Changes in diets of river otters in Prince William Sound, Alaska: effects of the *Exxon Valdez* oil spill

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We studied the effects of the *Exxon Valdez* oil spill on the diets of river otters (*Lutra canadensis*) from oiled and nonoiled areas of Prince William Sound, Alaska, U.S.A., in 1989 and 1990. On the basis of identification of prey remains in their feces, otters fed principally on marine, bottom-dwelling fishes. Marine gastropods, bivalves, and crustaceans composed most of the invertebrates in the diet of otters; freshwater and terrestrial food items seldom occurred in their feces. The diets of otters included 149 different taxa, most of which rarely occurred in their feces. Sixty-five taxa occurred ≥5 times in our combined data set. Species richness and diversity of prey remains in otter feces were similar on oiled and nonoiled study areas in late winter (April) 1989 (before the oil spill) and during summer (June–October) 1989 following the spill. By summer (July–September) 1990, however, there were significant declines in the richness and diversity of species (mostly bony fish, molluscs, and bivalves) in otter diets on the oiled area. Likewise, the relative abundance of prey remains in otter feces showed strong differences between areas and years, and an area by year interaction. Members of the Perciformes and Archaeogastropoda declined from 1989 to 1990 on the oiled area while they increased on the nonoiled site; Malacostraca exhibited the opposite pattern. These outcomes, when considered with other data on body mass and blood chemistry, strongly suggest that some effects of the oil spill on otters were delayed.

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Nous avons étudié les effets du déversement accidentel de mazout par l'*Exxon Valdez* sur le régime alimentaire et la Loutre de rivière (*Lutra canadensis*) dans des zones affectées et des zones non affectées du détroit de Prince William, Alaska, É.-U., en 1989 et 1990. D'après l'analyse des restes de proies dans les fèces, les loutres se nourrissaient surtout de poissons marins benthiques. Les gastropodes, les bivalves et les crustacés marins constituaient la plus grande partie de la fraction d'invertébrés dans le régime des loutres; les fèces contenaient peu d'aliments consommés en eau douce ou sur terre. Cent quarante-neuf taxons différents ont été inventoriés dans les fèces, la plupart selon un taux de fréquence faible. Soixante-cinq taxons ont été trouvés ≥5 fois dans toutes nos données combinées. La richesse en espèces et la diversité des restes de proies dans les fèces étaient semblables dans les zones affectées et dans les zones non affectées à la fin de l'hiver (avril) 1989 (avant le déversement) et durant l'été (juin–octobre) 1989, après le déversement. À l'été (juillet–août) de 1990, cependant, des chutes importantes de la richesse en espèces et de la diversité (surtout des poissons osseux, des mollusques et des bivalves) ont été enregistrées dans le régime des loutres de la région affectée par le mazout. De même, l'abondance relative des restes de proies dans les fèces des loutres a diminué et il y avait de fortes différences entre les zones et entre les années et dans une même zone d'une année à l'autre. Les perciformes et les archéogastropodes ont diminué de 1989 à 1990 dans la zone affectée, alors qu'ils ont augmenté à un site non touché; la tendance inverse a été enregistrée chez les malacostracés. Ces résultats, examinés conjointement avec d'autres données sur la masse corporelle et la chimie du sang, semblent indiquer fortement que certains effets du déversement de mazout sur les loutres se sont manifestés à retardement.

[Traduit par la Rédaction]

Introduction

River otters (*Lutra canadensis*) inhabit marine environments along the shoreline of Prince William Sound, Alaska. These mustelids feed principally upon marine fish and invertebrates in subtidal and intertidal zones (Larsen 1984; Woolington 1984). Crude oil, spilled from the grounding of the tanker *Exxon Valdez* in late March 1989, spread southwesterly through Prince William Sound, contaminating extensive areas inhabited by river otters and their prey (Fig. 1). Moreover, river otters are sensitive to a variety of aquatic pollutants, and therefore serve as a good indicator of the effects of the oil spill on mammals (Duffy et al. 1993).

We hypothesized that if the oil spill affected the use of food by river otters, we should detect such changes in prey remains in otter feces over time. Likewise, we postulated that differences should occur in the diets of otters (as indexed by fecal remains) between oiled and nonoiled areas within Prince William Sound.

Methods

Study area

Intensive research on river otters was conducted primarily at the following two study sites: Herring Bay and surrounding areas on northern Knight Island (60°30′N, 147°4′W), which received heavy oiling; and Esther Passage (61°53′N, 147°55′W), which was about 40 km to the northwest and received no oil from the spill (Fig. 1). These study areas, each with about 80 km of shoreline, are ecologically similar. Shorelines in the Sound are steep and rocky, with many inlets and small bays. Terrestrial vegetation is dominated by

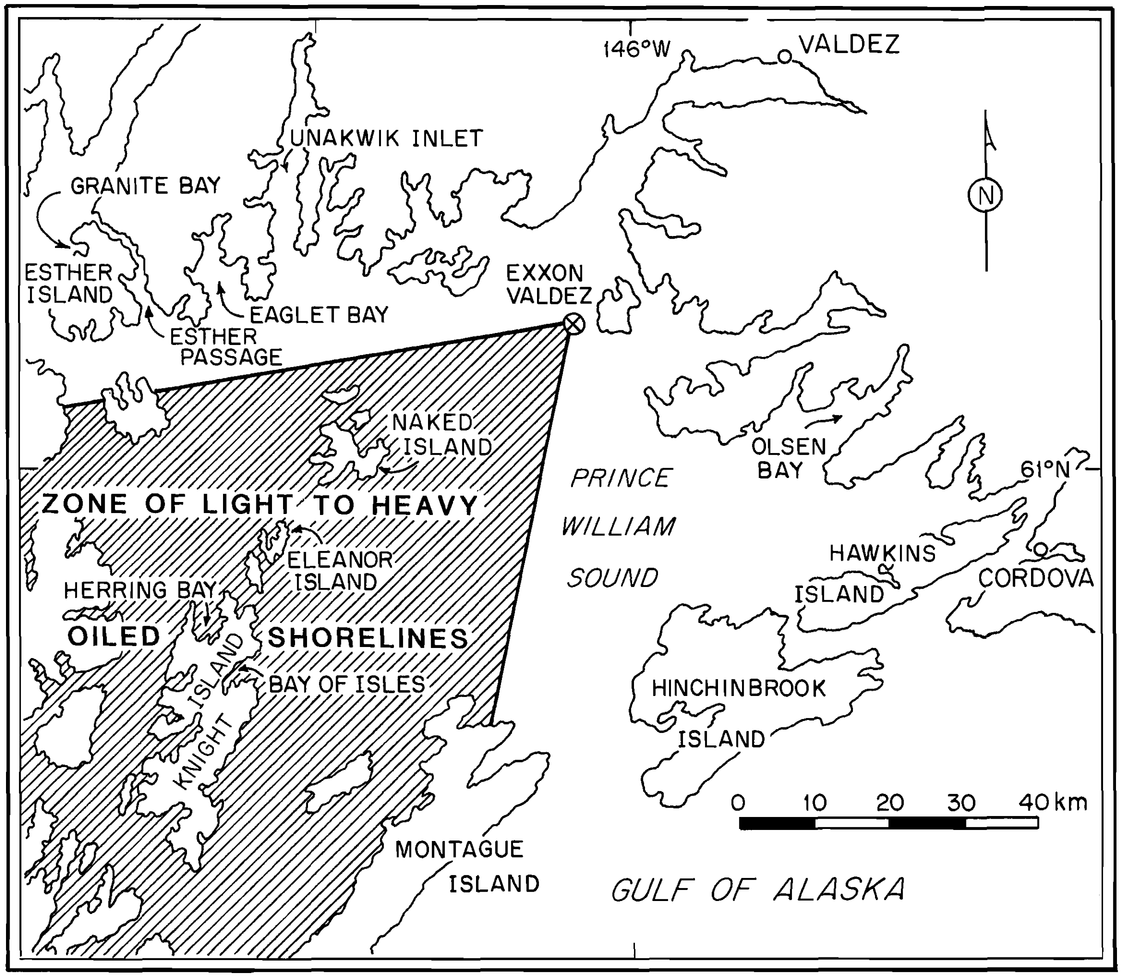

FIG. 1. The general path of crude oil spilled from the *Exxon Valdez* grounding in Prince William Sound, Alaska, U.S.A., in late March 1989. Intensive studies of river otters were conducted in the vicinity of northern Knight Island (oiled) and Esther Island (nonoiled).

old-growth forest composed mostly of hemlock (*Tsuga heterophylla*) and spruce (*Picea sitchensis*) near the shore; alpine tundra occurs at higher elevations. The Sound possesses a maritime climate and receives >200 cm of annual precipitation. The densities of river otters and their sign (latrine sites) were similar on both study areas (Testa et al. 1994), and river otters, which were implanted with radio-frequency transmitters and radioisotopes for other aspects of this study, did not move between Herring Bay and Esther Passage. All methods used in this study were approved by an independent Animal Welfare Committee at the University of Alaska Fairbanks.

Location and selection of latrine sites

In early April 1989, while crude oil was fresh on Knight Island, the shoreline both within the area of the spill and immediately to the north was searched for active latrine sites of river otters. Using small boats, biologists searched along the shore for signs of recent use by river otters. During the preliminary search, those sites that appeared to have been used recently by otters were flagged. Flagged sites were then evaluated, and those having ≥10 recent otter scats (feces), with ground vegetation and litter fall modified by otter activity, were selected for the study. Generally there were well-established trails and a central area of low vegetation or bare ground. Recently deposited scats were those that retained their structure and were not dissolved as a result of being "washed out" by heavy precipitation.

Once selected, the latrine site was cleaned of all feces, the search area was delimited with flagging, and the site was sketched in a field notebook. A permanent marker was placed in a nearby location visible from the water. The locations of those latrine sites were plotted on a 1 : 63 000 map from the U.S. Geological Survey to facilitate relocation. During this initial phase, latrine sites in Granite Bay, Esther Passage, and Eaglet Bay were selected for the source of nonoiled or control data. Our initial intent was not to locate every latrine site along a section of shoreline, but to obtain an adequate number of sites to provide data on rates of scat deposition. The north end of Knight Island, including Herring Bay, Louis Bay, and adjacent smaller islands, was selected as the oiled study area. In June 1989, both areas were revisited and additional latrine sites were located. The sample size for the remainder of the field season in 1989 was 54 latrine sites in the oiled area and 59 sites in the nonoiled area.

In 1990, in response to the needs of other aspects of this study to follow otters implanted with telemetry transmitters, the boundary of the nonoiled area was modified so that Granite Bay and Eaglet Bay were excluded. Both oiled and nonoiled areas were intensively searched again, this time to locate all active latrine sites. Criteria for selection and marking procedures were the same in both years. Additionally, approximately 15% of each study area was searched on foot to determine how often active sites were missed by searches from the skiff. Only one additional latrine site was discovered in this manner. For the 1990 field season, 113 latrine sites from the nonoiled area and 131 latrine sites from the oiled area were located.

During the initial cleaning and selection of active latrine sites in both study years, no effort was made to enumerate the scats present. The high volume of feces, particularly in instances where scats were protected from weather, likely represented many months of fecal deposition by otters. On subsequent visits in 1989, the number of scats collected from each site was recorded. When large groups of scats occurred, which could not be counted accurately, the number present was estimated on the basis of the average size of scats and the total volume of feces accumulated at the latrine. All otter feces were gathered, placed in plastic bags, labeled, and frozen. These sites were cleaned of all feces, so only new scats would be gathered in subsequent sampling efforts. To ensure that all scats were removed, each site was cleaned by two or more people, who covered the entire area independently. Scats gathered from a particular site were combined into a single sample. The procedures used to collect scats in 1990 differed slightly from those employed in 1989. In 1990, these sites were revisited after 2–3 days so that fresh scat could be collected as part of a mark–recapture study (Testa et al. 1994). This may have reduced the number of scats collected in the following month slightly, but persistence of intact otter scats for more than 2–3 weeks in heavy precipitation is considered unlikely (Jenkins and Burrows 1980).

Timing of sampling of latrines

The large volume of scat recovered from latrine sites in Herring Bay and the Esther Island area immediately following the spill (early April) was deposited by otters in late winter 1989, and thus represents diets before the oil spill. Latrine sites from oiled and nonoiled areas were sampled near midmonth for otter feces five times in summer 1989 (June, July, August, September, and October) and three times in summer 1990 (July, August, and September). We assume that otter feces collected from the same latrine site during different surveys were independent samples. Thus, samples from multiple surveys each summer were pooled into a single sample for statistical analysis. Otters have large (>20 km of shoreline), overlapping home ranges (R.T. Bowyer, J.W. Testa, and J.B. Faro, unpublished data), and many different otters had the opportunity to defecate at a latrine between surveys. We observed up to 15 otters at a latrine site, and isotope-labeled feces from otters (Testa et al. 1994) indicated that a single otter defecated at up to seven different latrine sites over 2–3 days. Any potential lack of independence is further minimized because we did not analyze feces from all latrine sites during each survey; samples were selected haphazardly within each survey. Overall, summer feces were analyzed from each latrine site in Herring Bay an average of 1.8 and 1.2 times in 1989 and 1990, respectively. Similarly, otter feces collected during summer from Esther Passage were sampled from each latrine site an average of 1.7 times in 1989 and 1.6 times in 1990. Laboratory resources and time did not allow the analysis of all samples.

Fecal analysis

Prey remains of feces were analyzed in a manner similar to that reported by Bowyer et al. (1983). Scat samples were washed in individual nylon-stocking bags to remove soft materials and then were air dried. The entire sample or a 10- to 20-g portion of it was then examined under a dissection microscope to identify food items to the lowest possible taxonomic level. A reference collection of skeletal remains of fish and invertebrates was used to aid in identification. Keys to otoliths (Morrow 1979), scales (Lagler 1974), and mammal hair (Adorjan and Kolenosky 1969) also were used. Bird remains and feathers were identified using a reference collection and available literature (Chandler 1916).

Species richness and diversity

For purposes of statistical analysis, we considered a species to be the lowest taxonomic level we were able to identify. This probably underestimates species richness for taxa for which we were unable to identify prey items below the family or genus level, and may overestimate richness where we created an "unidentified" food category for an item already found in the diet. This procedure, however, provides a valid method of making comparisons between oiled and nonoiled areas because samples were treated identically. We evaluated species diversity (H) with the Shannon–Wiener index:

[1] $H = -\Sigma P_i \ln P_i$

where P_i is the proportional occurrence of a species across latrine sites. We then rescaled H so that it was expressed as the relative number of species (Ricklefs 1973, pp. 686–687):

[2] $\text{Diversity} = e^H$

The species contained in the diet of otters living in marine environments are many and diverse (Larsen 1984). Thus, the occurrence of rare species might affect our comparison between oiled and nonoiled areas by including prey seldom consumed by otters. To control for this, we restricted our analyses of richness and diversity to species (i.e., unique food items) that occurred ≥5 times in the entire data set. Moreover, we arbitrarily eliminated taxa (classes) that did not contain ≥10% of all species identified; this results in a conservative analysis restricted to the most commonly identified food items. Then we used curve-linear regressions of the cumulative number of species identified against number of latrine sites sampled to assess whether an adequate sample was available to make comparisons (between areas and years). We judged that sample size was sufficient when a pronounced asymptote of this regression line occurred. The difference in species richness between oiled and nonoiled areas was evaluated with a χ^2 test; changes in the presence or absence of taxa among sampling periods were examined with the McNemar test for the significance of changes (Siegel 1956, pp. 63–67).

Relative species abundance

We examined prey remains in otter feces in two separate ways: the number of species present and their occurrence across latrine sites (species richness and diversity), and the relative abundance of species within latrine sites. Species abundance within latrine sites was assessed by calculating the proportional occurrence of food items by survey and site. These data also contain a bias related to the number of scats collected from a latrine site. Sites with more scats would be likely to have more species. Moreover, each species would represent a smaller proportion of the species present as the number of food items increased at a latrine site. Thus, we used multivariate analysis of variance (MANOVA), weighted by the number of scats at each latrine site, to evaluate the effects of area and year on diet. Percentage data were arcsine transformed to meet assumptions of this analysis. Likewise, to avoid this bias we present adjusted (least squares) means for the relative abundance of food groups based on the proportional occurrence of these prey at a latrine site weighted by the number of scats in that sample.

Results

Species richness and diversity

The diet of river otters inhabiting coastlines within Prince William Sound was highly diverse. In total, we recorded 149 "species" (i.e., the lowest unique taxonomic unit we could identify) in otter feces (Fig. 2; a list of species has been submitted to the Depository of Unpublished Data[1]). Many of these species were rare. To avoid undue influences from rare species, we eliminated any species that occurred ≤5 times in the entire data set, leaving 65 more common ones, composed mostly of bony fish, gastropods, and bivalves (Fig. 2). To assure adequate sample sizes for comparing oiled (Herring Bay) and nonoiled (Esther Passage) study areas, we further limited our analyses to taxa (fish, gastropods, and bivalves) that composed most of the prey remains in otter feces (Fig. 2). Curve-linear regressions of the cumulative number of unique food items (species) against the number of latrine sites sampled suggest that adequate samples were analyzed for both study sites (oiled and nonoiled) for summer (June–October) 1989 and summer (July–September) 1990, but perhaps not

[1]Copies of the list of species may be purchased from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada.

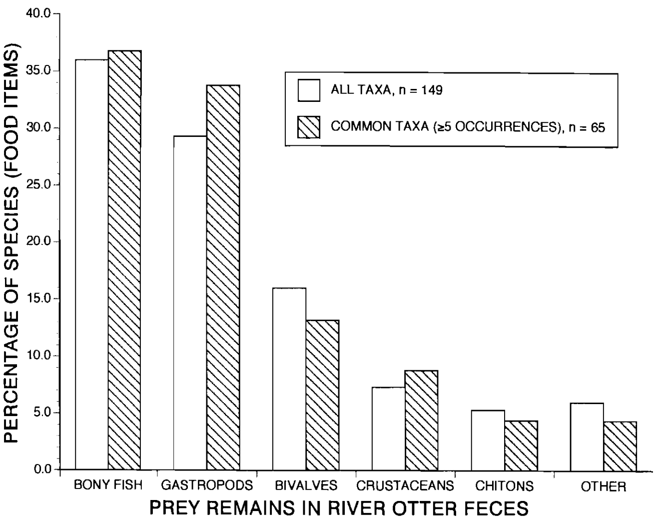

FIG. 2. Percentages of prey species in the feces of river otters in Prince William Sound, Alaska, U.S.A., 1989–1990.

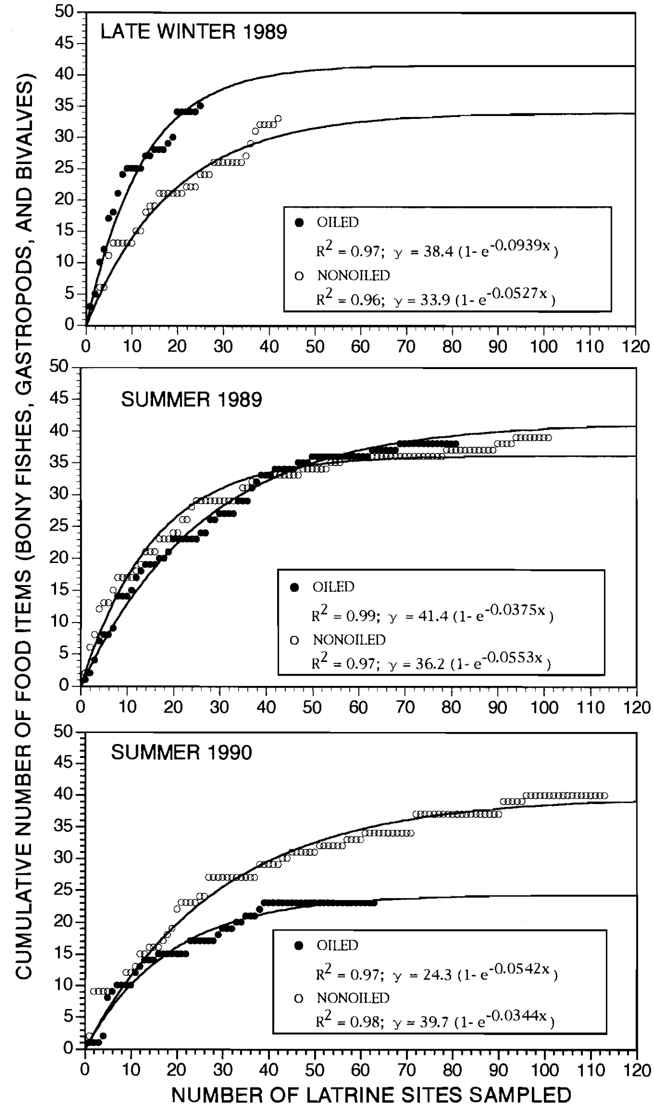

FIG. 3. Curve-linear regressions of cumulative number of unique food items (species) occurring ≥5 times in the feces of river otters against number of latrine sites sampled in Prince William Sound, Alaska, U.S.A. Equations are $Y = \alpha(1 - e^{-\beta x})$, where α is the asymptote and β is the slope. Note that adequate sample sizes were obtained for summer 1989 and summer 1990 (strong asymptotes), but that data for late winter 1989 may underestimate species richness.

for late winter (April) 1989 (Fig. 3). These analyses also suggest that there was a tendency for species richness in otter diets to decline over time on the oiled compared with the nonoiled area (Fig. 3). Species richness and diversity, however, did not differ significantly between oiled and non-oiled areas in late winter 1989 prior to the oil spill (Fig. 4). Likewise, differences in species richness evident by summer 1989 (Fig. 3) were not yet significant (Fig. 4). By summer 1990, however, a tremendous change in species richness and diversity had occurred, with the complete loss of 18 common species (49 total species) from the diets of otters on the oiled area (Fig. 4). The missing species were mostly bony fish (43%), gastropods (27%), and bivalves (12%). To further investigate this change, we examined species that remained the same (unchanged), disappeared from diets (lost), or were added to diets on both oiled and nonoiled areas with the McNemar test for significance of changes. Comparisons were made between late winter 1989 (before the oil spill) and summer 1989 (after the oil spill), and then again from summer 1989 to summer 1990. The only significant change was in the comparison of the oiled area between summer 1989 and summer 1990 (Fig. 5). Many species were common to both study areas in late winter 1989 and summer 1989. By summer 1990 there were significant changes in the distribution of species in otter scats between study sites (Fig. 6), with the loss of species from the oiled area being largely responsible for this difference.

Relative species abundance

We also examined the relative abundance of food items within latrine sites, by weighting the proportional occurrence of food items at a latrine by the number of scats collected from that site. Likewise, we pooled species into 18 taxonomic groups (Table 1) to have samples of sufficient size for analysis. Weighted MANOVA (18, 342 df), with taxonomic groups in the diet as dependent variables and area (oiled vs. nonoiled) and years (summer 1989 vs. summer 1990) and their interaction as main effects, indicated significant overall differences between areas (F = 9.19, $P < 0.001$), years (F = 4.31, $P < 0.001$), and a year by area interaction (F = 3.66, $P < 0.001$). Effects of oiling on the taxonomic groups in otter diets are most clearly interpreted from year by area interactions because changes in the abundance of these groups were in opposite directions on the two study areas from 1989 to 1990; groups exhibiting this pattern were Perciformes, Archaeogastropoda, and Malacostraca (Table 1). Inasmuch as the nonoiled area served as a control, area effects also are of interest; these were most pronounced for Pleuronectiformes and Scorpaeniformes (Table 1).

When both species richness (Fig. 4) and abundance (Table 1) are considered, it is clear that otters fed most often on taxa of bottom-dwelling fish. Otters also foraged on gastropods, bivalves, and crustaceans that represent life forms occurring in close association with the intertidal and subtidal substrates. Terrestrial or freshwater species of any taxa occurred rarely in the diet of otters (Table 1).

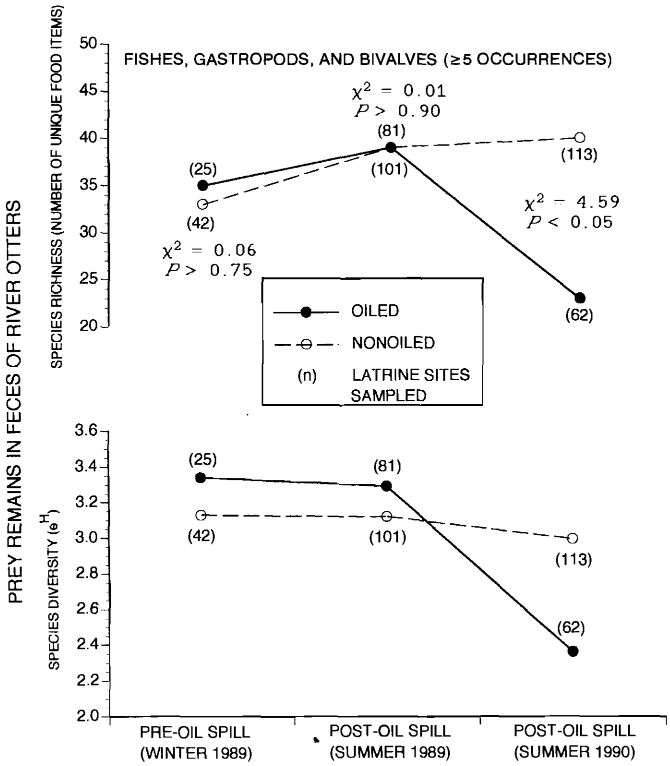

FIG. 4. Differences in species richness and diversity between oiled and nonoiled areas of Prince William Sound, Alaska, U.S.A.

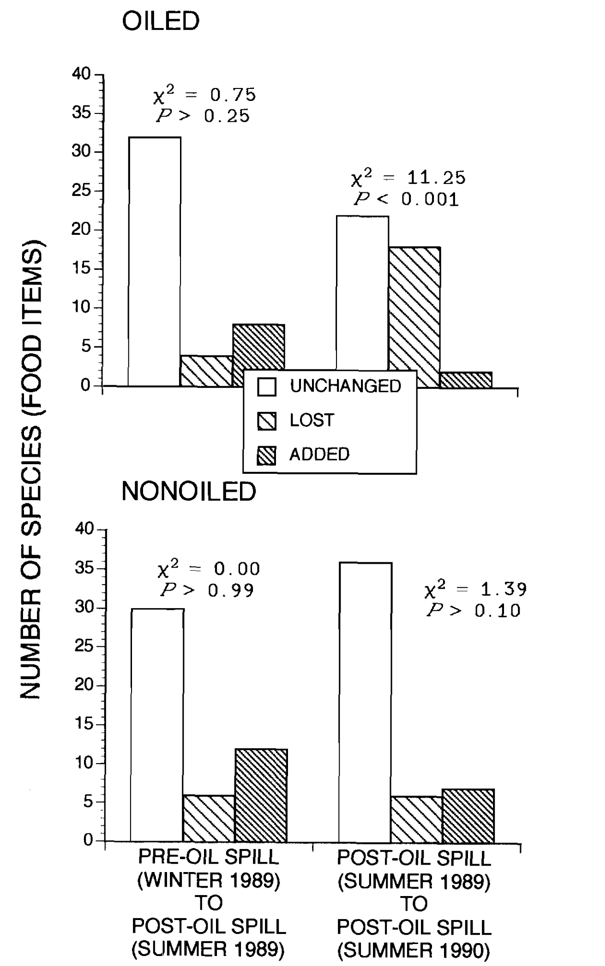

FIG. 5. Changes in prey species in the feces of river otters from Prince William Sound, Alaska, U.S.A. Note that significant changes occurred on the oiled but not the nonoiled area. The statistics are from the McNemar test for significance of changes.

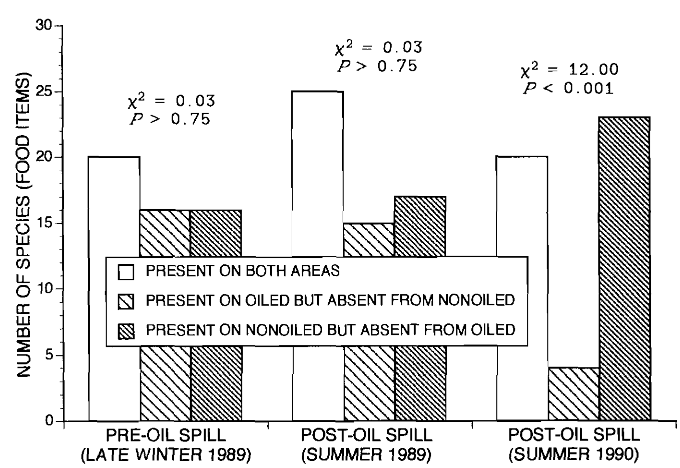

FIG. 6. A comparison of prey remains in the feces of river otters on oiled and nonoiled areas of Prince William Sound, Alaska, U.S.A., 1989–1990. Note that significant differences did not occur until summer 1990.

Discussion

Changes in species richness and diversity

Changes in the species richness and diversity of otter diets on the oiled area, which did not occur on the nonoiled area (Fig. 4), suggest that the effects of the oil spill were not clearly manifested in our data set until summer 1990, over 1 year after the spill and following a major effort to clean oil from shorelines. This time lag may have been related to the movement of oil from intertidal areas in 1989 to subtidal habitats in 1990 (S.C. Jewett, personal communication). Further, this change is not the result of otters feeding on different taxa between study sites. Taxa common to the diets of otters living in both areas in 1989 declined on the oiled site in 1990 (Figs. 5, 6). We know of no other factor except oil (or activities to clean contaminated shorelines) across these 80-km study sites that might be responsible for such differences. Moreover, the analysis of scats confirms that primary prey species of otters are those known to depend on intertidal and subtidal habitat that were exposed to oil.

Care must be used in interpreting our data. Oil contamination might affect diets of otters in many ways. Changes in prey remains in otter feces could result from variation in prey abundance, otters avoiding oil-contaminated prey or feeding areas, changes in the vulnerability of prey, or debilitated otters being less able to capture some types of prey. We cannot discriminate among these possibilities. Likewise, we recognize that it is not possible to reconstruct the biomass of taxa consumed by otters from their feces because we do not know the digestibility of various prey. More digestible food items are undoubtedly underrepresented in our samples. We also observed the shells of mussels (*Mytilus edulis*) and scallops (*Chlamys*) that ostensibly were consumed by otters at latrine sites; soft body parts of these bivalves would not be detected using our methods. Nonetheless, inherent biases in this methodology are the same for both areas and therefore allow a valid comparison between years as well as oiled and nonoiled

TABLE 1. Differences in prey remains in the feces of river otters from oiled (Herring Bay) and nonoiled (Esther Passage) study areas in Prince William Sound, Alaska, during summer (postspill) 1989 and 1990

	Oiled (%)		Nonoiled (%)		
Taxonomic group[a]	1989 (n = 82)	1990 (n = 63)	1989 (n = 102)	1990 (n = 90)	Differences
Unidentified Osteichthyes	9.8	36.7	16.7	30.4	Y
Perciformes	15.8	7.1	0.8	6.2	A, Y*A
Gadiformes	10.9	4.5	6.3	5.9	ns
Pleuronectiformes	0.0	<0.1	2.0	1.6	A
Scorpaeniformes	18.0	10.1	4.0	2.9	A
Unidentified Gastropoda	0.9	1.1	8.2	3.0	ns
Archaeogastropoda	2.1	0.0	0.7	0.9	Y, Y*A
Patellogastropoda	4.2	5.4	7.0	4.5	ns
Mesogastropoda and Cephalaspidea	4.5	1.3	5.5	3.9	Y
Unidentified Bivalva	3.9	2.7	5.6	6.9	Y
Veneroida and myoida	1.4	1.6	1.9	0.5	ns
Mytiloida	2.0	1.1	2.5	3.0	ns
Ostreoida	0.9	0.0	1.4	0.2	Y
Polyplacophora	1.5	0.5	2.6	0.3	Y
Malacostraca	4.2	7.2	16.6	9.0	Y, Y*A
Majidae and Cancridae	16.5	12.3	18.4	11.6	Y
Paguridae	1.8	0.0	2.3	0.4	Y
Other					
Insecta and Aves	2.5	7.5	3.8	7.1	Y

NOTE: Percentages are given as adjusted means weighted by the number of scats at each latrine site; sample sizes were obtained by pooling data from latrine sites across surveys. Statistical analyses are a posteriori comparisons from a MANOVA. ns, not significant ($P > 0.05$); Y, significant year effect ($P \leq 0.05$); A, significant area effect ($P \leq 0.05$); Y*A, significant interaction ($P \leq 0.05$).

[a]Some common names and further subdivisions of taxa have been submitted to the Depository of Unpublished Data (see text footnote 1).

study sites. Moreover, changes in species richness (Fig. 4) resulted from the complete disappearance of some taxa from the diet of otters (Figs. 5, 6); this outcome cannot be explained by differential digestibility of prey.

Changes in relative abundance

In addition to differences in digestibility, another potential problem exists in our data (Table 1). Because of the small number of samples analyzed for some surveys, it was necessary to pool data across each summer. This should not bias our comparison between oiled and nonoiled areas because the two data bases were treated identically. Nevertheless, this pooling of data requires us to assume that each latrine site represents an independent sample (when sites were each sampled an average of 1.2–1.8 times during summer). This has little effect on our test of hypotheses, however; even reducing the denominator degrees of freedom by half (i.e., 171 df) in our MANOVA still results in significant ($P < 0.001$) effects of area, year, and the year by area interaction on the abundance of prey items.

To the degree that the nonoiled area serves as a control, differences in the abundance of prey in otter feces between areas may be attributed to oiling. Certainly, species richness and diversity of prey in otter diets were generally similar for both areas prior to and immediately following the spill (Fig. 3); our analysis may underestimate richness on the oiled area because of fewer samples than from the nonoiled area (Fig. 3). Nonetheless, differences in species abundance in otter feces between areas from 1989 to 1990 (Table 1) should be interpreted with caution. Flatfish (Pleuronectiformes) were more abundant, and sculpin (Scorpaeniformes) less abundant on the nonoiled than on the oiled study site. Unidentified bivalves also were more common in otter feces from the nonoiled area (Table 1).

Food taxa showing interactions between year and area are of greater interest because the direction of change between years is different for oiled and nonoiled areas: the inference that the oil spill caused such changes is far stronger than for a comparison based on area differences alone. Remains of lances, gunnels, and searchers (Perciformes) declined on the oiled area whereas they increased in the feces of otters from the nonoiled site; this same pattern held for keyhole limpets and margarites (Archaeogastropoda) (Table 1). Crustaceans (Malacostraca), however, exhibited an opposite pattern (Table 1). Declines in bivalves and keyhole limpets in the diet of otters from the oiled area might be expected. These taxa are sessile as adults and occur mostly in intertidal areas that received heavy oiling. Marine fish, however, constituted much of the diet of otters in this study (Fig. 2, Table 1) and other studies of coastline populations in Alaska (Larsen 1984; Woolington 1984). Changes in the abundance of fish in their diet, therefore, would be expected to have the greatest consequences for marine populations of river otters. Indeed, Kruuk et al. (1991) noted that the abundance of fish was an important factor in the population dynamics of European otters (*Lutra lutra*) living in marine environments. Evidence that the changes in diets we noted may affect otter populations in Prince William Sound was provided by Duffy et al. (1993); otters from Herring Bay (oiled area) had significantly lower body mass than animals from Esther Passage (nonoiled area), as well as elevated haptoglobin levels in blood serum, suggesting that otters experienced toxicological effects from oil contamination. Otters inhabiting oiled areas throughout broad regions of Prince William Sound had elevated levels of blood haptoglobin and abandoned use of latrine sites at high rates in 1991 (Duffy et al. 1994). We believe that too much emphasis has been placed on the more immediate effects of the oil spill, and suggest that there is a need for long-term studies of otters and other vertebrates to adequately evaluate this catastrophe.

Acknowledgments

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