect of year in both analyses (Table 2). As for red algae in channels, we interpret these results as random variation among years that was unrelated to oiling.
Estimates of Settlement Substrate Availability.—Open Coast. The surface area covered by red algae or AHB on submerged roots was calculated by multiplying the average surface area of roots by the mean percent cover of red algae or AHB (Fig. 3). On the unoiled open coast, red algae covered ~10 cm²/root from years 2–5 post-spill. At oiled sites, red algae were essentially absent in the second year after the spill, increasing to ~15 cm²/root 5 years after oiling. Because vertical distribution data showed the entire submerged root surface suitable for red algae, percent cover and percent of root surface area occupied by red algae were identical.

When the effects of habitat reduction were taken into account, we estimated that ~1.6 m² of submerged root surfaces 100 m⁻¹ shoreline were covered by red algae in year 5 post-spill at both oiled and unoiled sites. Thus, although there was a 33% reduction in the amount of submerged root surfaces at unoiled sites, an increase in the percent cover of red algae in year 5 post-spill at oiled sites balanced the amount of lost habitat and approximately as much red algae was potentially available as juvenile habitat at both oiled and unoiled sites 5 years after the spill.

AHB covered ~20 cm²/root⁻¹ at unoiled sites from 1987–1991 (Fig. 3), occupying 8.2–14.3% of the root surface calculated as suitable for AHB. At oiled sites, <10 cm²/root⁻¹ was covered with AHB for years 2–4 post-spill (~5% of the root surface calculated suitable for AHB). In year 5 post-spill, cover of AHB approximately doubled, to 15.5 cm²/root⁻¹, but was still 25% less than at unoiled sites. When these values were compared with the potential surface area suitable for AHB (cm²/root⁻¹ >40 cm deep), ~13% of the calculated area was covered with AHB at unoiled sites and ~11.5% at oiled sites 5 years after the spill.

On a 100 m section of shoreline in 1991, we estimated that ~3.2 m² of root surfaces would be covered with AHB at unoiled sites; at oiled sites, only 1.7 m² of root surfaces would be covered with AHB. Thus, AHB covered approximately 25% less space on a per root basis 5 years after the spill; when changes in the number of submerged roots 100 m⁻¹ of mangrove fringe were factored in, there was 47% less surface covered with AHB at oiled than unoiled sites.
CHANNELS AND LAGOONS. In channels and lagoons, estimated surface area covered by red algae ranged from $15-30 \text{ cm}^2 \cdot \text{root}^{-1}$ at both oiled and unoiled sites in years 2–5 post-spill (Fig. 4). Thus on a per root basis, there was approximately as much surface area covered by red algae at oiled and unoiled sites (Table 2). However, when the reduction in root density related to oiling was factored in, red algae in 1991 were estimated to cover $6.0 \text{ m}^2 \cdot 100 \text{ m}^{-1}$ shoreline at unoiled sites and $2.2 \text{ m}^2 \cdot 100 \text{ m}^{-1}$ shoreline at oiled sites. This threefold difference may be an overestimate of average differences between oiled and unoiled sites, because cover of red algae was high at unoiled sites in 1991 (Table 2, Fig. 4). However, there was probably on average at least twice as much surface area $100 \text{ m}^{-1}$ shoreline covered with red algae at unoiled than oiled sites.

Results were similar for cover of AHB. On a per root basis, AHB covered approximately as much surface area at oiled as unoiled sites (Fig. 4). When reductions in the density of roots were factored in, we estimated that AHB in 1991 covered $2.0 \text{ m}^2 \cdot 100 \text{ m}^{-1}$ shoreline at unoiled sites and $1.3 \text{ m}^2 \cdot 100 \text{ m}^{-1}$ shoreline at oiled sites.

**DISCUSSION**

*Patterns of Habitat Loss.*—The Bahía las Minas oil spill killed sections of shoreline fringed with red mangroves, reducing the amount of habitat for associated sessile and mobile species. Reductions in the density of roots within surviving fringe further decreased potential habitat. Additional losses of potential habitat due to decreases in cover of sessile organisms on roots varied with location in the estuary. In channels, there were no significant effects of oiling on root size or on the amount of root surfaces covered with red algae or AHB between the second and fifth years after the spill. Thus reductions of habitat estimated for post-larval spiny lobsters and other mobile species were directly proportional to structural losses in the mangrove fringe.

On the open coast, and for isopods in channels, results were more complex. AHB covered $50\%$ less surface area on surviving roots at oiled than unoiled sites for years 2–4 post-spill ($10\%$ of suitable root surfaces (area $>40 \text{ cm}$ deep) at unoiled sites, $5\%$ at oiled sites). Thus, there was a $50\%$ reduction in the amount of AHB independent of reductions in the surface area of submerged prop roots. In year 5 post-spill, the strength of this difference decreased to $25\%$. When added to reductions in amount of shoreline fringed with red mangroves and to decreases in density of submerged prop roots in surviving oiled fringe, a total reduction of $47\%$ of the potential habitat for mobile organisms using AHB as shelter was lost 5 years after the oil spill.

Results were also strong for wood-boring isopods in channels. In May 1991, the density of submerged prop roots was reduced by $40\%$ at oiled sites relative to unoiled sites. On remaining prop roots at oiled sites, isopod holes containing isopods were $42\%$ less common than at unoiled sites. However, this appeared due to a qualitative change in the state of submerged prop roots in oiled mangrove fringe, rather than a direct (toxicity) effect of oil. At oiled sites a greater proportion of submerged prop roots in the mangrove fringe were dead (Garrity et al., 1994) and isopods primarily burrow into the soft, uncorticated tissue near growing tips of live roots (Ellison and Farnsworth, 1990). Overall these changes led to a reduction of over $60\%$ in the number of submerged prop roots containing isopods at oiled sites 5 years after the oil spill (634 roots with isopods $100 \text{ m}^{-1}$ shoreline vs. 1,610 roots with isopods $100 \text{ m}^{-1}$ shoreline).
Hydrocarbon Contamination as a Continuing Factor.—Oil spills differ from natural disasters such as hurricanes in that chemical contamination may become chronic and affect recovery processes over the long term. Oil may damage organisms by direct contact (smothering) or by the effects of toxic hydrocarbon compounds (Bayne et al., 1982; Capuzzo, 1987; Levings et al., 1994). The direct effects of tarry compounds fade relatively quickly as they weather and harden. In contrast, toxic hydrocarbons deposited in anoxic soft sediments may persist for decades and exert continuing negative effects when leached from sediment reservoirs (Corredor et al., 1990; Teal et al., 1992; Burns et al., 1994).

In Bahía las Minas, bivalves accumulated high tissue levels of hydrocarbons at sheltered sites through at least 5 years post-spill and surprisingly unweathered oil residues were found at some heavily oiled sites (Burns et al., 1994; Burns and Yelle-Simmons, 1994; Levings et al., 1994). Lower cover of AHB on the open coast in years 2–4 post-spill could have been related to the presence of toxic compounds leaching from sediments (Burns and Yelle-Simmons, 1994) or to other physical changes in the habitat (i.e., increased light levels due to canopy thinning, Garrity et al., 1994). Levels of tissue hydrocarbon in bivalves at sheltered sites within Bahía las Minas were high enough that growth and reproduction were probably significantly reduced (Bayne et al., 1982; Levings et al., 1994). Unfortunately, no tissue hydrocarbon data are available for the open coast.

The effects of toxic hydrocarbons on the epibiota cannot yet be fully evaluated, and many questions remain unanswered more than 5 years after the spill. The lack of statistically significant changes in the percent of live roots with boring isopods or cover of red algae and of AHB in channels is puzzling, given the significantly reduced percent cover and high tissue burdens of hydrocarbons of oysters from the same sites (Crassostrea virginica, Levings et al., 1994). Data presented here start in the second or third year after the spill, when some effects of oiling may have been declining. Direct measurement of biomass or productivity might suggest a different interpretation. For example, growth of red algae at oiled sites may have been stimulated by the presence of hydrocarbons (Capuzzo, 1987) or by increased light levels after defoliation (Garrity et al., 1994). Isopods were present at oiled sites, but may have had altered population dynamics (Krebs and Burns, 1977) not detectable with our data. Separation of the effects of toxicants from those of physical changes to the habitat is especially important in biogenically-structured habitats, where decreases in the abundance of associated organisms could be caused both by loss of the habitat-structuring species and by continuing toxic effects.

Potential Effects on Associated Mobile Species.—For each year since the oil spill, the amount of fringing red mangrove suitable for associated mobile species was reduced at oiled sites. In 1991, 5 years post-spill, we estimated that ~40–50% of the potential substrate for juvenile spiny lobsters remained lost in both channels and the open coast. There were no significant differences in root size in channels after oiling, and differences on the open coast were lessening in the fifth year after the spill. Thus after 5 years, the estimated number of roots-unit⁻¹ shoreline was the most important component of habitat losses (quantitative reductions in juvenile habitat), while changes in root length were less important (qualitative changes). There was also an additional loss of AHB beyond reductions in suitable habitat, but the strength of this effect had declined to ~25% in year 5 post-spill. In contrast, for wood-boring isopods both the quantitative reduction in prop root density and the qualitative increase in the proportion of dead roots at oiled sites
affected isopod abundance. Only as the mangrove fringe becomes re-established will this lost habitat return.

This measure of potential habitat has two major components: (1) meters of shoreline fringed with red mangroves and (2) the density and physical state of submerged prop roots within the mangrove fringe. An oil spill might kill few mangroves, but if the density of submerged prop roots declines after oiling, substantial reductions in fringing habitat could occur, yet pass undetected. Additionally, analyses performed only on a per root basis, such as those of percent cover, may falsely indicate that communities may have returned to approximate pre-spill levels. Reductions in productivity caused by oiling will persist until the amount of substrate (in this case, submerged root surfaces) also returns to pre-spill levels. Similarly, Cubit and Connor (1994) report that populations of most small invertebrates living in beds of algal turfs on reef flats rebounded to the same levels at oiled and unoiled sites within 15 months post-spill. However, there were reductions in the absolute amount of algal turf at oiled sites immediately after the oil spill, and 2 years post-spill, there were disproportionate reductions of algal turfs during a period of extreme low water levels at oiled as compared to unoiled sites. These losses of algal turf both also constituted oil-related reductions in associated invertebrate populations. They concluded that “oil-caused reductions of habitat should be considered as deleterious for populations of small invertebrates as the direct lethal effects of oil.”

The overall functional impact of oil-induced damage on mobile species associated with mangrove roots will vary in part with how much of an area’s population depends upon fringing red mangroves. In areas where the submerged surfaces of prop roots of fringing mangroves constitute a large percentage of the potential habitat, negative effects on local populations of associated mobile species should be strong and detectable, despite natural inter-annual variation in recruitment and population size. On the other hand, where other potential settlement sites exist, there may be no substantial reductions. Mobile species which lack alternative habitats would probably be more strongly affected by reductions in fringing mangroves (Sheridan, 1992).

Planning for implementation of the Oil Pollution Act of 1990 is currently underway. Mangroves fringe an estimated 60–75% of the tropical and subtropical shorelines of the world, including subtropical Florida and the Caribbean basin (McGill, 1958; Odum et al., 1982). Despite the vulnerability of mangrove forests and the frequency of oil spills near them, relatively little is known about direct or indirect effects of oiling (Getter et al., 1981; Lewis, 1983; Jacobi and Schaeffer-Novelli, 1990; Burns et al., 1993). Our estimates for mobile crustaceans indicate that indirect effects of oiling may be common and are potentially strong. We here suggest that contingency plans put a high priority on keeping oil out of fringing red mangroves, and that damage projections that are part of contingency planning routinely consider long-term effects on associated species.

ACKNOWLEDGMENTS

K. Burns, R. Carney, J. Cubit and R. Green provided essential advice throughout the project. S. Loo de Lao assisted in statistical analyses. We thank two anonymous reviewers for helpful comments. Data collection was funded by the Smithsonian International Environmental Sciences Program and by contracts 14-12-001-30355 and 14-12-0001-30393 between the Minerals Management Service of the U.S. Department of the Interior and the Smithsonian Institution. We thank Recursos Marinos of the Republic of Panama for permission to work in Panama and the Smithsonian Tropical Research Institute for facilities.
LITERATURE CITED


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DATE ACCEPTED: December 8, 1993.

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