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COMPREHENSIVE REVIEW AND CRITICAL SYNTHESIS OF THE LITERATURE ON RECOVERY OF ECOSYSTEMS FOLLOWING DISTURBANCES:

MARINE INVERTEBRATE COMMUNITIES

by

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EXECUTIVE SUMMARY

This paper is a comprehensive review and critical synthesis of the readily available literature on recovery of marine benthic invertebrate communities following disturbances. It was commissioned by the staff of the Oil Spill Restoration Planning Office to assist them in their management of Alaska's Prince William Sound area following the oil spill of the *Exxon Valdez*.

Benthic invertebrate communities are very productive, rich in species and support food webs that include commercially and ecologically important species. These communities are vulnerable to disturbances, including storm damage, sewage pollution and oil pollution. Many scientific studies have described the recovery of these communities after a disturbance.

This document summarises 79 of these recovery studies. In particular, it addresses the following issues: (a) recovery time; (b) abiotic factors that affect recovery; (c) management practices; and (d) recommended approach to determine when recovery has occurred.

(a) Recovery time. The general conclusions were :

1. Most studies reported that recovery did not occur in the time allowed by the investigators. [Most studies were conducted for less than three years.] This makes discussion of recovery times difficult and forces one to examine trends in the recovery times found in the studies.
2. Recovery was more likely after a small disturbance than after a large disturbance.
3. Recovery was equally as likely in intertidal and subtidal habitats.
4. Recovery was more likely after a non-oiling disturbance than after an oiling disturbance.
5. Recovery was more likely after oiling of hard substrates than after oiling of soft substrates.
6. Recovery times of invertebrate communities after an oiling event are estimated to be 10 - 20 years for communities on hard substrates and 10 - 25 years for communities on soft substrates.

(b) Abiotic factors that affect recovery. Recovery is generally slower (a) after a large oil spill than after a small oil spill, (b) in soft sediments than on hard sediments, (c) in the high intertidal zone than in the low intertidal zone, and (d) at high latitudes than at temperate latitudes.

(c) Management practices. Many management practices may influence recovery. In particular, I point out the problems associated with clean-up and bioremediation, and suggest that transplantation of some species should be considered.

(d) Recommended approach to determine when recovery has occurred. I believe that the following six points are crucial to conducting a successful study.

1. A definition of recovery is necessary. I suggest: "Complete recovery of an invertebrate community after an oil spill occurs when (a) all the species that were present before the oil spill are again present; (b) each of these species has reached their original abundances and biomasses, (c) each of these species has reached their original age distributions, and (d) all individuals are as healthy (as measured by growth rates) and productive (as measured by reproductive condition) as the individuals that were present at the time of the oil spill." In the absence of pre-spill data, original conditions (i.e.,

abundances, biomasses, age distributions, growth rates and productivities) should be estimated from several unoiled communities in similar physical/chemical environments.

2. The hypotheses being tested should be clearly stated. The following hypotheses are appropriate: that there are no significant differences in (a) the species that are present in oiled and unoiled areas; (b) the abundances and biomasses of the species in oiled and unoiled areas; (c) the age distributions of the species in oiled and unoiled areas; and (d) the growth rates and reproductive condition of individuals in oiled and unoiled areas.

3. None of the 79 studies provides a good example of how to conduct a recovery study (defined as testing the hypotheses cited in #2 above). It is clear that if a study is to stand up to scrutiny it will have to be a careful and thorough study planned by competant statisticians and biologists familiar with the Alaskan ecosystem.

4. Natural communities are spatially and temporally heterogenous. This means (a) that it is necessary to study many unoiled and many oiled sites so that the range of natural variability can be determined, (b) that a large area should be sampled at each site, and (c) that many samples are required for reliable estimates of population densities.

5. All the results that are necessary and sufficient to test the hypotheses should be presented in the research report.

6. Details about "important species" (e.g., those that are numerically dominant, provide much of the structure to the community, or play an important role in the dynamics of the system) should also be presented. An analysis of the recovery of the community therefore requires a detailed knowledge of the community.

1.0 INTRODUCTION

1.1 Background

On 24 March 1989 the tanker *Exxon Valdez* ran aground in Alaska's Prince William Sound causing the largest oil spill in U.S. history. Approximately 11 million gallons of North Slope crude was lost at sea. The oil spread over an area of >900 square miles and oiled 1, 244 miles of the shorelines in the Prince William Sound, and on the Kenai Peninsula, Alaska Peninsula and Kodiak Island (Alaska Department of Environmental Conservation, 1989).

A tremendous clean-up and restoration effort has followed the spill and the managers of this effort would like to know what to expect in the recovery of these habitats. In particular, they would like answers to questions such as: How long will recovery take? What factors are likely to affect recovery? What indicators of recovery should the biologists be measuring? In an attempt to answer these questions for benthic marine invertebrate communities I have reviewed the literature on recovery of invertebrate communities after various disturbances, including oil spills.

Benthic invertebrate communities in the intertidal and shallow subtidal zones are particularly vulnerable to oil spills because much of the oil is deposited and concentrated in these habitats (National Research Council 1985) and, because most invertebrates are relatively immobile, they are unable to escape the toxic and smothering effects of oiling. The recovery of these communities is relatively slow, i.e., several years, and the damage caused by an oil spill can often still be detected several years after a major spill (e.g., Southward and Southward 1978).

Benthic invertebrate communities are very productive, rich in species and support complex food webs that frequently include commercially and ecologically important species. For instance, the benthic invertebrates in Alaska support many species of bottom feeding fish (e.g., black rockfish), birds (e.g., oystercatchers), and mammals (e.g., gray whale, sea otter, brown bear, black bear, even man -- subsistence harvesting of mussels and clams). Also many benthic invertebrates have planktonic larvae and these become important components of planktonic food webs which include pelagic fishes (e.g., salmon, herring), birds (e.g., puffins, kittiwakes, murres, bald eagles), and mammals (e.g., harbor seals). Damages to the benthic invertebrate communities can therefore have wide-spread effects.

The **effects** of disturbances on benthic invertebrate communities have been well studied, particularly during the past 20 years (e.g., Kvitek et al. in press, see Connell and Keough 1985, and Sousa 1985, for reviews). However, long-term studies of **recovery** in these communities are rare -- I have found only 79 studies that deal with recovery and most of these (62%) followed recovery for a rather short time -- three years or less. My review of these recovery studies expands upon earlier reviews by Mann and Clark (1978), Thistle (1981), and Ganning et al. (1984), and provides a different perspective to the review by Baker et al. (1990).

1.2 Objectives

There are two objectives to this paper:

1. To review the readily available literature on recovery of marine invertebrate communities after a disturbance. I will focus on the rate of recovery and factors that may affect recovery.
2. To extrapolate the information obtained in the review to the injured Alaskan ecosystem. In particular, to identify the most practical indicators of recovery to measure, and to recommend an approach to determine when recovery has occurred.

2.0 TECHNICAL APPROACH

2.1 Information Retrieval and Sources of Data

I searched in many places for papers dealing with the recovery of marine invertebrate communities. These included:

GENERAL REFERENCES

1. Aquatic Sciences and Fisheries Abstracts -- 1982 to 1990. Using the key words: oil-spills-benthic; intertidal-recruitment; intertidal-succession; subtidal-succession; disturbance-recovery-invertebrates; disturbance-recovery-marine; and oil-invertebrates.

2. The reference lists in: Vesco and Gillard 1980; Sousa 1984; Foster et al. 1988.

OIL POLLUTION REFERENCES

3. Oil Spill Public Information Center's Collection List (1366 entries) -- June 1991.

4. Proceedings of the American Petroleum Institute Oil Spill Conferences from 1975 through 1991 (e.g., American Petroleum Institute 1991).

5. The reference lists in: National Research Council 1975, 1985; Wolfe 1976; Stevenson 1978; Cox 1980; Cairns and Buikema 1984; Boesch and Rabalais 1987; Mielke 1990; Houghton et al. 1991a.

6. Marine Pollution Bulletin for the years 1985 through 1990.

DREDGING and DRILLING MUD REFERENCES

7. The reference lists in: Kester et al. 1982; National Research Council 1983; Ketchum et al. 1985; Cullinane et al. 1990.

EARTHQUAKES, LANDLEVEL CHANGES and NUCLEAR TESTING REFERENCES

8. The reference lists in: Kirkwood 1971; National Research Council 1971, 1973; Merritt and Fuller 1977.

9. Citation Index for recent citations of: Hubbard 1971; Baxter 1971; Haven 1971; O'Clair 1977; Lebednik and Palmisano 1977.

2.2 Analysis and Synthesis

Papers were excluded from the review if: (1) they dealt with the effect of a disturbance and not recovery after the disturbance (e.g., Maki 1991, see Teal and Howarth 1984, and National Research Council 1985 for reviews of effects); (2) they dealt with only the effect of oil on the physiology, biochemistry or behavior of species (e.g., Percy 1977, see National Research Council 1985 for review); and (3) they were not in English (e.g., NOAA-CNEXO 1982). Thus the papers that are included in this review deal with the population and community level recovery after many kinds of disturbances (from whale feeding excavations to oil and sewage spills), in several different habitats (from subtidal soft sediments to rocky shores), and from many parts of the world (from the Straits of Magellan to Norway).

I grouped the papers according to the nature of the habitat (soft substrates and hard substrates, intertidal and subtidal), the size of the disturbance (small, if less than square meters; medium if square meters; and large if square kilometers), and the type of disturbance (non-organic, organic, and oil pollution).

3.0 REVIEW OF READILY AVAILABLE INFORMATION ON RECOVERY

3.1 Benthic Invertebrates

3.1.1 Rate, Duration, and Degree of Recovery Following Disturbance

It is important to define what is meant by the terms disturbance and recovery. Disturbance is "a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established" (Sousa 1984). Typical disturbances in benthic invertebrate communities are oil pollution, sewage pollution, the shearing force of large waves, and the foraging activities of animals, such as whales.

The majority of the papers discussed below do not define recovery, however their implied definition was usually "the return of all population densities to pre-disturbance levels or to undisturbed levels". For the purposes of this section I have chosen to keep to this definition. However, in Section 4.2.1 I discuss further the definition of recovery.

Here I review many different types of disturbances and deal with soft and hard sediments separately because there are some differences in the recovery of their benthic invertebrate communities.

SOFT SUBSTRATES

A) Succession model

The effects of organic pollution on infaunal invertebrate communities have been studied for many years and a general model has emerged of the succession that occurs in these communities during recovery (Pearson and Rosenberg 1978, Rhoads and Germano 1982). Figure 1A describes part of this model. In general, a heavy input of organic material (e.g., sewage, pulp-mill effluent) onto the sediment reduces the oxygen content of

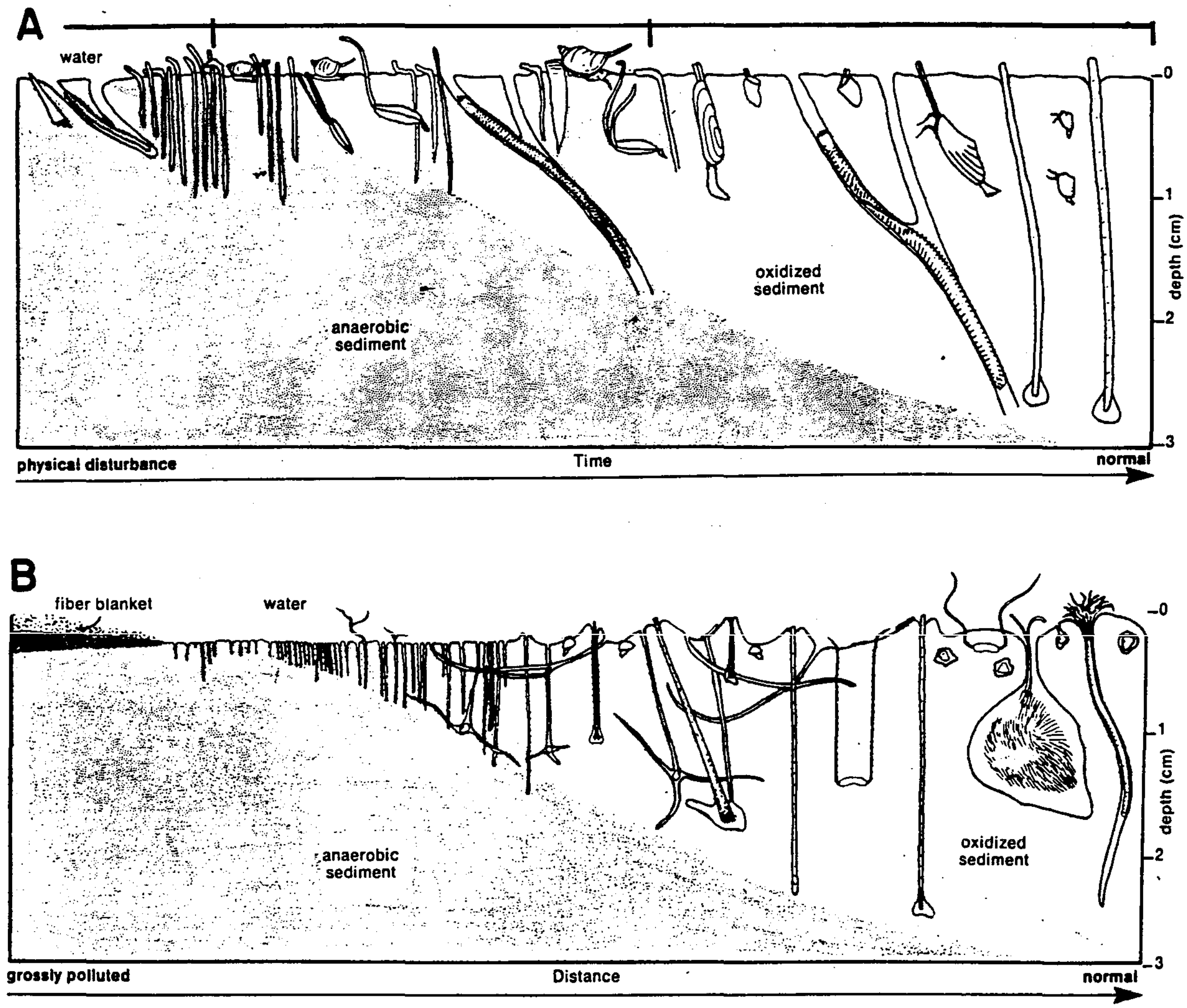

Figure 1. A diagram showing the variations in a typical benthic infauna community. The changes that occur in time during recovery from a disturbance (A) and the changes that occur in space around a source of pollution (B). From Rhoads and Germano (1982); used without permission.

the sediment and a black anaerobic layer rises to the sediment surface. The combination of high sulphide, low pH, and low oxygen concentrations in anaerobic sediment may cause complete defaunation. With no further input of organic material, currents carry away some of the organic material, conditions improve and a few macroinvertebrate species invade. These opportunistic, or "pioneer", species are usually epibenthic or surface-dwelling species (e.g., small tubiculous polychaetes) that are able to tolerate the conditions and take advantage of the rich organic material available. As conditions improve further and oxygen penetrates farther into the sediment, other species invade. These species, called "equilibrium" species or late succession species, include sub-surface deposit feeders whose burrowing activities result in further aeration of the sediment. Finally, these late succession species grow large, other late succession species invade, some (or all) of the opportunists drop out, and the community is indistinguishable from an undisturbed community.

Notice that the succession began when the area was invaded by relatively small, abundant, surface dwelling polychaete opportunists and ended when the area was inhabited by a suite of relatively large, rare, deep dwelling late succession species that include polychaetes, mollucs, crustaceans and echinoderms. Not only does the diversity of phyla increase but the number of foraging modes also increases, from non-selective sub-surface deposit feeders (e.g., *Capitella*) and carnivores, to suspension-feeders, omnivores, carnivores, and selective surface deposit feeders (Pearson and Rosenberg 1978).

The second part of the model describes how three important community characteristics (total number of species, total number of individuals, and total biomass) change during recovery of the community following an organic pollution event (Pearson and Rosenberg 1978; Figure 2). The total number of species increases steadily but then declines slightly because the opportunistic species tend to drop out. The total number of individuals rises very rapidly because the opportunists can be very dense but as the opportunists are replaced by late succession species the number of individuals drops quickly and eventually levels off at a relatively low number. The total biomass tends to increase steadily to a plateau usually with two peaks -- one early in the succession when opportunists are abundant and the other in the middle of succession when the greatest number of species are present in the community.

The end point of the succession is termed the "climax." This climax may only exist as an average condition on a relatively large spatial scale because frequent disturbances will prevent all parts of the habitat from reaching the climax state at the same time (Sousa 1984). The habitat will appear spatially heterogenous, i.e., many small patches at different stages of succession will be scattered in the large climax community.

The successional patterns described here also occur in space (Figure 1B). As one proceeds from a point source of organic pollution one will find in turn: an afaunal area, an area dominated by surface dwelling polychaetes, an area where there is a mixture of opportunistic and late succession species (transitional), and finally an area dominated by late succession species. This spatial pattern has been studied more than the temporal pattern (e.g., Pearson 1975, Swartz et al. 1986).

An important aspect of this model is that the composition of the early and late communities are quite predictable. The opportunistic species that invade during the initial stages of recovery from enrichment are distributed world-wide and the composition of the community they form is usually very similar from place to place (Pearson and Rosenberg 1978). It is therefore predictable. The late succession species that form the community during the final stage of recovery are more locally distributed and the "normal" communities they form differ from site to site depending on the habitat and the faunal region. However, the composition of these "normal" communities is predictable from

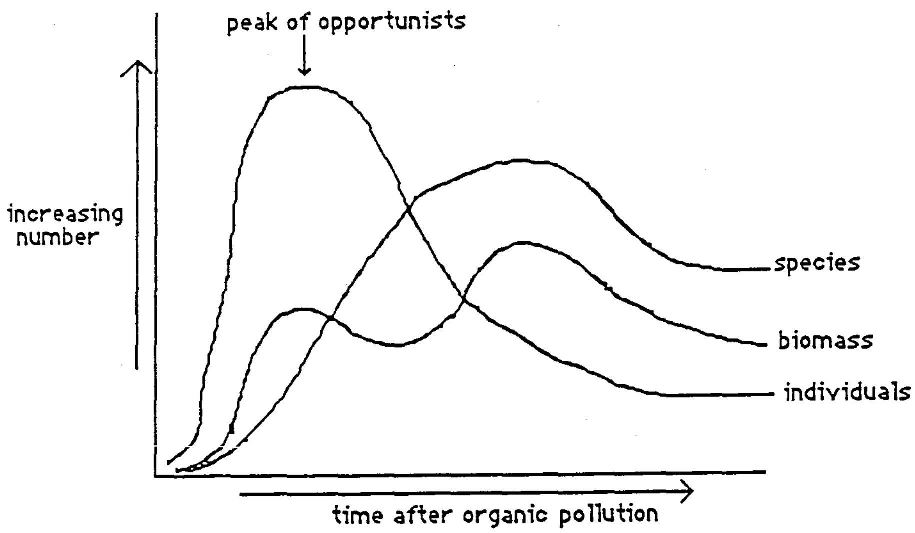

Figure 2. The fluctuations that occur in the number of species, number of individuals, and total biomass during the recovery of a typical benthic infauna community. From Pearson and Rosenberg (1978).

undisturbed areas nearby. Only the transitional community is unpredictable. This is because both the recruitment of the late succession species and the elimination of the opportunistic species is unpredictable.

Another important aspect of this succession is that a large number of species at a site does not necessarily indicate a fully recovered community. Actually a fully recovered site has fewer species, fewer individuals and less biomass than a partially recovered site. It will probably have the following characteristics: the anaerobic layer will be deep, several phyla will be present and several feeding modes will be present. However, a site can be considered to have fully recovered only when it is structurally and functionally indistinguishable from undisturbed reference sites.

B) Recovery times

Fifty-three studies dealt with the recovery of invertebrate communities in soft bottom habitats (Table 1). In deciding whether an area had recovered or not, I adopted the decision of each author, i.e., if the author determined that the area had recovered then I entered it as a "Yes", and if the author determined that it had not recovered then I entered it as a "No". The words "yes" and "no" could be replaced with "recovered" and "recovering".

a. Non-organic disturbances

A few studies dealt with the recovery of invertebrate communities after they were disturbed by animals, e.g., crabs, rays and walruses. These disturbances tended to be on a relatively small scale -- even the excavations made by the gray whales are usually less than $50m^2$ in size (Oliver and Slattery 1985). Recovery of these communities was relatively rapid -- some recovery had occurred in just a few days and in most cases full recovery was expected to occur within one year. Recovery occurred relatively quickly in other small scale disturbances as well, e.g., experimental pits made to mimic the effects of animal foraging activities (e.g., Savidge and Taghon 1988) and experimentally defaunated areas (e.g., Zajac and Whitlatch 1982a, b). Most authors attributed this to the rapid invasion of small areas by animals from the water column and the surrounding areas.

Recovery from more extensive disturbances, such as following dredging, a red tide, an earthquake or a hurricane, were slower -- recovery had not been completed in any of these cases and most of the studies had lasted for more than one year. One study found that recovery had not occurred in an area of mine tailings after 12 years (Ellis and Hoover 1990a, b).

b. Anthropogenic pollution

Organic pollution and oil pollution have been described as similar -- both forms of pollution are frequently extensive and affect the sediment and its inhabitants in similar ways (Glémarec 1986). Several studies dealt with the recovery of invertebrate communities following an organic pollution event (Table 1). Most commonly the authors reported that recovery was not complete, but recovery did occur in one case (Rosenberg 1976).

Rosenberg (1976) monitored the subtidal benthic community in the Saltkallefjord before and after a paper mill stopped dumping organic material. He found that recovery of the community was slowest in the most polluted sites; after approximately six years these sites had partially recovered -- they had the same number of species as the less polluted sites but the species compositions were not similar. After eight years, however, the

Table 1. A summary of the papers dealing with the recovery of marine invertebrate communities after a disturbance. For each paper the type of disturbance (dist.) and its size (Sm. = small, M = medium, L = large) are given. The time is either the recovery time (if recovery occurred) or the time between the disturbance and the last visit to the site (if recovery did not occur). The community is determined to have recovered if the authors said it had recovered or if the disturbed site was indistinguishable from a reference site. Quotes from the papers are included to amplify the answers. "REF" refers to the type of reference site(s) used (S = space, i.e., undisturbed site(s), T = time, i.e., the same site(s) prior to disturbance); "exp." = experimental; and "defaun." = defaunation. In addition, an * indicates that pollution was the source of the disturbance and, although it was substantially reduced, it was not completely eliminated. The Bibliography contains the full citation and abstract of each of these papers.

DIST. and SIZE	HABITAT	SITE	TIME	RECOVERY OF COMMUNITY ?	REF.	SOURCE
Soft Substrates						
Non-organic disturbance						
exp. pits, Sm.	intertidal	Oregon	24 days	**Yes**, "harpacticoids, juvenile spionids, cumaceans, and tanaids returned rapidly to ambient densities"	S	Savidge & Taghon 1988
crabs, Sm.	subtidal	Scotland	1 mo.	**Yes**, "the community returned to its original state within 25 to 30 days"	S	Hall et al. 1991
rays, Sm.	subtidal	S. California	1-1.5 mo	**Yes**, "the third phase of colonization is the gradual return of several numerically dominant species to predisturbance densities on a scale of 4-6 weeks"	S	Van Blaricom 1982
walruses, Sm.	subtidal	Bering Sea	2.5 mo.	**No**, "the infauna had not recovered by this time"	S	Oliver et al. 1985
exp. mounds, Sm.	intertidal	Scotland	4.5 mo.	**No**, "numbers remained low throughout the recovery period, being only 50% of the control population"	S	McLusky et al. 1983
exp. pits, Sm.	intertidal	Scotland	4.5 mo.	**Yes**, "the basins had populations equal to the controls"	S	McLusky et al. 1983
whales, Sm.	subtidal	Bering Sea & Brit. Columbia	7 mo.	**Yes**, "community patterns probably were re-established within the experimental excavations"	S	Oliver & Slattery 1985

Table 1 (cont.)

Soft Substrates Non-organic disturbance (cont.)

DIST. and SIZE	HABITAT	SITE	TIME	RECOVERY OF COMMUNITY ?	REF.	SOURCE
exp. defaun., Sm.	subtidal	Connecticut	1.08 yr.	Yes, "recovery to ambient conditions occurred rapidly in the lower reach, while successional changes in the middle and upper basins continued at least until the end of the winter"	S	Zajac & Whitlatch 1982a, b
exp. defaun., Sm.	subtidal	Lake Erie	2.17 yrs.	No, "late colonizers ... reached natural abundances only after several months if at all"	S	Soster & McCall 1990
dredging, M.	subtidal	Italy	6 mo.	No, "the 6-month post-dredging communities still showed a noticeable qualitative dissimilarity with respect to the predredging period and neighbouring non-dredged areas"	T & S	Pagliai et al. 1985
dredging, M.	subtidal	New York	11 mo.	No, "the bay sediments exhibited an overall reduction in epi- and infaunal populations, which did not approach recovery levels 11 mo. after dredging"	T	Kaplan et al. 1974
drill cuttings, M.	subtidal	New Jersey	6 mo.	No, "although polychaete species composition was unaffected by the drilling, polychaete densities were significantly lowered"	T & S	Maurer et al. 1981
drill cuttings, M.	subtidal	North Sea	1.33 yrs.	No, "results ... indicate partial recovery of macrofaunal communities"	T & S	Mair et al. 1987
red tide, M.	intertidal	Florida	2 yrs.	No, "although species composition was fairly constant, the distribution of individuals among species changed greatly"	T	Dauer & Simon 1976
mine tailings, M.	subtidal	West Canada	12 yrs.	No, "biological differences between tailing and non-tailing areas remain after 12 years"	S	Ellis & Hoover 1990a, b
earthquake, L.	intertidal	Alaska	1 yr.	No?, "some species have apparently experienced little reproduction since the earthquake"	T	Hubbard 1971

Table 1 (cont.)
Soft Substrates Non-organic disturbance (cont.)

earthquake, L.	intertidal	Alaska	1 yr.	No, post-earthquake clam abundances were 64% the (estimated) pre-earthquake abundances	T	Baxter 1971
hurricane, L.	subtidal	Chesapeake Bay	2.5 yrs.	No, "the deep mud bottom community ... had not recovered 2.5 years after the storm"	T	Boesch et al. 1976
Anthropogenic pollution						
organic, L.	subtidal	L.A. Harbor	1 yr.	No, but there was an "upgrading of species composition from a polluted to a semi-healthy species composition in the immediate area"*	None	Reish et al. 1980
organic, L.	subtidal	Sweden	4 yrs.	No, but "the echinoderms, which were the dominating animal group ... began to be re-established"*	T	Rosenberg 1972
organic, L.	subtidal	England	7 yrs.	No, "in the middle reaches a fauna tolerant of organic pollution is very abundant"*	S	Shillabeer & Tapp 1989
organic, L.	subtidal	Sweden	8 yrs.	Yes, "the basic recovery ... took five years, and ... after eight years it was not possible to distinguish between a normal and a recovery -influenced succession"*	T & S	Rosenberg 1976
organic, L.	subtidal	Texas	12 yrs.	No, but "it was evident that the Neches river estuary had been greatly improved"*	None	Harrel & Hall 1991
Oil pollution						
exp. oiling, Sm.	salt marsh	Georgia	5 mo.	Yes, "increased periwinkle density in the oiled area was due to recolonization of the area by juvenile forms"	T & S	Lee et al. 1981

Table 1 (cont.)
Soft Substrates Oil pollution (cont.)

exp oiled mud, Sm.	intertidal	Wales	10 mo.	No, "total faunal density and abundance of certain species remain depressed for the duration of the experiment"	S	Dixon 1987
exp oiling, Sm.	intertidal	Virginia	10 mo.	No, oligochaetes, polychaetes and amphipods more abundant in control even after 39 wks.	S	Bender et al. 1977
exp oiling, Sm.	intertidal	Washington	1.25 yrs.	No, "for individual species densities as well as overall abundance ... oiled substrates had recovered only about one-half"	S	Vanderhorst et al. 1980
oil spill, M.	subtidal	L.A. Harbor	11 mo.	No, "population levels appeared normal ... although total numbers have not equalled the (pre-oiling) levels"*	T & S	Reish et al. 1980
oil spill, L.	subtidal	Sweden	10 mo.	No, "the soft bottom community did not show even the beginning of a recovery"	T	Linden et al. 1979
oil spill, L.	eelgrass	France	1 yr.	No, but "recovery took place relatively rapidly... all numbers were at the same level as the year before, the filter feeding amphipoda being the only exception"	T	Jacobs 1980
oil spill, L.	subtidal	France	1 yr.	No, "one year later, several species eliminated from the polluted area, had still not yet begun to recover"	T	Cabioch 1980
oil spill, L.	intertidal	Alaska	1.25 yrs.	No, "shoreline treatment and oil contamination each caused major negetive impacts ... but the effects of the treatment predominated"	S	Houghton et al. 1991a, b
oil spill, L.	coral & mangroves	Panama Canal	1.5 yrs.	No, "after 1.5 years only some organisms in areas exposed to the open sea have recovered"	T & S	Jackson et al. 1989

Table 1 (cont.)
Soft Substrates Oil pollution (cont.)

oil spill, L.	intertidal	Washington	2.5 yrs.	No, bivalve biomass and infaunal species number still higher in unoiled site *	S	Blaylock & Houghton 1989
oil spill, L.	intertidal	Arctic	2 yrs.	No, "neither in 1979 or 1980 were living macrobenthic organisms recorded"	S	Gulliksen & Taasen 1982
oil spill, L.	intertidal	France	2 yrs.	No, "the original community has been replaced by a new community containing a very small number of tolerant species"	T & S	Laubier 1980
oil spill, L.	subtidal	France	2 yrs.	No, "there is no question that on a quantitative basis the stricken communties have not yet recovered to their previous richness and diversity"	T & S	Laubier 1980
oil spill, L.	subtidal	Nova Scotia	2.25 yrs.	No, "longer term effects involved extensive mortalities of *Mya arenaria* and *Spartina alterniflora*."	None	Thomas 1973
oil spill, L.	saltmarsh	S. Chile	2.33 yrs.	No, "observations ... at the east inlet of Puerto Espora demonstrated that the benthic macrobiota is still very scarce"	S	Guzman & Campodonico 1981
oil pollution, L.	subtidal	Finland	3 yrs.	No, "3 or 4 years is not long enough for monitoring the final stages of a postabatement succession"	S	Leppäkoski & Lindström 1978
oil spill, L.	intertidal	France	3 yrs.	No, "the biological environment has not returned to its pristine condition "	T & S	Conan 1982
oil spill, L.	salt marsh	Massachusetts	3 yrs.	No, "the interstitial fauna ... showed an extremely reduced number of individuals and species"	S	Hampson & Moul 1978
oil spill, L.	subtidal	Baltic	3.4 yrs.	No, "full recovery is likely to require more than 5 years and may take a decade or more"	T & S	Elmgren et al. 1983

Table 1 (cont.)
Soft Substrates Oil pollution (cont.)

oil spill, L.	intertidal	California	5 yrs.	**No**, "the present densities (of *Emerita analoga* and *Nepthys californiensis*) have not approached the pre-oil status for this area"	T	Chan 1977
oil spill, L.	intertidal	Massachusetts	5 yrs.	**No**, "after more than five years the fauna had only slightly recovered"	S	Michael et al. 1975, Sanders 1978, Sanders et al. 1980
oil spill, L.	subtidal	Massachusetts	5 yrs.	**No**, "recovery had begun but it was not very far advanced"	S	Michael et al. 1975 Sanders 1978, Sanders et al. 1980,
oil spill, L.	salt marsh	Nova Scotia	5 yrs.	**No**, "soft-shell clams ... have shown persistent mortalities proportional to oil content of the sediment"	None	Thomas 1977
oil spill, L.	subtidal	France	5.5 yrs.	**Yes**, recovery of the fauna took between 66 mo. (# individuals and species) and 84 mo. (biomass)	None?	Glémarec 1986
oil spill, L.	intertidal	Massachusetts	7 yrs.	**No**, "the persistent reduction in fiddler crab populations observed at Wild Harbor at least 7 years after the original oil spill"	S	Krebs & Burns 1977
oil spill, L.	intertidal	Nova Scotia	7 yrs.	**No**, "species diversity was uniformly higher at control than oiled stations. Analysis of abundance and biomass data ... showed a significant overall difference between oiled and control stations"	S	Thomas 1978
oil spill, L.	subtidal	France	8 yrs.	**No**, "the amphipod populations ... have not yet fully recovered 8 years after the pollution"	T	Dauvin 1987
oil spill, L.	intertidal	France	10 yrs.	**No**, "the amphipod populations ...were in the least advanced state of recovery"	T	Dauvin & Gentil 1990
oil spill, L.	subtidal	France	10 yrs.	**Yes**, "the population structure tended towards a return to the inital situation"	T	Ibanez & Dauvin 1988

Table 1 (cont.)

Hard Substrates

Non-organic disturbances

exp. removal, Sm.	intertidal	Oregon	1.75-. 3.17 yrs.	Yes, "the timing and magnitude of successful barnacle recruitment appeared to cause much of the variation in the rate of succession"	S	Farrell 1991
exp. removal, Sm.	intertidal	Washington	3 yrs.	No, "when members of a sparse, isolated group of mussels were lost, no recovery was seen within periods ranging up to 3 yr."	T & S	Dethier 1984
exp. removal, Sm.	intertidal	California	3 yrs.	No, "*Mytilus californianus* did not recruit to the patches from the plankton during the 3 years"	T & S	Sousa 1984
exp. removal, Sm.	intertidal	California	4 yrs	Yes, "leads to development of ... the equivalent late successional stage in a minimum of 4 years"	T & S	Sousa 1979(a & b), 1980
exp. removal, Sm.	intertidal	Washington	5.5 yrs.	Yes, "recovery should occur in roughly 40 mo."	T & S	Paine & Levin 1981
nuclear test, M.	intertidal	Alaska	3.5 yrs.	No, "significant changes were still observed in some plots 3.5 years after the test"	T & S?	Lebednik & Palmisano 1977
nuclear test, M.	intertidal	Alaska	3.75 yrs.	No, "plot 1 is the only plot ... to show signs of recolonization by intertidal organisms after 33 months post-event"	T & S	O'Clair 1977
earthquake, L.	intertidal	Alaska	1.25 yrs.	No, "the inferred climax community had not yet become established in the post-earthquake intertidal zone"	S	Haven 1971
earthquake, L.	intertidal	Chile	4 yrs.	No, "rapid invasion by barnacles" but "no settlement of the competitively dominant inter-tidal mussel"	S	Castilla 1988, Castilla & Oliva 1990
earthquake, L.	intertidal	Alaska	5 yrs.	Yes, "with some exceptions these communities have returned to essentially their pre-earthquake condition"	S	Haven 1971

Table 1 (cont.)
Hard Substrates
Oil pollution

exp. oiling, Sm.	mesocosms	Norway	1 yr.	**No**, "most responses were back to normal, and population regeneration of mussels and amphipods had started, but some physiological dysfunctions were still detected"	T & S	Bakke 1986
exp. oiling, Sm. + dispersants	subtidal	Panama	1.7 yrs.	**No**, "recovery of sea urchins was complete after 1 year but the recovery of corals and other encrusting organisms will probably take several years"	T & S	Ballou et al. 1989
oil spill, M. + dispersants	intertidal	Ireland	2 yrs	**Yes**, "the rocky-shore littoral community ... had largely recovered from the effects of the oil spill"	S	Flower 1983
oil spill, M.	intertidal	Washington	2.5 yrs.	**Yes**, "the area affected has returned to an apparently normal state as determined by our level of investigation"*	S	Clark et al. 1975
oil spill, M.	intertidal	Wahington	5 yrs.	**Yes**, "the community balance in this rocky intertidal ecosystem does not appear to be markedly altered"*	S	Clark et al. 1978
oil spill, L.	intertidal	Sweden	1 yr.	**No**, "the recovery of the littoral fauna was well under way one year after the spill but was not yet complete"	T	Linden et al. 1979
oil spill, L.	intertidal	sub-Antarctic	1 yr.	**No**, "densities of marine invertebrates appeared to have been markedly reduced in the lower littoral and sublittoral zones"	S	Pople et al. 1990
oil spill, L.	intertidal	Alaska	1.25 yr.	**No**, "lower densities of limpets and littorines" and *Nucella lamellosa* in oiled sites	S	Houghton et al. 1991a, b
oil spill, L.	intertidal	France	2 yrs.	**Yes**, "the recovery of areas exposed to waves, currents and winds is almost complete"	T & S	Laubier 1980

Table 1 (cont.)

Hard Substrates	Oil pollution (cont.)					
oil spill, L.	intertidal	Nova Scotia	2.25 yrs.	No, "longer term effects involved extensive mortalities of *Fucus spiralis*"	None	Thomas 1973
oil spill, L.	intertidal	Baltic	4 yrs.	Yes, "no significant evidence of lasting detrimental effects can be found when natural annual variations ... are taken into account"	S	Notini 1978
oil spill, L.	intertidal	Nova Scotia	5 yrs.	No, "sporelings of fucoid algae have repeatedly settled in this zone but have never survived to a size where they could be identified"	None	Thomas 1977
oil spill, L.	intertidal	California	5 yrs.	No, "crab numbers are only half the pre-spill numbers"	T	Chan 1977
oil spill, L.	intertidal	Nova Scotia	7 yrs.	No, "species diversity was uniformly higher at control than oiled stations. Analysis of abundance and biomass data ... showed a significant overall difference between oiled and control stations"	S	Thomas 1978
oil spill, L.	intertidal	Shetland Is.	9 yrs.	No, "the biological communities at the sites that were cleaned mechanically were obliterated and still have not recovered"	T & S	Rolan & Gallagher 1991
oil spill, L. + dispersants	intertidal	England	10 yrs.	No, "lightly oiled, wave-beaten rocks that received light dispersant treatment showed the most complete return to normal, taking about 5-8 yr; heavily oiled places that received repeated application of dispersants have taken 9-10 yr and may not be completely normal yet"	T	Southward & Southward 1978

compositions of the most polluted and least polluted sites were similar, and they were similar to that recorded prior to the establishment of the paper mill, forty years earlier.

c. Oil pollution

Many studies dealt with the recovery of benthic infaunal communities after being oiled (Table 1). The scale of the oil pollution ranged from small experimental oilings to major oil spills.

The recovery of invertebrates after a small scale oiling was slow. Above, I pointed out that recovery in small areas is usually fast, but when oil is applied to the sediment the recovery is slower. For example, in the study by Vanderhorst et al. (1980), recovery was not complete after 16 months. Although the species lists were similar in the control and oiled sites, the abundances of the species were significantly lower in the oiled sites.

Only two of the 25 studies describing the recovery of soft bottom invertebrate communities after a large-scale oiling found full recovery (Glémarec 1986, Ibanez and Dauvin 1988; Table 1). The recovery times for these studies were 5.5 years, and 10 years, respectively. More typically the researchers return to a site three to ten years after an oil spill, and determine that recovery still has not occurred (e.g., Thomas 1977).

I suspect that insufficient time has been allowed for full recovery to occur at most of these study sites. I conclude that the recovery of soft sediment invertebrate communities after an oil spill can take longer than ten years, but how much longer one cannot say.

HARD SUBSTRATES

A) Succession

Succession on rocky shores has been well studied in temperate zones (e.g., Dayton 1971, Lubchenco 1983, Sousa 1984, Farrell 1991) and a general view of the process has emerged (Paine and Levin 1981). In the absence of disturbance, the competitive dominant species spreads out and occupies nearly 100% of the primary space. For example, mussels are the competitive dominant on exposed Washington shores and they can form beds that cover 100% of the rock surface (Dayton 1971). Disturbance by waves, logs or starfish predation opens gaps in the beds of the competitive dominant. These gaps are relatively small, usually less than 1m^2 (Paine and Levin 1981). Small gaps are filled by the growth or movement of animals from the surrounding area. Large gaps are invaded by these means and by the settlement of species out of the plankton. The first settlers are usually small algal species, followed by barnacles and worms, and finally by the dominant large algae and/or mussels. Thus a succession generally occurs, but this succession is not particularly predictable -- the rates at which species invade depend upon the presence of their larvae in the water column and inhibition of one species by another can occur. Frequently a shoreline looks like a mozaic where the matrix of the competitive dominant is interrupted by scattered patches of other species at different stages of succession.

An important principle has come out of these studies -- the intermediate disturbance principle: the highest number of species is found in a system with an intermediate degree of disturbance (Paine 1966, Connell 1978). If the combined disturbance from all sources (e.g., predation, wave action) is low, then the system becomes dominated by the competitive dominant and its attendant species (i.e., a relatively low number of species). If the combined disturbance is high, then few opportunities arise for most species to recruit successfully -- therefore the total number of species is again low. Only when the combined disturbance is intermediate do conditions favour a large number of species. This pattern is usually studied in space, i.e., at several places at the same time, but it is also observed at one place over time, i.e., during the recovery of invertebrate communities after a disturbance (Connell 1978). In this respect recovery on hard sediments is similar to that in soft sediments -- the greatest number of species occur before full recovery. Therefore, again, the presence of a large number of species does not necessarily indicate that a site has recovered.

An important feature of the studies that have led to these generalizations about succession on rocky shores is that the disturbances examined are unlike oil pollution -- the bare spaces, or gaps, are relatively small and organic enrichment is rarely involved. However, Southward and Southward (1978) stated that the general sequence of recolonization after the Torrey Canyon oil spill was similar to that described above for small-scale experiments where the rocks were scraped clean.

B) Recovery times

I reviewed 26 studies that dealt with the recovery of invertebrate communities on hard substrates (Table 1). In this section, as above, in deciding whether an area had recovered or not, I adopted the decision of each author, i.e., if the author determined that the area had recovered then I entered it as a "Yes", and if the author determined that it had not recovered then I entered it as a "No". The words "yes" and "no" could be replaced with "recovered" and "recovering".

a. Non-organic disturbances

Several studies in Table 1 deal with the recovery of rocky shore invertebrate communities after non-organic disturbances. Recovery was relatively common and rapid -- between 1.75 years (Farrell 1991) and 5.5 years (Paine and Levin 1981); however, some sites had not recovered after more than three years (e.g., O'Clair 1977, Castilla 1988).

Boulder beaches are common in Alaska and the recovery of the communities on boulder beaches is therefore of special interest. Sousa (1979a, 1979b, 1980) showed that the recovery of early successional assemblages on boulder beaches takes approximately 5 months, middle successional assemblages 2.5 years, and late successional assemblages a minimum of 4 years.

Landslides and elevation changes resulting from earthquakes and nuclear testing are examples of extreme physical disturbances. Uplifting from the 1964 Alaska earthquake and the 1971 "Cannikin" nuclear test caused a die-off of most species whose elevation was raised. These species were being replaced by others that generally occur higher up the shore (e.g., O'Clair 1977, Haven 1971).

It must be remembered that these disturbances are not necessarily similar to oil spills because several were relatively small and none involved the addition of toxic organic material.

b. Oil pollution

Many studies have dealt with the recovery of rocky shore invertebrate communities after oiling (Table 1). In general, recovery was common and occurred relatively quickly (five years or less) after small and medium sized oil spills, but recovery was less common and occurred relatively slowly after large spills (even after ten years a site may not be fully recovered).

Southward and Southward (1978) noted that "heavily oiled places that received repeated application of dispersants have taken nine to ten years and may not be completely normal yet." Thomas (1978) found that, seven years after an oil spill, the oiled communities still did not resemble the unoiled communities. The fucoid algae (e.g., *Fucus*), in particular, were slow to recover.

CONCLUSIONS

Whereas Table 1 contains the details of recovery of invertebrate communities Table 2 shows an overview of Table 1. The general trends are:

1. Most of the studies report that recovery did not occur in the time allowed by the investigators. Recovery occurred in only 24% of the studies (Table 2). This means that either: recovery was going to occur in all cases but the assessment of recovery was conducted too early, i.e. prior to recovery (Teal 1990, Harding 1990); or recovery was not going to occur in all cases because the systems were irreparably damaged and will never recover to their pre-disturbance conditions.

2. Recovery was more likely after a small disturbance than after a large disturbance. Recovery was reported in 50% of the studies following a small disturbance, 25% of the studies following a medium disturbance, and in only 13% of the studies following a large disturbance (Table 2). This suggests that recovery times are relatively fast after a small disturbance but slow after a large disturbance.

3. Recovery was equally as likely in intertidal and subtidal habitats. Recovery was reported in 25% of the intertidal studies and 19% of the subtidal studies (Table 2).

4. Recovery was more likely after a non-oiling disturbance than after an oiling disturbance. Recovery was reported in 33% of the stuidies following a non-oiling disturbance and in only 17% of the studies following an oiling disturbance (Table 2). This suggests that recovery times are relatively fast after a non-oiling disturbance but slow after an oiling disturbance. A reason for these trends is that oil persists longer than other disturbances (e.g., sewage); Ganning et al. (1984) estimated that the minimum residence time of oil on mud flats was 10 years..

5. Recovery was more likely after oiling of hard substrates than after oiling of soft substrates. Recovery was reported in 31% of the studies of oiling of hard substrates and in only 10% of the studies of oiling of soft substrates (Table 2). Again, this suggests that recovery times are relatively fast on hard substrates but slow in soft substrates. One reason for these trends is that oil persists longer in soft sediments than on hard substrates (Vandermeulen 1977; see Section 3.1.2 for further discussion).

6. Recovery times of invertebrate communities after an oiling event are estimated to be 10 - 20 years for communities on hard substrates and 10 - 25 years for communities on soft substrates. Recovery occurred in only 17% of the oiling studies thus making calculations of mean recovery times impossible (Table 2). However, with what data we have at present, it appears that these estimates of 10 - 20 years and 10 - 25 years are reasonable.

Table 2. The number of studies that recorded full recovery (yes) and incomplete recovery (no) of invertebrate communities. They are grouped according to the size of the disturbance, nature of the habitat, nature of the disturbance, and oiling in different habitats. The studies are from Table 1.

INVERTEBRATE COMMUNITY RECOVERY				
	YES	NO	TOTAL	% YES
total	19	60	79	24 %
size of disturbance				
small	10	10	20	50 %
medium	3	9	12	25 %
large	6	41	47	13 %
nature of habitat				
intertidal	12	36	48	25 %
subtidal	6	25	31	19 %
nature of disturbance				
not oiled	11	22	33	33 %
oiled	8	38	46	17 %
oiling in different habitats				
oiling of soft substrates	3	27	30	10 %
oiling of hard substrates	5	11	16	31 %

These recovery time estimates are similar to those estimated by most others (e.g., Vandermeulen 1978 -- 5 to 15 years). Only the Exxon Corporation biologists who reviewed the literature on recovery of cold water marine environments after oil spills suggest much faster recovery time estimates (Baker et al. 1990). They concluded that "rocky shores usually recover in 2 to 3 years. Other shorelines show substantial recovery in 1 to 5 years with the exception of sheltered, highly productive shores (e.g., salt marshes), which may take 10 years or more to recover." Their lower estimated recovery times can be partly attributed to their definition of recovery (see Section 4.2.1).

However, the Exxon Corporation biologists tended to use references selectively. Their paper covers the same topics as mine -- it includes a section on the benthic environment and a table (their Table 7) which is much like my Table 1. When a comparison is made of the two tables it is obvious that theirs omits some important references -- the relatively long-term studies of soft sediments that found the recovery to be incomplete (e.g., Elmgren et al. 1983, Sanders 1978, Sanders et al. 1980, Thomas 1977, Dauvin 1987). In addition, in some cases, they chose to present the rosiest picture. For example, Southward and Southward (1978) state that "lightly oiled, wave-beaten rocks that received light dispersant treatment showed the most complete return to normal, taking about 5-8 years; heavily oiled places that received repeated application of dispersants have taken 9-10 years and may not be completely normal yet." Baker et al. (1990) describe these results in their table as "good recovery after 2 years." It is clear that the paper by Baker and her colleagues must be read with some skeptism.

3.1.2 Effects of Abiotic Factors on Recovery

Because recovery occurred in so few of the studies cited in Table 1, it is extremely difficult to make correlations between abiotic factors and recovery times. However, drawing on the data and observations presented in the papers, I conclude that four abiotic factors influence recovery.

NATURE OF THE OIL SPILL

It has been noted that each spill is unique because numerous variables affect spill impact. These include type of spill, duration of exposure, volume and type of oil, oil state and age (degree of weathering), weather, season, use of dispersants, etc. (Straughan 1972). However, the severity of the oil spill and its areal extent appear to affect the recovery time most (Southward and Southward 1978, Sanders et al. 1980); high concentrations of oil will kill more of the resident species, making recovery slower, and large areas killed by oiling take longer for invertebrates to recolonize, partly because large areas are recolonized primarily by larvae and partly because sources of new individuals are far away (Sousa 1984).

HABITAT

Recovery is slower in soft sediments than on rocky shores (Vandermeulen 1977, Table 2). The main reason for this appears to be the lingering effects of oil in soft sediments. The time taken for oil to weather and disperse after an oil spill depends on the water flow in the habitat (National Research Council 1985). Ganning et al. (1984) reported that the estimated minimum residence time of oil spilled in the following habitats was: 6 months on rocky shores, 4 years on sandy shores, and 10 years on mud flats. Factors that promote oil retention are weak tidal action, weak currents and fine sediments

(Vandermeulen 1977, Gundlach 1987). Although recovery starts as soon as organisms can tolerate the conditions, which is well before all the oil has dissappeared, it appears that the residual hydrocarbons retard recovery of the invertebrate communities by taking up space, by killing individuals, and by reducing their reproductive output (Southward and Southward 1978).

Also lingering oil may cause "delayed effects". The effects of an oil spill may be delayed up to three years after the spill; however the cause-and-effect relationship is often difficult to demonstrate. Conan (1982) gives two examples: was the death of all the intertidal individuals of the species *Tellina fabula* (a clam) several months after an oil spill due to oil? Also, was the poor recruitment of *Tellina fabula* and *Donax vittatus* for the two years following a spill due to oil?

The disturbance level in the habitat will also influence the recovery time because a frequently disturbed habitat will have younger adults than an infrequently disturbed habitat. For instance, intertidal boulders are frequently disturbed by large waves that cause the boulders to roll over and thereby crush or smother the organisms growing on them (Sousa 1979a, b); stable rocky shores are also affected by the large waves but less so (Dayton 1971). Thus, stands of old organisms are rare on boulder beaches but common on stable rocky shores. One would therefore predict that recovery would be faster on boulders than on stable rocky shores.

TIDAL HEIGHT

Position in the intertidal zone is important to the recovery of the community after a disturbance -- low- and mid-tidal communities recover more quickly than high-tidal communities (e.g., Farrell 1991). This appears to be related to the amount of time underwater and its influence on growth rates and larval survivorship.

Position in the intertidal zone is also important to the natural self-cleaning of stranded oil -- oil stranded half-way up the shore is removed more quickly than oil stranded at the top of the shore (Vandermeulen 1977, Thomas 1977, 1978). This appears to be due to the amount of time underwater and the differing forces of waves in the low and high intertidal.

The recovery of the high intertidal species is likely to take a long time partly because recovery is naturally slower than that of the mid-tidal species and partly because oil stranded in the high intertidal zone slows the process still further. Describing the recovery of the intertidal communities five years after the Arrow oil spill, Thomas (1977) stated that "recolonization has proceeded from lower to higher levels but has not yet occurred in the high tide zone."

TEMPERATURE

Cool temperatures slow biological processes. Cold water organisms are longer lived, have longer generation times, lower fecundity and slower growth rates than their warm water counterparts (Southward and Southward 1978, Roberts 1989). Recovery of invertebrate communities is therefore expected to proceed more slowly at high latitudes (Dunbar 1968, Southward and Southward 1978, Clarke 1979). The only study that I found that tested this idea was by Oliver and Slattery (1981) -- unfortunately it is an abstract from the proceedings of a meeting and it is therefore sadly incomplete (no time scales are given). However, they report on the recovery of benthic infauna to defaunated soft-bottom habitats in and around Monterey Bay and in Antarctica. They state that the rate of succession "was dramatically extended at the cold polar latitude."

3.1.3 Dependency of Recovery on Habitat Protection, Changes in Management Practices, and Other Restoration Approaches

Given sufficient time, full recovery after an oil spill is likely to occur naturally. It will probably take a long time in areas (a) that were heavily oiled, (b) that were heavily oiled and destructively cleaned, (c) where the sediments are soft, and (d) where the oiling was extensive (see Section 3.1.2). In order to speed recovery, managers will want to consider restoration options.

One option is to do nothing. Teal (1990) advises against active restoration. He states that it is best to leave the area alone after picking up as much oil as possible. He believes that we know so little about the ecosystems we are trying to restore that we could do more harm than good.

Below I discuss other restoration options -- clean-up, bioremediation, habitat protection and transplantation.

THE CLEAN-UP OF AN OIL SPILL

Stranded oil disperses slowly and so cleaning up as much of the stranded oil as possible is an important first step on the road to recovery of the system. However, many of the methods used to clean-up oil spills appear to be more harmful than the oil itself. For instance, in 1967 after the Torrey Canyon spill off England, 10,000 tons of toxic dispersants (also called detergents) were used in the cleaning operations, and most of the invertebrate mortalities could be attributed to the dispersants rather than the oil (Southward and Southward 1978). More recently, mechanical removal (Rolan and Gallagher 1991) and high pressure hot water (Broman et al. 1983, Houghton et al. 1991a) have been used to clean oiled shores, but both treatments also kill many organisms.

These studies show that the effects of the cleaning are detrimental to the invertebrate communities both in the short-term (Broman et al. 1983, Houghton et al. 1991a) and in the long-term (Rolan and Gallagher 1991). Recovery is likely to be slower in cleaned areas because, in general, very large clearings take longer to recover than patches that have some of the original inhabitants intact (Sousa 1984, Smith and Brumsickle 1989).

Thomas (1978) believes that some clean-up methods on rocky shores do more harm than good, but suggested that clean-up of oil from soft sediments would promote recovery. He stated that "if clean-up methods for lagoons could be improved so that oil could be removed without sediment penetration or disturbance, clean-up should help to minimize oil pollution effects" (Thomas 1978). However, this is easier said than done.

BIOREMEDIATION TO SPEED-UP RECOVERY

In most bioremediation, a nitrogen-phosphorus fertilizer is sprayed onto the stranded oil. This fertilizer provides extra nutrients for naturally occurring micro-organisms (i.e., bacteria and fungi) that break down oil. This technique, long employed against toxic wastes, can more than double the speed of oil removal (EPA 1990). The micro-organisms feed on the oil, reduce its toxicity, and increase its removal by waves and currents (Lee and Levy 1991). Two problems with this approach are that bacteria may not be active below the top few inches of soft sediments and that micro-organisms are relatively slow to break-down oil in cold marine habitats (Cretney et al. 1978, Atlas et al. 1978). The first large-scale use of bioremediation took place in Prince William Sound during 1989, as a series of experiments. The preliminary results of the experiments look promising (EPA 1990, Chianelli et al. 1991), but the effects on long-term recovery of the communities are not known.

HABITAT PROTECTION DURING RECOVERY

None of the studies described in Table 1 compared the recovery of communities in habitats that were protected from humans to recovery in unprotected habitats. However, there are a few studies on rocky shores that indicate that human interference -- trampling, souvenir collection, handling, and bait collection -- does have a negative effect on the community (Zedler 1978, Beauchamp and Gowling 1982, Ghazanshahi et al. 1983, Addessi 1992). Therefore, limiting human access to a community would likely promote recovery.

TRANSPLANTATION OF SPECIES

Another option is to transplant species into the disturbed sites. Species' recovery rates will depend on life-history characteristics and tolerance of oil. The species that have larvae in the plankton all, or most, of the year will recruit quickly into large disturbed spaces. On the other hand, the species whose larvae are rarely found in the plankton or whose larvae have extremely short-range dispersal, will recruit slowly into the same patches. Species with poor larval recruitment include many asteroids and some echinoids (Simenstad, pers. com.). Examples of species with short-range dispersal are soft corals (Gerrodette 1981), amphipods (Cabioch 1980), some *Octopus* (Hochberg and Fields 1980), many of the snails in the order Neogastropoda (Abbott and Haderlie 1980), and several species of algae (Dayton 1973, Paine 1979, Sousa 1984). Most of these propagules disperse less than 2m from the adult. Recruitment of such species to disturbed patches will correlate with the abundance of propagule-releasing adults in the immediate vicinity of the clearing. Thus the complete recolonization of large bare areas by these types of species will take a very long time. These short-range dispersal species would be the most likely to benefit from transplantation. Short-range dispersal is also more common in the Arctic than in temperate waters (Thorson 1950).

The alga, *Fucus*, is a short-range dispersal species (Brawley 1992) that is an important species on hard substrates in Alaska -- it is common and provides cover and food for many invertebrate species. The recovery of *Fucus* may well determine the pattern of recovery for the community as a whole. To speed the recovery of *Fucus*, particularly in large disturbed areas, managers may consider transplanting plants into the area.

Unfortunately there is little information on how to conduct the restoration of marine communities. The restoration of kelp beds in southern California may provide an example for the restoration of the damaged ecosystems in Alaska. *Macrocystis pyrifera*, the giant kelp, forms the main component of southern California's kelp forests. Although an adult plant produces millions of spores, and although the spores and gametes are planktivorous, colonization of disturbed areas can be slow. Population declines of this species around sewer outfalls and power plants, and during warm water years, have stimulated many attempts at restoration (see Foster and Schiel 1985 for review). Transplants have been made of three stages in the life-cycle of the plant -- adult sporophytes, juvenile sporophytes and microscopic sporophytes. Most restoration attempts using these methods have not had suitable controls, so their success rates are difficult to determine (Foster and Schiel 1985). However, *Macrocystis* has returned to some of the transplanted areas.

If transplantation of *Fucus* and other organisms is attempted, I recommend that care be taken to not damage the areas from which the transplants are taken. In addition, I recommend that any major restoration project begin with an experimental phase so that the success rates of different methods can be evaluated. This will help rule out techniques that don't work and will help identify promising approaches that can be developed further (see PERL 1990). This research will provide valuable information on restoration techniques (a subject about which little is known) as well as further our knowledge of the Alaskan ecosystems. All major restoration projects should be continually evaluated with a long-term monitoring program that will allow managers to take advantage of unforeseen benefits and to address unexpected problems quickly.

4.0 EXTRAPOLATION TO THE INJURED ALASKAN ECOSYSTEM

4.1 Identification of Most Practical and Cost Effective Indicators of Recovery to Measure

What is needed to determine whether recovery has occurred is an extensive study of the abundances, biomasses, age distributions, growth rates and reproductive condition of all the species influenced by the spill (see Section 4.2). If any of these characteristics goes unmeasured then a conclusion that recovery has occurred may be criticized. However, should insufficient funds be available to conduct a thorough study it is appropriate to consider alternative approaches.

"Indicator species" have been used extensively in pollution studies. Indicator species are those species which, by their presence and abundance, provide some indication of the prevailing environmental conditions. The best indicator species are those that have narrow and specific environmental tolerances, because they will show a marked response to quite small changes in environmental quality (Abel 1989). However, indicator species provide only a general overview of the approximate position of the community in the successional process, i.e., whether the community is generally in the early or the late successional stage.

A viable alternative to examining all the invertebrates is to sample only "target species." These are species that are abundant in certain zones, are key space occupiers, or are consumers known to play an important role in community structure (Dethier 1991). Sampling only target species would have the advantage of reducing costs and allowing increased replication. Dethier (1991) compiled a list of recommended target organisms for the Washington coast and I have repeated it here (Table 3A). I have added a short list of suggested target species for the Alaskan coast from Houghton et al. (1990a; Table 3B).

There are two problems with the target species approach. First, in considering oil effects, "confining sampling to dominant species might miss a significant oil effect, or underestimate the degree of impact" (Dethier 1991). And second, "in considering recovery from oil spills it is important to take into account not only the dominant species, which might recolonize and recover quickly, but also the uncommon ones which may take longer to return to former abundances (e.g., because of limited dispersal or small 'source' populations)" (Dethier 1991).

However, I suggest that a sound determination of recovery after an oil spill could be based on the study of the abundances, biomasses, age distributions, growth rates and reproductive condition of several target species. The choice of target species will be critical. Houghton et al. (1990a) have begun a target species study of growth rates in Prince William Sound but their study is of four molluscs only. I suggest that target species should come from several different phyla, a few different feeding modes, and mostly from late successional stages.

Table 3. Target species recommended for intensive sampling effort on the Washington coast (Dethier 1991) and on the Alaskan coast (Houghton et al. 1990a).

WASHINGTON COAST

ROCKY SHORES

Wave-exposed	**Wave-protected**
Eudistylia vancouveri	*Fucus* spp.
Mytilus californianus	*Endocladia muricata*
Mytilus edulis	*Mastocarpus papillatus*
Pollicipes polymerus	*Neorhodomela larix*
Anthopleura elegantissima	*Phaeostrophion irregulare*
Nucella spp.	*Lacuna* spp.
Pisaster ochraceus	
Katharina tunicata	
Endocladia muricata	
Mastocarpus papillatus	
Corallina vancouveriensis	
Dilsea californica	

COBBLE SHORES	SANDY SHORES
Fucus spp.	*Eohaustorius* spp.
Gelidium coulteri	*Excirolana* spp.
Phyllospadix spp.	*Euzonus mucronatus*
Odonthalia floccosa	total number of polychaetes
Tegula funebralis	
Hemigrapsus spp.	
Leptasterias hexactis	

ALASKAN COAST

ROCKY SHORES	BOULDER/COBBLE SHORES
Fucus spp.	*Fucus* spp.
red algae	red algae
Mytilus edulis	green algae
Nucella lamellosa	Lottiidae
Pagurus spp.	

SOFT SUBSTRATES

polychaeta
gastropoda
bivalvia
crustacea

4.2 Recommended Approach to Determine When Recovery has Occurred

4.2.1 Definition of Recovery

It is important that in any study of recovery one state one's objectives clearly and define what one will or will not accept as a fully recovered ecosystem. The objectives will guide the entire project, including the sampling design, statistical tests and conclusions. Without clear objectives, the work will result in a poorly directed sampling design and weak conclusions.

If one's objective is to determine whether an area has fully recovered from an oil spill then one must define what one will accept as recovered. Most of the researchers in Table 1 did not explicitly define recovery but their implicit definition was:

- "the return of all population densities to pre-disturbance levels or undisturbed levels."

However, there are many other possible definitions of recovery.

- American Heritage Dictionary (1973): "return to a normal condition; the getting back of something lost."
- Ganning et al. (1984): "the restoration to original functional and structural conditions with original species present in original numbers."
- Ganning et al. (1984): "returning the ecosystem to within the limits of natural variability."
- Lewis (1982): "complete recovery (has occurred when) there are no discernable after-effects."
- Boesch et al. (1987): "complete recovery is the time required for a disturbed community to exhibit variation that is within the bounds of variation seen in undisturbed, control areas."
- Conan (1982): "a new stable age distribution and equilibrium species assemblages attained".
- National Research Council (1975; page 91): "Complete recovery means that (1) the faunal and floral constituents that were present before the oil spill are again present and (2) they have their full complement of constituent age classes."
- Committee on Restoration of Aquatic Ecosystems, National Research Council (in press) " the return of an ecosytem to a close approximation of its condition prior to disturbance."

None of these definitions is completely satisfactory. They give a general description of the term but few specifics. I suggest the following definition of recovery -- it is a combination of the above definitions:

- Boland (this report): "Complete recovery after an oil spill occurs when (1) all the species that were present before the oil spill are again present; (2) each of these species has reached their original abundances and biomasses, (3) each of these species has reached their original age distributions, and (4) all individuals are as healthy (as measured by growth rates) and productive (as measured by reproductive condition) as the individuals that were present at the time of the oil spill." In the absence of pre-spill data, original conditions should be estimated from several unoiled communities in similar physical/chemical environments.

Prespill data on species abundances, biomasses, age distributions, growth rates and reproductive conditions are necessary for determining when recovery has occurred, however these data are usually unavailable. In these cases, studies of many unoiled sites must be conducted instead. These unoiled sites should be chosen carefully and should include all the habitats that were oiled. All the appropriate data should be collected in the unoiled sites soon after the oil spill and used as the baseline data representing the prespill conditions in the oiled sites.

Therefore, when one is testing for recovery one is testing the hypotheses that there are no significant differences in (1) the species that are present in oiled and unoiled areas; (2) the abundances and biomasses of the species in oiled and unoiled areas; (3) the age distributions of the species in oiled and unoiled areas; and (4) the growth rates and reproductive condition of individuals in oiled and unoiled areas.

Notice that the recovered community does not have to be identical to the undisturbed community, only not statistically different from the undisturbed community, i.e., it is varying within the bounds exhibited by undisturbed systems (see definition by Boesch et al. 1987).

Notice also that my definition, like those above, focuses on the structure of the community rather than on its functioning. Too little is known about the functioning of marine communities to include it in the definition. One hopes that when the structure returns the functioning will return too.

My definition of recovery is based upon that used by many researchers and the dictionary definition. However, the biologists working for The Exxon Corporation have recently proposed a different definition of recovery and this is:

- Baker et al. (1990): "recovery is marked by the re-establishment of a healthy biological community in which the plants and animals characteristic of that community are present and functioning normally. It may not have the same composition or age structure as that which was present before the damage, and will continue to show further change and development." This definition is very different from all the others outlined above in that it will consider a community recovered when it is only on the road to recovery. This is unacceptable. For instance, using this definition one may consider a mussel bed to have recovered if the rocks are completely covered with healthy opportunistic species such as green algae.

The defintion of recovery of Baker et al. (1990) leads them to estimate recovery times that are relatively fast. For instance, they say that "rocky shores usually recover in 2 to 3 years. Other shorelines show substantial recovery in 1 to 5 years with the exception of sheltered, highly productive shores (e.g., salt marshes), which may take 10 years or more to recover." In subtidal sand and mud systems "recovery times are 1 to 5 years, but they can be 10 years or longer in exceptional cases" (Baker et al. 1990). My literature survey suggests that recovery times are longer than these, and in general, these numbers should be doubled to obtain true estimates of recovery times (Section 3.1.1).

In conclusion, the definition of recovery is an extremely important part of any study of recovery.

4.2.2. Methods to be used in a Recovery Study

The researchers need to test the hypotheses that there are no significant difference in (1) the species that are present in oiled and unoiled areas; (2) the abundances and biomasses of the species in oiled and unoiled areas; (3) the age distributions of the species in oiled and unoiled areas; and (4) the growth rates and reproductive condition of individuals in oiled and unoiled areas.

Notice first, that no mention has been made of summarizing statistics such as species diversity, total number of species, total biomass or total number of individuals -- as we have seen in Section 3.1.1, these numbers cannot be used to show when recovery has occurred. Second, that identifications need to be made to the species level. Some research has shown that little information is lost when identifications are made to the family level, but this applies to only some analyses, e.g., ordinations (Warwick 1988).

In my opinion, none of the papers cited in Table 1 provides a good example of how to conduct a recovery study. Sanders et al. (1980) critized past research on recovery by saying that the researchers have arrived at "conclusions that are, at best, equivocal interpretations of insufficient and ambiguous data. Such inadequacies are usual in many pollution-related studies of benthic ecology, including those in which important decisions are based." It is clear that if a study is to stand up to scrutiny it will have to be a careful and thorough study planned by competant statisticians and biologists familiar with the Alaskan ecosystem. Many books and papers describe appropriate sampling programs and methods to be used for studying marine benthos (e.g., Green 1979, Gauch 1982, Holme and McIntyre 1984, Mead 1988, Underwood 1981, Hurlbert 1984, Stewart-Oaten et al. 1986, Carney 1987, Gray et al. 1988, Krebs 1989, PERL 1990, Dethier 1991), and these sources should be consulted.

Natural communities are spatially and temporally heterogenous. This means:
(1) that it is necessary to study many sites nearby that were not oiled and many sites within the oiled area so that the range of natural variability can be determined (Mann 1978, Ganning et al. 1984);
(2) that a large area should be randomly sampled at each site; because communities change with water depth, a useful design is stratified random sampling in which one blocks with water depth (Gray et al. 1988); and
(3) that a large number of samples are required for reliable estimates of population densities; even to estimate population densities to within 20-40% of their true value may require several hundred samples at each site (Abel 1989). Even well funded studies such as Houghton et al (1990a) often fail in all three respects.

4.2.3. Results and Conclusions of a Recovery Study

All the results that are necessary and sufficient to test the hypotheses should be presented in the research report. Frequently researchers collect a lot of information but report only species diversity. Some also report total biomass and total abundance but rarely do papers go beyond these summarizing statistics and describe the abundances of individual species. This is a weakness because, as we have seen above (Figure 2), "climax" communities do not have the greatest number of species, biomasses, or individuals. Also, these summarizing statistics cannot be used to test the hypotheses.

Details about "important species" (e.g., those that are numerically dominant, provide much of the structure to the community, or play an important role in the dynamics of the system) should also be presented. An analysis of the recovery of the community therefore requires a detailed knowledge of the functioning of the community.

Finally, the conclusions of any recovery study should be clearly presented.

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8.0 ANNOTATED BIBLIOGRAPHY

Here follows a detailed description of each of the recovery papers reviewed in Table 1. It includes the abstracts of each paper taken verbatim from the original papers. Three papers (Flower 1983, Glémarec 1986, Guzman and Campodonico 1981) did not have abstracts and for these I wrote a brief summary of their findings.

Bakke, T. 1986

Experimental Long Term Oil Pollution in a Boreal Rocky Shore Environment

Norwegian Institute for Water Research

Environment Canada. Proceedings of 9th annual Arctic and marine oil spill program technical seminar 17: 167-178.

ABSTRACT

The paper presents the design, experimental range and an overview of the results of a large scale mesocosm experiment performed during 1979 to 1985 at the Marine Research Station Solbergstrand, Eastern Norway. The aim of the experiment was to investigate the effects of continuous sublethal exposure to diesel oil on a cold temperate rocky shore community. The monthly mean temperature range of the mesocosm was 0.6-18.9°C during the six years the experiment lasted. The mesocosm communities were established in 1979 by transplantation of rocks with sessile organisms to four flow-through concrete basins (8x5x1.5 meters) equipped with wave generators and tide simulation. The communities were allowed to develop undisturbed for three years, whereafter two of the basins were exposed continuously to a diesel oil in seawater emulsion at mean levels of 130 and 30 µg/liter respectively (fluorescence analysis). The two remaining basins acted as controls. The oil exposure lasted from September 1982 to September 1984. After that the communities were followed for redcovery for one year. The experiment covered a range of subprojects aimed at studying the effects on general community structure, community recruitment and metabolism, population dynamics and genetics, physiology, cell chemistry, histology and tissure hydrocarbon levels of key species. The effects ranged from population collapse (blue mussel, amphipods), reduced growth (bladder wrack, kelp, mussels) and recruitment (winkles, barnacles), reduced primary production, increased cover of opportunistic green algae, reduced feeding and energy utilization (mussels, winkles), accumulation of hydrocarbons in algae and animals, to cyto- and biochemical stress indications (mussels, winkles). The effects were in most cases dependent on season. Relation to dose was not always found. The population genetics did not indicate any short term selection due to the oil. After one year recovery, most responses were back to normal, and population regeneration of mussels and amphipods had started, but some physiological dysfunctions were still detected.

Ballou, T.G., S.C. Hess, R.E. Dodge, A.H. Knap, and T.D. Sleeter. 1989.

Effects of untreated and chemically dispersed oil on tropical marine communities: a long-term field experiment.

Wibur Smith Associates, P.O. Box 92, Columbia, South Carolina 29201.

Proceedings of 1989 International Oil Spill Conference, American Petroleum Institute, p447-454.

ABSTRACT

A multidisciplinary long-term field experiment was conducted to evaluate the use of chemical dispersants to reduce the adverse environmental effects of oil spills in nearshore, tropical waters. Three study sites, whose intertidal and subtidal components consisted of mangroves, seagrass beds, and coral reefs, were studies in detail before, during and after exposure to untreated crude oil or chemically dispersed oil. This study simulated an unusually high ("worst case") exposure level of dispersed oil and a moderate exposure level of untreated oil. The third site served as an untreated reference site. Assessments were made of the distribution and extent of contamination by hydrocarbons over time, and the short- and long-term effects on survival, abundance, and growth of the dominant flora and fauna of each habitat. The whole, untreated oil had severe, long-term effects on survival of mangroves and associated fauna, and relatively minor effects on seagrasses, corals, and associated organisms. Chemically dispersed oil caused declines in the abundance of corals, sea urchins, and other reef organisms, reduced coral growth rate in one species, and had minor or no effects on seagrasses and mangroves. Conclusions were drawn from these results on decision making for actual spills based on trade-offs between dispersing or not dispersing the oil.

This report deals only with the major results of the study. A large number of parameters were monitored, but in the interest of brevity only the most important aspects of the study are reported here. A detailed description of the methods used and a complete presentation and discussion of results is given in Ballou et al.

Baxter, R.E. 1971.

Earthquake effects on clams of Prince William Sound

Alaska Department of Fish and Game.

In: National Research Council. 1971. The Great Alaska Earthquake of 1964. National Academy of Sciences, Washington, D.C.

ABSTRACT

The changes in land elevations associated with the Alaska earthquake of 1964 affected the intertidal populations of hard-shell clams in the Prince William Sound. Mortality was estimated at 36%. Studies established that 29% of the surviving hard-shell clams were in the optimum habitat zone between mean low water and lowest low water; before the earthquake, 82% of the hard-shell clams were in the optimum zone. No species of hard-shell clam is in danger of disappearing from the fauna of Prine William Sound. Ninety-nine species of pelecypodss were tentatively identified during studies in the Sound.

Bender, M.E., E.A. Shearls, R.P. Ayres, C.H. Hershner, and R.J. Hugget. 1977.

Ecological effects of experimental oil spills on Eastern Coastal Plain estuarine ecosystems.

Virginia Institute of Marine Science, Gloucester Point, Virginia 23062.

Proceedings of 1977 International Oil Spill Conference, American Petroleum Institute, p505-509.

ABSTRACT

Five segments of a mesohaline marsh located off the York River in Virginia were physically isolated from the surrounding area, except for allowing subtidal flow, and dosed with fresh and artificially weathered South Louisiana crude oil. The experimental design and field site utilized in this study are described. The mini-ecosystems each contained about 695 sq. m. of marsh, 100 sq m of open water and 15 sq m of intertidal mud flat. In September 1975, three barrels (570l) of each of the experimental oils were spilled into replicate systems.

Overall, the artificially weathered oil was shown to have as great an ecological impact on the communities as the fresh crude. Phytoplankton and fish populations all showed declines following the spills in the weathered oil systems. Phytoplankton production declined immediately after both spills but had recovered to control values within seven days. Species composition was not affected by the oils, while perihyton biomass, as measured by ATP, increased after both treatments. Marsh grass production was reduced in both spill units. Benthic animals, showing population declines after both oil, included nereid polychaetes, insect larvae and amphipods. Oligochaete populations decreases shortly after the fresh crude spill, returned to normal within 30 days, and then declined again relaive to the control in both treatments 11 weeks after the spill. Mortalities of fish, *Fundulus heteroclitus*, held in live boxes were noted only in the weathered treatment systems.

Blaylock, W.M., and J.P. Houghton. 1989.

Infaunal recovery at Ediz Hook following the *Arco* Anchorage oil spill

Dames & Moore, 500 Market Place Tower, 2025 First Avenue, Seattle, Washington 98121

Proceedings of the 1989 American Petroleum Institute oil spill conference: 421-426.

ABSTRACT

The Arco Anchorage crude oil spill occurred near Ediz Hook, in Port Angeles, Washington, in 1985. Following the spill, replicate infaunal sampling was carried out during five summer and winter seasons at a series of transects that ranged from relatively clean and unaffected by the spill to industrialized sites that had received heavy oiling. Average wet weight biomass, abundance, species diversity, and number of species were calculated for all samples. Analysis of variance was used to test for differences in these parameters over time within a transect. A statistically significant increase in average biomass, density, and species diversity was seen at several heavily oiled stations over time. A similar pattern was not seen at an unoiled reference station. Biomass, density, and number of species had significant negative correlations with sediment hydrocarbon concentration. A widespread settlement of bivalves was observed in October 1986 samples. Several species from this settlement (e.g., *Macoma nasuta* and *Clinocardium nuttallii*) were present in successively larger sized classes in subsequent samplings. The industrialized nature of Ediz Hook and pollution events unrelated to the oil spill probably limited the degree of recovery and recolonization documented at several of the transects.

Boesch, D.F., R.J. Diaz, and R.W. Virnstein. 1976

Effects of Tropical Storm Agnes on Soft-bottom Macrobenthic Communities of the James and York Estuaries and the Lower Chesapeake Bay

Virginia Institute of Marine Science, Gloucester Point, Virginia 23062

Chesapeake Science 17: 246-259

ABSTRACT

Macrobenthos was studied at 58 previously surveyed stations following the drastic salinity reductions caused by Tropical Storm Agnes. Effects were greatest in the lower, polyhaline portions of the James and York estuaries, where many abundant species were eliminated from shallow bottoms due to the usually low salinities and several species were eliminated or reduced in abundance on deeper bottoms due to the somewhat reduced salinity but, more importantly, to low oxygen concentrations resulting to strong density stratification of the water masses. Irruptions of opportunistic species followed these perturbations and the deep mud bottom community in the lower York estuary had not recovered 2 1/2 years after the storm. The primary alteration to usually mesohaline communities was an infusion of species more abundant in oligohaline and/or shallow brackish habitats. Communities in usually oligohaline or tidal freshwater reaches of the James and York estuaries and those at the mouth of the bay were hardly affected by Agnes.

Cabioch, L. 1980.

Pollution of subtidal sediments and disturbance of benthic animal communities.

Station Biologique, 29211 Roskoff, France.

Ambio 9: 294-296

ABSTRACT

In the sublittoral areas, the organisms most affected by *Amoco Cadiz* oil were living in fine sediments on the bottoms of bays and estuaries. A few sensitive species were completely wiped out in the polluted area. The author notes that for some species, repopulation is proving to be difficult.

Castilla, J.C. 1988.

Earthquake-caused coastal uplift and its effects on rocky intertidal communities.

Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago , Chile

Science 242: 440-443

ABSTRACT

The coastal uplift (approximately 40 to 60 centimeters) associated with the Chilean earthquake of 3 March 1985 caused extensive mortality of intertidal organisms at the Estación Costera de Investigaciones Marinas, Las Cruces. The kelp belt of the laminarian *Lessonia nigrescens* was particularly affected. Most of the primary space liberated at the upper border of this belt was invaded by species of barnacles, which showed an opportunistic colonization strategy. Drastic modifications in the environment such as coastal uplift, subsistence, or the effects of the El Niño phenomenon are characteristic of the southern Pacific. Modifications in the marine ecosystem that generate catastrophic and widespread mortalities of intertidal organisms can affect species composition, diversity, or local biogeography.

Castilla, J.C. and D. Oliva. 1990

Ecological consequences of coseismic uplift on the intertidal kelp belts of *Lessonia nigrescens*

Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile.

Estuarine, Coastal and Shelf Science 31: 45-56.

ABSTRACT

Coseismic uplift from the Chilean earthquake of 3 March 1985 caused changes in the biomass and vertical zonation of rocky intertidal organisms at four sites along 150 Km of the central Chilean coast. The 11-60cm uplift causedwidespread mortality mainly of the dominant intertidal kelp *Lessonia nigrescens*, reducing its biomass in the upper part of its pre-earthquake range and altering the vertical zonation. The *L. nigrescens* belt shrank from the top by about 0.5-1m within 1 year of the shock, then expanded downward by about 1m. An important part of the primary space liberated at the pre-earthquake upper border of *Lessonia* was invaded by the barnacles *Chthamalus scabrosus* and *Jelius cirratus*. None of the foregoing changes occured at the two control sites located outside the shock area. The ecological effects of these recurrent sudden and drastic environmental processes on the rocky intertidal communities include the liberation of the primary space, enhancement of mosaic areas and modification of the vertical zonation of competitively dominant organisms.

Chan, G.L. 1977.

The five-year recruitment of marine life after the 1971 San Francisco oil spill.

College of Marin, Kentfield, California.

Proceedings of 1977 International Oil Spill Conference, American Petroleum Institute, p543-545.

ABSTRACT

On January 18, 1971, two Standard Oil tankers collided underneath the Golden Gate Bridge, releasing about 840,000 gallons of Bunker C fuel. An estimated 4.2 million to7.5 million intertidal invertebrates, chiefly barnacles, were smothered by the oil. Five-year observations of marine life recruitment following the spill indicate that population densities of some marine species have significantly increased in the San Fransisco Bay area intertidal zones at Sausalito and Duxbury Reef. With some fluctuations, the barnacles *Balanus glandula* and *Chthamalus dalli* have increased from July 1971 to May 1976--from 93 to 189 barnacles per dm^2 at Sausalito and from nine to 34 per dm^2 at Duxbury Reef. The large bed of mussels, *Mytilus californianus*, showed a steady rise from $5.9/m^2$ in April 1971 to $14.0/dm^2$ in July 1976. The desity of mobile organisms, such as limpets, snails, crabs, and starfish, all show cyclical variations; some show an overall increase. The limpets, *Collisella spp*., which suffered high mortality during the spill have increased threefold over pre-oil counts.

In 1975, some significantly low sample means were recorded for barnacles in Sausalito and for 18 composite species at Duxbury Reef, probably due to natural ecological forces. The five-year recruitment (1971-1976), however, shows no evidence of lasting detrimental effects of Bunker C. oil on the populations of marine life within the transect sites.

Clark, R.C. Jr., J.S. Finley, B.G. Patten and E. DeNike. 1975

Long-term chemical and biological effects of a persistent oil spill following the grounding of the *General M.C. Meigs*

National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, Washington

Proceedings of the 1975 Conference on Prevention and Control of Oil Pollution, API/USCG/EPA, San Francisco, CA, 25-27 March 1975.

ABSTRACT

Petroleum hydrocarbon uptake patterns and observations of plant and animal populations of an intertidal community exposed continually since January 1972 to small quantities of a Navy Special Fuel Oil residue from the grounded unmanned troopship General M.C. Meigs were obtained by an interagency team of oceanographers, biologists, chemists, and engineers. Although the tar-ball-like character of the released oil served to limit its coverage, specific members of the intertidal community showed effects of the persistence of the spill. This report describes the long-term observations and analyses made since the grounding of the 622-foot military transport on a rich and productive intertidal regime.

Clark, R.C., B.G. Patten and E.E. DeNike. 1978.

Observations of a Cold-Water Intertidal Community After 5 Years of a Low Level, Persistent Oil Spill from the *General M.C. Meigs*

Environmental Conservation Division, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, Seattle, Wash. 98112, USA

J. Fish Res. Board Can. 35: 754-765.

ABSTRACT

A rich and productive intertidal community was exposed continually for over 5 yr to small quantities of a Navy Special fuel oil from the unmanned troopship *General M.C. Meigs* that came aground on the Washington coast in January 1972. Observations of animal and plant populations and their petroleum hydrocarbon uptake patterns showed early evidence of contamination and the persistence of the oil spill throughout the study period. Abnormal and dead urchins, and loss of algal fronds and pigment were observed in localized areas near the wreck for at least 1 yr. Within 2 mo of the accident, paraffinic hydrocarbons had been taken up by prominent members of the community and continued to appear in certain species even after 5 yr. Although changes were seen in certain species during the early days of this persistent low-level pollution incident, the community balance in this rocky.intertidal ecosystem does not appear to have been markedly altered.

Conan, G. 1982.

The long-term effects of the *Amoco Cadiz* oil spill

Centre Océanologique de Bretagne (C.N.E.X.O.), B.P. 337, 29273 Brest Cedex, France

Phil. Trans. R. Soc. Lond. B. 297: 323-333

ABSTRACT

The supertanker *Amoco Cadiz* wrecked on the coast of northern Brittany in April 1978. The resulting spill of 223,000 t of crude oil polluted some 360 km of rocky or sandy shores, salt marshes and estuaries.

An immediate mortality impact was observed. Populations of bivalves, periwinkles, limpets, peracarid crustaceans, heart urchins and sea birds were the most severely affected. Populations of polychaete worms, large crustaceans and coastal fishes were less affected. Three to six generations (5-10 years for bivalves but up to 60 years for birds) may be necessary before populations retrieve their stable age distribution.

Delayed effects on mortality, growth and recruitment were still observed up to 3 years after the spill. Estuarine flat fishes and mullets had reduced growth, fecundity and recruitment; they were affected by fin rot disease. Populations of clams and nematodes in the meiofauna declined one year after the spill. Weathered oil is still present in low-energy areas.

Species with short life cycles tend to replace long-lived species. A fauna of cirratulid and capitellid polychaete worms now prevails in sandy to muddy areas. For several clam populations, recruitment remains unstable. Three years after the spill it is still premature to decide how long it will take before populations and ecosystems reach their former or new equilibria.

Dauer, D.M. and J.L. Simon, 1976.

Repopulation of the polychaete fauna of an intertidal habitat following natural defaunation: species equilibrium

Department of Biology, University of South Florida, Tampa, Florida 33620.

Oecologia 22: 99-117

ABSTRACT

During summer, 1971, a massive outbreak of red tide resulted in defaunation of a previously characterized sandy, mtertidal habitat in upper Old Tampa Bay, Tampa, Florida. Repopulation of the polychaete fauna was studied from August 1971, to July 1973. A transect composed of 4 stations running from just below mean high water to just below mean low water was quantitatively sampled each month for species composition, densities of individual populations, biomass, and distribution of age classes.

Analysis of the rates of immigration and extinction, and the resulting colonization curve showed that repopulation conformed to the species equilibrium model of MacArthur and Wilson. Immigration was rapid with an equilibrium number of species becoming established in the 11th month. Although species composition was fairly constant, the distribution of individuals among species changed greatly.

In contrast to the ideas of Thorson, adult dispersal was shown to be a significant factor in the establishment of benthic populations with larval settlement being more significant in maintenance of the populations.

The community is viewed as a system in which species composition is determined primarily by the physical attributes of the area, and the density dominance of any species is dampened by the vagaries of adult dispersal and larval settlement. Such a system could be used to explain the relatively large number of species which belong to the same trophic type and yet occupy the same habitat.

Dauvin, Jean-Claude. 1987.

Evolution a Long Terme (1978-1986) des Populations d'Amphipodes des Sables Fins de la Pierre Noire (Baie de Morlaix, Manche Occidentale) Après la Catastrophe de l'Amoco Cadiz

CNRS-LP 4601 et Université P. et M. Curie (Paris VI), 29211 Roscoff, France

Marine Environmental Research 21: 247-273

ABSTRACT

Greatly reduced in 1978 by the *Amoco Cadiz* oil spill, the amphipod populations of the fine sand community of Pierre Noire in the Bay of Morlaix, have not yet fully recovered 8 years after the pollution. The sublittoral sandy-mud benthic communities in the western part of the English Channel show a discontinuous distribution, occurring in isolated zones which are localized in estuaries and bays. The amphipods, which are characteristic of these communities and lack a pelagic larva, form insular populations. This insular distribution delays their re-introduction to the fine sand community of Pierre Noire. Moreover, the biological and demographic characteristics of the species entail limited periods of recolonisation and increase in population.

Dauvin, J-C., and F. Gentil. 1990.

Conditions of the Peracarid populations of subtidal communities in northern Brittany ten years after the *Amoco Cadiz* oil spill.

CNRS-LP 4601 et Université P. et M. Curie (Paris Vl), 29211 Roscoff, France.

Marine Pollution Bulletin 21: 123-130.

ABSTRACT

Peracarid populations were greatly reduced in 1978 by oil from the *Amoco Cadiz*. Ten years after the spill, a benthic survey was conducted in the soft-bottom infra-littoral communities of the bays of Morlaix and Lannion and the Aber Wrac'h channel to study the rate of recovery of peracarid populations. Living in isolated populations in fine sand and muddy sand communities with low potential for immigration, the recolonization and the reconstitution of these disturbed populations was expected to be slow. The amphipod populations from the subtidal channel of Aber Wrac'h, which were initially the most affected by the oil spill were in the least advanced state of recovery. Some species present in abundance before the oil spill have not rediscovered. Novertheless, ten years after the oil spill, most of the populations had completely recovered.

Dethier, M.N. 1984.

Disturbance and recovery in intertidal pools: maintenance of mosaic patterns

University of Washington, Friday Harbor Laboratories, Friday Harbor, Washington 98250.

Ecological Monographs 54: 99-118.

ABSTRACT

The species composition of pools in the intertidal zone on the coast of Washington State varies greatly from pool to pool and from time to time. While assemblages change somewhat predictably from the low- to the high-intertidal zone (presumably owing to different stress tolerances of the species), the variance among pools at a given tidal height cannot be ascribed to such physical factors. Some pools at each height are dominated by one species that monopolizes space on the rock or in the water column and modifies the pool environment. Each dominant species, once established, can spread rapidly through a pool (either by vegetative growth or by enhanced recruitment of its conspecifics) and is thus potentially self-perpetuating. When abundant, most dominants appear to prevent potential competitors from settling and surviving by monopolization of resources, abrasion of the substratum, and/or collection of sediment. Six such dominants were identified for Washington tidepools: from low to high pools, these are (1) the surfgrass *Phyllospadix scouleri,* (2) articulated coralline algoa, (3) the mussel *Mytilus californianus* (exposed shores), (4) the cloning anemone *Anthopleura elegantissima* (more protected shores), (5) the red alga *Rhodomela larix*, and (6) the green alga *Cladophora* sp. Colonial diatoms also appear capable of cominating low pools in the absence of wave disturbance. However, each dominant monopolizes only 20-50% of the polls at anyh height.

Disturbnces, defined here as a loss of biomass exceeding 10% cover of a sessile species within 6 months and caused by extrinsic forces, were observed frequently in regularly censused tidepools. Disturbance agents included waves, excessive heat, wave-driven logs or rocks, and unusual influxes of predators and herbivores. Severe disturbances (those affecting a large proportion of the organisms in a pool) tended to occur in high pools in the summer (due to heat stress) and low pools in the winter (due to wave damage). Overall, a disturbance occurred in every pool studied an average of every 1.6 years. About half of the 231 observed disturbances affected one of the six dominant species. The frequencies of these disturbances ranged from one every 2-5 years, and recovery of the species to its original level required 3 months to over 2 years. Some species (e.g., *Rhodomela*) were disturbed frequently but recovered quickly because of rapid vegetative growth. However if asexual propagation was not possible, such as when the entire population of a species was removed from a pool, the slowness and irregularity of recruitment of sexual propagules greatly impeded recover. Experimental manipulations involving the total removal of dominant species from pools showed that such large disturbances often require over three years for recovery. The irregularity of planktonic recruitment can be compounded by the presence of herbivores, which can remove most settling organisms from the substratum, or by the absence of other organisms that are necessary for the settlement of a dominant (e.g., seed-attachment sites for *Phyllospadix*).

The combination of high disturbance frequency and slow rates of recovery makes it impossible for any dominant to occupy all the pools in its tidal range at any one time. Disturgbance is viewed in these habitats as the stochastic factor overlying other, more predictabl, community-structuring factors such as tidal height, pool size, wave exposure, and levels of herbivory, predation, and competation. Thus combined deterministic processes and random events operate to produce a complex mosaic of species assemblages in pools in one region. None of the tidepool asemblages is "stable" over many generations; rather, they seem to exist in a dynamic state where disturbances are an integral structuring factor.

Dixon, I.M.T. 1987.

Experimental application of oil-based muds and cuttings to seabed sediments

Oil Pollution Reasearch Unit, Field Studies Council, Orielton Field Centre, Pembroke, Dyfed, U.K.

In: J. Kuiper and W.J. Van den Brink (eds.). Fate and effects of oil in marine ecosystems. Martinus Nijhoff Publishers, Dordrecht, Netherlands.

ABSTRACT

Between September 1984 and July 1985, a field experiment was carried out in Milford Haven to follow the macrofaunal effects and subsequent recovery from a single application of used diesel and 'low-tox' oil based muds (OBM). Six treatments, including two levels of cuttings addition, were investigated and each was replicated three times in a randomised block experimental design. The cuttings' treatments were designed to give surficial sediment hydrocarbon concentrations of about 5000 ppm (high dose) and 400 ppm (low dose). Treatments were applied by divers to marked seabed plots (2m x 2m). Core samples were taken for hydrocarbon, sedimentological and macrofaunal analysis prior to treatment and then subsequently at 2 weeks, 1 month and then 2 monthly intervals for a total period of 10 months.

Prior to treatment no hydrocarbon or biological gradients across the experimental site were discernible. Following treatment, sediment hydrocarbon concentrations tended to fall rapidly within the first month, followed by a period of slower removal. Evidence of OMB contamination had disappeared from the low-dose plots after 4-6 months. In the high-dose plots hydrocarbon levels had all fallen almost to within the background range of values by 10 months, but slight contamination was still evident on all GLC traces.

Faunal disturbance was minor and significant effects were mainly recorded from the high-dose plots where the initial effect of oiled cuttings addition was to depress faunal density, species richness and diversity relative to controls. Population reductions were observed in a number of species but no expansion of opportunists occured. In the high-dose plots, total faunal density and the abundance of certain species remained depressed for the duration of the experiment. Faunal disturbance occurred more rapidly following diesel treatment than with low-tox treatment; reflecting the greater acute toxicity of the former. After 1 or 2 months, however, the longer term effects of low-tox OBM's became indistinguishable from those of the diesel treatment.

Ellis, D.V. and P.M. Hoover. 1990a.

Benthos on tailings beds from an abandoned coastal mine

Biology Department, University of Victory, Victory, B.C., Canada V8W2Y2.

Marine Pollution Bulletin 21: 477-480

ABSTRACT

The marine benthos which had recolonized the site of a mine tailing dischage 12 years after mining activiy had ceased was compared to an adjacent area in which no tailings were found. Test (tailings) and Reference (no tailings) sampling stations consistently separated in a series of 6 cluster analyses. They invariably provided the last linkages, thus demonstrating that biological differences between tailing and non-tniling areas remain after 12 years. Tailing station faunas were less diverse than those at non-tailing stations, and each had chnracteristic faunas. Shallow (25 m) and deep (100 m) stntions clustered together for both Test and Reference trnnsects, but were significantly different ($P<0.05$). There was a progressive increase in diversity from, shallow to deep stations, and from tailings to no tailings, and there were different highly abundant species at each station. The pattern of clusters and their significance was not affected by reducing taxa for the analyses to only those fully identified to species. Screening specimens from deposits using 2 mm and 0.5 mm mesh sieves, gave paired data sets, which clustered together for each sampling station. Only in one case were these sieve clusters significantly different, suggesting that sieve mesh size in this investigation did not seriously influence results.

Ellis, D.V. and P.M. Hoover. 1990b.

Benthos recolonizing mine tailings in British Columbia fiords

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Marine Mining 9:441-457

ABSTRACT

A comparison of the benthic species occuring in three British Columbia fiords into which mine tailings have been discharged was undertaken to demonstrate colonizing species which may be targeted for reclaimation of fishery feedstock. Data were drawn from three sources: Island Copper MIne, still in operation, and Anaconda Britannia Copper Mine and AMAX Kitsault Molybdenum Mine, both of which have ceased operation. Apparent deposite feeding polychaetes dominated in all areas, with sedentary forms representing the largest numbers of specimens and taxa in recovering sites, while errant (mobile) polychaetes were dominant in the most highly impacted areas. Other taxa, such as crustaceans and molluscs, were found in progressively larger numbers on recovering beds. Predischarge benthic fauna differed from fauna occurring during discharge, which in turn differed from fauna at sites in which discharge activities have ceased (although progressive changes were demonstated). Reclamation studies require knowledge of the dominant colonizing species, their biology, especially feeding habits, and procedures for fertilizing organically poor tailing beds.

Elmgren, R., S. Hansson, U. Larsson, B. Sundelin, and P. Boehm. 1983.

The *Tsesis* oil spill: acute and long-term impact on the benthos

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Marine Biology 73: 51-65

ABSTRACT

The "Tsesis" oil spill in October 1977 resulted in the release of over 1000 tons of medium grade fuel oil in an archipelago in the brackish Baltic Sea. Considerable oil quantities reached the benthos by sedimentation. Within 16 d benthic amphipods of the genus *Pontoporeia*, as well as the polychaete *Harmothoe sarsi* Kinberg, showed reduction to less than 5% of pre-spill biomasses at the most impacted station. The clam *Macoma balthica* (L.) was more resistant, and showed little or no mortality, but was heavily contaminated by oil (about 2000 $\mu g\ g^{-1}$ dry wt total hydrocarbons). The meiofauna was strongly affected, with ostracods, harpacticoids, Turbellaria and kinorhynchs showing clear reductions in abunance, while nematodes, as a group, were more resistant. In the winter following the spill gravid *Pontoporeia affinis* Lindström females showed a statistically significant increase in the frequency of abnormal or undifferentiated eggs. Food-chain transfer of oil to flounder [*Platichthys flesus* (L.)] was indicated. Not until the second summer after the spill were the first signs of recovery noted at the most heavily impacted station: Amphipods, *H. sarsi* and harpacticoids increased and the oil concentrations in *M. balthica* decreased (to about 1000 $\mu g\ g^{-1}$). In the area where amphipods had been virtually eliminated, there was an unusually heavy recruitment of *M. balthica*, reaching 4000 juveniles, of 1.5-2 mm length, per square metre, probably from settling in summer 1978. Three years after the spill *Pontoporeia* spp. biomass was still depressed in the most affected area, while *H. sarsi* showed normal biomass, and *M. balthica* abundance was inflated. Oil concentrations in *M. balthica* (about 250 $\mu g\ g^{-1}$) and flounder were only slightly elevated and the oil could no longer be confidently ascribed to "Tsesis" origin, even using GC/MS-analysis. Recovery was thus underway, but the long lifespan of *M. balthica* implies that the disturbed community composition may persist for many years at this station. Full recovery is likely to require more than 5 yr and may take a decade or more. An effort to evaluate the accumulated monetary loss to fishery from the accident indicates that direct costs of shoreline cleanup and vessel damage were considerably greater.

Farrell, T. 1991.

Models and mechanisms of succession: an example from a rocky intertidal community

Department of Zoology, Oregon State University, Corvallis, Oregon 97331 USA

Ecological Monographs. 61: 95-113

ABSTRACT

An investigation of the processes that cause succession was performed in an intertidal community on the central Oregon coast. The community was dominated by barnacles and several species of macroalgae. The sucessional sequence was determined at three different sites by clearing sets of plots in a way that mimicked natural disturbance. Succession at each of these sites followed the same general sequence. A barnacle, *Chthamalus dalli*, first colonized the plots and was later replaced by a second barnacle, *Balanus glandula*. The macroalgae *Pelvetiopsis limitata, Fucus distichus,* and *Endocladia muricata* colonized the plots only after *Balanus* was established. While the order of species arrival and departure was consistent, the rate of succession varied greatly among sites. The sequence of community development that was observed at one site over a 36-mo period occurred in <12 mo in a nearby area. Differences in the rate of succession appeared to result from variation in the timing of successful *Balanus* recruitment.

The mechanisms of succession were investigated in a series of field experiments. An experiment with *Balanus*-removal, *Chthamalus*-removal, and control plots was used to assess the interactions between barnacles. A direct interaction, competition for space with *Balanus*, caused *Chthamalus* to decrease in abundance as succession proceeded. *Chthamalus* did not affect the establishment of *Balanus*. Successful *Balanus* recruitment depended on occasional periods of larval settlement followed by periods of favorable weather. At all three sites, algal colonization was dependent on the presence of barnacles. *Balanus* greatly facilitated algal colonization, while *Chthamalus* only weakly facilitated algal colonization. Facilitation of algal colonization by epoxy-filled barnacle tests indicated that facilitation resulted from barnacle tests altering the substrate, rather than the activities of the living animals. A factorial experiment involving manipulations of barnacle and consumer (limpet) abundances demonstrated that the facilitation of algae by barnacles is an indirect interaction that is mediated by limpets. Barnacles decreased limpet foraging activity and thereby increased algal abundance.

Succession in this community is complicated by several processes that are not included in traditional views of succession. (1) Not all early successional species have the same effect on the establishment of later successional species. This results in spatial variation in the rate of succession. (2) The model of succession is different in each step in the successional sequence. The *Chthamalus-Balanus* interaction is an example of the tolerance model, while the barnacle-algal interaction is an example of the facilitation model. (3) Both direct and indirect interactions between species determine the course of succession.

The results of this study support a general model that predicts the effect of consumers on the rate of succession. Consumers slowed succession in this community in two ways. First, limpets delayed the establishment of *Balanus* and the competitive exclusion of *Chthamalus*. Second, limpets delayed the establishment of macroalgae. Previous studies inmarine and terrestrial habitats have found that consumers may slow, accelerate, or have no effect on the rate of succession and these observations are consistent with the predictions of this general model.

Flower, R.J. 1983

Some effects of a small oil spill on the littoral community at Rathlin Island, Co. Antrim

School of Biological and Environmental Studies, The New University of Ulster, Coleraine.

Irish Naturalists' Journal 21: 117-120

ABSTRACT

(by PERL) The trawler, *Ella Hewitt*, sank in Church Bay, Rathlin Island, during November 1962. Small quantities of bunker oil leaked from the trawler until 21 September 1978 when the Royal Navy destroyed the wreck with controlled explosions. This caused about 170 tons of oil to be washed onto the shores of Church Bay. Attempts were made to remove the stranded oil from the rocky shores (chemical dispersants) and sandy beach (mechanical methods). In order to determine the long-term effects of the oil on the rocky shores, observations were made during May 1979 and November 1980. During May 1979, one transect was run on an oiled shore and one was run on a similar unoiled shore, approximately 120m away. The abundances of invertebrates and algae were similar along the two transects, however the sea anemone, *Actinia equina*, was abundant at the unoiled site and rare at the oiled site. During November 1980 the abundances of the sea anemone were similar along the two transects. Therefore I conclude that the rocky shore organisms had recovered from the effects of the oil spill within two years.

Glémarec, M. 1986.

Ecological impact of an oil spill: utilization of biological indicators

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Water Science and Technology 18: 203-211

ABSTRACT

(By PERL) The ecological effects of the Amoco Cadiz oil spill were gauged by studying the recovery of sand-dwelling macrofauna at two subtidal sites -- lightly oiled and heavily oiled. [Hydrocarbon levels: at lightly oiled site < 700 ug/g for "a few months," and at heavily oiled site > 1000 ug/g for "over one year."]

At the lightly oiled site many macroinvertebrate species survived the disturbance and recovery of the fauna to the "normal" number of species took approximately 30 months. At the heavily oiled site all species were destroyed and recovery of the fauna took between 66 months (number of indivuals and number of species) and 84 months (biomass). At this site the number of species actually overshot the "normal" number of species between 36 and 66 months after the disturbance.

Oil acts like sewage in that it overloads the sediment with organic material and anoxic conditions occur. A succession of species occurs: first opportunistic species, then other tolerant species, and finally sensitive species are added to the community. However, this succession was rough -- sensitive species were present at 14 months although recovery was at approximately 66 months. The total number of sensitive individuals does not appear to be a good indication of the recovery of the ecosystem; the presence of specific sensitive species, on the other hand, may be a good indication that the community has recovered. The sensitive species suggested as indicators of recovery were: *Apseudes latreilli*, *Lanice* (polychaete) and *Ampelisca* (amphipod). [Opportunistic species were: Oligochaetes and the polychaetes *Scolelepis fuliginosa*, *Capitella capitata*, *Capitellides giardi*.]

Gulliksen, B. and J.P. Taasen. 1982.

Effect of an Oil Spill in Spitzbergen in 1978

Department of Marine Biology, Tromso Museum, University of Tromso, P.O. Box 2550, N-9001 Tromso, Norway.

Marine Pollution Bulletin 13: 96-98.

ABSTRACT

The oil content in the sediment and the marine life along the arctic shores of Van Mijenfjord, Spitzbergen, were investigated about two years after a spill from diesel storage tanks. High values of oil were recorded in the sediment along the shore near the tanks. The shore fauna is generally poor in these areas and the only biological effect detected was the disappearance of the amphipod *Gammarus setosus* from the surface layers.

Guzman, L. and I. Campodonico. 1981.

Studies after the *Metula* oil spill in the Straits of Magellan, Chile.

Dept. of Hydrobiology, Instituto de la Patagonia, Punta Arenas, Chile.

Proceedings of the Petromar 1980 conference: 363-376.

ABSTRACT

(by PERL) The *Metula* ran aground during August 1974, releasing approximately 40, 000 tons of oil. Much of the oil was washed ashore and approximately 250km of shoreline was oiled. This paper summarizes many observations made at the oiled sites and many papers published on the oil spill.

Hall, S.J., D.J. Basford, M.R. Robertson, D.G. Raffaelli, and I. Tuck. 1991

Patterns of recolonisation and the importance of pit-digging by the crab *Cancer pagurus* in a subtidal sand habitat

SOAFD Marine Laboratory, PO Box 101, Victoria Road, Aberdeen AB9 8DB, Scotland.

Marine Ecology Progress Series 72: 93-102

ABSTRACT

The nature and level of disturbance to a benthic community caused by the pit-digging activities of the crab *Cancer pagurus* were examined in a shallow sub-tidal sand habitat on the west coast of Scotland. From observations by acoustic tracking we estimate that each individual digs between 6 and 7 pits per day, with a total of 20 pits dug in a 1000 m^2 area each day. Recolonisahon of simulated crab pits suggest that the community returned to its original state within 25 to 30 d. This was achieved initially by erosion from the surrounding sediments followed by the random arrival of adult colonists from the available benthic pool. Feeding or other competitive interactions within disturbed patches were not altered sufficiently to be reflected as changes in the relative abundance of taxa. We estimate that 3.6% of the habitat will be at some stage of recovery from disturbance by pit-digging at this time of year.

Hampson, G.R. and E.T. Moul. 1978.

No 2 fuel oil spill in Bourne, Massachusetts: immediate assessment of the effects on marine invertebrates and a 3-year study of growth and recovery of a salt marsh.

Woods Hole Oceanographic Institution, Woods Hole, Mass. 02543.

J. Fish. Res. Board Can. 35: 731-744.

ABSTRACT

On October 9, 1974 the oil barge *Bouchard 65* loaded with 73,000 barrels of oil spilled what was initially thought by the Coast Guard to be a few barrels and later raised to an undetermined amount of No. 2 fuel oil off the west entrance of the Cape Cod Canal in Buzzards Bay, Massachusetts (anchor site C, Fig. 1). Within the following 2-week period, oil from the barge was found contained along the west side of Bassett's Island and inner Red Brook Harbor, a distance of 5.0 km from the site of the spillage. Qualitative samples of dead and moribund marine invertebrates were collected in tide pools and slight depressions along the beaches. A collection consisting of 4360 invertebrates comprising 105 species, plus 2 species of fish were found in 8 samples. Noticeable effects of the oil on the salt-marsh plant community were also observed. A detailed quantitative examination was begun to determine the effects of the oil on various components of the affected salt-marsh community in Winsor Cove compared to a selected control site. From data collected in September 1977, the marsh grass in the lower intertidal zone in Winsor Cove has shown an inability to reestablish itself by either reseeding or rhizome growth. The associated sediments show a correspondingly high concentration of petroleum hydrocarbons impregnated in the peat substrate. Erosion rates measured in the affected area, as a result of the 3 year period of marsh degeneration, were 24 times greater than the control site. Microscopic algae were collected during the sampling period and those present were considered least sensitive to environmental changes. Examination of the interstitial fauna found in the study area in the summer of 1977 showed an extremely reduced number of individuals and species.

Harrel, R.C. and M.A. Hall. 1991

Macrobenthic community structure before and after pollution abatement in the Neches River estuary (Texas)

Lamar University, Department of Biology P.0. Box 10037, Beaumont, TX 77710, USA

Hydrobiologia 211: 241-252

ABSTRACT

Macrobenthos and physicochemical conditions in the lower 39 km of the Neches River estuary were studied from August, 1984 to May, 1985. The results were compared with data collected in 1971-1972. Between 1972 and 1984 the permitted BOD waste load in the tidal Neches River was reduced from 12325 kg d to 8717 kg d. River discharge and dissolved oxygen concentrations were consistently higher and salinity was lower, during the same seasons, during the 1984-1985 study. A total of 50 taxa of macrobenthos were collected in 1971-1972 and 104 taxa were collected in 1984-1985. The numbers of taxa per collection at each station in 1984-1985 were at least twice those found in 1971-1972. Minimum densities in 1984-1985 were much higher than the maximum densities in 1971-1972 at all stations. Patterns of dominance, Sorenson's similarity index, and diversity *(d)* values indicated improved water quality in 1984-1985. Statistical analysis of macrobenthic diversity indicated significant differences between upper estuary and lower estuary stations in 1971-1972. No significant differences were found in 1984-1985. Significant differences in numbers of taxa, macrobenthos densities, and *d* values between the two studies were found. Reductions of waste loads, increased river discharge, and deepening of the navigation channel were among the factors that probably contributed most to the changes in community structure of the macrobenthos observed.

Haven, S.B. 1971

Effects of land-level changes on intertidal invertebrates, with discussion of postearthquake ecological succession

Simon Fraser University.

In: National Research Council (ed.). The Great Alaska Earthquake of 1964: Biology. National Academy Press, Washington, D.C.

ABSTRACT

Investigations were carried out in summer 1965 on the effects of land-level changes and other factors associated with the March 1964 earthquake on intertidal invertebrate populations in Prince William Sound, Alaska.

Effects of the earthquake varied with type of habitat and organism and with the amount and direction of land-level change. In general, organisms lifted above their normal vertical ranges were killed.

Postearthquake community development (in terms of similarity to inferred preearthquake conditions) had in general proceeded most rapidly in the *Laminaria* zone and less rapidly upward and signifcantly less rapidly on maximally uplifted shores than on the less strongly affected shores elsewhere.

In areas of maximum uplift, the postearthquake intertidal communities had to develop entirely anew. The fauna was greatly reduced-many species were absent, many others rare-compared to the time before the earthquake, except in the *Laminaria* zone, which supported a near-normal fauna.

Evidence for ecological succession was provided by four main aspects of the postearthquake rocky shore communities that were significantly different from inferred preearthquake conditions: the dominance by algal films rather than *Verrucaria* in the uppermost zone; the dominance of *Balanus balanoides* in the midlittoral zone; the attachment of mussels to underlying algae; and, in the maximally uplifted area, the dominance of *Porphyra* rather than *Fucus*, correlated with the scarcity of grazing gastropods. Additional aspects of succession in rocky shore and level bottom habitats are discussed

Houghton, J.P., D.C. Lees, H. Teas, H.L. Cumberland, S. Landing, W.B. Driskell and T.A.Ebert 1991a

Evaluation and condition of intertidal and shallow subtidal biota in Prince William Sound following the *Exxon Valdez* oil spill and subsequent shoreline treatment

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NOAA, WASC Contract No. 50ABNC-0-00121

ABSTRACT

The effect and extent of shoreline treatment in areas affected by the *Exxon Valdez* oil spill will greatly complicate assessment of the long-term impacts of treatment and the oil alone. Because much of the heavily oiled shoreline was washed with high-pressure hot water at least once, and because so little of the oiled shoreline was left untreated, only a limited number of areas remain where comparisons may be made to distinguish between effects of oiling and the effects oiling plus treatment. Lack of specificity in the available treatment information (e.g., equipment, temperature, duration, bioremediation application rates, and repetitions) also complicates separation of effects of individual treatment approaches.

Nevertheless, the results from this study to date provide a strong basis to argue that conditions spanning a broad spectrum of biological properties reflect both the influences of hydrocarbon contamination and the intrusive shoreline treatment. The high number of cases in which the null hypothesis of no impact from oiling and/or treatment was rejected is impressive. It is clear, based on the number of rejections and the high levels of significance observed in many cases, that the data provided by this study strongly support the conclusion that hydrocarbon contamination and high pressure, hot-water treatment each caused major adverse impacts to the intertidal biota of western Prince William Sound, but that the effects of the treatment predominated. Moreover, it appears likely that the treatment, while removing oil from the upper and mid-littoral zones, where its effects were somewhat restricted to relatively tolerant organisms such a barnacles, rockeweed, and mussels, transported the remobilized oil into the lower intertidal and shallow subtidal zones, where the oil was placed into contact with relatively more sensitive and productive organisms such as hardshelled clams and crustaceans.

Houghton, J.P., D.C. Lees, W.B. Driskell and A.J. Mearns. 1991b.

Impacts of the *Exxon Valdez* spill and subsequent cleanup on intertidal biota -- 1year later

Pentec Environmental, Inc., 120 West Dayton, Edmonds, Washington 98020

Proceedings of the 1991 International Oil Spill Conference, American Petroleum Institute, p467-475.

ABSTRACT

A substantial amount of the crude oil which spilled from the tanker *Exxon Valdez* on March 24, 1989, was deposited on beaches in Prince Williams Sound. Major beach cleanup activities began in May and continued throughout the summer of 1989. Additional cleanup activities occured during the summer of 1990. A study was conducted in 1989 to document the short-term impact to biota of hot water wash treatments. Additional field surveys were conducted in the summer of 1990 to evaluate recovery of littoral habitats from the effects of oiling and shoreline treatment. Stratified-random sampling was used to assess epibiota and infauna at 27 sites, representing several habitats and degrees of disturbance.

Preliminary data evaluations indicate that treaatment methodologies applied in 1989 had varied effects on intertidal assemblages. Some treated rocky beaches were stripped of flora and fauna at mid- and upper intertidal elevations and showed relatively little colonization by mid summer 1990. On other oiled rocky beaches that recieved less severe or no treatment, the majority of the community dominants remained in place and significant recolonization was underway. Protected sand and gravel beaches subjected to hydraulic treatments displayed greatly altered beach morphology. Finer sands and gravels were flushed from upper intertidal elevations, often burying the lower beach in several centimeters of sediment, resulting in major reductions in infauna in 1990. Oiled but untreated sand and gravel beaches had a rich and varied infauna. The effects of 1989 shoreline treatment activities on intertidal flora and fauna were significant and widespread and will greatly complicate assessment of the long-term impacts of the oil itself.

Hubbard, J.D. 1971.

Distribution and abundance of intertidal invertibrates at Olsen Bay in Prince William Sound, Alaska, One Year after the 1964 earthquake

University of Wisconsin at Sheboygan

In: National Research Council (ed.). The Great Alaska Earthquake of 1964: Biology. National Academy Press, Washington, D.C.

ABSTRACT

In the summer of 1965, the Bureau of Commercial Fisheries began a study of intertidal invertebrates in the Olsen Bay area of Prince Williams Sound; this included an evaluation of the effect on intertiidal organisms of uplift caused by the 1964 Alaska earthquake. Intensive sampling of four areas representative of the three most common types of habitat in this protected bay revealed a vertical distribution and abundance of invertebrate species strongly influenced by substrate composition and tidal exposure. Mean tide level (+6.2 ft) exhibited particular importance as the upper limit of numerous organisms. It was found that the uplift produced measurable changes in the distributions of certain bivalve mollusks. Amount of uplift, approximately 3.0 to 3.5 ft in Olsen Bay, could be estimated by comparing the positions of some of these organisms before and after the earthquake. The most obvious and reliable quantitative index of the uplift was provided by pre- and postearthquake limits of barnacle populations, whereas supportive evidence was obtained from examination of certain bivalve mollusk distributions. Differential mortality, noted especially between different species of mollusks and between different age-classes of certain species, was apparently attributable to earthquake-related processes. While reproductive success of some species appeared unaffected by the earthquake, other species have apparently experienced little reproduction since the earthquake.

Ibanez, F. and J-C Dauvin. 1988.

Long-term changes (1977 to 1987) in a muddy fine sand Abra alba-Melinna palmata community from the Western English Channel: multivariate time-series analysis

CEROV, Station Zoologique, BP 28, F-06230 Villefranche-sur-Mer, France.

Mar. Ecol. Prog. Ser. 49: 65-81.

ABSTRACT

Long-term monitoring for 10 years (1977 to 1987) of the muddy fine sand community of the Bay of Morlaix (N. France) has allowed us to determine the principal stages of structural succession following pollution by the hydrocarbons of the *Amoco Cadiz* (1978). Abundance of 30 main species and biomasses of 30 categories were investigated. Regular series were obtained by averaging values from each season, resulting in 40 sequential observations. General trends and seasonal variations were extracted by the Eigen-Filtering method which takes into account the shortness of the annual sampling. Principal component analysis of the covariance matrix of the general trends exhibits 7 successive periods of temporal community changes. This succession is a function of changes in direction in gradients within the populations. The community developed through a successional phase following the oil spill, with establishment at first of a community of opportunists, followed by a colonisation of the polychaete *Lanice conchilega* and finally by reestablishment of the original community pre-Amoco Cadiz. An attempt to classify the species according to their seasonal variations is proposed using a semi-quantitative approach. Results show a concentration of maximal abundances in summer and autumn, and of minimal abundances in winter. The dissimilarity correlograms of the densities and the biomasses were used after rearranging the species into 3 trophic groups. The different behaviour of trophic groups is related to recolonization after the oil spill and to organic matter in the sediment.

Jackson, J.B.C. et al. 1989.

Ecological effects of a major oil spill on Panamanian coastal marine communities.

STRI, Apartado 2072, Balboa, Republic of Panama.

Science 243: 37-44.

ABSTRACT

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

Jacobs, R. 1980.

Effects of the *Amoco Cadiz* oil spill on the seagrass community at Roscoff with special reference to the benthic infauna

Laboratory of Aquatic Ecology, Catholic University, Toernooiveld, 6525 ED Nijmegen, The Netherlands

Mar. Ecol. Prog. Ser. 2: 207-212

ABSTRACT

The benthic fauna of an eelgrass (*Zostera marina L.*) community has been investigated at Roscoff (France) from October 1977 to April 1979. The impact of the *Amoco Cadiz* oil spill of March 1978 on the community was studied. Direct effects on the eelgrass itself were only local during the first weeks after the spill, when many plants had black, 'burnt' leaves. This was, however, a temporary phenomenon, for the production of new leaf tissue continued normally. Effects on the benthic fauna were observed directly after the arrival of the oil at Roscoff. A sharp decrease in numbers of both individuals and species occurred - mainly caused by an almost total disappearance of the smaller Crustacea and Echinodermata, and a serious numerical decrease in other groups. Recovery took place relatively rapidly. In the beginning of 1979 all numbers were at the same level as the year before, the filter feeding Amphipoda being the only exception: on 1 May 1979 they were still absent.

Kaplan, E.H., J.R. Welker and M.G. Kraus. 1974.

Some effects of dredging on populations of macrobenthic organisms

Biology Dept., Hofstra University, Hempstead, NY 11550.

Fishery Bulletin 72: 445-480.

ABSTRACT

Populations of epi- and infauna were studied from 10 mo before to 11 mo after a navigation channel was dredged through a small, shallow lagoon. A new sampler which penetrated 20-30 cm into the substratum was used.

Current velocities and sedimentation patterns were changed due to an altered distribution of tidal currents, although flushing time was not appreciably altered.

Values of certain particulate and dissolved nutrients changed after dredging, but no correlation was observed between animal populations and fluctuations in nutrients.

Significant reductions in standing crop figures and species and specimen numbers occurred in both the bay and the dredged channel. *Mercenaria mercenaria* populations were reduced, but there was no evidence of mass mortality. Recovery of biomass in the channel was affected by sediment composition, but seasonal and sediment type variations were not significant in the bay as a whole.

Goose Creek had a high predredging epi-and infaunal standing crop estimated at 36.83 g/m^2, but the number of organisms/m^2 was relatively low, indicating a preponderance of large forms.

Productivity of Goose Creek was calculated at 89.87 $g/m^2/yr$ before dredging and 31.18 $g/m^2/yr$ after dredging. Productivity figures for the mixed peripheral marsh were calculated and the annual loss due to replacement of 10.87 ha of marsh by spoil areas was estimated at 49,487 kg. Altered land usage patterns tended to fix this loss on a permanent basis.

The unusually profound effects of dredging reported for Goose Creek are attributed to its small size and shallowness.

Krebs, C.T. and K.A. Burns 1977.

Long-term effects of an oil spill on populations of the salt-marsh crab *Uca pugnax*

Division of Natural Science and Mathematics, St. Mary's College, St. Mary's City, Maryland 20686

Science 197: 484-487

ABSTRACT

A spill of fuel oil at West Falmouth, Massachusetts, in 1969, contaminated contiguous salt marshes with up to 6000 microgramsof oil per gram (ppm) of wet mud and affected local populations of *Uca Pugnax*. Directly related to high-sediment oil content were reduced ratio of females to males, reduced juvenile settlement, heavy overwinter mortality, incorporation of oil into body tissues, behavioral disorders such as locomotion impairment, and abnormal burrow construction. Concentrations of weathered fuel oil greater than 1000 ppm were directly toxic to adults, while those of 100 to 200 ppm were toxic to juveniles. Cumulative effects occured at lower concentrations. Recovery of the marsh from this relatively small oil spill is still incomplete after 7 years.

Laubier, L. 1980.

The *Amoco Cadiz* oil spill: an ecological impact study

Centre National pour l'Exploitation des Oceans, 66, avenue d'Iena, 75116-Paris, France.

Ambio 9: 268-276

ABSTRACT

When the *Amoco Cadiz* ran aground off the coast of France in March, 1978, 223,000 tons of oil spilled into the ocean. After two years, major studies show the recovery of areas exposed to waves, currents and winds is almost complete. But oil persists in areas protected from the physical movement of the sea, and there are sublethal long-range effects on the reproduction of marine organisms.

Lebednik, P.A. and J.F. Palmisano. 1977.

Ecology of marine algae

Fisheries Research Institute, University of Washington, Seattle Washington.

In M.L. Merritt and R.G. Fuller (eds.). The environment of Amchitka Island, Alaska. Technical Information Center..

ABSTRACT

The rocky shores of Amchita Island are densely carpeted by marine algal communities, which, beyond the coast exposed by the tides, are characterized by extensive floating kelp beds. An unusual feature of the intertidal area of the southeastern third of the island if the occurance of wide, often extremely flat, rock benches at about mean tide level.

The Milrow nuclear test affected about 4 ha (10acres) of littoral vegetation when an uplift of about 12 cm (5in.) occured on an intertidal rock bench. Mortality was extensive in the upper portions of all zones 6 months after the disturbance, and significant changes were still occuring when last observed, 3 1/2 years after Milrow. The Cannikin nuclear test resulted in uplifting to a maximum of 1 m (3ft). Mortality of the littoral vegetation was severe along 1.9 km (1.2 miles) of coast, including areas with 0.5 to 1 m of uplift. Moderate mortality was observed along an additional 1.5 km (1 mile) of coast, and mortality was detectable along a further 2.7 km (1.7 miles) of coast. Significant changes in vegetation were reported to be occuring nearly 3 years after Cannikin. A normal littoral vegetation will eventually return to both the Milrow and the Cannikin disturbed areas. The lifting of some rock benches above the midlittoral area as a result of the Cannikin test has resulted in significant permanent reduction in the area available to most littoral species.

Lee, R. F., B. Dornseif, F. Gonsoulin, K. Tenore and R. Hanson. 1981.

Fate and Effects of a Heavy Fuel Oil Spill on a Georgia Salt Marsh

Skidaway Institute of Oceanography, PO Box 13687, Savannah, Georgia 31406, USA

Marine Environmental Research 5: 125-143

ABSTRACT

Addition of a heavy oil to a Spartina salt marsh in the autumn resulted in high concentrations of polycyclic aromatic hydrocarbons in sediment and benthic animals. The highest concentrations of phenanthrene, chrysene and fluoranthene in the sediment were 112, 105 and 75 ng/g sediment, respectively. These concentrations rapidly decreased during the 20 week period following the spill. The times for these hydrocarbons to decrease to 50% of their highest values, i.e. half-life, were approximately 100, 70 and 30, days in sediment, mussels and oysters, respectively. Benthic macrofauna species showed three responses to oil addition which included no change, an increase, or a decrease in the population. No changes were noted in populations of fiddler crabs (*Uca pugnax*), oysters (*Crassostrea virginica*), and mussels (*Modiolus demissus*). Mud snails (*Nassarius obsoleta*) increased in density after the spill due to immigration of adult snails from untreated areas to scavenge on animals killed by the oil. Many of the adult periwinkles (*Littorina irrorata*) were killed by the oil. In the spring, juvenile periwinkles recolonised to oiled areas as a result of larvae settling.

Leppakoski, E.J. and L.S. Lindstrom. 1978.

Recovery of benthic macrofauna from chronic pollution in the sea area off a refinery plant, southwest Finland.

Institute of Biology, Abo Akademi, SF-20500 Abo, Finland.

J. Fish Res. Board Can. 35: 766-775.

ABSTRACT

Quantitative field studies (density, wet weight biomass, Shannon diversity, species richness, evenness of distribution) on benthic sublittoral macrofauna were made in the vicinity of an oil refinery in southwest Finland before and after the installation of a new wastewater treatment plant that reduced the amount of oil and liquid effluents by ca. 90-95%. The number of species and species diversity increased during the 1st and 2nd year after pollution abatement at the stations close to the former outflows. The amphipods *Pontoporeia affinis, Corophium volutator*, and *C. lacustre,* midge largae of the *Chironomus plumosus*-group, the oligochaete *Tubifex costatus*, the polychaetes *Harmothoe sarsi* and *Polydora redeki*, and the bivalve *Cardium* sp. were the most successful recolonizers of the 23 taxa sampled. The strong lethal effect of oil-contaminated sediments upon *Chironomus plumosus* larvae decreased markedly in laboratory experiments (LT50 was estimated at 7 d in 1973 and at 28 d in 1974; in 1975, 80-90% of the larvae survived for 28 d). Details of postabatement succession are discussed. The results demonstrate not only the recovery from chronic oil pollution but also the degree of ecological damage caused by previous continuous discharge of oil.

Linden, O., R. Elmgren and P. Boehm. 1979.

The *Tsesis* oil spill: its impact on the coastal ecosystem of the Baltic Sea.

Swedish Water and Air Pollution Research Institute (IVL), Studsvik, S-611 82 Nykoping, Sweden.

Ambio 8: 244-253.

ABSTRACT

The Tsesis oil spill was relatively minor by international standards - roughly 1000 tons of medium grade fuel oil. However, severe effects were observed, at least locally, in the pelagic, littoral and benthic ecosystems and the speed of recovery varied greatly. The plankton communities were back to normal after about one month, but it took a year before the littoral communities showed considerable recovery and within that time soft bottom community did not show even the beginning of a recovery.

Mair, J.McD., I. Matheson and J.F. Appelbee. 1987.

Offshore macrobenthic recovery in the Murchison field following the termination of drill-cuttings discharges

Institute of Offshore Engineering, Heriot-Watt University, Research Park, Riccarton, Edinburgh EH14 4AS, UK

Marine Pollution Bulletin 18: 628-634.

ABSTRACT

The effects of discharged drilling cuttings contaminated with oil-based drilling fluids on the macrobenthos surrounding several North Sea oil-production platforms have been well documented. Areas of biological effect ranging from highly modified benthic communities, through transitional zones to undisturbed zones have been identified and characterized. Results are presented from a series of studies at the Murchison oil field which indicate partial recovery of macrofaunal communities around the production platform after cuttings discharges had ceased. Eventual rates of recovery of affected macrobenthic communities around production platforms are discussed in terms of persistence of oil in the drilling cuttings and the rates of degradation of the oil and its toxic components.

McLusky, D.S., F.E. Anderson and S. Wolfe-Murphy. 1983.

Distribution and population recovery of *Arenicola marina* and other benthic fauna after bait digging.

Department of Biology, The University of Stirling, Stirling FK9 4LA, Scotland.

Mar. Ecol. Prog. Ser. 11: 173-179.

ABSTRACT

Effects of bait digging on distribution and population recovery of *Arenicola marina*, *Hydrobia ulvae* and *Macoma balthica* have been investigated on trial plots at Blackness, Forth estuary (Scotland). *A. marina* rapidly recolonised the basins created by digging, but had reduced populations on the dug mounds. Its populations were dislocated for over 3 mo after digging. *H. ulvae* and *M. balthica* showed enhanced populations on the mounds for up to 2 wk, but were otherwise unaffected by digging. Factors influencing the mode of population recovery are discussed; it is suggested that enhanced basin populations of recolonising *A. marina* are due substantially to above-surface migration of worms into areas with increased levels of organic matter.

Maurer, D., W. Leathem and C. Menzie. 1981.

The impact of drilling fluid and well cuttings on polychaete feeding guilds from the US northeastern continental shelf.

College of Marine Studies, University of Delaware, Lewes, Delaware 19958.

Mar. Poll. Bull. 12:342-347

ABSTRACT

The effect of recent drilling operations (fluid and well cuttings) on polychaete feeding guilds from continental shelf off Atlantic City, New Jersey, was examined. Although there were some adverse effects on macrobenthos from 2160 metric tons of cuttings and mud solids discharged into the marine environment, the composition of polchaete feeding guilds remained essentially unchanged. This key trophic relationship between polychaetes and the changing environment due to the drilling operation was apparently uninterupted. This relationship remains to be examined in other natural and perturbed habitats.

Michael, A.D., C.R. Van Raalte, and L.S. Brown. 1975.

Long-term effects of an oil spill at West Falmouth, Massachusetts

Marine Biological Laboratory, Woods Hole, Massachusetts.

Proceedings of 1975 International Oil Spill Conference, American Petroleum Institute, p573-582.

ABSTRACT

A small spill of No. 2 fuel oil occured near Wild Harbor, Massachusetts, in September 1969. The benthic fauna of Wild Harbor Marsh, boat basin, and offshore area was sampled through the fourth and fifth year after the spill (1973, 1974). Sediment sampels were analyzed for the presence of petroleum hydrocarbons. Gas chromatography produced evidence of hydeocarbons typical of weathered fuel oil in the sediments of the marsh, boat basin, and two offshore stations. The numbers of benthic species at the offshore stations and the marsh were slightly, but significantly, lower than those found at control stations but not in the case of the marsh. The boat basin was still heavily affected. Some stations were charaterized by the presence of opportunistic species The recovery process in terms of the total benthos has leveled off, but there was evidence for further recovery during the course of the study.

Notini, M. **1978.**

Long-term effects of an oil spill on *Fucus* macrofauna in a small Baltic bay

Swedish Water and Air Pollution Research Institute, IVL Baltic Sea Laboratory, Studsvik, Fack, S-611 01 Nyköping, Sweden.

J. Fish. Res. Board Can. 35: 745-753.

ABSTRACT

On October 6, 1970, the small tanker *Irini* ran aground in the southern part of the Stockholm archipelago, releasing about 1000 t of medium and heavy fuel oil. Approximately 400 t drifted into a small bay, Gästviken, wiping out nearly the entire littoral fauna. Most of the oil was collected mechanically during the winter, and by May 1971 cleanup operations were completed. The recruitment of the bladder wrack (*Fucus vesiculosus*) community in the bay was observed at intervals over a 5-yr period. Significantly increased macrofauna population densities were found for a number of species in the 1974 and 1976 samples compared to those of 1971 and 1972. From June-July 1971 to June 1976, the mean numbers of individuals for all species rose from about 280 to 1000/100 g *Fucus* dry weight (d.w.). The bivalve *Mytilus edulis* increased in number from 0 to about 45, the gastropod *Theodoxus fluviatilis* from 0 to about 160, the amphipod *Gammarus* spp. from about 40 to 580, the isopods *Idotea* spp. from about 5 to 35, and *Iaera* spp. from almost 0 to about 10/100 g *Fucus*. Larvae of Chironomidae were the only group found with a decreased density between the first and sixth summers after the spill, with 240 and 145 individuals, respectively. The data obtained are discussed in relation to conditions in a nearby unpolluted bay and to normally occurring cyclic variations.

O'Clair, C.E. 1977.

Marine Invertebrates in Rocky Intertidal Communities

Fisheries Research Institute, University of Washington, Seattle, Washington.

In: Merritt and Fuller (eds.). 1977. The Environment of Amchitka Island, Alaska. Technical Information Center, Energy and Research and Development Administration.

ABSTRACT

Previous knowledge of Aleutian marine benthic invertebrates was based on few observations and collections, the history of which is summarized. In this study three belt transects (one sampled once and two sampled seven times) and two intertidal arrays (sampled twice each) of 0.25-m^2 quadrats were used for descriptive studies of intertidal communities at Amchitka Island. These communities are dominated by algae at all tidal levels. Three communities are dominated by algae at all tidal levels. Three communities designated according to their dominant macrophytes are the *Laminaria* community, the *Alaria-Hedophyllum* community, and the Halosaccion-Fucus community. Invertebrates in these communities are mostly inconspecious. Despite the large proportion of North American species in the fauna of Amchitka, species that play key roles in structuring intertidal communities elsewhere on the west coast of North America are absent or in low abundance at Amchitka. Invertebrates in subtidal communities are discussed briefly. An annotated list of over 365 littoral and sublittoral invertebrate species is appended.

Seven zoogeographical elements were recognized in the shallow-water marine fauna of Amchitka. The greatest proportion of species are North Pacific or North American in their distribution. Two oceanographic features (the Alaskan Stream and the Kamchatka Current) and one geologic feature (the Aleutian "stepping-stone" islands between Amchitka and the Asian and North American mainlands) increase the immigration rates of North American species over Asiatic species.

The effects of Cannikin were determined with the use of two intertidal arrays of fixed 0.25-m^2 quadrats (totaling 40 plots) examined twice preevent and ten times postevent (over 33 months) and an intertidal grid (control) sampled randomly once preevent and twice (over 9 months) postevent. The rate of die-off and emigration of intertidal species in maximally uplifted (as much as 1 m) areas depended on exposure to open ocean waves. Most preevent intertidal species were replaced by supralittoral fringe species.

Oliver, J.S. and P.N. Slattery. 1985

Destruction and opportunity on the sea floor: effects of gray whale feeding

Moss Landing Marine Laboratories, P.O. Box 223, Moss Landing, California 95039, USA.

Ecology 66: 1965-1975

ABSTRACT

Gray whales (*Eschrichtius robustus*) are highly disruptive bottom feeders that remove infaunal invertebrate prey and sediments by suction. The response of the benthos to gray whale feeding was examined in the primary feeding grounds of the Bering Sea dn in an ecological analog of these prey communities along the west coast of Vancouver Island. Prey communities were dominated by ampeliscid and other amphipod crustaceans that formed dense tube mats. Large feeding excavations (often 2-20m^2) were rapidly colonized by scavenging lysianassid amphipods, especially *Anonyx* spp., that attacked injured and dislodged infauna. Many of the attacked animals were small crustaceans (< 1 cm long) and polychaete worms. *Anonyx* spp. was 20-30 times more abundant inside fresh excavations than in the surrounding tube mat, where they dispersed within hours after the initial feeding disturbance. A smaller species of lysianassid, *Orchomene minuta*, invaded less rapidly and remained much longer in excavations than the larger, *Anonyx* spp. Natural scavenging events outside feeding excavations revealed that lysianassids commonly fed on relatively small crustacean carcasses (< 3 cm long). Within days and weeks, gray whale feeding excavations trapped organic debris. Most invading species were much more abundant in debris patches compared to debris-free areas of the same excavations. The number of some colonists remained elevated in disturbed areas for > 2 mo. Early colonists were characterized by much greater abundances inside excavations relative to the adjacent tube mat. Two numerically dominant groups of tube-dwelling amphipods were not characterized by a large pulse of abundance inside excavations. *Ampelisca* and *Protomedeia* gradually colonized pits. They also swam less frequently than the early colonists, and probably had more infaunal habits. Gray whale feeding clearly has a dramatic impact on the structure of benthic communities, and also may enhance the population size of several secondary prey.

Oliver, J.S., R. Kvitek and P. Slattery. 1985.

Walrus feeding disturbance: scavenging habits and recolonization of the Bering Sea benthos

Moss Landing Marine Laboratories, Moss Landing, CA 95039.

J. Exp. Mar. Biol. Ecol. 91: 233-246.

ABSTRACT

Walruses *(Odobenus rosmarus* Illiger) influenced the structure of macrobenthic assemblages in a variety of ways as they excavated their major bivalve prey from soft sediments. Benthic animals were attracted to discarded bivalve shells and they colonized pits and furrows made during prey excavation. Discarded shells contained soft tissues that were eaten by several invertebrate scavengers. The most abundant and widespread scavenger was the sea star, *Asterias amurensis* Lutken. Sea stars out-competed brittle stars *(Amphiodia craterodmeta* Clark) for fresh scavenging events. They also attacked brittle stars under shells in the laboratory, and thus may have obtained two meals from discarded shells by eating remnant tissue and by consuming animals that used the shell as a habitat. In nature, brittle stars were abundant under discarded shells. In experiments, brittle stars invaded shells with soft tissue in the absence of sea stars, but not in their presence. In other experiments, brittle stars were most abundant under shells with soft tissue, but were also attracted to shells without organic matter. Large brittle stars were more abundant under shells than in the surrounding bottom, and the reverse was true of small individuals. Bottom communities recovered gradually inside experimental feeding excavations, which were not invaded by large numbers of opponunistic infaunal or epifaunal invertebrates. This is in contrast to gray whale feeding excavations, which are colonized by a large number of opportunistic peracarid crustaceans.

Pagliai, A., A. Varriale, R. Crema, M. Galletti, and R. Zunarelli. 1985.

Environmental Impact of Extensive Dredging in a Coastal Marine Area

Institute of Zoology, the University of Modena, 41100 Modena, Italy.

Marine Pollution Bulletin 16: 483-488.

ABSTRACT

An area of the Thyrrenian Sea in the Gulf of Cagliari, Sardinia, Italy, was investigated before, during and after extensive dredging operations to create an access channel for oil tankers to reach a refinery. The observed abiotic parameters were not greatly affected, but the benthic macrofauna was completely eliminated from the dredged area. Recolonization of this area by the macrobenthos was very rapid. Six months after dredging, benthic communities had main structural parameters very similar to those of the predredging period and neighbouring non-dredged areas. However, the six month post dredging communities still showed a noticeable qualitative dissimilarity with respect to the predredging period and neighbouring non-dredged areas. Communities in the neighbouring non-dredged zones were unaffected by the large scale dredging. These results are only in fact in agreement with those reported in previous investigations into the effects of dredging of the benthic biota. They suggest that the environmental impact of this human induced disturbance may be quite variable from case to case, also in dependence of the concomitant action of other pollutants.

Paine, R.T. and S.A. Levin. 1981.

Intertidal landscapes: disturbance and the dynamics of pattern

Department of Zoology, University of Washington, Seattle, Washington 98195.

Ecological Monographs 51: 145-178.

ABSTRACT

The mussel *Mytilus californianus* is a competitive dominant on wave-swept rocky intertidal shores. Mussel beds may exist as extensive monocultures; more often they are an ever-changing mosaic of many species which inhabit wave-generated patches or gaps. This paper describes observations and experiments designed to measure the critical parameters of a model of patch birth and death, and to use the model to predict the spatial structure of mussel beds. Most measurements were made at Tatoosh Island, Washington, USA, from 1970-1979.

Patch size ranged at birth from a single mussel to 38 m^2; the distribution of patch sizes approximates the lognormal. Birth rates varied seasonally and regionally. At Tatoosh the rate of patch formation varied during six winters from 0.4-5.4% of the mussels removed per month. The disturbance regime during the summer and at two mainland sites was 5-10 times less. Annual disturbance patterns tended to be synchronous within 11 sites on one face of Tatoosh over a 10-year interval, and over larger distances (16km) along the coastline. The pattern was asynchronous, however, among four Tatoosh lacalities. Patch birth rate, and mean and maximum size at birth can be used as adequate indices of disturbance.

Patch disappearance (death) occurs by three mechanisms. Very small patches disappear almost immediately due to a leaning response of the border mussels (0.2 cm/d). Intermediate-sized patches (<3.0 m^2) are eventually obliterated by lateral movement of the peripheral mussels: estimates based on 94 experimental patches yield a mean shrinking rate of 0.05 cm/d from each of two principal dimensions. Depth of the adjacent mussel bed accounts for much of the local variation in closing rate. In very large patches, mussels must recruit as larvae from the plankton. Recovery begins at an average patch age of 26 months; rate of space occupation, primarily due to individual growth, is 2.0-2.5%/month.

Winter birth rates suggest a mean turnover time (rotation period) for mussel beds varying from 8.1-34.7 years, depending on the location. The minimal value is in close agreement with both observed and calculated minimal recovery times.

Projections of total patch area, based on the model, are accurate to within 5% of that observed. Using a method for determining the age of patches, based on a growth curve of the barnacle *Balanus cariosus*, the model permits predictions of the age-size structure of the patch population. The model predicts with excellent resolution the distribution of patch area in relation to time since last disturbance. The most detailed models which include size structure within age categories are inconclusive due to small sample size. Predictions are good for large patches, the major determinants of environmental patterns, but cannot deal adequately with smaller patches because of stochastic effects.

Colonization data are given in relation to patch age, size and intertidal position. We suggest that the reproductive season of certian long-lived, patch-dependent species is moulded by the disturbance regime. The necessary and vital connection between disturbance which generates spatial pattern and species richness in communities open to invasion is discussed.

Pople, A., R.D. Simpson, and S.C. Cairns. 1990.

An incident of Southern Ocean oil pollution: effects of a spillage of diesel fuel on the rocky shore of Maquarie Island (sub-Antactic)

Department of Zoology, University of New England, Armidale, N.S.W., 2351, Austalia.

Aust. J. Mar. Freshwater Res. 41: 603-20.

ABSTRACT

On 3 December 1987, the Australian resupply ship *Nella Dan* ran aground at Macquarie Island, releasing approximately 270 000 L of oil, mostly light marine diesel, into the sea. This represented one of the few spills to have occured in southern hemisphere cold waters. Following the spill, thousands of marine invertebrates were washed up dead on beaches along 2 Km of the shore. Twelve months after the spill, a study was conducted to examine the shore community in 5 zones at 2 oil-affected and 2 control locations three sites were examined within each of these locations. Densities of marine invertebrates appeared to have been markedly reduced in the lower litttoral and sublittoral zones in the vicinity of the wreck In the upper littoral zones, algal cover and invertebrate abundance were similar at oil-affected and control locations. The significance of the oil spill and its long-term effects are disscussed.

Reish, D.J., D. F. Soule and J. D. Soule. 1980.

The benthic biological conditions of Los Angeles-Long Beach Harbors: results of 28 years of investigations and monitoring.

Dept. of Biology, California State University, Long Beach, Long Beach, California, 90720.

Helgolander Meeresunters 34: 193-205.

ABSTRACT

Los Angeles-Long Beach Harbors were a grossly polluted body of water at the time of the initiation of benthic biological studies in 1951. Industrial, domestic and storm wastes were discharged into these waters with little or no treatment. The inner harbor waters contained little or no dissolved oxygen and much of the benthos was azoic or possessed a stressed community. However, the outer harbor water mass contained adequate dissolved oxygen, and the benthos supported a rich fauna dominated by many species of polychaetes. A pollution abatement program was initiated in 1968 and today many former wastes have been eliminated or are being diverted to treatment plants for processing. The benthic fauna changed markedly and rapidly following this environmental clean-up. Peaks in population were reached throughout the harbor in 1973-1974 which was followed by a slight decline then stability. An oil tanker explosion, pre-treatment of fish-cannery wastes then diversion of these wastes to a sewage treatment plant, and a change from primary to secondary treatment of sewage brought about changes in the benthic fauna. In the latter instance, benthic populations of polychaetes, fish populations and the number of birds feeding within the area decreased significantly.

Rolan, R.G. and R. Gallagher. 1991.

Recovery of intertidal biotic communities at Sullom Voe following the *Esso Bernicia* oil spill of 1978.

British Petroleum America, 200 Public Square, Cleveland, Ohio 44114.

Proceedings of the 1991 International Oil Spill Conference, American Petroleum Institute, p461-465.

ABSTRACT

In December 1978, the *Esso Bernicia* spilled 8,000 barrels of Bunker C oil during a berthing accident near Sullom Voe Oil Terminal. About 100 miles of shoreline were oiled, much of that span heavily. Sullom Voe is a bay of the Shetland Islands, north of Scotland, An area environmentally similar to Prince William Sound. The highly indented, rocky shoreline is inhabited by typical intertidal communties characterized by fucoid algae (rockweed), barnacles, and snails. Biological survey data for the interdidal communties had been collected for three years prior to the spill.

During The cleanup, most of the shores that were accessible to heavy equipment were stripped of oily rock, cobble, and gravel. Other fairly accessible areas were hand-cleaned. Dispersants were tried on a few shores, but were ineffective. Many of the less accessible locations were not cleaned at all.

The oiled shorelines were resurveyed every year from 1979 through 1987, except 1982 and 1983. Except for the mechanically cleaned areas, the biological communities in the rocky intertidal zone returned to very near normal within the first year, and have remained so in spite of the presence of traces of weathered oil. Normal populations of snails and small crustaceans have thrived in intimate contact with ashphaltic residues that still remain in some locations. In contrast, the biological communities at the sites that were cleaned mechanically were obliterated, and still had not fully recovered after almost nine years.

Rosenberg, R. 1972

Benthic faunal recovery in a Swedish fjord following the closure of a sulphite pulp mill

Swedish Water and Air Pollution Research Laboratory, Box 4052, S-400 40 Gothenburg, Sweden.

Oikos 23: 92-108.

ABSTRACT

During 1968-70, the recovery of the benthic macrofauna was investigated at 53 stations in Saltkallefjord, an inner branch of Gullmarsfjord on the west coast of Sweden. Physico-chemical analyses have shown that the water quality in Saltkallefjord improved as a result of reduced waste water discharge subsequent to discontinuance of production of sulphite pulp in 1966.

After 1968, the benthic macrofauna has colonized fjord areas which earlier in the 1960's were azoic, or occupied by a poor fauna only. During May-October, 1969, a successive monthly increase of the number of species appeared in these areas. Classification of some species in the succession is subject to discussion.

Rosenberg, R., 1976

Benthic faunal dynamics during succession following pollution abatement in Swedish estuary

Swedish Water and Air Pollution Research Laboratory, Gothenburg

Oikos 27: 414-427

ABSTRACT

The recovery of benthic communities has been studied continuously since the closure of a sulphite pulp mill in 1966. The previous, increasing organic enrichment in the estuary had deteriorated the marine environment and reduced the fauna over large areas. The succession of the macrobenthic communities to a level where the recovery process was indistinguishable from annual fluctuations to that recorded forty years earlier. The successional changes in number of species, individuals and biomass are illustrated for the total fauna as well as for dominating groups. The sequential changes of some numerically dominant populations showed a bell-shaped curve patter. During the first years after pollution abatement, when polychaetes dominated, these population changes were drastic but evened out in later seral stages. The role of larval recruitment in succession is discussed. Three diversity indices were used to assess the community structure: Shannon's formula, its measurement of evenness, and Sanders rarefaction technique. As tools for assessing pollution or recovery, the two former had to be used with care, as the highest values were recorded at the beginning of the recovery process when the individuals found were few but evenly distributed among the few species present. The rarefaction technique and the measure of species richness were more satisfactory for this kind of assessment.

Sanders, H. L. 1978.

Florida oil spill impact on the Buzzards Bay benthic fauna: West Falmouth

Woods Hole Oceanographic Institution, Woods Hole. Mass. 02543, USA.

J. Fish. Res. Board Can. 35: 717-730.

ABSTRACT

No matter what criterion is used to measure the effects of the *Florida* oil spill, the densities and species composition and the array of statistical methods demonstrate that the same hierarchical pattern emerges. Densities and species composition remain stable over time at the minimally oiled and unoiled stations, but display considerable fluctuations and marked changes at the more heavily oiled stations. With simple presence or absence data, highest fidelity is present at the marginally oiled stations, lower fidelity at the intermediately oiled stations, and lowest fidelity at the severely oiled stations. The discrepancy index measures mean yearly differences in faunal composition at each of the stations. Very large and large differences are documented for the severely and intermediately oiled stations but only small differences are found for the marginally oiled stations. The coefficient of variation is a measure of faunal variability throughout the entire sampling period for each of the stations. Faunal variation remains very high at the severely and intermediately oiled stations but low at the marginally oiled sites. Cluster analysis reveals profound temporal changes in the fauna from samples collected at the severely and intermediately oiled stations but demonstrates a much more homogeneous pattern with only small seasonal changes from samples obtained at the marginally oiled stations.

Sanders, H.L., J.F. Grassle, G. 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, Massachusetts.

Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, 02543.

J. Mar. Res. 38: 265-380.

ABSTRACT

To determine carefully the effects on the marine and extuarine benthos of Number 2 fuel oil spilled by the barge FLORIDA off West Falmouth, Massachusetts, we sampled for many months along an onshore-offshore gradient of pollution, and less intensively at unoiled sites. Analyses of hydrocarbons established that pollution was greatest and most persistent in the intertidal and subtidal zones of Wild Harbor River, less severe in degree and duration at stations farthest from shore. A variety of concurrent analyses showed that disturbance of the fauna was most severe and longest lasting at the most heavily oiled sites, and least severe but perceptible at lightly oiled stations. Patterns of disturbance were not related to granulometry of the sediments. Plants, crustaceans, fish, and birds suffered both high mortality immediately after the spill, and physiological and behavioral abnormalities directly related to high concentrations of the fuel oil. Five years after the spill its effects on the biota were still detectable, and partly degraded #2 fuel oil was still present in the sediments in Wild Harbor River and estuary.

Savidge, W.B. and G.L. Taghon. 1988.

Passive and active components of colonization following two types of disturbance on intertidal sandflat

Mark O. Hatfield Marine Science Center, Oregon State University, Newport, Oregon.

J. Exp. Mar. Biol. 115: 137-155

ABSTRACT

Immigration of small benthic invertebrates into two types of disturbed patches, small depressions and patches of azoic sand, was compared. Rates of recolonization differed between patch types, with numerical recovery in depressions occurring more quickly than in defaunated sediments. The results suggest that colonization by most taxa was dominated by passive advection. The effects of both disturbance types on faunal abundances were of short duration.

Shillabeer, N. and J.F. Tapp. 1989.

Improvements in the benthic fauna of the Tees Estuary after a period of reduced pollution loadings.

ICI Brixham Laboratory, Freshwater Quarry, Brixham, Devon TQ5 8BA, UK.

Marine Pollution Bulletin 20: 119-123

ABSTRACT

The Tees Estuary (north east England) has been industrialized since the nineteenth century and used for the disposal of industrial amd domestic waste. Its physical nature has been changed by canalization amd dredging. In 1970 a number of water quality objectives were established by the Northumbrian River Board and local industry, and during the 1970s water quality improved.

Classification analysis identihes three faunal associations within the estuary. The seaward end of the estuary has a typical estuarine fauna, and the middle reaches are dominated by an abundant fauna tolerant of organic pollution. Species diversity and abundance increased between 1979 and 1985 with a penetration of marine fauna into the estuary and increase in abundance in the middle reaches.

Soster, F.M., and P.L. McCall. 1990.

Benthos response to disturbance in western Lake Erie: field experiments

Department of Geology and Geography, DePauw University, Greencastle, IN 46135, USA

Can. J. Fish. Aquat. Sci. 47: 1970-1985

ABSTRACT

Open space (defaunated sediment) was provided on the floor of Lake Erie on 11 occasions during different seasons over a 26-mo period. The benthic community that developed was sampled over time and compared with the nearby undisturbed bottom community. A consistent succession of functional and adaptive types was observed. Early colonizers - the ostracod *Physocypria globula*, the nadid oligochaete *Vejdovskyella intermedia*, and the chironomid, *Chironomus plumosus* - exceeded their natural bottom abundances by 2-7 x within 40 d, but decreased in abundance later. They are small and mobile, live and feed close to the sediment-water interface, and reproduce often. Late colonizers - *Limnodrilus* spp., *llyodrilus templetoni*, and pisidiid bivalves - reached natural abundances only after several months if at all. They are large, deep infaunal dwellers that grow slowly and reproduce late in life. An intermediate group - *Arcteonais lomondi, Specaria josinae, Pristina acuminata, Dero digitata, Procladius* sp., and *Coelotanypus* sp. - reached their natural abundances early but did not exceed them. This successional sequence of functional and adaptive types appears to be a general response by both shallow freshwater sublittoral and shallow marine subtidal macrofauna to space-providing disturbances despite radical taxonomic dissimilarity.

Sousa, W.P. 1979a.

Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity.

Dept of Zoology, University of California, Berkeley, California 94720.

Ecology 60: 1225-1239.

ABSTRACT

The effects of disturbance on local species diversity were investigated in an algal-dominated intertidal boulder field in southern California. In this habitat, the major form of disturbance occurs when waves, generated by winter storms, overturn boulders. These natural physical disturbances open space, interrupt successional sequences, and determine local levels of species diversity. Because small boulders are more frequently overturned than larger ones,.the plants and sessile animals of boulder fields are distributed in a patchwork of successional stages.

Boulders which are subjected to intermediate disturbance frequencies are usually less dominated than those which are very frequently disturbed, and always less dominated than those which are seldom disturbed. In all seasons most small boulders have fewer species than those of intermediate size. Large boulders also usually have fewer species, except in the spring, when defoliation of the algal canopy during the previous winter has opened space for colonization. Species richness on these boulders declines during summer months, and is less than that on boulders of intermediate size in the fall.

Small boulders, with a shorter disturbance interval, support only sparse early successional communities of the green alga, *Ulva*, and barnacles. Large, infrequently disturbed boulders are dominated by the late successional red alga, *Gigartina canaliculata*. Intermediate-sized boulders support the most diverse communities composed of *Ulva,* barnacles, several middle successional species of red algae, and *Gigartina canaliculata.* Comparison of the pattern of succession on experimentally stabilized boulders with that on unstable ones confirms that differences in the frequency of disturbance are reponsible for the above patterns of species composition.

The frequency of disturbance also determines the degree of between-boulder variation in species composition and diversity. Small boulders which are frequently overturned sample the available pool of spores and larvae more often. As a result, a greater number of different species occur as single dominants on these boulders. Boulders with an intermediate probability of being disturbed are most variable in species diversity. Assemblages on these boulders range from being dominated by a single species to being very diverse while most communities on boulders which are frequently or seldom disturbed are strongly dominated.

Observations on the local densities of three species of middle successional red algae over two year-long periods indicate that most of these are variable in time. More local populations went extinct or became newly established on boulders than remained constant in size. These species persist globally in the boulder field mosaic by colonizing recent openings created by disturbances. These results lend support to a nonequilibrium view of community structure and, along with other studies suggest that disturbances which open space are necessary for the maintenance of diversity in most communities of sessile organisms.

Sousa, W.P. 1979b.

Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community

Dept of Zoology, University of California, Berkeley, California 94720.

Ecological Monographs 49: 227-254.

ABSTRACT

Mechanisms of ecological succession were investigated by field experiments in a rocky intertidal algal community in southern California. The study site was an algal-dominated boulder field in the low intertidal zone. The major form of natural disturbance which clears space in this system is the overturning of boulders by wave action. Algal populations recolonize cleared surfaces either through vegetative regrowth of surviving individuals or by recruitment from spores.

Boulders which are experimentally cleared and concrete blocks are colonized within the first month by a mat of the green alga, *Ulva*. In the fall and winter of the first year after clearing, several species of perennial red algae including *Gelidium coulteri, Gigartina leptorhynchos, Rhodoglossum affine*, and *Gigartina canaliculata* colonize the surface. If there is no intervening disturbance, *Gigartina canaliculata* gradually dominates the community holding 60-90% of the cover after a period of 2 to 3 years. If undisturbed, this monoculture persists through vegetative reproduction, resisting invasion by all other species. During succession diversity increases initially as species colonize a bare surface but declines later as one species monopolizes the space.

Several contemporary theories concerning the mechanisms of ecological succession were tested. The early successional alga, *Ulva*, was found to inhibit the recruitment of perennial red algae. This competition for settling space is an important feature of the successional process. *Ulva* is the best competitor for this space; it reproduces throughout the year and quickly becomes established on newly cleared substrates. As long as these early colonists remain healthy and undamaged, they preempt colonization by perennial red algae which have highly seasonal recruitment and slower growth.

Selective grazing on *Ulva* by the crab, *Pachygrapsus crassipes*, breaks this inhibition and accelerates succession to a community of long-lived red algae. Grazing by small molluscs, expecially limpets, has no long-term effect on the successional sequence. Their grazing temporarily enhances the recruitment of the barnacle, *Chthamalus fissus*, by clearing space in the mat of algal sporelings and diatoms which develops on recently denuded rock surfaces.

Where locally abundant, middle successional red algae also slow the invasion and growth of the late successional dominant, *Gigartina canaliculata*. This alga replaces middle successional species because it is less susceptible to damage by desiccation and overgrowth by epiphytes.

The results of this study do not support either the classical facilitation model or the tolerance (competitive) model of ecological succession. Once early colonists secure the available space/light, they resist rather than facilitate the invasion of subsequent colonists. Early colonists are not killed by direct interference competition with late successional species which grow up through their canopy; rather, early colonists can successfully inhibit the recruitment and growth of these species. Successional sequences occur because species which dominate early in a succession are more susceptible to the rigors of the physical environment and to attacks by natural enemies than late successional species. Late species colonize and grow to maturity when early species are killed and space is opened. Only late in a successional sequence, when large clearings become a mosaic of small openings, does direct competition with surrounding adult plants of late successional species contribute to the decline in cover of the remaining early species. Studies of succession in a number of terrestrial and marine communities lend support to this inhibition model.

Sousa, W.P. 1980.

The responses of a community to disturbance: the importance of successional age and species' life histories.

Dept of Zoology, University of California, Berkeley, California 94720.

Oecologia 45: 72-81.

ABSTRACT

The responses of different successional stages of a temperate intertidal algal community to disturbance were investigated with a field experiment. The experiment was conducted in a low intertidal boulder field in southern California. In this habitat, the top surfaces of boulders are covered with algae. The composition of the assemblage on any particular boulder depends on the length of time since it was last overturned by wave action. When a boulder is overturned, the algae on what was formerly the top surface, are killed in whole or part by a combination of sea urchin grazing, anoxia, light levels below compensation intensity, and mechanical damage caused by crushing or abrasion. The length of time that a boulder remains overturned and the local abundance of sea urchins determines the intensity of the disturbance. When the boulder is righted, recolonization begins either by vegetative regrowth of survivors and/or by spores from outside.

Using a three-factorial design, this natural form of disturbance was experimentally mimicked and the responses of three different successional stages of the algal community monitored. Boulders in each successional category were overturned for periods of 17, 27 and 54 days in areas with and without sea urchins, then righted. Two aspects of community response to perturbation were evaluated. These were (1) the assemblage's ability to resist change and (2) its ability, if altered, to adjust to some semblance of its original state. The resistance of each assemblage and of its component species to change was measured by the percent decrease in algal cover and by the decline in percent similarity of the community to its original composition. The recovery rate of each assemblage and of the cover lost by each species during the first 35 days following a disturbance was measured by the rate of increase in percent similarity to the original composition and the percent reestablishment of lost cover.

The experimental evidence demonstrates that the successional stages of the producer level of an intertidal algal community differ significantly in their responses to distrubance. Early successional communities suffer more damage from a given level of perturbation but recover more quickly that either middle or late successional communities. Damage to any particular assemblage of algae, irrespective of successional age, is more extensive and recovery slower, the longer the boulder is overturned and/or sea urchins are present. Several thresholds in these responses were also identified.

Differences in community responses and non-linearities in these responses were attributable to the life history characteristics of the component species rather than emergent properties of the assemblage. These characteristics have evolved in response to a variety of recurrent natural disturbances. This interpretation is in agreement with recent critical reevaluations of the trends and mechanisms of successional change in natural communities.

Sousa, W.P. 1984.

Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession

Dept of Zoology, University of California, Berkeley, California 94720.

Ecology 65: 1918-1935.

ABSTRACT

Localized disturbances transform most assemblages of sessile organisms into mosaics of patches differing in characteristics such as size and age (time since last disturbed). This mosaic nature of natural communities is especially evident on exposed intertidal shores along the northwest coast of North America, where the competitively dominant mussel, *Mytilus californianus*, occupies much of the space at mid-tidal levels. Nearly continuous beds of this species are interrupted by patches of open space generated mainly by the shearing forces of winter storm waves. These patches serve as foci for the recruitment, growth, and reproduction of many competitively inferior, "fugitive" species, including both algae and sessile invertebrates. These species are doomed to local extinction as the lateral encroachment of adult mussels closes the patch and excludes them from the area.

This study examined the dynamics of algal succession within experimental patches cleared in mussel beds. In particular, two potentially important sources of variation in successional dynamics were investigated: (1) the size of the patch when first created, and (2) the location of the patch with respect to potential sources of propagules.

The size of a cleared patch was found to influence strongly the course of algal succession. This effect was largely indirect, resulting from an interaction between patch size and grazing intensity. Small patches support higher densities of grazers, especially limpets, than do large patches. As a consequence the assemblages of algae that develop within small and large patches differ markedly. The assemblage in small patches includes grazer-resistent but apparently competitively inferior species, whereas that in large patches is composed of grazer-vulnerable but competitively superior species. Small patches appear to serve as refuges from competition for grazer-resistent species.

Recruitment was variable among the experimental patches. Percent cover of several species was found to be highly correlated with the cover of epizoic conspecific adults within 1 m of the edge of the patch. This result suggests that a number of the species inhabiting patches within mussel beds may disperse their propagules over relatively short distances. For such species, patch dispersion may influence the regional dynamics of their populations.

Southward, A.J., and E.C. Southward. 1978.

Recolonization of rocky shores in Cornwall after use of toxic dispersants to clean up the *Torrey Canyon* spill.

Marine Biological Association, Citadel Hill, Plymouth, U.K.

J. Fish Res. Board Can. 35: 682-706.

ABSTRACT

Fourteen thousand tons of Kuwait crude oil, reduced from 18,000 tons by weathering at sea, was stranded along 150 km of the coast of West Cornwall, England, in March 1967. The oil was treated with 10,000 tons of toxic dispersants during cleaning operations. By itself the oil was not very toxic, although it killed some limpets and barnacles, and most of the mortalities that followed cleaning were due to the dispersants. There was a graded effect. Most animals and some algae were killed on the shores treated heavily with dispersants, while a few animals and most algae survived in places less heavily treated. However, long stretches of coast were contaminated to some extent by drifting of patches of oil and dispersants along the shore and by indiscriminate dispersant use in remote coves. The general sequence of recolonization was similar to that which has been found after small-scale experiments, where the rocks were scraped clean, or where limpets were removed, but took longer to complete. There was first a rapid "greening" by the alga *Enteromorpha;* then a heavy settlement and growth of perennial brown algae (*Fucus* species), leading to loss of surviving barnacles. A settlement of limpets and other grazing animals followed, with eventual removal or loss of the brown algae. The final phases were a reduction in the limpet population and a resettlement of barnacles. Lightly oiled, wave-beaten rocks that received light dispersant treatment showed the most complete return to normal, taking about 5-8 years; heavily oiled places that received repeated application of dispersants have taken 9-10 years and may not be completely normal yet. Most common species returned within 10 years, but one rare hermit crab is still missing from places directly treated with dispersants. The early recolonization by algae resulted in a raising of the upper limit of *Laminaria digitata* and *Himanthalia elongata* by as much as 2 m in wave-beaten places, demonstrating that grazing pressure by limpets must be one of the factors controlling the zonation of these plants. Later, other species of plants and animals were found higher up the shore than usual, under the shade and shelter provided by the dense canopy of *Fucus*. Fluctuations in the populations of algae and herbivorous animals during the course of the recolonization illustrate the importance of biological interactions in controlling the structure of intertidal communites. Pollution disturbance affects the herbivores more than plants, hence the point of stability of the community is shifted towards the sheltered shore condition of low species richness and greater biomass.

Thomas, M.L.W. 1973.

Effects of Bunker C oil on intertidal and lagoonal biota in Chedabucto Bay, Nova Scotia

Department of Biology, University of New Brunswick, Saint John, N.B.

J. Fish. Res. Board Can. 30: 83-90

ABSTRACT

In February 1970, a large spill of Bunker C oil occurred in Chedabucto Bay, Nova Scotia. The incident was of particular interest since large spills of this type of oil had not previously been studied. Further interest was added by the unusually cold temperatures and by the nonuse of detergents in cleanup. The effects of the oil on intertidal and lagoonal biota have been followed since the accident. Many rocky shores and lagoons were heavily oiled. On exposed shores, oil has decreased steadily since oil stopped coming ashore in mid-1970 and by August 1971 only small amounts remained. In sheltered areas, particularly lagoons, heavy oil contamination remains. The summer remobilisation and subsequent redeposition of oil added a chronic aspect to the pollution. Initial effects of oil involved minor smothering of fauna and tearing loose of algae. Longer term effects involved extensive mortalities of *Fucus spiralis* on rocky shores and *Mya arenaria* and *Spartina alterniflora* in lagoons. Other biota were not visually affected. In all three affected species, mortalities took place either continuously or only in the second year of pollution. Causes of death are unknown. It is recommended that in all intertidal areas very heavy oil deposits should be mechanically removed and the remainder of the oil left to natural degradation.

Thomas, M.L.W. 1977.

Long term biological effects of Bunker C oil in the intertidal zone

Department of Biology, University of New Brunswick, Saint John, New Brunswick, Canada

Proceedings of the Seattle Symposium. 238-246.

ABSTRACT

In February, 1970 a large spill of Bunker C oil occurred in Chedabucto Bay, Nova Scotia, Canada when the tanker "Arrow" grounded. Oil from the tanker has persisted for over six years on rocks and in intertidal sediments on the shores of the bay. During this period mortalities of common species in all major communities on both exposed and sheltered shores have occurred. On rocky shores, the dominant fucoid algae suffered heavy initial mortalities which were more severe at high tidal levels. Recolonization has proceeded from lower to higher levels but has not yet occurred in the high tide zone. Delayed recolonization appears to be related to long term toxicity. In salt-marsh and sheltered lagoonal communities, the dominant grass, salt marsh cord grass, suffered heavy mortality delayed one year from the initial spill, recovery commenced two years later and is proceeding steadily. Soft-shell clams in lagoonal sediments have shown persistent mortalities proportional to oil content of sediments. This pattern appears to be a result of direct toxicity, environmental change caused by oil and sub-lethal metabolic effects.

Thomas, M.L.W. 1978.

Comparison of oiled and unoiled intertidal communities in Chedabucto Bay, Nova Scotia.

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J. Fish Res. Board Can. 35: 707-716.

ABSTRACT

During 1976, detailed surveys of four oiled and four unoiled control stations, each subdivided into seven standardized intertidal levels, were carried out in Chedabucto Bay. Seventy-one species were found, 14 unique to control and 9 to oiled locations. Species diversity was uniformly higher at control than oiled stations. No differences in horizontal zonation of major species were apparent. Analysis of abundance and biomass data for the eight stations and seven tidal levels showed a significant overall difference between oiled and control situations. However, no particular station or tidal level was significantly different from any other. Ten species accounted for most of the variance between oiled and control stations. Six of these were more important at controls and four more important at oiled stations. The flora were particularly affected at oiled stations and species dominant on both sedimentary and rocky shores at all but the lowest tidal levels have been reduced. Length and weight data for the clam *Mya arenaria* showed significantly lower values at oiled stations, but that for the periwinkle *Littorina littorea* showed the opposite. The length-weight relationship for both of these species showed a significantly lower increase in weight per unit of length at oiled than at control stations. Oiled stations showed significantly greater concentrations of oil in biota and sediments than unoiled, where concentrations were essentially at background levels.

VanBlaricom, G.R. 1982.

Experimental analyses of structural regulation in a marine sand community exposed to oceanic swell

Scripps Institution of Oceanography, University of California at San Diego, La Jolla, California 92093.

Ecological Monographs 52: 283-305.

ABSTRACT

The development of general theories concerning the origin and maintenance of community organization in marine sedimentary environments will benefit from studies of similar processes in the widest possible range of habitat types. The roles of predation and disturbance by large epibenthos are thought to be significant in many such habitats, but the bulk of recent experimental confirmation comes from shallow areas protected from oceanic swell. This field experimental study examines relationships among demersal predators, predator-caused local disturbance, infauna, and infaunal food resources in an exposed marine sand habitat at 17 m depth in southern California, USA.

Manipulation of predator densities with exclusion cages, simulation of biological disturbance, and study of dispersal and habitat selection of infauna showed the importance of recurrent local disturbances by the rays *Urolophus halleri* and *Myliobatis californica*, which dig pits to expose prey but clear other infauna in the process. Benthic invertebrate populations show complex but reproducible patterns of reoccupation of disturbed sites. The most striking aspect of these patterns is active selection of recently formed pits by certain species. Ray pits are sites of accumulation for organic material on which most of the infauna feed. Experiments showed that populations which rapidly colonize new ray pits are responding to the concentration of food resources which are otherwise sparsely distributed. Responses of infauna to ray disturbance are correclated with postlarval swimming capability and method of feeding. Early colonists are active nocturnal swimmers that feed on detritus at the sand-water interface. Such features allow efficient exploitation of patchy, ephemeral concentrations of organic matter. Later arrivals are primarily subsurface feeders with limited swimming activity. The relative abundances of infauna are sensitive to seasonal changes in ray disturbance rates. Early pit colonists predominate when disturbance rates are high. The ray disturbance phenomenon produces a persistent mosaic of patches in various stages of infaunal recolonization.

Other experiments showed the importance of predation by sea stars (*Astropecten verrilli*) and speckled sand dabs (*Citharichthys stigmaeus*). Sea stars consume crab larvae soon after they settle to the bottom and begin metamorphosis. During the study, recruitments of two crabs, *Cancer gracilis* and *Portunus xantusii*, were much reduced by sea star predation. A caging experiment indicated that high-density populations of *P. xantusii* have important negative effects on some infaunal populations. Thus, sea star predation on young crabs is important to the maintenance of infaunal community organization. Sand dabs consume infauna, which are flushed into the water column or onto the sand surface by digging rays. This commensal behavior constitutes an important additional source of mortality for populations that are otherwise unavailable as food for sand dabs, which are visual predators.

Vanderhorst, J.R., J.W. Blaylock, P. Wilkinson, M. Wilkinson and G. Fellingham. 1980.

Recovery of Strait of Juan de Fuca intertidal habitat following experimental contamination with oil.

Batelle, Pacific Northwest Laboratories, Marine Research Laboratory, Sequim, Washington 98382.

Report for the Office of Environmental Engineering and Technology, Office of Research and Development, U.S. Environmental Protection Agency, Washington, D.C. 20460.

ABSTRACT

This is a second year interim report on the effects of experimental oiling with Prudhoe Bay crude oil on recovery of intertidal infauna and epi-fauna of the Strait of Juan de Fuca, Washington State. It describes completed studies of the recovery of infauna as recovery rate relates to the experimental oiling, the site of study, tidal height, season of study, and duration of recovery. The report also describes the methods and initial results of studies of the effects from experimental oiling on epifauna colonization of hard substrates.

Full recovery is defined within the experimental framework for infauna as that composition and density of species which had colonized trays of untreated coarse substrate within the 15-month study period. The relevance of this definition is supported by presentation of data on composition and density of infauna at adjacent baseline stations as measured by other investigators. In terms of species composition, nearly full recovery of oiled substrates occurred in 15 months. For individual species densities, as well as overall abundance, however, oiled substrates had recovered only about one-half in 15 months. Total hydrocarbons in treated substrates were reduced from initial concentration by 85 and 97% for fine and coarse sediments, respectively, in 15 months. Based on rate of loss between 3 and 15 months, it is speculated that total hydrocarbons would have reached background levels in 18.5 months. Analyzed saturate compounds appeared to be lost from treated sediments at a rate similar to total oil. Analyzed aromatic compounds exhibited a much more rapid reduction in concentration than did saturate compounds or total oil.

As analyzed experimental variables, the site of study, tidal height, and sediment type, produced significant effects on the density of primary biological species. Overall, there were much higher densities at two feet below Mean Lower Low Water (MLLW) than at MLLW. Overall abundance appeared about equal between sediment types. Although not analyzed statistically, there appeared to be an order of magnitude higher density in the summer-fall experimental period than in the spring-summer experimental period.

The most severe effects from oiling on infauna density, as an expression of recovery, were seen for detritivorous and herbivorous species. The species for which significant effects on recovery were demonstrated were among those identified as having major trophic importance for a variety of bottom feeding fishes by other Strait of Juan de Fuca investigators.

The experimental oil treatment, while perhaps a "worst" case in the sense that the oil was mixed in sediment, was well within the concentration measured in sediments following some actual oil spills.

Zajac, R. and R.B. Whitlatch. 1982a.

Responses of estuarine infauna to disturbance. I. Spatial and temporal variation of initial recolonization

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Mar. Ecol. Prog. Ser. 10: 1-14.

ABSTRACT

Responses to disturbance of estuarine infauna were studied to test the hypothesis that seasonality, the estuarine environmental gradient and sediment composition would significantly affect recolonization. The study was conducted in a small estuary located in southeastern Connecticut, USA, using controlled disturbance experiments and sampling of the ambient infauna. Species composition in experimental plots and ambient sediments usually did not differ, either on a seasonal or areal basis. Numerically dominant species usually included the polychaetes *Streblospio benedicti, Capitella* spp. and *Polydora ligni,* and the oligochaete *Peloscolex gabriellae.* Other species included the polychaetes *Scoloplos fragilis, Hobsonia florida* and *Nereis virens,* the hemichordate *Saccoglossus kowaleski,* and the amphipods *Microdeutopus gryllotalpa* and *Corophium insidiosum.* At times, densities of these species exceeded or were equivalent to dominant species densities in experimental plots. There were usually significant differences in recolonization and ambient population dynamics due to seasonality and estuarine position. The effects of sediment composition on recolonization patterns of the various species were generally not significant. Seasonal trends in ambient and recolonization species densities were similar, with the highest responses to disturbance in the spring and summer. As ambient densities declined during the fall and winter, responses to disturbance did likewise. On an areal basis, the highest responses to disturbance occurred in the middle and upper portions of the estuary. Ambient densities followed a similar pattern, but peak densities in the early spring (May, 1979) were found in the lower portion of the estuary. Based on differences between ambient and recolonization population densities, only 1 species, *Polydora ligni,* exhibited a regular opportunistic response. Other species exhibited opportunistic responses, but in only 1 or 2 mo during the study. It is apparent, therefore, that species responses to disturbance were quite variable and no general pattern of recolonization could be applied to Alewife Cove with respect to seasonality and estuarine position. Due to this variation, and the historical component involved in disturbed habitats, hypotheses correlating species responses to disturbance with life history adaptations may not be generally applicable to estuarine soft-bottom communities.

Zajac, R. and R.B. Whitlatch. 1982b.

Responses of estuarine infauna to disturbance. II. Spatial and temporal variation of succession

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ABSTRACT

Infaunal successional patterns in Alewife Cove, a small estuary in southeastern Connecticut, USA, varied significantly seasonally and along the estuarine environmental gradient. Each study site exhibited different patterns of change in species composition and abundance. However, suites of species found during succession did not differ greatly from those found in ambient sediments. Species which exhibited the most variable population changes during succession were numerically dominant tubiculous polychaetes *(Streblospio benedicti, Capitella* spp., *Polydora ligni,* and an oligochaete *(Peloscolex gabriellae).* Other species which exhibited significant activity were the polychaetes *Scoloplos fragilis, Hobsonia florida and Nereis virens,* the hemichordate *Saccoglossus kowaleski,* and the amphipods *Microdeutopus gryllotalpa* and *Corophium insidiosum.* At certain times, densities of these species exceeded or were equivalent to dominant species densities in ambient sediments and experimental plots. Timing of disturbance greatly influenced succession. Succession after an early spring disturbance was characterized by peak species densities and numbers. Succession following a fall disturbance was abbreviated with few species at low densities, while after a summer disturbance intermediate trends were found. Classification analysis of similarity between ambient and successional community structure indicated that recovery to ambient conditions occurred rapidly in the lower reach (14 to 30 d), while successional changes in the middle and upper basins continued at least until the end of the winter. It is apparent that estuarine succession can be quite variable and that re-establishment of community structure may occur over various time scales with no set seral stages. The physical and biological processes appearing to be important determinants of estuarine succession include (1) timing of disturbance, (2) habitat in which the disturbance takes place, (3) reproductive periodicity of infauna, (4) ambient population dynamics which generate the pool of recolonizers, (5) abiotic and biotic factors (e.g. food and space resources that affect the preceding 4 factors).