

YALE PEABODY MUSEUM

P.O. BOX 208118 | NEW HAVEN CT 06520-8118 USA | PEABODY.YALE. EDU

JOURNAL OF MARINE RESEARCH

The *Journal of Marine Research*, one of the oldest journals in American marine science, published important peer-reviewed original research on a broad array of topics in physical, biological, and chemical oceanography vital to the academic oceanographic community in the long and rich tradition of the Sears Foundation for Marine Research at Yale University.

An archive of all issues from 1937 to 2021 (Volume 1–79) are available through EliScholar, a digital platform for scholarly publishing provided by Yale University Library at <https://elischolar.library.yale.edu/>.

Requests for permission to clear rights for use of this content should be directed to the authors, their estates, or other representatives. The *Journal of Marine Research* has no contact information beyond the affiliations listed in the published articles. We ask that you provide attribution to the *Journal of Marine Research*.

Yale University provides access to these materials for educational and research purposes only. Copyright or other proprietary rights to content contained in this document may be held by individuals or entities other than, or in addition to, Yale University. You are solely responsible for determining the ownership of the copyright, and for obtaining permission for your intended use. Yale University makes no warranty that your distribution, reproduction, or other use of these materials will not infringe the rights of third parties.



This work is licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License.
<https://creativecommons.org/licenses/by-nc-sa/4.0/>



Differential responses of two nearshore infaunal assemblages to experimental petroleum additions

by Jeffrey L. Hyland,^{1,2} Eva J. Hoffman¹ and Donald K. Phelps³

ABSTRACT

Empirical support is provided for the hypothesis that benthic communities found in relatively constant and predictable environments are less stable (resistant and resilient) following unusual disturbances than lower-diversity communities found in more inconstant and unpredictable environments. A less diverse benthic community (i.e., the *Streblospio-Tubificoides* assemblage) inhabiting an inconstant and unpredictable, shallow marsh cove was disturbed less and recovered faster from an experimental addition of No. 2 fuel oil, than the more diverse benthos (i.e., the *Nucula-Mediomastus* assemblage) inhabiting a relatively more constant and predictable, deeper coastal embayment. Disturbed sediment had a stimulatory effect on most populations in the marsh and an inhibitory effect on most populations in the bay. Initial amount and subsequent behavior of oil were similar in the two environments. Thus, differential responses of the two communities are attributable to intrinsic biological properties rather than differences in levels or composition of oil.

1. Introduction

This paper presents results of an *in situ* study of the responses of two macro-infaunal assemblages, observed in the vicinity of Narragansett Bay, Rhode Island, to experimental additions of No. 2 fuel oil. One of these assemblages is dominated by the polychaete *Streblospio benedicti* and oligochaete *Tubificoides brownae*, the other is dominated by the bivalve *Nucula annulata* and polychaete *Mediomastus ambiseta*. Both assemblages consist of a variety of marine and estuarine organisms inhabiting nearshore subtidal muddy substrates. The former assemblage is less diverse, consists of a greater proportion of eurytolerant and opportunistic species, and is found in a more inconstant and unpredictable local environment (Hyland, 1981).

Studying the responses of two disparate infaunal assemblages to an equivalent disturbance has enabled us to test a recent hypothesis that provides a theoretical basis for prediction of relative stability in marine and estuarine benthic communities. Specifically, we conducted a study to examine the hypothesis that simple, low-diversity

1. Graduate School of Oceanography, University of Rhode Island, Narragansett, Rhode Island, 02882, U.S.A.

2. Present address: Battelle New England Marine Research Laboratory, 397 Washington Street, Duxbury, Massachusetts, 02332, U.S.A.

3. Environmental Protection Agency, South Ferry Road, Narragansett, Rhode Island, 02882, U.S.A.

communities found in inconstant and unpredictable environments are inherently more stable than the diverse communities characteristic of more constant and predictable environments. This hypothesis, which we will refer to as the "response to disturbance hypothesis," is a corollary to the "stability-time hypothesis" of Sanders (1968, 1969) and has been presented in various forms by Slobodkin and Sanders (1969), Copeland (1970), Boesch (1974), and Boesch and Rosenberg (1981).

The term stability has several meanings (Orians, 1975). Here it refers to the ability of a system to maintain or return to an initial state after an external disturbance (either a man-induced or an unusual natural disturbance) and includes two components, resistance or the ability to withstand the source of disturbance without change, and resilience or the degree and speed at which the system returns to a normal state following the disturbance (Boesch, 1974). The terms inconstant and unpredictable describe environments in which the variances of environmental parameters around their mean values are both relatively high and unpredictable (Slobodkin and Sanders, 1969).

The response to disturbance hypothesis is based on the deduction that low-diversity communities inhabiting naturally inconstant and unpredictable environments should be more stable following general disturbances (including man-induced disturbances) because constituent fauna are more resistant, due to broad physiological tolerances, and because they are more resilient, due to life-history and dispersal adaptations that facilitate rapid colonization of the disturbed substrate (Boesch and Rosenberg, 1981). In environments that are more constant and predictable over long periods, there is less of a demand on species to reproduce, grow, and recruit rapidly, or to adapt to a broad range of environmental conditions; therefore these species acquire more conservative growth and reproductive properties, and at the same time they become more specialized, hence more sensitive to abnormal conditions.

The belief that complex, diverse communities are less stable than simple, low-diversity communities is at variance with conventional views on this subject, which were widely accepted prior to the last decade (see review by Goodman, 1975). Support however is provided by May (1974) who demonstrates through use of mathematical models that low-diversity systems are more stable than higher-diversity, more complex systems. Recent field studies addressing this subject provide additional empirical support (Boesch and Rosenberg, 1981) although to date relatively few of these have been conducted.

While the response to disturbance hypothesis can apply to general disturbances, we chose to examine responses to disturbances caused by petroleum hydrocarbons, a major pollution source in developed coastal regions. No. 2 fuel oil was selected because of its reported toxicity (Sanders *et al.*, 1980) and its wide distribution for use as home heating oil.

The overall experimental approach used in this study was to monitor relative responses of the *Nucula-Mediomastus* and *Streblospio-Tubificoides* assemblages to

equivalent additions of No. 2 fuel oil in experimental sediment chambers deployed in each of the two study areas. Responses were monitored throughout a one-year period. Composition and levels of No. 2 fuel oil were measured throughout the study by gas chromatography and mass spectrometry.

2. Description of study areas and assemblages

Our choice of the *Streblospio-Tubificoides* and *Nucula-Mediomastus* assemblages resulted from a conscious effort to select two assemblages that have different enough structure and composition to permit a test of the response to disturbance hypothesis, yet that share some basic attributes so that legitimate comparisons could be made. The two assemblages are similar in the sense that both are subtidal, macro-infaunal assemblages; the faunas of both were sampled within the same size range (with a 300- μm screen); and both inhabit similar types of substrate (poorly-sorted, medium to coarse silts with comparable amounts of organic matter). Structure and composition of the two assemblages however are distinctly different, which we assume is largely the result of differences in salinity regimes and the constancy and predictability of the two local environments.

The *Streblospio-Tubificoides* assemblage is found in a more inconstant and unpredictable environment, in a shallow marsh cove bordering the Pettaquamscutt River, Rhode Island (referred to as the marsh site, Fig. 1). Water depth in the area is approximately one meter. Salinities are extremely variable ranging from upper-oligohaline to mid-polyhaline (e.g., 5.0–23.0‰). Temperatures vary over short periods (e.g., at least 2°C within one tidal cycle) as well as seasonally (e.g., 0.0–25.0°C August 1977 to August 1978). At times during the winter the entire cove is covered by ice. Also, at times, particularly during the spring, sporadic surges of fresh water from a storm drainage ditch enter the head of the cove and cause unpredictable variations in salinity.

In contrast, the *Nucula-Mediomastus* assemblage is found in a more constant and predictable nearshore environment, in a much deeper area (approximately 9 m) in southcentral Narragansett Bay (referred to as the bay site, Fig. 1). Salinities in this area are high and stable (e.g., 29.5 to 31.0‰, August 1977 to August 1978); and although temperatures vary widely seasonally (e.g., 1.8 to 21.1°C, August 1977 to August 1978) they are relatively stable over shorter periods (e.g., only 0.5°C variation recorded within a one-week sampling period during September, 1979; data provided by EPA, Narragansett, R.I.).

The *Streblospio-Tubificoides* assemblage is less diverse (i.e., it has fewer species) than the *Nucula-Mediomastus* assemblage, as shown by comparison of species numbers in Tables 1 and 2. Moreover, this assemblage has greater proportions of opportunistic species (with a large potential for growth, reproduction, and rapid recruitment) and eurytolerant species that are resistant to a wide variety of environmental disturbances.

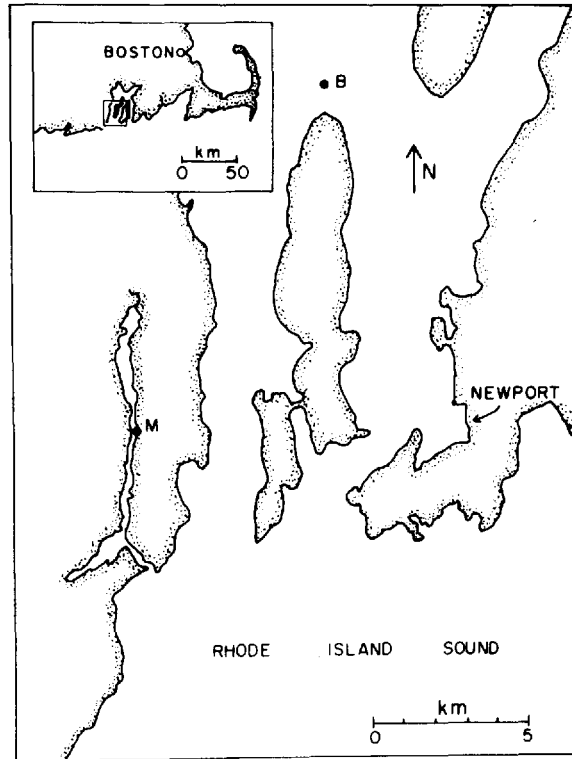


Figure 1. Map of Narragansett Bay showing location of bay (B) and marsh (M) study sites.

The *Streblospio-Tubificoides* assemblage is defined by its two most abundant species, the polychaete *Streblospio benedicti* and oligochaete *Tubificoides brownae*. *Tubificoides brownae* is one of several recently described species from the east coast of the United States (Brinkhurst and Baker, 1979) which in the past were often identified as *Pelosclex gabriellae*. Co-dominants in this assemblage (i.e., among the five most abundant species on a given sampling occasion) include the polychaetes *Nereis succinea*, *Scoloplos robustus*, *Heteromastus filiformis*, and *Hosbonia florida*, and the amphipods *Ampelisca abdita* and *Gammarus mucronatus*. Species which are not ranked as dominants but are still important numerically include the polychaete *Eteone heteropoda*, bivalve *Macoma balthica*, and crab *Rhithropanopeus harrisi*. The classic opportunistic polychaetes *Capitella capitata* and *Polydora ligni* (Grassle and Grassle,

Table 1. Total number of species found on various sampling occasions at the bay and marsh sites (per ten combined, replicate 0.0042 m² samples).

	Aug 77	Sept 77	Dec 77	Apr 78	Aug 78	Overall
Bay	28	31	28	26	38	56
Marsh	13	14	11	14	13	25

Table 2. Average number of species found per each replicate sample of the natural bottom (0.0042 m²) on various sampling occasions at the bay and marsh sites. Asterisks indicate significant differences at the 5% level in comparison to corresponding values for the Bay, based on results of Student *T*-tests.

	Aug 77	Sept 77	Dec 77	Apr 78	Aug 78
Bay	11.4	13.0	11.9	11.7	15.8
Marsh	7.6*	5.4*	5.8*	5.8*	6.6*

1974) are present throughout the area in low abundances, but appear in increased proportions whenever disturbed or new substrates are available. Members of this assemblage have been reported in disturbed environments throughout the world (Pearson and Rosenberg, 1978).

In contrast, the *Nucula-Mediomastus* assemblage is characterized by a greater number of species (Tables 1 and 2). Moreover, while eurytolerant and opportunistic species are present, there are larger proportions of species that are more conservative (with less potential for rapid colonization of new or disturbed substrate) and that are generally more sensitive to disturbance.

The *Nucula-Mediomastus* assemblage is defined by its two most abundant species, the bivalve *Nucula annulata* and polychaete *Mediomastus ambiseta*. Co-dominants include the bivalves *Yoldia limatula* and *Mulinia lateralis*, the gastropods *Turbonilla* sp., *Acteocina canaliculata*, and *Nassarius trivittatus*, the polychaetes *Nephtys incisa* and *Polycirrus eximius*, and the amphipods *Ampelisca abdita* and *Unciola irrorata*. Species which are not ranked as dominants but are still important numerically include the polychaetes *Asychis elongata*, *Ninoe nigripes*, *Tharyx* sp., and *Pholoe minuta*, and the bivalve *Macoma tenta*. The bivalve *Pitar morrhua* has a low relative abundance but is important due to its large biomass. *Polydora ligni* and *Capitella capitata* are present in low abundances. Rhoads et al. (1978) refer to the similar *Nucula-Nephtys* assemblage, reported from Buzzards Bay (Sanders, 1958) and Long Island Sound (Sanders, 1956; Rhoads et al., 1978), as an "equilibrium community."

For further detail on these assemblages see Hyland (1981).

3. Methods

a. Treatment and in situ monitoring of infaunal samples. A total of 240 sediment samples were collected for infaunal analysis. Samples were collected by scuba, in capped butyrate tubes that had an inner diameter of 7.3 cm (0.0042 m²) and that were 15 cm long. Table 3 summarizes the sampling strategy.

Ten replicate samples of the natural bottom were collected from each of the two study sites on five separate occasions, during August, September, and December of 1977, and April and August of 1978. During the initial August 1977 sampling, an additional 70 cores were collected from each site to use as oiled and control sediment chambers. These were returned to the laboratory immediately after collection and

Table 3. Number of samples for infaunal analysis. Natural bottom samples (NB), oiled samples (O), controls (C).

	Aug 77			Sept 77		Dec 77		Apr 78			Aug 78	
	NB	O	C	NB	O	NB	O	NB	O	C	NB	O
Bay	10	10	10	10	10	10	10	10	10	10	10	10
Marsh	10	10	10	10	10	10	10	10	10	10	10	10

placed in tanks of flowing seawater. The caps were removed and replaced with 300- μ m screen covers to prevent animals from escaping. Otherwise, they were left intact.

Fifty of the 70 chambers from each site were kept in a separate tank and were treated with No. 2 fuel oil. Oil was injected directly into the sediment of each chamber with an automatic syringe. An attempt was made to inject the oil in a number of positions to minimize patchiness and to distribute it equally at all depths. Enough oil was added initially to yield a nominal concentration of 10 mg/g dry weight sediment. This level was selected because it was anticipated as being high enough to produce measurable biological responses, yet was not regarded as being unrealistically high. Comparable levels were reported after the West Falmouth spill (Sanders *et al.*, 1980) and are found in the upper Narragansett Bay, Rhode Island, in areas receiving chronic oil discharges (Farrington and Quinn, 1973).

Ten of the 50 oiled chambers and ten of the remaining 20 unoled chambers from each site were maintained in laboratory tanks for a period of 48 hours to assess initial impact. The ten unoled chambers served as controls to assess any initial effects induced by the experimental technique itself.

The remaining 40 oiled chambers and ten unoled chambers were capped and then returned to the field within 48 hours after the initial collection. To facilitate their deployment, chambers were contained in compartmentalized boxes fabricated from PVC. Oiled and unoled chambers were contained in separate boxes. Each box was buried back into the mud, such that the tops of the chambers were flush with the surrounding mud surface. Chamber caps were removed after burial.

A set of ten oiled chambers were collected from each site at the same time that natural bottom samples were collected, i.e. during September 1977 (1 mo. after oiling), December 1977 (4 mo. after oiling), April 1978 (8 mo. after oiling) and August 1978 (12 mo. after oiling). In addition, the remaining ten unoled chambers were collected during the April 1978 sampling period to assess any long-term effects induced by the technique.

Once collected, samples were sieved on a 300- μ m screen and the contents on the screen preserved in 10% buffered formalin with phloxine B added to facilitate sorting. Organisms were removed from the debris, enumerated, and identified to the species level wherever possible. Colonial coelenterates and ectoprocts, larval forms, and smaller meiofaunal members, such as the nematodes, copepods and forams, were omitted from analysis. Complete species lists can be obtained from the senior author.

b. Hydrocarbon analysis. Eight additional sediment cores were collected from each site during the initial sampling period for hydrocarbon monitoring. Oil was introduced to each sample as described above. One sample from each site was frozen immediately after oiling, and the remaining seven were placed in tanks of flowing seawater. After 48 hours, a second was frozen, and the remaining six were returned to the field and buried flush with the surrounding sediment surface as described above. One sample was then retrieved from each site at periods of one week, two weeks, one month, four months, eight months, and one year after deployment. An additional sample of the natural bottom was collected for hydrocarbon analysis each time an oiled sample was retrieved. After collection, all samples were frozen until analyzed.

Prior to analysis, each sample was partially thawed and subdivided into three equal sections, 0–5 cm (surface), 5–10 cm (middle), and 10–15 cm (bottom). In addition, a surficial section (0–1 cm) was taken from each marsh sample, and subsequently from a single oiled sample maintained in the bay for eight months (from 6/79 to 1/80).

After addition of $n\text{-C}_{22}$ and chrysene internal standards, approximately 1 to 30 g (dry weight) of sediment were extracted with 0.5 N KOH in methanol under reflux conditions for $2\frac{1}{2}$ hours. The mixture was filtered, and the filtrate was extracted three times with petroleum ether. The petroleum ether was evaporated under reduced pressure below 30°C on a rotary evaporator to approximately 1 ml. The extract was then charged to a fully activated silica gel column, as described by Hoffman and Quinn (1978). The f_1 fraction (i.e., saturated hydrocarbons) and f_2 fraction (i.e., aromatics and other unsaturated hydrocarbons) were eluted with hexane and an 80–20 mixture of hexane and dichloromethane, respectively. These fractions were each evaporated down to a volume of 0.1 ml, and 1 μl of each was injected on a Hewlett Packard 5840 gas chromatograph equipped with an automatic liquid sampler and a 20-m long, OV-101 glass capillary column. The concentration of hydrocarbons in each fraction was then determined by comparing the area under the internal standard peak to the sample area. The identity of specific aromatic compounds was confirmed by gas chromatography/mass spectrometry. These analyses were performed on a 30-m, OV-101 column in a Shimadzu Model GC-4CM gas chromatograph with splitless injection. The chromatograph was coupled to a Finnigan 1015 mass spectrometer equipped with a Systems Industries data system and Riber 400 D-8 software.

c. Analysis of community responses. Response of each assemblage to petroleum addition was evaluated by comparing changes in community structure and composition in oiled sediment chambers to corresponding samples of the natural bottom and unoiled control chambers. We focus here on changes in two community measures, numbers of species and individual species abundances. While more complicated approaches to data analysis were attempted, these simple measures revealed the clearest patterns of community response to disturbance.

Changes in numbers of species were examined with reference to both average and total species numbers. Results are presented graphically. Changes in species abun-

Table 4. Hydrocarbon concentrations ($\mu\text{g/g}$ dry weight) in oiled and natural bottom samples of marsh sediment.

	Oiled				
	0-1 cm	0-5 cm	5-10 cm	10-15 cm	ave
Initial	54300	33500	6170	543	13400
2 days	35500	19800	5900	306	8670
1 wk	35500	25500	4490	523	10200
2 wk	46200	32800	2530	166	11800
1 mo	11300	11800	4530	454	5590
4 mo	5900	13400	3380	173	5650
8 mo	254	11000	5350	102	5480
1 yr	750	8250	4720	523	4500
	Natural Bottom				
	0-1 cm	0-5 cm	5-10 cm	10-15 cm	ave
Mean \pm S.D. for 4 sampling occasions	114 \pm 10	114 \pm 19	79 \pm 26	52 \pm 30	82 \pm 20

dances were examined for those species that were abundant enough to recognize patterns. These species were divided into three categories: those that showed net decreases in oiled samples (sensitive species), those that showed no consistent changes (resistant species), and those that showed net increases (resistant species with stimulated population growth). Distributions of abundance with time for those species that showed population changes are also presented graphically.

Analyses of variance and *t*-tests were the primary methods used to measure statistical differences; an alpha value of 0.01 was selected as the significance level. Tests for differences in abundance were performed on log-transformed ($\log_{10}x + 1$) data. Concordance analysis (Kendall, 1975) was also used to test for trends in the ranking of relative abundances in the various sample types.

4. Results

a. Hydrocarbons. Natural bottom samples of the bay and marsh contained similar levels of hydrocarbons (Tables 4 and 5). Concentrations of total hydrocarbons averaged over all depths and sampling periods were 111 $\mu\text{g/g}$ dry wt. sediment for the bay and 82 $\mu\text{g/g}$ for the marsh. These levels are typical of moderately clean areas of Narragansett Bay (Farrington and Quinn, 1973). Chromatograms of the f_1 fractions from both areas, however, contained a noticeable unresolved complex mixture (UCM) revealing low background levels of degraded petroleum hydrocarbons (Fig. 2). Ratios of f_1 to f_2 fractions were slightly higher for the bay, due to the larger size of the UCM in bay samples and the larger proportion of resolved components in marsh samples.

Table 5. Hydrocarbon concentrations ($\mu\text{g/g}$ dry weight) in oiled and natural bottom samples of bay sediment.

	Oiled				
	0-1 cm*	0-5 cm	5-10 cm	10-15 cm	ave
Initial	—	36400	2880	271	13200
2 days	—	35200	1760	150	12400
1 wk	—	37000	3290	63	13500
2 wk	—	19500	2070	360	7310
1 mo	—	9160	5820	1160	5380
4 mo	—	2540	21300	805	8220
8 mo	177†	4360	4480	1280	3370
1 yr	—	12600	3410	436	5480

	Natural Bottom				
	0-1 cm	0-5 cm	5-10 cm	10-15 cm	ave
Mean \pm S.D. for 8 sampling occasions	—	149 \pm 29	94 \pm 30	70 \pm 21	111 \pm 32

*The 0-1 cm section was not monitored routinely in the bay series.

†This sample was initially oiled in June, 1979 and deployed for eight months. All other samples were oiled in August, 1977 and deployed for the periods shown.

Oil behaved similarly in the two environments. This was a fortunate occurrence considering the original objective to examine differential community responses to an equivalent source of perturbation. Several trends in the hydrocarbon data (Tables 4 and 5) illustrate this important point. First, in both series of oiled samples, there was an initial concentration of approximately 13,000 $\mu\text{g/g}$ averaged over all depths. Second, although an attempt was made initially to add the oil to the chambers uniformly from top to bottom, in both series oil was immediately redistributed such that greater than 80% was found in the top five centimeters of sediment. Presumably this resulted from the oil either migrating through pore waters or through puncture holes made during initial oil injection. Third, there was a similar net loss of oil with time. In both series, initial concentrations (averaged over all depths) dropped by 60% to approximately 5000 $\mu\text{g/g}$ by the end of the first month, and then remained near this level for the rest of the year. Again, this loss presumably resulted from physical processes.

A fourth similarity is that in either series, regardless of depth, there was no qualitative chemical change in oil composition as a result of preferential weathering of certain hydrocarbon classes over others. This is illustrated in Table 6 which presents ratios of $n\text{-C}_{18}$ to phytane in the top five centimeters of oiled bay and marsh sediment as a function of time. Since microbial action affects normal alkanes at a faster rate than branched alkanes, a decreasing ratio of $n\text{-C}_{18}$ to phytane would provide evidence of preferential weathering. These data do not reveal any trend distinguishable from

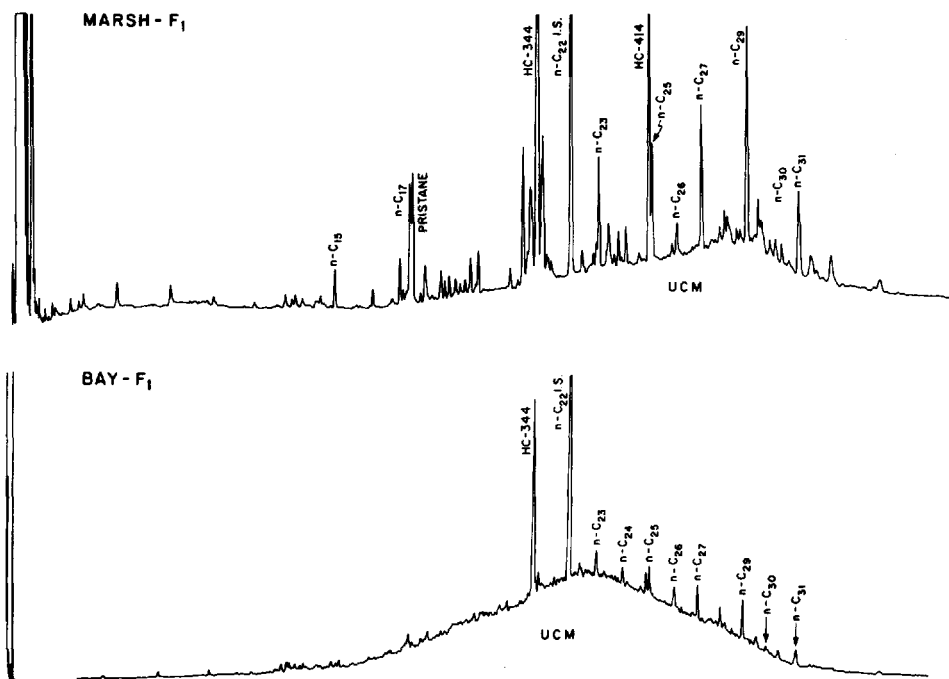


Figure 2. Gas chromatograms of the saturated (f_1) hydrocarbon fraction from natural bottom samples of the bay and marsh.

background variability. Several other indicators were evaluated, but similarly none revealed changes in oil composition. These included ratios of $n\text{-C}_{17}$ to pristane, percent resolved hydrocarbons relative to total hydrocarbons, percent f_1 and f_2 fractions relative to total hydrocarbons, ratios of $n\text{-C}_{10}$ to $n\text{-C}_{17}$, ratios of $n\text{-C}_{13}$ to $n\text{-C}_{17}$, and ratios of $n\text{-C}_{10}$ through $n\text{-C}_{19}$ to $n\text{-C}_{13}$.

There was no evidence of preferential weathering even in the uppermost centimeter of sediment, where one might expect a large amount of microbial activity. This is illustrated in Figures 3 and 4, which compare chromatograms of fresh No. 2 fuel oil with chromatograms of the uppermost centimeter of oiled marsh sediment deployed for eight months. Chromatograms of bay sediment, although not provided, show similar results. There is no indication of a loss of lower molecular weight alkanes and

Table 6. Ratios of $n\text{-C}_{18}$ to phytane in the top five centimeters of oiled marsh and bay sediment. Values in parentheses refer to number of sample splits run to evaluate variability within a sample.

	Initial	2 days	1 wk	2 wk	1 mo	4 mo	8 mo	1 yr
Bay	4.93	4.43 ± 1.25(4)	3.17	4.81	4.85	4.36	3.88	3.92
Marsh	4.88	4.98	5.18	3.04	5.05	4.71	5.00	3.96
No. 2 fuel oil	= 5.02 ± 0.07(2)							

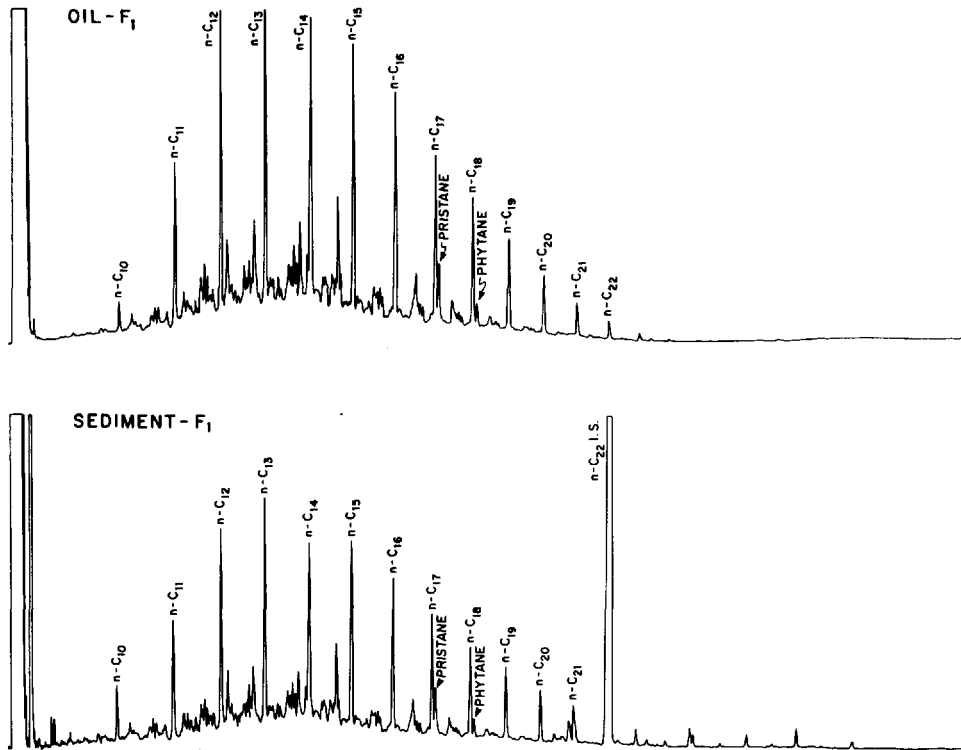


Figure 3. Gas chromatograms of the saturated (f_1) hydrocarbon fraction from fresh no. 2 fuel oil and from experimentally oiled marsh sediment maintained *in situ* for eight months.

aromatics relative to compounds of higher molecular weight, no indication of preferential alkane degradation compared to isoprenoids (e.g., nC₁₇/pristane and nC₁₈/phytane), nor any trend of preferential aromatic losses or enrichments with time. Chromatograms of both fresh oil and surficial sediment contain similar proportions of normal alkanes ranging from nC₁₀ to nC₂₂, with a maximum around nC₁₂ to nC₁₆; pristane and phytane isoprenoids; the unresolved envelope of numerous isomeric and homologous hydrocarbons, including aromatics and cycloalkanes; and toxic aromatics, including low-boiling C₂ to C₇ alkylated benzenes, and higher-boiling compounds such as naphthalene and C₁ to C₄ alkylated naphthalenes.

Changes in the chemical composition of oil as it degrades in sediments have been noted in other field (Spies and Davis, 1979; Hershner and Lake, 1980; Sanders *et al.*, 1980) and mesocosm (Gearing *et al.*, 1980) studies. Several factors could have prevented detection of these changes in the present study. First, a large amount of unweathered No. 2 fuel oil was injected directly into the sediment at various depths, including those below the redox potential discontinuity (RPD) layer where degradation is normally limited due to anaerobic conditions. Second, the normal position of the

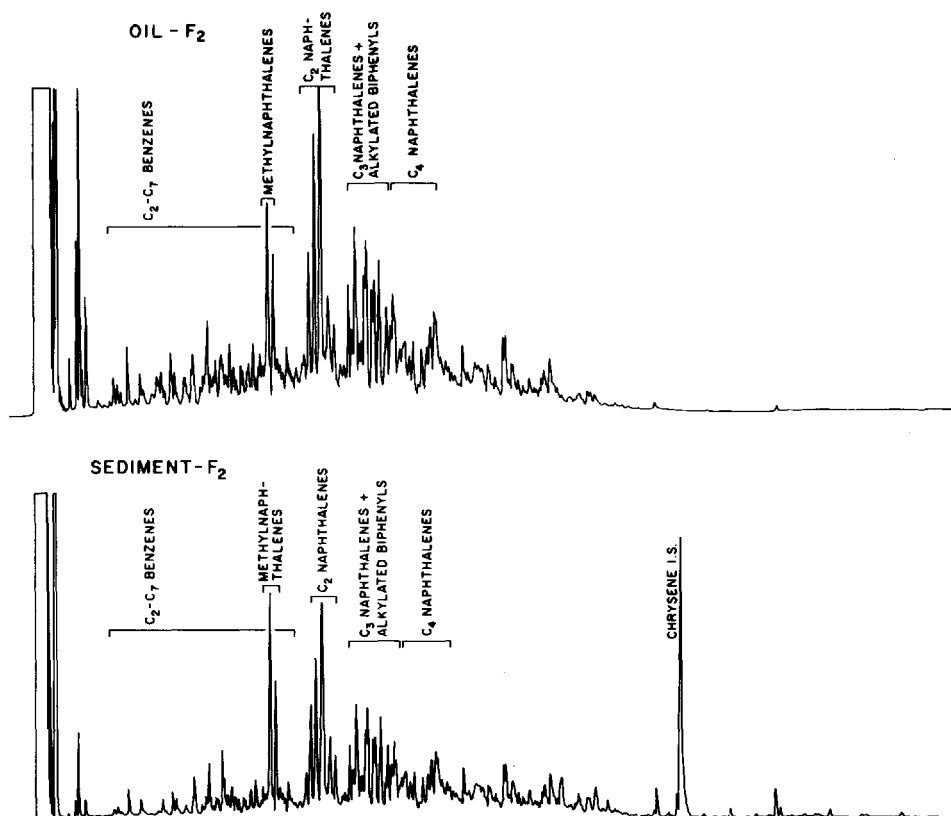


Figure 4. Gas chromatograms of the unsaturated (f_2) hydrocarbon fraction from fresh no. 2 fuel oil and from experimentally oiled marsh sediment maintained *in situ* for eight months.

RPD layer could have been raised closer to the sediment-water interface due to the highly disturbed condition of oiled sediment; thus, bacterial attack may have been restricted to a very thin surface layer. Lastly, any evidence of preferential weathering due to bacterial or chemical processes in the surface layer was probably masked by the relatively large reservoirs of fresh oil remaining in the chambers. Other studies similarly document minimal oil degradation over comparable time periods, once the oil has penetrated the sediment at depth (Ward *et al.*, 1980; Anderson *et al.*, 1978) or in areas where the oil is present in large amounts (Sanders *et al.*, 1980).

A final result regarding hydrocarbons is that although oil tended to concentrate in the overall upper five centimeters of sediment, oil in the very top surficial layer (upper 1 cm) behaved differently and showed a substantial decline with time. Analysis of the surficial sections of marsh samples showed a decrease in oil concentration from an initial 54,300 $\mu\text{g/g}$ to 11,300 $\mu\text{g/g}$ after one month, to 5900 $\mu\text{g/g}$ after four months, to a minimum of 254 $\mu\text{g/g}$ after eight months (Table 4). The one analysis performed on

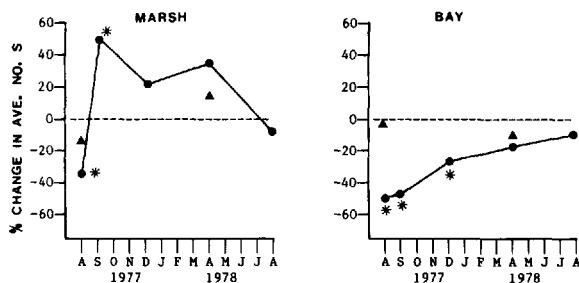


Figure 5. Percent change in the average number of species (S) in oiled samples relative to the natural bottom (dots) and in controls relative to the natural bottom (triangles). Asterisks indicate significant differences at the 1% level based on results of student *T*-test and analysis of variance. Oil was added August, 1977.

the surficial section of a bay sample (which was oiled and analyzed after eight months of *in situ* placement) showed a similar decline to $177 \mu\text{g/g}$ (Table 5). As reported above, we did not detect changes in oil composition at any depth, including the uppermost centimeter. A quantitative loss of oil with no measurable change in oil composition suggests that contaminated sediment in the top one centimeter was being removed physically through resuspension, carried away from the immediate area, and then replaced by deposition of new sediment from surrounding uncontaminated areas. The resuspension-deposition process could have been caused by prior winter storms, since both test sites were in relatively shallow water. McCall (1977) reports that a single storm in Long Island Sound produced a one-centimeter thick layer of resuspended sediment at a site where the depth was 14 meters.

b. Changes in numbers of species. Figure 4 shows changes in the average number of species in oiled and control samples relative to the natural bottom. In the bay, 48 hours after oil was added, 50% fewer species were found in oiled samples than in the natural bottom. This significant loss coincided with the appearance of dead and moribund animals on the sediment surface. There was a subsequent recruitment of species, but at a gradual rate. One to four months after oiling, there were still significantly fewer species. Eight months after oiling, again there were fewer species, although at this time the difference was statistically insignificant. Twelve months after oiling, the average number of species in oiled samples almost reached the number found in the natural bottom (only 9% fewer species in oiled samples). Average numbers of species in unoiled control samples were not significantly different from natural bottom samples for both occasions when controls were monitored (i.e., 48 hours and eight months after oiling) indicating that differences between oiled and natural bottom samples were attributable largely to the effects of oil. However, there were slightly fewer species in controls than in natural bottom samples, particularly on the eight-month sampling occasion. Although insignificant, these differences together with differences in species abun-

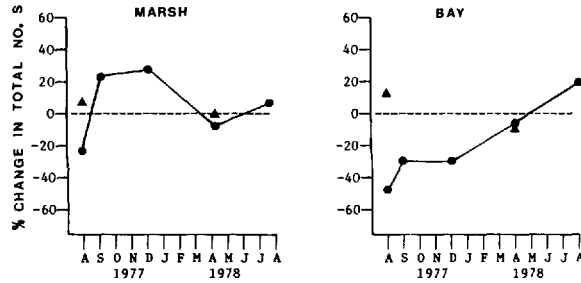


Figure 6. Percent change in the total number of species (from ten combined replicates) in oiled samples relative to the natural bottom (dots) and in controls relative to the natural bottom (triangles). Oil was added August, 1977.

dances (which are discussed below) suggest that changes in oiled samples were due partly to adverse conditions caused by the chamber itself.

Changes in the total number of species from combined replicates of the bay (Fig. 6) followed a pattern similar to the average species number, although on the final sampling occasion there were 21% more species in oiled samples than in the natural bottom. This final increase in species was due to the appearance of several numerically rare species not previously encountered in any bay samples. These species, sometimes represented by a single individual, included the polychaetes *Clymenella torquata* and *Harmothoe extenuata*; the molluscs *Mya arenaria*, *Crepidula fornicata* and an unidentified juvenile razor clam; and the crustaceans *Corophium* sp., *Luconacia incerta*, *Pagurus longicarpus*, and a juvenile *Cancer irroratus*. It is difficult to evaluate the cause or significance of this event. The importance of rare species in any sample collection is hard to evaluate and could be the result of chance alone. Furthermore, *Pagurus*, *Crepidula* and *Cancer* are actually members of the epifauna. Nonetheless, the appearance of so many of these species only in oiled samples indicates that the oil still had some effect on the structure of the bay assemblage twelve months after the initial oiling.

Generally, species in the bay that moved back into oiled samples following the initial disturbance were members of the natural ambient community. However, there are a few exceptions. *Capitella capitata* was found only once in natural bottom samples (one individual) while it was consistently abundant in oiled samples until the last sampling occasion (see next section). Also, as noted above several numerically rare species were found only in oiled samples on the final sampling occasion.

Contrasting responses were observed in the marsh. Dead and moribund animals were found in oiled samples 48 hours after oiling, however as Figure 5 shows, the average number of species at this time was reduced by only 33% in comparison to the natural bottom. This initial loss was statistically significant but less severe than in the bay. Furthermore, oiled marsh samples showed an extremely rapid recruitment of species. Within one month after oiling, there were significantly more (48% more)

species in oiled samples than in samples of the natural bottom. Increases in average species number persisted through the following winter (four months later) and spring (eight months later) although these increases were not statistically significant. Twelve months after oiling, the average number of species in oiled samples returned to approximately the same number found in the natural bottom. As in the bay, average numbers of species in unoiled control samples of the marsh were not significantly different from natural bottom samples for both occasions when controls were monitored. However, again values for control samples were between values for natural bottom and oiled samples, suggesting that species responses in oiled samples were due partly to the sediment chamber itself.

Changes in the total number of species from combined replicates of the marsh (Fig. 6) followed a pattern similar to the average species number. However, in this case the increase of species in oiled samples relative to the natural bottom had subsided by the eighth month following oil addition.

The additional species found in oiled samples of the marsh generally were not unique to these samples. As in the bay, species that recruited to oiled samples were usually members of the natural ambient community. Exceptions are *Polydora ligni*, *Capitella capitata*, and *Nemertea* sp. All three species occurred at relatively high densities in oiled samples. However, *Nemertea* sp. never occurred in natural bottom samples, and *Capitella* and *Polydora* occurred in natural bottom samples at extremely low densities.

c. Changes in species abundances. Table 7 categorizes species in the bay and marsh according to their abundance patterns following oil addition. Results show that most species in the bay (65%) were sensitive to disturbance, while most species in the marsh (69%) were resistant with stimulated population growth. Resistant species which showed no distinct changes in abundance occurred in both places in relatively low proportions.

Changes in abundance with time for sensitive bay species are presented in Figure 7. Typically, there was a loss of individuals in oiled samples within 48 hours after oil was added (in August 1977). Several recruitment patterns followed. Densities of *Nephtys incisa* were restored within four months. *Macoma tenta*, *Ampelisca abdita*, and *Unciola irrorata* gradually recruited to oiled samples, and either approximated or exceeded natural bottom densities by the following summer, twelve months after oil addition. *Mediomastus ambiseta* followed a similar recruitment pattern, with peak densities occurring in the following summer; although values for oiled samples remained below natural bottom values on the final two sampling occasions. Densities of *Ninoe nigripes*, *Asychis elongata*, *Nassarius trivittatus*, *Pholoe minuta*, and *Polycirrus eximius* remained low in oiled samples throughout the study period, revealing long-term population effects; although, note that densities of *Ninoe*, *Asychis*, and *Nassarius* in oiled samples are not significantly different from natural bottom samples

Table 7. Lists of sensitive, resistant, and stimulated species in the bay and marsh, based on abundance patterns following oil addition. Relative proportions of each species category are expressed as % of total species in each respective list.

	<i>Bay</i>	<i>Marsh</i>
1. Sensitive species with reduced populations	<i>Ninoe nigripes</i> <i>Asychis elongata</i> <i>Pholoe minuta</i> <i>Nephtys incisa</i> <i>Mediomastus ambiseta</i> <i>Polycirrus eximius</i> <i>Macoma tenta</i> <i>Acteocina canaliculata</i> <i>Nassarius trivittatus</i> <i>Unciola irrorata</i> <i>Ampelisca abdita</i>	<i>Scoloplos robustus</i> <i>Ampelisca abdita</i>
% Total	64.7%	15.4%
2. Resistant species with no population changes	<i>Mulinia lateralis</i> <i>Yoldia limatula</i> <i>Turbonilla</i> sp. <i>Tharyx</i> sp.	<i>Eteone heteropoda</i> <i>Heteromastus filiformis</i>
% Total	23.5%	15.4%
3. Resistant species with stimulated population growth	<i>Nucula annulata</i> <i>Capitella capitata</i>	<i>Tubificoides brownae</i> <i>Streblospio benedicti</i> <i>Nereis succinea</i> <i>Capitella capitata</i> <i>Polydora ligni</i> <i>Hobsonia florida</i> <i>Macoma balthica</i> <i>Rhithropanopeus harrisii</i> <i>Nemertea</i> sp.
% Total	11.8%	69.2%

on the final sampling occasion. *Acteocina canaliculata* showed a similar pattern of persistent reductions in oiled samples, except that on one occasion (December) there were more animals in oiled samples than in the natural bottom.

Nucula annulata and *Capitella capitata* were the only species in the bay that showed distinct population irruptions in oiled samples. Densities of these species are plotted in Figure 8. *Capitella* was the faster colonizer of the two and invaded oiled samples within the first month following oil addition. Densities of both species peaked by December, declined slightly by April, and then returned to natural bottom densities by the final sampling in August 1978. Densities of these two species declined as other more sensitive species increased in abundance.

There were no consistently large increases or decreases in densities of *Mulinia lateralis*, *Yoldia limatula*, *Turbonilla* sp., or *Tharyx* sp. following an oil addition.

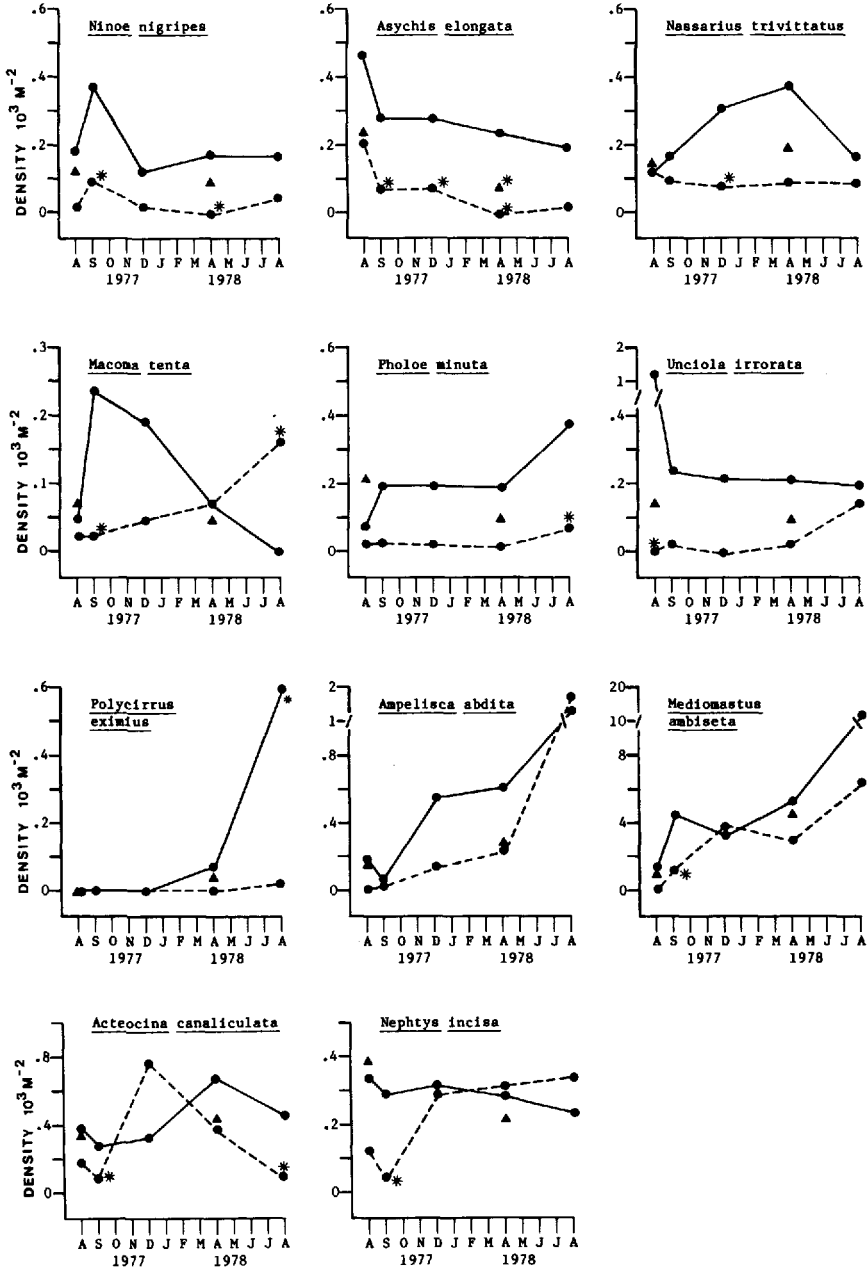


Figure 7. Species in the bay showing net decreases in density of oiled samples. Natural bottom samples (solid lines), controls (triangles), oiled samples (broken lines). Asterisks indicate significant differences at the 1% level in comparison to natural bottom. Oil was added August, 1977.

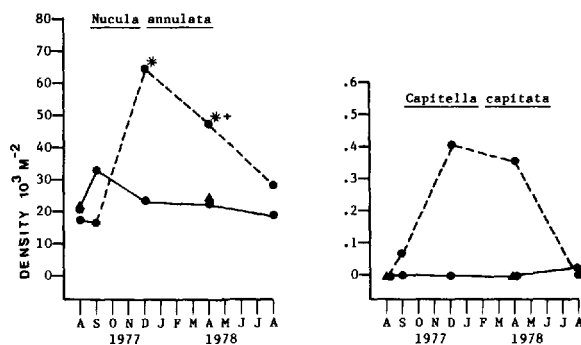


Figure 8. Species in the bay showing net increases in density of oiled samples. Natural bottom samples (solid lines), controls (triangles), oiled samples (broken lines). Asterisks indicate significant differences at the 1% level in comparison to natural bottom. Crosses indicate significant differences at the 1% level in comparison to controls. Oil was added August, 1977.

These species are listed in Table 7 as resistant species. Their abundances are presented in Table 8. There is a caveat in the case of *Tharyx*, which showed some signs of sensitivity. This species occurred in the natural bottom and not in oiled samples on three out of five sampling occasions. In spite of this result, we have identified it as a resistant species, since over all there was no strong, consistent pattern of sensitivity; densities in natural bottom samples were not significantly higher on these three occasions, and on remaining occasions densities were either comparable or slightly higher in oiled samples.

Densities in control sediment chambers for the bay were not significantly different from corresponding natural bottom samples for all species shown in Figures 7 and 8,

Table 8. Abundances (# individuals/0.042 m²) in natural bottom (NB), control (C), and oiled (O) samples for resistant bay and marsh species.

	Aug 1977			Sept 1977		Dec 1977		Apr 1978			Aug 1978	
	NB	C	O	NB	O	NB	O	NB	C	O	NB	O
Bay												
<i>Mulinia lateralis</i>	—	—	—	42	35	46	45	32	15	8	5	2
<i>Yoldia limatula</i>	25	24	26	19	4	13	22	6	9	19	29	31
<i>Turbonilla</i> sp.	47	36	22	24	17	12	12	35	32	44	21	9
<i>Tharyx</i> sp.†	4	3	—	3	—	2	7	9	8	6	9	—
Marsh												
<i>Eteone heteropoda</i>	17	5	2	1	1	1	2	5	3	5	1	—
<i>Heteromastus filiformis</i> †	2	7	8	5	12	3	—	12	1*	—*	12	1

*Significant difference at the 1% level in comparison to natural bottom.

†Species shows some signs of sensitivity; note text.

except *Asychis elongata*. Average density of *Asychis* in control chambers was significantly reduced eight months after deployment. The fact that only one species was significantly reduced in controls suggests that density changes observed in oiled samples for most bay species were largely the result of oil addition. However, when species abundances are ranked from highest to lowest in the three sample types, there is a tendency for the ranks for control samples to lie between those for oiled and natural bottom samples. On both the 48-hour and eight-month sampling occasions, abundance ranks are usually highest in natural bottom samples, intermediate in controls, and lowest in oiled samples. Values of Kendall's coefficient of concordance (Kendall, 1975), which measures the communality of the rankings from one species to the next, are significant at an alpha level of 0.01. This trend, which is reflected to some extent in the average species number (discussed above), suggests that altered sediment conditions induced by the chamber itself contributed to reduced abundances of these species in oiled samples.

Figure 9 shows changes in abundance with time for those species in the marsh whose populations were stimulated following oil addition. Densities in oiled samples dropped immediately after oiling for some species—*Streblospio benedicti*, *Nereis succinea*, *Tubificoides brownae*, and *Hobsonia florida*. Remaining species at this time were either absent or present in low abundance in all sample types. Typically, over the next several months, densities in oiled samples increased above natural bottom densities (often to significantly higher levels) and then approximated natural bottom densities by the final sampling period. Colonization of oiled samples was extremely rapid for most of these species. *Polydora ligni*, *Capitella capitata*, *Rhithropanopeus harrisi*, *Hobsonia florida*, *Nereis succinea* and *Streblospio benedicti* all had higher (usually significantly higher) densities in oiled samples within the first month after oil addition. *Tubificoides brownae*, *Macoma balthica*, and *Nemertea* sp. increased in oiled samples by the fourth month after oil addition.

Scoloplos robustus and *Ampelisca abdita* were the only species in the marsh that showed a consistent pattern of sensitivity to disturbed sediment (Fig. 10). Both species were significantly reduced immediately after oiling. Reductions generally persisted until the following April, eight months after oil addition.

There were no consistently large increases or decreases in densities of either *Eteone heteropoda* or *Heteromastus filiformis* following oil addition. These species are listed in Table 7 as resistant species. Their abundances are presented in Table 8. There is a caveat in the case of *Heteromastus*, which showed some signs of sensitivity. This species was less abundant in oiled samples than in the natural bottom on the last three sampling occasions, and showed a significant reduction on one of these occasions. In spite of this effect, we have identified *Heteromastus* as a resistant species, since over all there was no consistent pattern of sensitivity; the species, in fact, was more abundant in oiled samples than in the natural bottom during the first month when oil concentrations were the highest, particularly in the uppermost centimeter.

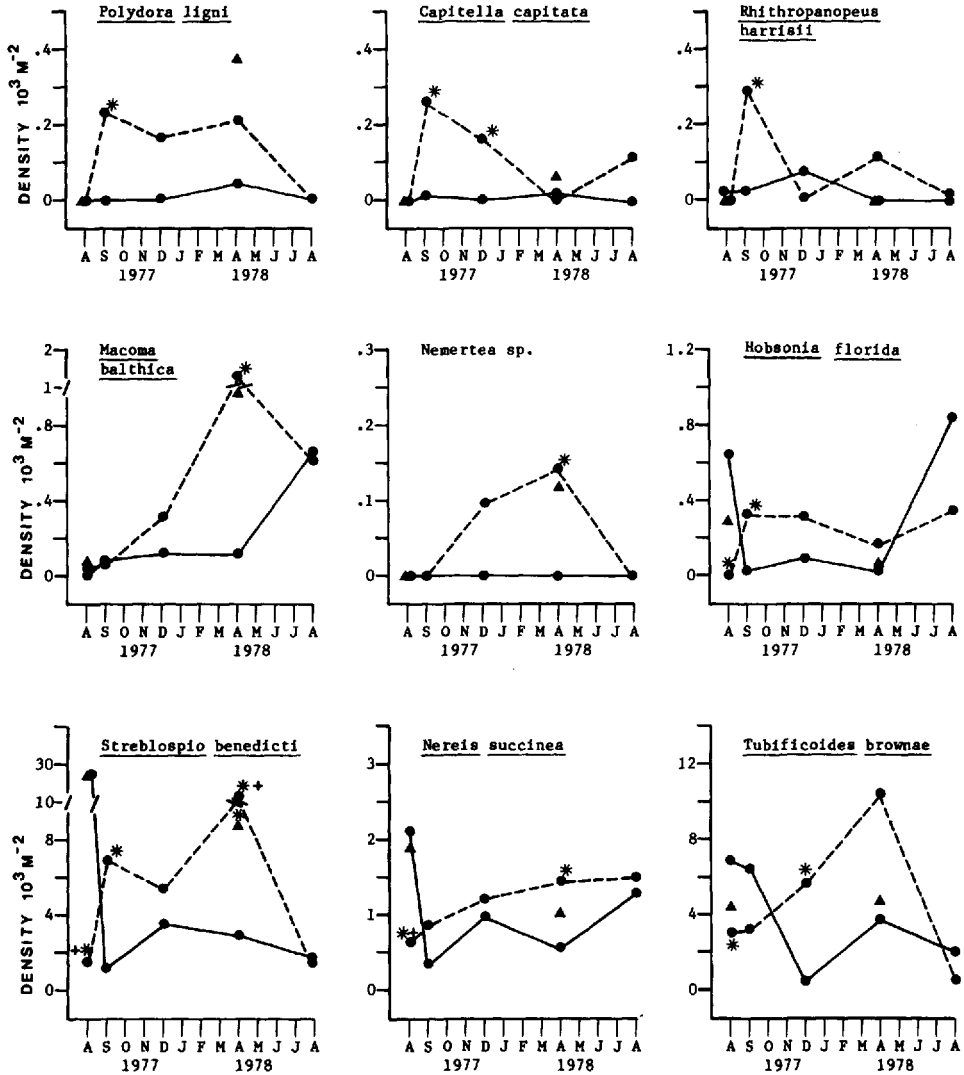


Figure 9. Species in the marsh showing net increases in density of oiled samples. Natural bottom samples (solid lines), controls (triangles), oiled samples (broken lines). Asterisks indicate significant differences at the 1% level in comparison to natural bottom. Crosses indicate significant differences at the 1% level in comparison to controls. Oil was added August, 1977.

Several species in the marsh showed abundance changes in control chambers that were similar to those observed in oiled chambers. *Scoloplos robustus* and *Ampelisca abdita* (Fig. 10) had significantly lower densities in both control and oiled sediment chambers than in natural bottom samples 48 hours after the start of the experiment. *Streblospio benedicti* (Fig. 9) had significantly higher densities in both control and

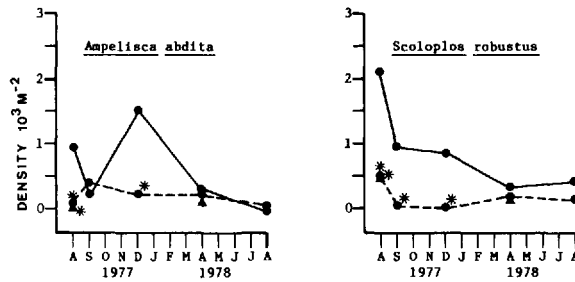


Figure 10. Species in the marsh showing net decreases in density of oiled samples. Natural bottom samples (solid lines), controls (triangles), oiled samples (broken lines). Asterisks indicate significant differences at the 1% level in comparison to natural bottom. Oil was added August, 1977.

oiled chambers than in natural bottom samples eight months after deployment. Furthermore, as in the bay, concordance analysis reveals that there is a significant tendency (at an alpha value of 0.01) for abundances in control samples for most marsh species to be ranked between values for natural bottom and oiled samples. On the 48-hour sampling occasion, abundance ranks are usually highest in natural bottom samples, intermediate in controls, and lowest in oiled samples. On the eight-month sampling occasion, ranks are usually highest in oiled samples, intermediate in controls, and lowest in natural bottom samples. These results suggest that altered sediment conditions induced by the chamber itself contributed to changes in abundances of these species in oiled samples.

5. Discussion

a. Possible causes of population changes in oiled and control sediment chambers. Most species in the marsh and a few species in the bay showed distinct population irruptions in oiled sediment chambers following the initial disturbance (Table 7). These increases were first detected one month after oil addition, once hydrocarbon levels dropped to about $5000 \mu\text{g/g}$ (averaged over all depths). We propose that besides having resisted toxic effects of the remaining oil, these species were stimulated by a surplus of food supplied by microbial enrichment of the disturbed sediment. All of these species are to some degree deposit feeders and can utilize this additional energy source. We cannot provide direct proof of this hypothesis since samples of the microbiota were not collected. However, this type of interaction has been demonstrated in other studies. Spies and Davis (1979) found that deposit feeders at a natural oil seep near Santa Barbara, California, had higher densities in comparison to a control site, and conclude that these species were supported by elevated densities of microbes (*Beggiatoa* sp. and *Desulfovibrio*) that utilized either the fresh oil or an excess of H_2S associated with the disturbed sediment condition. Similarly, Lock et al. (1981) found that populations of macroinvertebrates that colonized oil-soaked bricks placed in the

Muskeg River, Alberta, Canada were stimulated by enhanced bacterial and algal growth.

Gas chromatograms of oiled sediment in the present study did not reveal signs of bacterial attack of oil components. However, this process still could have occurred, with any evidence having been masked by the relatively large reservoirs of fresh oil still remaining in the sediments. Also, heterotrophic microbes which decompose organic compounds rather than oil, and chemosynthetic bacteria which derive energy from oxidation of H_2S may have been abundant even if bacteria responsible for oil decomposition were few. Fenchel and Riedl (1970) have discussed the importance of these latter microbial energy sources to benthic macrofauna. The altered condition of oiled sediment (e.g., increased organics and H_2S) would have enhanced these processes. Regardless of their origin, enhanced microbial supplies must have been depleted by the final sampling period, as evidenced by the convergence of macrofaunal densities in oiled and natural bottom samples.

Species in oiled samples (bay or marsh) did not show population irruptions of the size that McCall (1977) observed for initial colonizers of azoic mud deployed in Long Island Sound. Samples collected ten days after deployment in his study contained *Capitella capitata* and *Streblospio benedicti* at densities near $10^5/m^2$. Maximum densities of *Capitella* in the present study were $405/m^2$ in the bay and $262/m^2$ in the marsh. Maximum density of *Streblospio* (in the marsh) was much higher ($14,476/m^2$) however still nearly an order of magnitude lower than values reported by McCall. Two factors may have contributed to the smaller irruptions in the present study. First, oil could have prevented recruitment of some individuals within the populations. Second, as McCall (1977) has noted, densities of opportunists following a disturbance depend on how empty the substratum is of normal residents. In the present study, oiled sediment chambers were not completely defaunated as a result of the initial disturbance. Thus, organisms entering the sediment chambers competed with existing fauna for resources. Sanders *et al.* (1980) found that the largest irruptions of opportunists following the West Falmouth oil spill occurred at stations that were the most biologically denuded.

Population irruptions in oiled marsh sediments seemed to be due partly to conditions associated with the sediment chamber itself. Recall that on the eight-month sampling occasion most species that showed population irruptions in oiled sediment chambers showed similar increases in controls, although *Streblospio benedicti* was the only species with a statistically significant increase. It is possible that control sediments contained excess organics or H_2S , which may have built up due to restricted circulation of pore waters inside the chambers. As in oiled chambers, this could have stimulated growth of microbes capable of using these materials as energy sources and resulted in an increase in food for the deposit-feeding invertebrates. With a few exceptions (notably, *Polydora ligni*) densities in controls were usually between values for natural bottom and oiled samples, revealing the additional stimulatory effect caused by the

presence of oil. *Streblospio benedicti* showed a population irruption in oiled samples that was statistically significant in comparison to both control and natural bottom samples. Increases in oiled samples relative to controls were not significant for the remaining species.

Most species in the bay were sensitive to adverse conditions in oiled sediment (Table 7). Specific abundance patterns for these species are the result of a combination of factors: oil concentrations as a function of time and sediment depth, relative sensitivities of species to these levels, timing and mode of recruitment, and position of the species relative to sediment depth. Decreases in abundances 48 hours after oiling reflect a common sensitivity to the initial, extremely high oil concentration, which was about 13,000 $\mu\text{g/g}$ averaged over all depths, and almost three times this amount in the upper five centimeters. Within the first month a considerable amount of oil was lost, presumably through physical processes, leaving subsequent oil concentrations during the remainder of the study near 5000 $\mu\text{g/g}$ when averaged over all depths. After this initial loss of oil, some species were able to repopulate oiled sediment, and several recruitment patterns followed. Densities of *Nephtys incisa* were restored within four months, reflecting only short-term population effects. *Nephtys* are highly mobile, thus it was possible for both adults and established juveniles to migrate directly into oiled chambers from the surrounding sediment. Recruitment of *Macoma tenta*, *Ampelisca abdita*, and *Unciola irrorata* was delayed until the following spring to summer, between eight to twelve months after oil addition, reflecting longer-term population effects. These species were represented mostly by juveniles. Their appearance corresponds to the natural late-spring to summer peak recruitment period reported for this community (Grassle et al., 1981; Sanders et al., 1980). The timing also corresponds to the period when the top one centimeter of sediment, where these fauna were concentrated, contained low levels of oil (e.g., 177 $\mu\text{g/g}$ for the eight-month oiled bay samples). It is possible that these incoming juveniles did not survive after this final sampling period. Two of these species are amphipods; ampeliscid amphipods, in particular, are identified as being highly sensitive to oil toxicity (Sanders et al., 1980). *Mediomastus ambiseta* also showed the largest increase in oiled samples during the summer recruitment season, although densities were still lower than in natural bottom samples. Densities of *Ninoe nigripes*, *Asychis elongata*, *Nassarius trivittatus*, *Pholoe minuta*, *Polycirrus eximius*, and *Acteocina canaliculata* were low in oiled samples on most occasions throughout the study period, revealing a common sensitivity to the remaining oil levels and longer-term population effects.

Reduced abundances in oiled bay sediment seemed to be due partly to adverse conditions associated with the sediment chamber itself. Recall that most species on the 48-hour and eight-month sampling occasions had lower densities in both control and oiled samples than in natural bottom samples, although reductions in control samples were insignificant for all species except *Asychis elongata*. Reduced abundances in control chambers within the initial 48-hour laboratory phase were most likely due to

lower levels of oxygen caused during transport of the chambers from the field to the laboratory. Once in the laboratory, all chambers were kept in well-aerated tanks equipped with continuously flowing seawater. Longer-term reductions in abundance after eight months of *in situ* deployment were probably due to reduced levels of oxygen or other changes in pore-water chemistry (e.g., build-up of organics or increased levels of ammonia and H_2S) that resulted from restricted circulation of pore waters inside the chambers. Under such conditions, the RPD layer could have moved closer to the sediment surface, leaving a smaller amount of inhabitable space for many individuals. Adverse conditions in controls had the most notable effect on *Asychis elongata*. *Asychis* would have been particularly sensitive to an unusually shallow RPD layer, since it feeds head-down in the sediment five centimeters or more below the surface. In addition to the effects of restricted circulation, the relatively small size of the sediment chamber (diameter of 7.3 cm and height of 15 cm) may have placed physical limitations on some of the larger species like *Asychis*.

Densities in control chambers in the bay were usually between values for natural bottom and oiled samples, revealing the additional effect of oil toxicity. On no occasion, however, did densities in oiled samples show significant reductions when compared directly to controls.

Populations of two species in the marsh, *Scoloplos robustus* and *Ampelisca abdita*, showed significant reductions in control chambers after the initial 48-hour period in the laboratory. Other marsh species had lower densities in controls than in natural bottom samples on this same sampling occasion, although the differences were not significant. Similar to bay species, these species were possibly disturbed by a reduction in oxygen caused during transport of the chambers from the field to the laboratory.

b. Species responses in relation to life-history properties. Rapid colonization of oiled sediments in the marsh was facilitated by a large potential for growth and reproduction characteristic of many of these species. Several of the marsh species that showed population irruptions in oiled samples, including the two most abundant species, are well-known opportunists. Diaz (1980) for example has commented on the opportunistic nature of estuarine tubificid oligochaetes (such as *Tubificoides brownae*). Grassle and Grassle (1974) list *Streblospio benedicti*, *Capitella capitata*, and *Polydora ligni* as opportunists. All of these species are characterized by relatively small sizes, more than one generation per year, rapid growth, early maturation, ability to recruit rapidly, and high mortality. *Nereis succinea* is also usually regarded as an opportunist (e.g., Boesch, 1977), although as Grassle and Grassle (1974) point out, this species is less opportunistic than the above extreme opportunists, in the sense that it grows to a relatively large size, lives longer, and requires nearly a year to reach maturity.

Opportunistic species were present in the bay as well. For example, Grassle and Grassle (1974) list both *Capitella capitata* and *Mediomastus ambiseta* as opportunists, and *Ampelisca abdita* is listed as an opportunist by McCall (1977). However, of

these, *Capitella* was the only species that was also resistant to disturbance. *Mediomastus* and *Ampelisca* were both sensitive to disturbance.

Not all of the species in this study that showed population irruptions in oiled sediments are necessarily opportunists. For example, *Nucula annulata*, which showed population irruptions in oiled samples of the bay, is relatively conservative. It has a long mean life-span (at least seven years), a relatively low recruitment rate that approximates its death rate, and colonizes azoic sediments (that are not organically enriched) only in later successional stages (McCall, 1977; Rhoads et al., 1978). Larval recruitment and rapid growth of juveniles at the site of disturbance was not the primary mechanism causing increases in populations of *Nucula annulata* in oiled sediment chambers. Oiled sediments contained large proportions of adults and juveniles that were at least older than the duration of the experiment (based on size of the animals) which suggests that immigration of established animals from surrounding sediments into the oiled chambers was the primary source of population increases.

c. Relative stability. It is difficult to distinguish differences between levels of stability in various nearshore benthic communities. Most nearshore communities, even in deeper embayments, are composed of assortments of species that display a wide variety of life history properties (Boesch et al., 1976) and consequently show varying degrees of resistance and resilience in response to disturbance. Differential patterns of response to disturbance should be more distinguishable in offshore-nearshore comparisons.

Still, within a given nearshore area, it is expected that communities in the most inconstant and unpredictable environments will be composed of the largest proportions of resistant and resilient species. According to the response to disturbance hypothesis, an equivalent petroleum exposure should have a less catastrophic effect on these communities than on communities of more constant and predictable local environments. Results of the present study are consistent with this prediction.

The marsh assemblage was both more resistant and resilient following oil addition than the bay assemblage. Greater resistance in the marsh is indicated by the fact that a larger proportion of species survived initial impact, and by the fact that species continued to resist toxic effects throughout the study period. In fact, following initial impact most marsh species (69%) not only resisted oil toxicity (and any other adverse conditions caused by the sediment chamber) but were actually stimulated under these conditions. Another 15% of the species were resistant without showing population increases. Within only one month after oiling, there was a significant enrichment of species in oiled samples. Indications of species enrichment persisted through the following spring, eight months after oiling. By the final sampling (twelve months after oiling) measures of species richness for oiled samples dropped near the natural bottom values. Densities of most species followed a similar pattern: initial reductions in density 48 hours after oiling; subsequent population irruptions one to eight months later; and

return to background densities eight to twelve months after oiling. Recovery in the marsh was basically complete eight to twelve months after oiling.

That recovery in the marsh occurred in less than one year and that during this period the majority of species showed increased densities in oiled samples are striking results when considering the presence of a relatively large amount of fresh oil (approximately 5000 $\mu\text{g/g}$ averaged over all depths, after the first month) components of which are toxic to a wide variety of aquatic organisms (Hyland and Schneider, 1976).

Compared to the marsh assemblage, the bay assemblage was less resistant and resilient. Lower resistance is indicated by a greater loss of species during initial impact, and by a predominance of sensitive species (65%) whose populations were consistently reduced over several sampling occasions. Lower resilience is indicated by a longer overall recovery period and by slower recruitment of species and individuals. Numbers of species remained low in oiled samples for several months. Increases were more gradual with time. The average number of species was still lower (although not statistically lower) in oiled samples eight months after oiling and finally approximated the number found in natural bottom samples twelve months after oiling. While densities of several species recovered during the period of study, densities of several others had not fully recovered by the final sampling occasion. Only two species, *Nucula annulata* and *Capitella capitata*, showed the kind of population irruptions in oiled samples that were characteristic of most marsh species. There were some indications of recovery in the bay twelve months after oil addition (e.g., recovery of the average species number and abundances of some species). However, there were also indications that recovery was not yet complete (e.g., the increase in numerically rare species only in oiled samples on the final sampling occasion; and persistent reduction in abundances of several species). Full recovery in the bay requires longer than one year and perhaps several years. Effects of No. 2 fuel oil on subtidal assemblages in Buzzard Bay, Massachusetts, following the grounding of the barge *Florida*, lasted for at least 2½ years (Sanders *et al.*, 1980).

Results of this study are consistent with other recent studies which have addressed the subject of relative stability in marine and estuarine benthic communities. Grassle (1977) observed extremely slow colonization of experimental boxes of azoic sediment deployed on the continental slope (1,760 m) and much faster rates for sediment deployed in Buzzards Bay, Massachusetts (10 m). Boesch *et al.* (1976a) found that diverse benthic communities inhabiting normally more constant, polyhaline regions of the James and York River estuaries in Virginia were less stable from disturbances caused by Tropical Storm Agnes than lower-diversity communities inhabiting upper, oligohaline reaches of the estuaries. Similarly, Rhoads *et al.* (1978) observed slower colonization rates for infaunal species of a deeper, more stable bottom in Long Island Sound than in a shallower area more frequently disturbed by storms. High resistance and resilience in response to petroleum-induced disturbances have been noted for the estuarine meiobenthos (Alongi *et al.*, 1983).

6. Conclusions

1. We have provided empirical support of the response to disturbance hypothesis by comparing *in situ* responses of two disparate macro-infaunal assemblages to equivalent experimental additions of No. 2 fuel oil. This hypothesis predicts that less diverse communities which typically inhabit relatively inconstant and unpredictable environments are more stable from unusual disturbances than higher-diversity communities which typically inhabit relatively more constant and predictable environments.

2. One of the assemblages is dominated by the polychaete worm *Streblospio benedicti* and oligochaete worm *Tubificoides brownae*, the other is dominated by the protobranch clam *Nucula annulata* and the polychaete *Mediomastus ambiseta*. Both assemblages were sampled from subtidal, muddy substrates in the vicinity of Narragansett Bay, Rhode Island. The former assemblage is less diverse (fewer species) and is found in a more inconstant and unpredictable local environment, in a shallow oligohaline to polyhaline marsh cove bordering the Pettaquamscutt River. The latter assemblage is more diverse, and is found in a more constant and predictable local environment, in a much deeper area in south-central Narragansett Bay. Salinity in this area is high and more stable (29.5 to 31‰).

3. The *Streblospio-Tubificoides* assemblage was disturbed less and recovered faster from the experimental oil addition than the *Nucula-Mediomastus* assemblage. Disturbed sediment had a stimulatory effect on populations of most species in the marsh and an inhibitory effect on populations of most species in the bay. Several of the marsh species which showed population irruptions in oiled samples are well-known opportunists. Resistant and opportunistic species also inhabit the bay, but these comprise relatively smaller proportions of the total species.

4. Oil behaved similarly in the two environments. In both series, initial oil concentrations (about 13,000 $\mu\text{g/g}$ averaged over all depths) dropped within the first month to about 5000 $\mu\text{g/g}$. Presumably this loss was due to oil rising to the surface and entering the water column. Unweathered No. 2 fuel oil, including toxic aromatic compounds, persisted at this approximate level in both series for the remainder of the study. Any evidence of preferential weathering due to bacterial or chemical processes was apparently masked by the remaining reservoirs of fresh oil. Oil in the top one centimeter of sediment also showed no changes in composition, although by the eight-month sampling occasion (April, 1978) concentrations had dropped substantially to 177 $\mu\text{g/g}$ for the bay, and 254 $\mu\text{g/g}$ for the marsh. This loss may have been caused by resuspension of surficial sediment and deposition of new uncontaminated sediment from surrounding areas during prior winter storms.

5. The sediment chamber itself did not have significant short-term or long-term effects on species numbers, or on abundances of most species. However, there was a tendency for control values (for both species numbers and most species' abundances) to lie between values for natural bottom and oiled samples. Also, the sediment chamber did have significant effects on densities of some species. These results suggest that

benthic community responses were due partly to altered sediment conditions induced by the chamber itself and not solely to the presence of oil. Such effects do not alter conclusions regarding relative stability of the two assemblages in response to disturbance.

6. Predictions of the response to disturbance hypothesis may have far-reaching applications in management-related decisions. However, we must urge that additional empirical studies be performed on other communities and under a variety of field conditions to provide further tests of the limits of this hypothesis.

Acknowledgments. This paper was prepared from information extracted from a doctoral dissertation submitted by the senior author to the University of Rhode Island, Kingston, Rhode Island. Financial support for this research was provided by in-house funds from the Environmental Protection Agency, Narragansett, Rhode Island, and by EPA grant R-805477 to Dr. James Quinn, University of Rhode Island, Graduate School of Oceanography. The senior author was supported by graduate student appointments at the Narragansett EPA facility throughout the course of the study. Appreciation is extended to Dr. James Lake who supervised GC-MS analyses, to Elaina Kenyon who helped in sorting and enumerating benthic animals, and to Walter Galloway who helped in all phases of the field work. Appreciation is also extended to Dr. Frederick Grassle, Susan Brown-Leger, Dr. Donald Boesch, Dr. Robert Diaz, Sheldon Pratt, and Dr. John Scott for their assistance in species identifications. We thank Dr. Donald Boesch, Dr. Howard Sanders and Dr. William Lang for reviewing the manuscript. We also thank Patricia Younkens for typing the manuscript.

REFERENCES

- Alongi, D. M., D. F. Boesch and R. J. Diaz. 1983. Colonization of meiobenthos in oil-contaminated subtidal sands in the lower Chesapeake Bay. *Mar. Biol.*, 72, 325-335.
- Anderson, J. W., R. G. Riley and R. M. Bean. 1978. Recruitment of benthic animals as a function of petroleum hydrocarbon concentrations in the sediment. *J. Fish. Res. Board Can.*, 35, 776-790.
- Boesch, D. F. 1974. Diversity, stability and response to human disturbance in estuarine ecosystems, *in* Proceedings of the First International Congress of Ecology, Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands, 109-114.
- 1977. A new look at the zonation of benthos along the estuarine gradient, *in* Ecology of Marine Benthos, B. C. Coull, ed., University of South Carolina Press, Columbia, 245-266.
- Boesch, D. F., R. J. Diaz and R. W. Virnstein. 1976a. Effects of Tropical Storm Agnes on soft-bottom macrobenthic communities of the James and York Estuaries and the Lower Chesapeake Bay. *Chesapeake Science*, 17, 246-259.
- Boesch, D. F. and R. Rosenberg. 1981. Response to stress in marine benthic communities, *in* Stress Effects on Natural Ecosystems, G. W. Barrett and R. Rosenberg, eds., John H. Wiley and Sons, Inc., New York, 179-200.
- Boesch, D. F., M. L. Wass and R. W. Virnstein. 1976b. The dynamics of estuarine benthic communities, *in* Estuarine Processes, 1, M. Wiley, ed., Academic Press, New York, 177-196.
- Brinkhurst, R. O. and H. R. Baker. 1979. A review of the marine Tubificidae (Oligochaeta) of North America. *Can. J. Zool.*, 57, 1553-1569.
- Copeland, B. J. 1970. Estuarine classification and response to disturbances. *Trans. Amer. Fish. Soc.*, 99, 826-835.

- Diaz, R. J. 1980. Ecology of tidal freshwater and estuarine Tubificidae (Oligochaeta), in *Aquatic Oligochaete Biology*, R. O. Brinkhurst and D. G. Cook, eds., Plenum Press, N.Y., 319–330.
- Farrington, J. W. and J. G. Quinn. 1973. Petroleum hydrocarbons in Narragansett Bay. Survey of hydrocarbons in sediment and clams. *Estuar. Coast. Mar. Sci.*, 1, 71–79.
- Fenchel, T. and R. Riedl. 1970. The sulfide system. A new biotic community underneath the oxidized layer of marine sand-bottoms. *Mar. Biol.*, 7, 255–268.
- Gearing, P. J., J. N. Gearing, R. J. Pruell, T. J. Wade and J. G. Quinn. 1980. Partitioning of No. 2 fuel oil in controlled estuarine ecosystems. Sediments and suspended particulate matter. *Environ. Sci. Technol.*, 14, 1129–1136.
- Goodman, D. 1975. The theory of diversity-stability relationships in ecology. *The Quarterly Rev. of Biol.*, 50, 237–266.
- Grassle, J. F. 1977. Slow recolonization of deep-sea sediment. *Nature*, 265, 618–619.
- Grassle, J. F. and J. P. Grassle. 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes. *J. Mar. Res.*, 32, 253–284.
- Grassle, J. F., R. Elmgren and J. P. Grassle. 1981. Response of benthic communities in MERL ecosystems to low level, chronic additions of #2 fuel oil. *Mar. Environ. Res.*, 4, 279–297.
- Hershner, C. and J. Lake. 1980. Effects of chronic oil pollution on a salt-marsh grass community. *Mar. Biol.*, 56, 163–173.
- Hoffman, E. J. and J. G. Quinn. 1978. Methods development for hydrocarbon analyses of sediment samples, in *Chemical Studies Directed Towards Ecological Damage Assessment of Petroleum Discharges into the Marine Environment*, J. G. Quinn, ed., Progress Report, Grant No. R805477, URI Graduate School of Oceanography, Narragansett, RI, 16 pp.
- Hyland, J. L. 1981. Comparative structure and response to (petroleum) disturbance in two nearshore infaunal communities. Ph.D. dissertation, University of Rhode Island, Kingston, Rhode Island, 141 pp.
- Hyland, J. L. and E. D. Schneider. 1976. Petroleum hydrocarbons and their effects on marine organisms, populations, communities, and ecosystems, in *American Institute of Biological Sciences, Proceedings of symposium on "Sources, effects and sinks of hydrocarbons in the aquatic environment."* Aug. 9–11, 1976, Wash., D.C., 464–506.
- Kendall, M. 1975. *Rank Correlation Methods*. 4th ed. (2nd impression). Charles Griffin & Co. Ltd., London and High Wycombe, Great Britain, 202 pp.
- Lock, M. A., R. R. Wallace, D. R. Barton and S. Charton. 1981. The effects of synthetic crude oil on microbial and macroinvertebrate benthic river communities—Part I: colonization of synthetic crude oil contaminated substrata. *Environ. Pollut. (Ser. A.)*, 24, 207–217.
- May, R. M. 1974. *Stability and Complexity in Model Ecosystems*. 2nd ed. Princeton Univ. Press, Princeton, New Jersey, 265 pp.
- McCall, P. L. 1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. *J. Mar. Res.*, 35, 221–266.
- Orians, G. H. 1975. Diversity, stability and maturity in natural ecosystems, in *Unifying Concepts in Ecology*, W. H. van Dobben and R. H. Lowe-McConnell, eds., Dr. W. Junk Publ., The Hague, Netherlands, 139–150.
- Pearson, T. H. and R. Rosenberg. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. Mar. Biol. Ann. Rev.*, 16, 229–311.
- Rhoads, D. C., P. L. McCall and J. Y. Yingst. 1978. Disturbance and production on the estuarine seafloor. *Amer. Sci.*, 66, 577–586.
- Sanders, H. L. 1956. Oceanography of Long Island Sound, 1952–54, 10: The biology of marine bottom communities. *Bull. Bingham Oceanogr. Coll.*, 15, 345–414.

- 1958. Benthic studies in Buzzards Bay. I. Animal-sediment relationships. *Limnol. Oceanogr.*, 3, 245–258.
- 1968. Marine benthic diversity: a comparative study. *Amer. Natur.*, 102, 243–282.
- 1969. Benthic marine diversity and the stability-time hypothesis, *in* Diversity and Stability in Ecological Systems, G. M. Woodwell and H. H. Smith, eds., Brookhaven Symposia in Biology, No. 22, 71–81.
- Sanders, H. L., J. F. Grassle, G. R. Hampson, L. S. Morse, S. Garner-Price and C. C. Jones. 1980. Anatomy of an oil spill: long-term effects from the grounding of the barge *Florida* off West Falmouth, Mass. *J. Mar. Res.*, 38, 265–380.
- Slobodkin, L. B. and H. L. Sanders. 1969. On the contribution of environmental predictability to species diversity. *Brookhaven Symp.*, 22, 71–81.
- Spies, R. B. and P. H. Davis. 1979. The infaunal benthos of a natural oil seep in the Santa Barbara Channel. *Mar. Biol.*, 50, 227–237.
- Ward, D. M., R. M. Atlas, P. D. Boehm and J. A. Calder. 1980. Microbial biodegradation and chemical evolution of oil from the Amoco spill. *Ambio*, 9, 277–283.