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Oil Impacts on Marine Invertebrate Populations and Communities[1]

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SYNOPSIS. It is likely that roughly one billion gallons of oil enters our oceans each year as a result of man's activities. Only 8% of this input is believed to derive from natural sources. At least 22% is intentionally released as a function of normal tanker "operational discharges," 12% enters from accidental tanker spills and another 36% from runoff and municipal and industrial wastes.

Invertebrate populations and communities form the foundation for marine ecosystems and are continually subjected to stresses from both chronic and acute oil toxicity. The diversity of invertebrate taxa represented in the marine environment exhibit a wide range of responses to oil. Mortality is an obvious impact resulting from catastrophic spills or even chronic toxicity. Sublethal impacts on individuals are manifested by physiological, carcinogenic and cytogenetic effects. Impacts typically felt at the population level involve changes in abundance, age structure, population genetic structure, reproduction and reduced recruitment potential. Community level impacts are typified by modified interactions between competitors, predator/prey and symbionts. Most importantly, changes in community structure represented by altered trophic interactions tend to produce the most dramatic alterations to natural invertebrate assemblages.

Invertebrate communities respond to severe chronic oil pollution and/or acute catastrophic oil pollution in much the same way. Initial massive mortality and lowered community diversity is followed by extreme fluctuations in populations of opportunistic mobile and sessile fauna (and flora). Oscillations in population numbers slowly dampen over time and diversity slowly increases to original levels. The time over which these events occur depends on the type of oil, the extent of the initial contamination, habitat type, weather conditions, latitude, the species assemblages represented and a myriad of other complex factors.

INTRODUCTION

The coastal ocean is increasingly subjected to a myriad of pollutants. Oil is but one of numerous multiple stresses imposed upon diverse and productive invertebrate communities (Suchanek, 1994). During the early 1980s it was estimated that an average of 3.2×10^6 metric tons (nearly one billion gallons) of oil enter the sea each year, but the upper range of possible oil inputs may be as high as 8.8×10^6 metric tons per year (over two billion gallons) (N.R.C., 1985). This compares with an estimated average of over 6×10^6 metric tons per year for the period around 1970–1972 (N.R.C., 1973). From the more recent study, about 45% of the volume is believed to enter as a result of transportation related activities, including intentional holding tank purging activities associated with normal tanker operations (22%), and spills from tanker accidents (12%) that attract enormous media attention. Other sources include inputs from municipal and industrial sources including coastal refineries (*ca.* 31%), atmospheric

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deposition (*ca.* 9%), natural sources such as seeps (*ca.* 8%), urban and river runoff (*ca.* 5%), offshore oil production (*ca.* 2%) and ocean dumping (*ca.* 1%). Despite technological improvements in navigational and safety equipment, major oil spills continue to plague our coastal resources. As testimony to this fact, during the preparation of this paper another major oil spill (from the tanker Aegean Sea) has just occurred off the north coast of Spain releasing at least several millions of gallons of crude (Solomon, 1992), and as the manuscript was in editorial review, the U.S. tanker Brear grounded off the Shetland Islands; each tanker released more than 20 million gallons of oil into the marine environment, approximately twice the volume of the Exxon Valdez oil spill in Prince William Sound, Alaska in 1989. The significant effects of identified sources of chronic oil pollution, as well as the obvious catastrophic spills, on invertebrate populations and communities is cause for serious concern.

Invertebrate populations, especially those that live subtidally, are relatively obscure and rarely seen, except by the sport or research diver. Occasional glimpses into the subtidal realm are usually not sufficient to document or even notice long-term declines in population levels or shifting relationships between different competitors, predators or prey. Adding to the problem of obscurity, and a possible significant reason for it, is the fact that virtually no marine invertebrates are listed on any federal or state lists for endangered or threatened species, although fresh water invertebrates are well represented (USFWS, 1990). There is simply not enough information to evaluate population and community level changes in these invertebrate assemblages in order to determine which species are at risk of potential extinction or serious decline.

Even though intertidal invertebrate communities are the predictable recipients of spilled oil, and often suffer at least as much as birds and mammals, the "cuter" furry and feathered animals typically occupy most of the time on 30 sec video bites dedicated to media coverage of spectacular oil spills. This is part of the problem of public perception and ultimate lack of legislative attention paid to the problem of invertebrate conservation in general and marine coastal invertebrates in particular.

In this paper I provide some documentation for oil impacts on marine invertebrate populations and communities. Although I cannot really do justice to the topic in this short review, I have tried to present an overview, with selected examples, of the types of impacts experienced by invertebrates when exposed to oil in the marine environment.

OIL IN THE MARINE ENVIRONMENT

As identified above, oil enters the marine environment from many sources. Because oil is composed of many complex compounds, with a wide range of toxicities, it is often difficult to characterize the presence and movement of the many types of hydrocarbons in the marine environment, as well as the impact of these compounds on invertebrates. While there have been many laboratory experiments that have begun to identify the most toxic fractions of oil that cause the most damage, most generalizations of oil impacts on invertebrate populations and communities have been made from studies of spilled crude oil.

Crude oil in the coastal environment typically breaks up into three major components: a volatile component, a floating component and a sinking component. The volatile component can be 20–50% by volume, depending on the type of oil. This fraction quickly (days to weeks) evaporates into the atmosphere and dissolves into the water column, mostly affecting organisms with a large surface area to volume ratio such as plankton. The floating component is the fraction that typically affects rafting birds, floating mammals like sea otters and eventually drifts to shore to impact shoreline communities. Wave action on the sea surface and near shore whips this fraction into an aerated slurry called "mousse," often increasing the original volume several fold. It reduces the insulative and flotation functions of fur and feathers for vertebrates, but also suffocates shoreline invertebrates. Because of the floating nature of this fraction, and the limited mobility of most shoreline invertebrates, intertidal communities are especially vulnerable. Studies of past spills in temperate coastal habitats indicate that mousse affects most taxa indiscriminately, as most organisms heavily covered by such oil are typically killed. When it occurs (often depending on the relative density of the oil and the amount of sediment in the water column), the sinking component may severely impact subtidal communities.

Oil naturally undergoes weathering and consumption by indigenous marine bacteria. The problem with major oil spills is the fact that bacteria cannot consume the oil fast enough to reduce the biological impacts on other communities. Herein lies the problem of excess oil in the marine environment.

DIRECT EFFECTS OF OIL ON INDIVIDUAL TAXA

The proximate causes of invertebrate community impacts from oil pollution are clearly a result of effects at the individual level. These individual effects can be grouped into several general categories including: death, physiological effects, carcinogenic impacts and cytogenetic effects. Population wide impacts can be observed as changes in population structure (including effects on abundance, age and genetic variability), reduced recruitment and modified interactions between competitors, predator/prey, and/or symbionts.

The first major mechanism of impact for most invertebrates is by physical factors. Physical smothering by oil (exclusive of toxicity) will prevent respiration, inhibit or prevent movement, and create excess weight and/or shearing forces on mobile organisms to which oil adheres. This, in turn, may cause them to be carried away by waves or currents to the subtidal zone where they may be subject to predation or swept to the supratidal zone where they may die from desiccation.

There has been considerable debate over oil impacts on invertebrates at the individual level. For example, while some studies have shown that hydrocarbon concentrations in bivalves diminish over time, it is unclear whether those compounds are being depurated or metabolized (Clark, 1982*b*). It is obvious that those two disparate outcomes could lead to very different conclusions regarding the severity of impacts at the individual, population and community level.

Mortality as an impact and its effect on a population are rather self evident. Some generalizations derived from bioassays on a variety of marine invertebrates indicate that lethal effects result from soluble fractions of oil in the 1 to 100 parts per million range (Hyland and Schneider, 1976). For smaller, more sensitive larval and/or juvenile stages, mortality may occur at much lower concentrations (*e.g.*, 0.1–1.0 ppm).

The important consideration here is which individual species are affected and how extensively populations have been altered. If there are particular species within the community that contribute significantly to structuring and maintaining community interactions, then elimination of those species will have the most severe impact on the community as a whole (see below under Indirect Effects). If, on the other hand, those species that are killed make a relatively minor contribution to structuring the community, then the basic composition and integrity of the community is likely to remain intact or recover relatively quickly.

Individual genetic effects from petroleum hydrocarbons are not as widely recognized for invertebrates as for fishes. However, some studies have shown cytogenetic, cytotoxic and embryotoxic effects from oil or oil fractions in both sea urchins and bivalves. Hose and Puffer (1983) and Hose *et al.* (1983) demonstrated both cytologic and cytogenetic anomalies in the sea urchin *Strongylocentrotus purpuratus* as manifested by aberrant chromosome arrangements during mitosis from environmental levels of benzo(a)pyrene. Stiles (1992) showed cytogenetic impacts on early reproductive stages of the American oyster (*Crassostrea virginica*), including the following chromosomal abnormalities: anaphase bridges, laggard chromosomes, multipolar spindles, polyploidy, aneuploidy and chromosomally mosaic embryos. Some population genetic effects have been documented as a result of the West Falmouth, Massachusetts spill (Cole, 1978). Because of limited dispersal abilities of the oyster drill *Urosalpinx,* widespread mortality of this snail likely caused a "founder effect" in the recolonizing individuals, yielding greater year to year fluctuations in allozyme genotypes when compared with control populations.

Sublethal responses of marine invertebrates to oil (typically in the range of 1–10 ppb) will likely produce dramatic population level changes (Hyland and Schneider, 1976). The most common physiological functions altered by sublethal crude oil and/ or oil fractions are: reproduction, growth, respiration, excretion, chemoreception, feeding, movement, stimulus response and susceptibility to disease. Generally, refined products will produce more toxic effects than crude oil and the relative toxicity of oil is directly correlated with the proportion of aromatic hydrocarbons (Neff *et al.,* 1976). Below I provide documentation for selected studies on mostly sublethal effects for specific taxonomic or functional groups.

Meroplankton and holoplankton

On an individual basis larvae and/or juveniles would be expected to show more susceptibility to toxic fractions of oil because of their significantly higher surface area to volume ratio, which permits a more efficient uptake rate of the contaminant. During their dispersal phase, larvae may be affected by (1) impaired abilities to avoid predators, (2) reduced capacity to locate suitable settlement sites, (3) limited ability to attach and/or maintain initial attachment to the preferred settlement substratum, (4) lowered defensive abilities against predators or competitors, and (5) an inability to feed, grow or mature.

Plankton populations typically exhibit extreme temporal and spatial variability and this has somewhat hampered the assessment of oil impacts on this group. In general though, natural plankton populations have not shown the type of deleterious impacts that are characteristic of both laboratory experiments on plankton and sessile forms on intertidal shores (Kineman *et al.,* 1980; Davenport, 1982; Southward, 1982). To date, field studies have shown no lasting damage to planktonic communities (Davenport, 1982). It has been suggested, however, that holoplankton may be more susceptible to the effects of oil contamination than their temporary planktonic counterparts (Nelson-Smith, 1972). While there has not been an abundance of zooplankton studies following catastrophic spills, it must be assumed that because of the extreme mixing of the water column, most entrained zooplankton populations will be spared severe impacts and/or will recover relatively quickly. Oil impacts on plankton populations will most likely be limited to the immediate vicinity of the spilled oil for as long as it lasts in the water column.

Neuston are plankton that occupy the surface layer of the ocean. Recently there has been considerable attention paid to sea surface microlayers (Ermakov *et al.,* 1992; Gardiner and Hardy, 1992), surface layers that concentrate detritus, bacteria, neuston, and organic and inorganic compounds (including pollutants). How the compounds contained within these surface films interact with neuston and/or shoreline communities when surface slicks drift to shore is uncertain at this time, but it will likely be a fast emerging area of study.

Meiofauna

In two experimental releases of oil in the Baffin Island Oil Spill (BIOS) Project, oil was (1) dispersed directly into the water column and (2) released onto the water surface and allowed to strand on the shoreline. In a study of the impact of the dispersed oil on under-ice meiofauna, Cross and Martin (1987) showed that harpacticoid copepods were more sensitive than cyclopoid copepods and that cyclopoid nauplii density was also unaffected.

Cnidaria

Spangenberg (1987) documented numerous effects on cnidarians from exposure to Alaska Crude Petroleum (ACP). For the true jellyfish *Aurelia,* all compounds of ACP elicited retardation of strobilation initiation, and for some, cessation of strobilation entirely. And, for some groups of compounds, she showed numerous teratological effects: abnormal numbers of lappets, arms and rhopalia, irregular patterning, Siamese ephyra and reduction in both size and number of statoliths. There were also abnormalities in polyp morphology (multiple heads or stalks, fused parts, branched stalks, or clumped polyps) and behavior (altered swimming and pulsing). For various concentrations of petroleum water soluble fractions (WSF), the hydroid *Tubularia* exhibited neurological disorders, and alterations in chemosensory function and ingestion rates (Case *et al.*, 1987). And, in tests with other hydroids with symbiotic zooxanthellae, 24–48 hr exposures to WSF resulted in significant reductions in algal photosynthesis and carbon-translocation rates, but exposures of ≤3 hr did not produce these significant changes.

In contrast, some Cnidaria (anemones and some jellyfish) seem especially resistant to oil. The anemones *Anthopleura* and *Actinia* are species found surviving in waters with some of the most serious pollution, both from individual spills and chronic inputs (Nelson-Smith, 1972). However, other Cnidaria, such as the hydroid *Tubularia,* are much more sensitive, experiencing substantial mortality when subjected to only low concentrations of crude oil.

Research on impacts of oil on corals and especially coral communities is more limited. In addition to outright mortality, some experiments and field studies have shown the following sublethal effects on corals, especially hermatypic corals: diminished reproduction (especially manifested as decreased ovaria and planula per polyp, reduced female gonads per polyp, degeneration of the ova, and lack of gonadal development altogether), abnormal mouth opening and associated premature expulsion of planulae, altered feeding behavior and tactile responses, thinning of the coenosarc and changes in polyp pulsation rate (Loya and Rinkevich, 1980; N.R.C., 1985).

Crustacea

Case *et al.* (1987) showed that the WSF of crude oil resulted in specific chemosensory-induced brachycardia in the kelp crab *Pugettia,* affected food searching abilities in both *Pugettia* and *Cancer* and in general ultimately suppressed chemoreception abilities. Larvae of King crabs (*Paralithodes*) and shrimp (*Eualus*) exposed to WSF showed cessation of swimming and death within hours to days after exposure (Brodersen, 1987). Female Dungeness (*Cancer*) crabs held on oiled sediments through a reproductive cycle produced significantly fewer numbers of larvae than did controls, whereas Tanner crabs (*Chionoecetes*) showed no significant differences for number and viability of larvae (Babcock and Karinen, 1988).

Amphipods in general, and ampeliscid amphipods in particular, seem especially sensitive to oil, often not returning to prespill abundances for 5 or more years, which is likely related to the persistence of oil within sediments (Southward, 1982).

Most barnacles seem to have a tremendous tolerance for oil. Unless they are directly covered, and thereby die from smothering, they survive quite well even with oil surrounding their shell. Larvae even settle and survive on recently spilled oil, but may die when that layer eventually sloughs from the substratum. Goose-neck barnacles are often seen attached to floating tar balls at sea.

Echinodermata

Echinoderms seem especially sensitive to the toxic effects of oil, likely because of the large amount of exposed epidermis. Both seastars (*Pisaster*) and sea urchins (*Strongylocentrotus*) were eliminated for several years following the 1957 wreck of the Tampico Maru off the coast of Baja California (Nelson-Smith, 1972).

Both feeding rates and growth rates have been shown to be inhibited in the seastar *Evasterias troschelii* when exposed to WSF concentrations of crude oil greater than 0.12 ppm (O'Clair and Rice, 1985). For sea urchins (*Strongylocentrotus*), Vashchenko (1980) showed embryological abnormalities characterized by prominent delay of embryogenesis, asynchronism and production of non-viable larvae when exposed to hydrocarbon concentrations of 10–30 mg/liter. Mageau *et al.* (1987) also showed functional loss of tube foot and spine movement with an aged crude oil/Corexit dispersant mixture.

Mollusca

For mollusks, Connell and Miller (1981*a*, *b*) and Bayne *et al.* (1982) reviewed the effects of oil or oil fractions on many physiological functions. In general, sublethal concentrations of oil produce substantially reduced feeding rates and/or food detection ability (in *Crassostrea, Mytilus, Macoma, Mercenaria* and *Nassarius*), which probably results from direct ciliary inhibition. For bivalves and gastropods, respiration is sometimes increased at low concentrations, but decreased at higher concentrations. In general, there is an increase in energy expenditure and a decrease in feeding rates associated with oil, ultimately resulting in less energy for growth and reproduction. From a behavioral perspective, sublethal concentrations also reduce byssal thread production (resulting in weakened attachment strengths) and infaunal bivalve burrowing rates. Littorines (*Nassarius*) subjected to similar compounds have altered crawling rates, reduced feeding, decreased aggression and increased alarm responses. Oil may also disrupt normal gametogenesis, leading to asynchronous spawning with possible release of unripe gametes and lowered fitness (resulting from lower survival of suboptimal larvae). In bivalves, Mageau *et al.* (1987) showed ostial closure, loss of responsiveness to mechanical stimuli and narcosis.

Among mollusks, most limpets seem particularly sensitive to oil and their populations are often severely reduced during a major spill. Gastropods may also suffer significant mortality because they become encrusted with oil, overweighted and washed from the substratum into subtidal regions where they likely succumb to predation or into supratidal regions where they die from desiccation.

Some physiological effects on adults involve only minor alterations to normal functions. For example, a minor reduction in speed or movement may affect the organism's ability to elicit an effective predatory escape response.

Polychaeta

Some polychaeate species, especially *Capitella capitata,* proliferate after oil spills (*e.g.*, the West Falmouth spill—see Sanders, 1978); accordingly, *C. capitata* is often used as an indicator species to identify areas of heavy pollution. Cirratulids seem mostly immune, probably because their feeding tentacles are protected by a heavy secretion of mucus. The lugworm *Arenicola,* when exposed to high concentrations of fresh No. 2 fuel oil in sediments, is typically driven to the surface or stops sediment reworking and/or fecal cast production (Prouse and Gordon, 1976). This condition often results in death since it exposes them to predators (fish, birds, etc.) and prevents them from feeding. In parallel experiments, *Arenicola* was also shown to be affected by this same fuel oil in the water column, which resulted initially (after 5 hr) in reduced cast production, then emergence from the sediment (after 22 hr) and finally mortality (after 3 days).

Echiura

Although populations of the echiuroid worm (*Listriolobus*) declined sharply after the 1969 Santa Barbara blowout, they later recovered rather quickly and were found surviving in oil soaked sediments, indicating that their decline was possibly associated with some other cause and that they are likely more tolerant to oil (Nelson-Smith, 1972).

INDIRECT EFFECTS: TROPHIC CASCADING

Invertebrate communities are composed of species that have large influences on community structure and those that have little relative influence on community structure. Recently we have seen a great deal of attention paid to "trophic cascading" or "top-down" *versus* "bottom-up" forces that structure aquatic communities (Menge, 1992; Strong, 1992). Whatever the direction of influence, the important factor is that species at one trophic level can significantly influence species at other trophic levels, by virtue of being absent or present in large numbers. This can influence not only the relationship between species, but can affect the entire community structure (see Suchanek, 1994).

For example, when limpet populations are substantially reduced by oil, their grazing impacts are removed from the community. As found after some major spills, there may develop a luxuriant growth of algae (*e.g.*, *Enteromorpha* or *Fucus*). Fucoids or other large algae can also abrade or scour settling barnacle larvae from the substratum. As fucoids grow to adulthood, limpets and other grazers may not be able to remove them from the substratum, thereby changing community structure for several years (Nelson-Smith, 1972; Suchanek, 1979).

An example of the phenomenon of indirect effects is afforded from impacts on coastal marine mammals. If sea otter populations are severely impacted from an oil spill, their influence on nearshore invertebrates such as sea urchins and mussels will also be greatly modified. The absence of sea otters in a localized region would allow sea urchin populations to proliferate, reducing kelp beds, which in turn would reduce sedimentation in the nearshore environment, which in turn would tend to increase scour of the benthic substrata and encourage the development of a more hard substratum community rather than a soft substratum community (see Suchanek, 1994 for discussion).

Another example of indirect effects of oil (as a slick on the sea surface) would be to reduce light conditions (by 90%—Nelson-Smith, 1972), thereby affecting the efficiency of visual predators or reducing the photosynthetic rates of planktonic diatoms or submerged algae, which in turn would affect grazers on those food sources. It is uncertain what ultimate obvious or subtle changes may take place as the result of altered behavioral responses by various taxonomic groups, but these are changes that need to be considered when evaluating direct and indirect oil impacts on invertebrates.

ADDITIVE/SYNERGISTIC EFFECTS

Variables such as latitude, season, presence of floating ice and sediment in the water column may alter the responses of invertebrates to oil in the environment. Some specific examples provide insights to additive or synergistic effects on the responses of invertebrates to oil in their environment.

Arctic marine invertebrate communities may face special types of problems associated with exogenous stresses such as oil contamination. There is substantial evidence that oil may impose additive (and possibly synergistic) impacts with other stresses such as elevated salinities, experienced during the winter season in Arctic nearshore environments (Schneider, 1980). From laboratory toxicity tests on invertebrates, Rice *et al.* (1976) determined that Alaskan species may be slightly more sensitive than their more temperate counterparts. They stated, however, that this difference may only be a function of the greater toxicity of oil at lower temperatures (due to greater persistence of hydrocarbons) rather than a function of sensitivities. From a community level perspective, there are also fewer species in the Arctic and food chains are quite short. If one taxon were particularly impacted, there would likely be few replacement species. Therefore, once changed, this type of community would be less able to recover (Rice *et al.*, 1980).

Dispersants and oil together are thought to interact in a negatively synergistic manner, as evidenced by a particularly devastating impact when these chemicals were mixed during the clean-up operations following the 1967 grounding of the Torrey Canyon off the coast of Britain (Malins and Collier, 1981). Another additive factor is the amount of sediment present in the water column. Oil mixed with suspended sediment has been shown to migrate to distant areas, sometimes deeper, over a 1–2 yr period following a spill, resulting in secondary contamination of sites distant from the origin of the spill (Nelson-Smith, 1972; Sanders, 1978).

ECOSYSTEM STUDIES OF IMPACT/RECOVERY—A FEW CASE STUDIES

Initial impact and long-term ecosystem recovery from major oil spills have been documented in only a few cases. In general, the lasting impacts on invertebrate populations and communities are typically a function of the type and amount of oil spilled, its persistence, the type of habitat and species impacted, and the type of clean-up techniques used, if any. Below I provide a select few examples of spills and other oil introductions to the marine environment that have provided insights into understanding how invertebrates are impacted by oil. For a more complete accounting of other case studies, see N.R.C. (1985).

1967 Torrey Canyon spill

In March of 1967 the Torrey Canyon's grounding off the British coast of Cornwall spilled roughly 27,250,000 gal of oil, of which over 9,000,000 gal was believed to reach shore (Southward and Southward, 1978). Evaluation of oil impacts alone from this spill are nearly impossible, for huge amounts of dispersants were added (at a ratio of 10,000 tons of dispersant to 14,000 tons of oil) to reduce the spread of the oil. Following massive die-offs of intertidal invertebrates, including many grazers such as chitons, limpets anad other gastropods, the green fleshy algae *Enteromorpha* and *Ulva* colonized abundantly within a few months. Thereafter, fucoid algae colonized heavily. Within the next 2 years limpets (*Patella*) started to return in significant numbers. Normally sedentary, they had little to feed on and moved in "herds" grazing down any available fucoids. Over the ten year period following the spill *Patella* (as well as *Fucus*) experienced extreme population fluctuations. Another alteration to the intertidal community was a change in algal zonation patterns of *Laminaria* and *Hildenbrandia* by as much as 2 meters, shifting upwards most likely in response to reduced grazer populations, illustrating the importance of biological interactions in structuring these communities. By 1977 most common species had returned, but some were still completely absent. By 1981, 14 years after the spill, shoreline communities had not yet fully recovered (Southward, cited in Clark, 1982*b*).

1969 West Falmouth spill

The best documented spill for more protected habitats with soft mud/sand substrata was the West Falmouth spill of #2 diesel fuel. Here, the remobilization of oil (especially to subtidal regions) >1 year after the original spill contributed to much greater contamination of habitats than was originally caused by the initial impact. Virtually the entire benthic fauna was eradicated immediately following the spill and populations of the opportunistic polychaete *Capitella capitata* exploded to abundances of over 200,000/m^2 (Sanders, 1978). After *ca.* 7 months, this population crashed, giving way to less opportunistic infaunal species. Over the next 30 months there were numerous other population recruitments, explosions and crashes at the oil impacted site, but relatively stable populations at nearby non-oiled sites. In 1989, 20 years after the spill, oil traceable to the 1969 spill was still found in sediment cores to 15 cm depth at the most severely oiled site, but not at a nearby non-oiled comparison site (Teal *et al.,* 1992). For the most part these levels were very low and less than 1% of the marsh still remains significantly contaminated. The lasting nature of this oil was probably due to (1) the low energy environment (preventing removal by physical means), (2) the high organic content of the marsh sediments (promoting the sorption of the oil onto organic particles) and (3) the near zero oxygen concentrations of marsh sediments (which retarded microbial degradation). Tissues from fiddler crabs (*Uca*), that burrow into marsh sediments and derive their nutrition from detritus, showed the greatest level of continuing oil contamination. All other marsh organisms analyzed showed some trace contamination after 20 years, but levels were not significantly different between previously heavily oiled *versus* non-oiled sites.

1973 Naantali Harbor cleanup

In an interesting twist, a high quality oil waste water discharge treatment plant was installed at an oil refinery in Naantali Harbor in the Baltic Sea, Finland. This site was previously subjected to extreme oil contamination from refinery discharges (Leppakoski and Lindstrom, 1978). Benthic invertebrate populations were monitored before and after the installation with dramatic increases in species richness (55%), densities (*ca.* 400%) and biomass (*ca.* 2,000%) within 3 yr, indicating the magnitude of depression on community structure imposed by this environmental stress.

1977 Tsesis spill

This spill involved *ca.* 252,000 gal of mostly No. 5 fuel oil and some bunker oil released off the coast of Sweden in October 1977 (Kineman *et al.,* 1980). Oil was rapidly transported to the benthos where the taxonomic groups hit particularly hard were crustaceans and meiofauna. Amphipods and ostracods suffered especially high mortality (over 90% reductions) and the few remaining amphipods showed roughly 10% abnormal or undifferentiated embryos (compared with typical levels of *ca.* 1%).

1978 AMOCO Cadiz

Roughly 51,000,000 gal of Iranian and Arabian crude oil affected exposed rocky and sandy beaches, and some eelgrass beds and estuaries following this spill. Immediate mortality of most invertebrate community members was observed, especially bivalves, limpets, other gastropods, peracarid crustaceans and heart urchins (Conan, 1982). Meiofauna and harpactacoid copepods were drastically reduced and/or exhibited unbalanced seasonal cycles (Bodin and Boucher, 1982). After 3 months indigenous nematode populations showed dramatic declines in diversity and biomass; they were replaced by an extremely abundant opportunistic nematode species typically associated with eutrophic environments (Boucher *et al.,* 1982). After 3 years most communities were still perturbed and unbalanced (Glemarec and Hussenot, 1982) and delayed effects on mortality, growth and recruitment were documented (Conan, 1982). Species with short life cycles tended to replace species with longer life cycles.

Some baseline data were available for eelgrass beds in this region, indicating that recovery of this habitat type began relatively rapidly, within a year or so (den Hartog and Jacobs, 1980; Jacobs, 1980). Yet one year after the spill (Table 1), numerical abundance (N) and species richness (S) of all mobile fauna and infauna (from both upper and lower zones) were still reduced considerably below levels at comparable times before the spill (figures calculated from den Hartog and Jacobs, 1980; Jacobs, 1980).

In a 10 yr analysis of impacts from this spill on a muddy/sandy infaunal community in northern France, Ibanez and Dauvin (1988) identified 7 successive periods of temporal community change during recolonization. Similar to other large spills, there was a period of substantial population fluctuation in many species. This sequence developed through a series of successional phases with the establishment of opportunists, colonization of a polychaete (*Lanice*) and finally the re-establishment of the pre-spill assemblage.

1987 Nella Dan spill

In a relatively small spill, the Nella Dan released *ca.* 71,000 gal of mostly light diesel oil and was one of the few spills to occur in very cold sub-Antarctic waters (Macquarie Island, southwest of New Zealand; see Pople *et al.,* 1990). No pre-spill data existed. Comparisons of the spill site with control sites showed that this spill mostly affected species in the lower intertidal and subtidal regions. Those macrofauna that were affected the most were echinoderms and limpets, with lesser effects observed on chitons. After one year, the impact was still quite evident.

1989 Exxon Valdez

In March 1989 the Exxon Valdez spilled *ca.* 11,000,000 gal of Alaskan north slope crude into Prince William Sound (PWS), Alaska. The oil traveled rapidly southwest through and out of PWS into the Gulf of

TABLE 1. *Changes in cumulative numerical abundance of individuals (N) and species richness (S) for mobile fauna and infauna (at upper and lower tidal heights) in eelgrass beds one year after the Amoco Cadiz oil spill.*

Taxonomic group	Mobile fauna (N)	Mobile fauna (S)	Upper infauna (N)	Upper infauna (S)	Lower infauna (N)	Lower infauna (S)
Feb 1978	1,162	73	226	21	1,094	62
Feb 1979	439	51	127	19	509	42
% reduction	62.2	30.1	43.8	9.5	53.5	32.3

Alaska (GOA) and affected shoreline communities at least 500 miles from the spill origin, mostly along the region of the Shelikof Strait. At the time of this writing, most of the significant data (including my own) from this spill on the initial impact and recovery of invertebrate communities are still in preliminary stages and/or are being held from publication under litigation secrecy restrictions. Because of massive clean-up efforts (using chemicals and/or high-pressure/high-temperature water) on many shorelines mostly within Prince William Sound, it may also be difficult to determine whether impacts were caused by oil or by clean-up efforts.

To date some of the only data released from the Exxon Valdez spill are from a NOAA report on the differences between oiled sites that received cleaning treatments *versus* those that did not (*e.g.*, Houghton *et al.*, 1991), basically indicating that clean-up treatments apparently had a greater deleterious impact on shoreline communities than did oil alone. More recent preliminary qualitative reports indicate that the most significant impacts in Prince William Sound occurred in the upper intertidal zone, with limpets (*Tectura*) being the most affected (Hooten and Highsmith, 1992). Densities of subtidal crabs (*Telmessus*) and seastars (*Dermasterias*) were also significantly lower at oiled sites (Dean and Jewett, 1992). Populations of another adult seastar (*Pycnopodia*) seemed unaffected by the spill, but recruitment of this species was enhanced at oiled sites in 1991.

DISCUSSION AND CONCLUSIONS

Effects of oil, especially associated with major oil spills, on invertebrate populations and communities have received considerable attention. While most documented population and community level changes have focused on mortality as the primary impact, we need to expand our appreciation of less obvious changes to consider how systems are altered as a result of oil pollution or any other environmental stress. Changes in physiology, behavior or reproduction will all influence an organism's ability to feed, accurately perceive the surrounding environment, compete for resources or find mates, which can lead to significant changes in fitness. Direct, indirect, additive and synergistic effects at the individual level will all contribute greatly to the ultimate impacts felt at the population and community levels. While many ecosystem studies have shown that invertebrate communities display substantial recovery after only a few years, those systems with invertebrate population age structures that took 10–20 yr to develop will likely feel the long-term effects of a major perturbation to the system. Since many taxa such as echinoderms show stochastic or unpredictable recruitment patterns under normal conditions, it may also be hard to predict the recovery sequence or time needed to renew community level structure after an alteration from a major oil spill.

Despite many reports to the contrary, all or even most invertebrate communities subjected to major oil spills in the marine environment do not recover quickly (within a couple of years). For an excellent review of long-term studies of oil pollution see Clark (1982*a*). It is true that widespread mortality generally occurs in the immediate vicinity of a spill, and usually only during the initial contact with the oil. As evidenced by several spill studies, remobilization of oil to other regions (both subtidal and intertidal) typically results in additional mortality. In general, population and community structure are typically altered for periods of 2–15 years, depending mostly on the type and complexity of the community involved, the exposure regime of the habitat and the chemical composition of the oil and/or chemical treatments. Coastal habitats exposed to intense wave action will experience a scouring effect, sometimes called "self-cleansing" which reduces the time over which impacts are felt considerably. For more protected habitats which retain oil longer, community effects can be expected to persist longer.

The exposed shorelines of the eastern north Pacific (from California through British Columbia) are dominated by dense beds of the mussel *Mytilus californianus,* which support an extremely diverse associated community of over 300 taxa within the interstices of the mussel matrix (Suchanek, 1979, 1985, 1992; Seed and Suchanek, 1992). Currently there is an 18 yr ongoing study (initiated in 1974) of disturbance and recovery in these intertidal mussel beds on the outer exposed coast of Washington. Mathematically projected recovery rates for some artificially disturbed upper intertidal sites yield estimates of hundreds of years or more for complete recovery (Suchanek and Duggins, unpublished data; and see Seed and Suchanek, 1992). It is unlikely that recovery would take this amount of time, as some massive stochastic recruitment event will probably intervene, but it has not done so yet over the past 18 yr. Because oil is usually deposited at upper intertidal zones, and because the overall effects of oil tend to be the same as those associated with any other disturbance to the community (Southward, 1982), these types of communities (*i.e.*, diverse mussel bed communities) may be at some of the highest risk of long-term impact from a major spill in the eastern Pacific region.

The following generalizations can be applied to coastal marine invertebrate communities following a major oil spill. Initially there is significant mortality. In soft sediment habitats, infaunal polychaetes, bivalves and amphipods are particularly affected. On rocky shores the most significant impacts are experienced by mobile fauna such as echinoderms, crabs, gastropods, chitons and amphipods as well as some canopy-forming algae such as the rockweed *Fucus*. If the oil is especially thick it will also smother barnacles and/or mussels. In both cases opportunistic species typically invade the habitat and proliferate. Populations of invading species undergo wildly fluctuating boom and bust cycles with dampening amplitude over time. In soft sediments this scenario is played out with polychaetes (often with *Capitella capitata* as the opportunist) and nematodes. In rocky habitats, where grazer populations have been eliminated or severely reduced, green or brown algae proliferate quickly and often become dominant space occupiers for several years until both competition and herbivory return them to pre-spill levels. There may even be a shift in zonation patterns. These initial periods of rapid and prolific algal growth have led some to proclaim that widespread or even complete recovery is virtually immediate, but usually they do not represent the pre-spill complement of species.

Figure 1 provides a generalized scenario for typical changes in an invertebrate community following a catastrophic oil spill. The

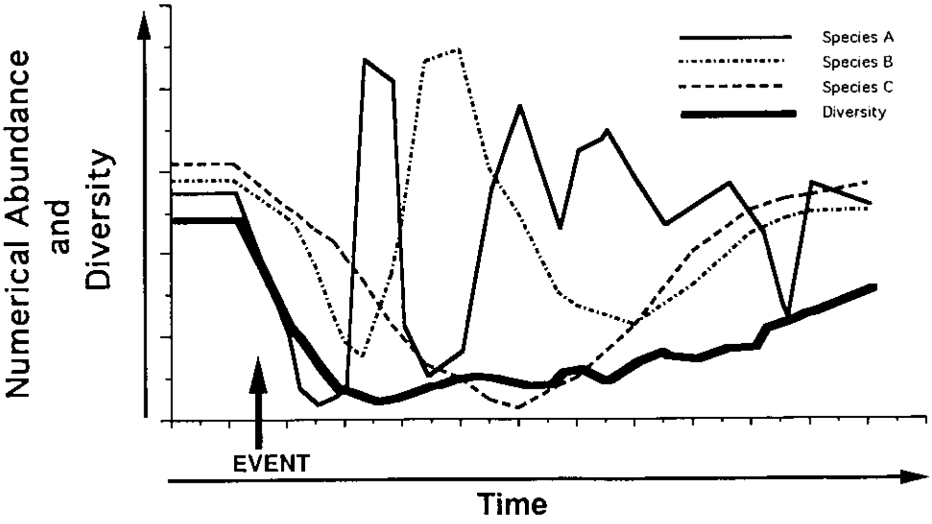

FIG. 1. Generalized effects on species richness and numerical abundance of invertebrate populations subjected to a major oil spill.

effects of chronic oil pollution usually mimic those effects from acute exposure to massive spills. There is usually a reduction in diversity, which is often compensated by an increase in numbers of a few resistant species.

Because oil affects virtually all invertebrate taxa (some more seriously than others), and because many marine invertebrate populations (especially subtidal ones) are mostly obscure, we need to start evaluating relative community health and long-term variability. As billions of gallons of hydrocarbons enter our oceans each year, they are imparting numerous direct, indirect, additive, synergistic and unknown effects on invertebrate communities. We need to monitor and control as carefully as possible all anthropogenic sources of hydrocarbons in the oceans, which likely account for over 90% of all inputs. In addition, we need to institute more research programs to first identify which invertebrates exist in specific marine habitats, especially those subjected to the highest levels of actual and potential impacts. Many areas have had virtually no basic taxonomic or descriptive studies, especially in more remote areas (such as the region impacted by the Exxon Valdez oil spill). Complex community and ecosystem level changes are all dependent on critical species-species interactions and these are driven by impacts at the individual level. Therefore, once we have defined these communities we need to identify and understand the ecological processes that control their long-term natural variability. Only with this understanding will we have the tools necessary to protect and conserve such diverse natural resources.

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