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Oil and Planktonic Ecosystems [and Discussion]

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Oil and planktonic ecosystems

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Information about the effects of oil and oil products upon planktonic organisms is much sparser than for nekton or benthos because of the problems of quantitative plankton analysis. The data available derive from three sources: laboratory experiments, studies with enclosed ecosystems and test organisms (e.g. Cepex, phytoplankton cages) and from field observations made in oil-affected areas.

Laboratory experiments have tended to be conducted at unrealistically high hydrocarbon concentrations upon planktonic species that are amenable to laboratory conditions. However, such investigations have shown that the early oil dispersants were very toxic and revealed the great differences between the toxicities of crude oils from various oil fields. Sublethal studies have shown that hydrocarbons, especially the high aromatic fractions, can damage development and alter behaviour and physiology in planktonic organisms. Biochemical investigations have demonstrated both accumulation and depuration of hydrocarbons (including carcinogens) in plankton.

Enclosed ecosystem experiments at low hydrocarbon concentrations (less than 40 ng g^{-1}) have demonstrated stimulation of microflagellates and small zooplankton (tintinnids and rotifers), whereas diatom populations were reduced and large zooplankton little affected. At higher concentrations (*ca.* 100 ng g^{-1}) phytoplankton production was little affected but copepod and predator populations collapsed.

Field studies have revealed no lasting damage to planktonic ecosystems caused by oil. Typically, oil spills are followed by rises in bacterial and yeast numbers (though the latter may be inhibited by oils with high aromatic fractions), temporary falls in zooplankton densities and increases in phytoplankton production. Chronically polluted inshore areas have been little studied; neustonic, arctic and coral reef ecosystems also merit further investigation. Cautious optimism is expressed about the usefulness of enzyme ratio and adenylate charge measurements in future field studies upon plankton.

Introduction

Hydrocarbons are natural not alien materials; the bulk of hydrocarbons, even including polycyclic aromatic carcinogens (King 1977), are produced by living biota and are thus a normal part of the chemical habitat of organisms. Smith (1954) estimated that the yearly hydrocarbon production by marine phytoplankton amounted to some 5 t km^{-2}, while estimates of annual crude oil discharge into the world ocean have ranged from 0.002 to 0.15 t km^{-2} (Chandler 1974; Wilson 1974). Spectacular tanker accidents or wellhead blowouts receive much public attention and undoubtedly cause high local concentrations, but their contribution to total environmental hydrocarbon loading is relatively minor.

It is known that oil may damage seabird populations and the fauna of enclosed inshore areas, but is there any evidence to suggest that planktonic ecosystems may be similarly affected by crude oil discharges? Quantitative studies of plankton populations lasting beyond a few days are extremely difficult (see Dicks 1976; Colebrook 1979), largely because of the three-dimensional mobile nature of the habitat, but also because of factors such as plankton patchiness (Cushing 1953), huge and rapid seasonal changes in species composition and diurnal vertical migrations by many of the zooplankton. There is therefore no possibility at present of using the sort of mathematically sophisticated analysis (e.g. log normal distribution (Gray 1979)) applicable to benthic populations, or of acquiring the detailed knowledge of population dynamics built up about some commercially important fish species.

In consequence, information about the effects of oil on planktonic organisms is much sparser than for larger nektonic or benthic forms and comes from three sources (in ascending order of closeness to natural conditions): laboratory experiments, experience with artificially enclosed ecosystems, and field observations made in chronically polluted areas or in the wake of oil spills.

Laboratory experiments

The results derived from laboratory investigations have contributed the bulk of the literature associated with oil, oil products and planktonic organisms. Laboratory studies with whole plankton samples are, as yet, very difficult. Many of the organisms of such samples are small and delicate, and zooplankton species can exhibit rapid changes in morphological or physiological state and nutritional requirements. In consequence, experiments have tended to be carried out upon easily managed species such as barnacle nauplii, the larger copepod species, fish eggs or pure bacterial or algal cultures. It seems probable that these hardy species do not have representative resistances to oil products. Even with these convenient organisms, experiments have tended to be short-term because of the difficulty of rearing them past events such as moulting, metamorphosis or yolk sac exhaustion. Coupled with this shortness of duration there has also been a common tendency towards the use of unrealistically high hydrocarbon concentrations, typical only of water in intimate contact with oil slicks. This last factor stems partly from the wish of some experimenters to obtain 'positive' results and it would seem desirable that far more studies should be performed in the future at total hydrocarbon concentrations below $1\ \mu g\ g^{-1}$. Laboratory experiments may be subdivided into two broad categories: toxicity tests and sublethal studies.

Toxicity tests

Despite the above disadvantages and the often-criticized crudity of toxicity tests and l.c._{50} values, laboratory experiments upon planktonic organisms have yielded much useful information. At the time of the *Torrey Canyon* incident they poinpointed the very toxic nature of early dispersant agents (Smith 1968) and the problem of oil–dispersant mixtures being more damaging than either of the constituents (see, for example, Lindén 1975; Gyllenberg & Lundqvist 1976; Hsiao *et al.* 1978). Subsequently they have demonstrated that oil and oil fractions may be toxic to freshwater and marine plankton, and that oil with a high aromatic content (especially of naphthalenes) usually has a greater toxicity than oils of a more aliphatic nature (see, for example, Anderson *et al.* 1977). Laboratory tests have also shown that weathered oil is much less toxic than fresh crude because of the evaporative loss of the more damaging volatile fractions (see, for example, Lee *et al.* 1978). Lee & Nicol (1977) showed that coastal zooplankton were more resistant to fuel oil contamination than oceanic zooplankton and that meroplankton tolerate higher concentrations than holopolankton. However, their results were obtained from experiments at rather high concentrations (4 μg g^{-1} total soluble organics and more). Toxicity tests continue to play an important role, for example in the testing of newer generations of less toxic dispersants.

Sublethal studies

Structural and rearing studies upon algal eggs and the meroplanktonic eggs and larvae of fish and invertebrates exposed to oil and oil constituents have shown evidence of sublethal genetic damage and impairment of development, growth and settlement (see, for example, Kühnhold 1977; Johnston 1977; Johns & Pechenik 1980). From an anthropomorphic viewpoint this may be disturbing, but it seems likely that the reduced fitness of such damaged organisms would make their prospects of survival under field conditions poor and their chances of influencing the gene pool of their species virtually negligible. In any case the short duration of many of the experiments showing such damage makes it doubtful whether the observed effects are truly sublethal; they may be the early stages in a drawn-out lethal response. Also, in most studies, concentrations sufficiently high to elicit developmental anomalies would only occur in areas where oily suspensions would probably foul organisms beyond the possibility of self-cleaning anyway. However, it remains possible that genetic or developmental damage too subtle for us to detect in plankton at present may occur at lower oil concentrations, and it is already clear that some organisms are particularly sensitive; Johnston (1977) demonstrated that *Fucus* eggs were damaged by hydrocarbons at only 0.1 μg g^{-1}.

A few studies have demonstrated that the presence of oil affects behaviour in planktonic organisms. Feeding tends to be depressed and food selection altered at hydrocarbon concentrations of around 250 ng g^{-1} hydrocarbons in the copepods *Acartia clausi* and *Acartia tonsa* (Berman & Heinle 1980). Blumer (1969) suggested that oil suppressed mate selection and escape resonses too. Percy (1976) demonstrated that amphipods were repelled by fresh crude oil; these animals are benthic–nektonic, but similar responses might be effective in those zooplankton that have control over their vertical position in the water column. More work in this area would be desirable, but tentatively it would see that the responses so far demonstrated at quite realistic concentrations, if representative, would help to localize oil damage to plankton by keeping 'clean' animals from feeding on or breeding with contaminated organisms.

Largely because of the small size of planktonic organisms, relatively few physiological or biochemical procedures may be easily performed on them. Oil products have been shown to have significant effects upon feeding rates, oxygen uptake and heart rates of zooplankton (see, for example, Anderson *et al.* 1977; Davenport *et al.* 1979) but the natural variability of these functions tends to mean that statistically significant alterations in rate are only induced by hydrocarbon concentrations that are close to lethal limits. Much more realistic studies have been carried out upon phytoplankton by Gordon & Prouse (1973), who worked with whole phytoplankton at low hydrocarbon concentrations (0–300 ng g^{-1}). At levels below 30–50 ng g^{-1} photosynthesis was stimulated, presumably by the presence of micronutrients, while above 50 ng g^{-1} there was progressive inhibition.

Perhaps most useful of all sublethal studies have been the chemical–biochemical investigations that have demonstrated both rapid accumulation and slower but nearly complete depuration of hydrocarbons in freshwater and marine plankton (see, for example, Kauss *et al.* 1973; Lee 1975; Neff *et al.* 1976; Varanishi & Malins 1977) and the metabolism of some aromatics, including carcinogens, by some zooplankton (see figure 1). However, here again there has to be a note of caution about the findings that plankton rid themselves of accumulated oil products fairly quickly; Corner *et al.* (1976) found that naphthalene accumulated from water was depurated quickly and almost completely by the copepod *Calanus helgolandicus* but that naphthalene accumulated from contaminated food (*Biddulphia* cells) was retained for much longer periods as well as being accumulated much more rapidly. In similar vein, Rossi & Anderson (1977) found that gravid female specimens of the polychaete *Neanthes arenaceodentata* retained naphthalenes in the egg lipids until the eggs were released. Although the resultant trochophores lost the naphthalenes very quickly it is clear that responses of different life cycle stages can be quite complex.

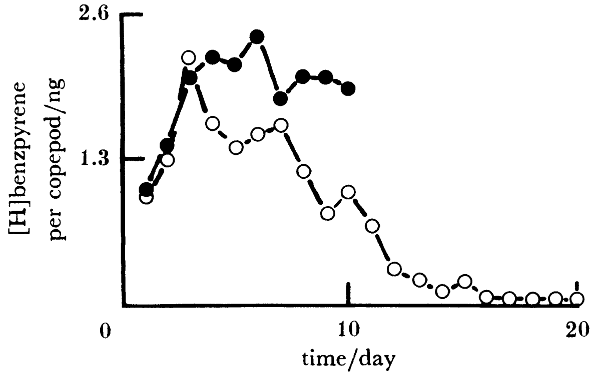

FIGURE 1. Uptake and discharge of benzpyrene by the copepod *Calanus pulchrus*. Solid circles represent animals exposed continually from time zero to [^{3}H]benzpyrene at 1 ng g^{-1} in seawater. Open circles represent copepods initially held in [^{3}H]benzpyrene at 1 ng g^{-1} but transferred after 3 days to clean seawater. (Redrawn from Lee (1975).)

ENCLOSED ECOSYSTEM EXPERIMENTS

At present, monitoring the biology of a moving water mass in the open ocean for any length of time is virtually impossible save at great expense, though it is conceivable that remote sensing by satellite may help to reduce costs in the future. An alternative approach has been to construct containers placed either on land or (perhaps more successfully) floating in the sea but moored in accessible sheltered water (for reviews see Lee *et al.* 1977; Davies & Gamble 1979). These enclosures have to contain self-sustaining ecosystems composed of several trophic levels; some have both benthic and pelagic components (these consist of tubes between seabed and water surface) while others (bags) just have a pelagic phase and a cod end to collect sinking material. Several sizes have been tried; small ones suffer from anomalies caused by the biomass living on the container walls, while large ones risk small-scale plankton patchiness with the attendant problems of sampling and statistical analysis. Enclosed ecosystem studies can also be criticized since diffusional or mixing processes within the containers will differ from those of the open sea because of the absence of wave action. Also, the plankton within the enclosures cannot be affected by outside biotic influences once an experiment has started. Thus there can be no input of meroplankton from the nekton or benthos (except for a limited benthic input in the tube-type enclosures) and the influence of nektonic predators will be absent. Finally, comparisons between the results of different experiments may be difficult because of seasonal changes in plankton composition. Despite these reservations, and the high cost of the construction and maintenance of containers, enclosures have already yielded valuable information about the effects of oil on plankton (they were earlier used in heavy metal studies). Oil exploration and exploitation in northern Canada and Alaska has led to fears about the possible effects of oil spills upon subarctic bodies of fresh water if oil transport pipelines should rupture. Enclosures placed in shallow subarctic lakes have been used with test oil spills to investigate this problem (see, for example, Hellebust *et al.* 1975; Snow & Scott 1975).

The best known of the marine enclosure studies have been the CEPEX (controlled ecosystem pollution experiments) series started in the Saanich Inlet of western Canada in the mid-1970s (Lee & Takahashi 1977; Lee *et al.* 1977). These used the rather toxic and naphthalene-rich no. 2 fuel oil in 60000 litre enclosures. The 1975 experiment was performed at a concentration of about 40 ng g^{-1} of added non-volatile hydrocarbons. This caused an increase in phytoplankton production and changed the plant community structure as well; there was a decrease in the population of the diatom *Ceraulina bergonii*, but a massive increase in the numbers of the microflagellate *Chrysochromulina kappa*. Large zooplankton were aparently unaffected (40 ng g^{-1} is about an order of magnitude below the known toxic levels for them), but small tintinnids and rotifers (which eat *C. kappa*) prospered greatly. Microbial degradation of aliphatic compounds increased rapidly after the addition of oil and so it would appear that microbial plankton numbers increased too. Loss of aromatic materials appeared to be partly caused by adsorption onto sinking particulate material, which would presumably represent a loss to the benthos in 'real' situations, but was also due to metabolism by zooplankton. Earlier experiments had yielded similar results with added non-volatile hydrocarbons at 20 ng g^{-1}, but 10 ng g^{-1} had no discernible effect.

More recent experiments at Loch Ewe in Scotland (Davies *et al.* 1980) have been carried out with a larger enclosure (*ca.* 300000 l) and involved the treatment of the trapped plankton with an initial concentration of 100 ng g^{-1} of hydrocarbons of North Sea oil extract. The results obtained were very different from those presented by the Canadian workers. Over 4–5 weeks, oil concentrations fell to 25 ng g^{-1}. Of this decrease in concentration, 50 ng g^{-1} was apparently lost with particulate material falling out of the water column. The remaining 25 ng g^{-1} was lost by evaporation or biodegradation. There was no evidence of any plant or microbial biomass increase associated with the addition of oil, and there appears to have been no significant effect on primary production or phytoplankton community structure. There was some evidence of enhanced naphthalene breakdown 8–10 days after oil addition, which indicates some increase in the micro-organisms capable of mineralizing naphthalene in the water column, but the most significant change in the make-up of the plankton lay in a marked reduction in the numbers of calanoid copepods. This population depression resulted both from direct hydrocarbon effects on the adults and from the failure of development of nauplii from copepod eggs. This reduction in copepod numbers led to a reduction in the numbers of predators; if repeated in nature this might have implications for fish recruitment though it has to be pointed out that the Loch Ewe experiment was performed at rather high concentrations, which would only be met close to oil slicks.

The experiments performed on enclosed areas of freshwater lakes by Snow & Scott (1975) yielded rather unexpected results. There appeared to be little effect on plankton of oil applied at 0.06 l m^{-2} apart from some indications of a build-up of blue-green algae, and the main deleterious effects were upon periphyton (which virtually disappeared) and upon insects, which were trapped in great numbers by the oil slicks in the first few weeks after the application of oil. Despite the shallowness of the lakes and the relatively large amounts of oil added, there was little sign of the presence of oil after 6–8 weeks. However, this comforting picture is disturbed by the much more detailed study of Federle *et al.* (1979). These workers combined laboratory studies with the investigation over several years of tundra pools which had been deliberately polluted with oil; they found that all zooplankton within a pool could be killed if the oil concentration was sufficiently high ($10\ \mathrm{l\ m^{-2}}$), that the resultant lack of grazing pressure seriously disturbed the phytoplankton community structure and that as much as 6 years elapsed before zooplankton returned and polluted pools began to resemble control ponds.

Two other approaches with enclosed pelagic organisms may be relevant. Pequegnat & Wastler (1980) exposed shellfish and finfish to polluted areas of the sea by holding them in large floating *porous* bags. The results obtained were promising and though technically difficult it might be feasible to duplicate this idea, which exposes test organisms to 'real' pollution, with planktonic enclosures. Secondly, there is the planktonic cage method pioneered by Jensen (1980) at Trondheim, Norway. Enclosed phytoplankton cultures are exposed to water-soluble pollutants in the environment by means of dialysis membranes. This approach has yielded valuable results in fjords polluted by heavy metals and has recently been applied to hydrocarbons; dissolved hydrocarbons do apparently penetrate the cellulose bags employed and have already been shown to retard growth in certain sensitive algae (Jensen, personal communication).

Field studies

The amount of fieldwork carried out on planktonic organisms exposed to hydrocarbon pollutants seems to be inversely related to the public nuisance of the pollution. Major spills have generated moderate amounts of information (though far less than for benthic organisms), whereas minor marine or inland spills have received little attention. Few data have been collected from areas exposed to chronic low level oil input. Particular difficulty in all cases arises in the choice of appropriate control populations. Many chronically affected areas have been exposed to hydrocarbons for decades and no reliable information exists about earlier populations. In the case of acute spills it is often difficult both to identify unaffected areas and to select similar plankton populations for controls.

Chronically affected areas

Baker (1976) reported on the ecological changes that occurred at Milford Haven during 10 years of its development as an oil port. As far as plankton was concerned she relied upon the surveys performed by Dias (1960) and Gabriel (1974) before and after industrialization. Small differences in the structure of plankton populations could be seen, but none could be regarded as representing deterioration or even exceeded likely natural fluctuations.

Hollaway *et al.* (1980) studied autochthonous bacterial plankton populations near an oil platform in the Gulf of Mexico that had been operational for some 18 years. ZoBell (1963) long ago showed that it was unlikely that any marine bacterial population would be injured by oil pollution, but it might have been expected that oil-degrading and sulphur-oxidizing bacteria would be found in the oil-affected area. Although the Buccaneer Field discharges 565 kg hydrocarbons and 15 kg sulphur daily, Hollaway *et al.* found that oil-degrading and sulphur-oxidizing bacteria only made up a small proportion (*ca.* 1 %) of the water column bacterial flora and that slightly heightened populations of these were found only very close (less than 1 km) to the production platform. Otherwise there were no major differences in the taxonomic or physiological make-up of water column bacteria between the oilfield and control ('oil-free') sites. Although this study suggests that low-level oil discharges are innocuous, at least to one component of the plankton, it might be argued that no site in the Gulf of Mexico can be regarded as oil-free and therefore that the controls were faulty. However, it is also worth stressing that neither the bacterial flora around the Buccaneer Field nor that of the control site showed any similarity to that occurring after oil spills (i.e. high densities of both oil-degrading and sulphur-oxidizing bacteria).

In some respects the Mediterranean Sea can be regarded as chronically oil polluted. This is particularly true of the neustonic component of the plankton (0–25 cm from the sea surface), which is exposed to the influence of petroleum aggregates (tar balls). Tar balls (mean diameter 10 mm, but ranging up to 130 mm) now occur in about 75 % of Mediterranean neuston samples and have a residence time of 1–3.5 months, according to Benzhitskiy & Polikarpov (1976). The proportion of samples containing aggregates rose by 6 % between 1971 and 1974 alone, but subsequent oil crises and changes in shipping and refinery practices make it difficult to predict whether that tendency has been sustained. By 1974 the fauna and flora attached to tar balls (e.g. goose barnacles, isopods and blue-green algae) in the Mediterranean were making up 20–30 % of the total neustonic biomass, thereby representing substantial eutrophication of the neustonic environment. It is also true that contamination by petroleum aggregates is the one manifestation of oil pollution that is evident even in mid-oceanic waters (Horn *et al.* 1970).

Acute pollution

Freshwater

Pollution of freshwater lakes and rivers by oil has been little studied; sewage, fertilizers or pesticides, or heavy metal pollutants have assumed more importance. Bunker fuel oil and crankcase oil are perhaps the most likely pollutants. Where spills have occurred, most interest has usually centred on fish rather than plankton. This is true also of chronically affected areas where tainting of fish by oily effluents (e.g. outboard motor discharges) has been regarded as more important than the effects upon organisms at lower trophic levels. McCauley (1966) studied the small Muddy River, Massachusetts, U.S.A., after a bunker oil spill that heavily polluted it (*ca.* 200 μg g^{-1} at the release site). The quantity of oil was sufficient to reduce oxygen tensions in the affected stretch of the stream by a significant amount but this did not kill the plankton. The density of plankton remained unaffected but there was some change in community structure, with some species (the sensitive ones?) disappearing while others (the opportunists?) prospered.

Marine

Although the effects of oil on marine organisms had been studied sporadically for many years, the first internationally coordinated study of the consequences of a large oil spill followed the 1967 *Torrey Canyon* incident. Interpretation of the data collected (see Smith 1968) was complicated by the large quantity (*ca.* 2.8 Ml) of dispersants used to 'clean up' the spill. The dispersants were far more toxic than the crude oil; nauplius larvae of the barnacle *Elminius modestus* survived many hours of exposure to crude oil at 100 μl l^{-1} but were killed in minutes by the same concentration of dispersant. Relatively little attention was paid to field plankton studies, but tow net samples collected beneath thin oil at sea during the emergency revealed apparently normal abundances of healthy copepods. In contrast, at sampling stations where large quantities of dispersants were used, the mortality of pilchard eggs was around 90 %

(cf. 50 % in control areas) and, though diatoms and dinoflagellates appeared normal, there were many dead cysts of *Pterosperma* spp. (Prasinophyceae).

Political or economic considerations mean that large oil spills are almost invariably sprayed with dispersants (though the latter are now far less toxic) which makes allocation of the cause of biological effects difficult. However, in 1977 a small tanker incident occurred in the Swedish archipelago of the northern Baltic Sea (the *Tsesis* spill; see Johansson *et al.* 1980) About 1000 t of oil was spilt, but approximately 700 t was recovered. The remaining 300 t was deliberately left untreated and the effects were monitored for one month. The amount of oil discharged was small, but the affected waters were shallow and sheltered so the situation could be regarded as a reasonable model of a larger oil spill occurring in open deeper water (with the slight reservation that the low salinity of the Baltic is unrepresentative). Close to the wreck the zooplankton biomass declined dramatically in the first few days after the spill. It is not clear whether this decline resulted from direct toxic effects or from avoidance behaviour by the animals. However, within 5 days there was a complete recovery. Oil contamination of individual members of the zooplankton (e.g. rotifers, copepods) was visible for 3 weeks but no change in community structure was noted. Phytoplankton biomass and productivity both increased transiently in the area; this change was probably caused by the absence of grazing zooplankton rather than by any direct stimulatory effect. Peak hydrocarbon concentrations 5 km from the *Tsesis* were around 50–60 ng g^{-1} (this level is above that likely to stimulate phytoplankton growth (Gordon & Prouse 1973); presumably levels closer to the wreck were far higher and probably exceeded the 250 ng g^{-1} level known to suppress feeding in some copepods. The increase in phytoplankton density was accompanied by a rise in bacterial plankton numbers, a feature of all oil spills studied so far.

Not only bacteria benefit from oil spills: planktonic yeast populations usually rise as they thrive upon paraffinic substrates (see, for example, Scheda & Bos 1966). However, in perhaps the best studied of all oil spills, that from the supertanker the *Amoco Cadiz*, yeast populations did not increase. The *Amoco Cadiz* wreck created a very serious oil incident made worse than most others by the high aromatic content of the discharged Iranian crude oil (*ca.* 30 % naphthalenes) and the severe weather, which dispersed oil deep into the water column. Yeast densities were very low (Ahearn & Crow 1980) and experiments showed that aromatic fractions of Iranian crude are inhibitory to them; high aromatic concentrations were recorded from copepods up to 100 km from the wreck (Mackie *et al.* 1978).

The disaster occurred on 16 March 1978, but by early April no differences in terms of zooplankton composition (including fish larvae) could be detected between affected and control offshore (more than 6.4 km from the coast) areas, according to Laubier (1978). However, the inshore 'abers' of the French coast, which are low-energy sheltered areas with a long turnover time, contained virtually no plankton during April. This was perhaps to be expected since oil levels of several micrograms per gram were recorded at the mouths of some abers (Spooner 1978). In Aber Benoît, a small estuary, abundant zooplankton was found 3 weeks after the wreck but there was much dead algal material and many dead animals. Remaining live copepods were obviously in very poor condition and may well have been moribund. Intermediate coastal areas showed intermediate effects; the spring plankton outburst was apparently depressed but no differences in population composition could be detected by June 1978 and it would appear that some replenishment from offshore areas had occurred.

Koster & Van Den Biggelaar (1980) found that development of the tuskshell *Dentalium* *vulgare* at the Roscoff marine laboratory was affected badly in 1978 by the *Amoco Cadiz* spill. Fertilization was poor (only 30%) and abnormal first cleavage was seen in 20% of eggs. Many trochophores were malformed and exhibited a very high mortality, but the surviving larvae appeared normal and the effect upon population dynamics must have been minimal since populations and developmental success returned to 1977 levels in 1979. This picture of rapid recovery is consistent with the data obtained from earlier and perhaps less toxic oil spills. Straughan (1969) monitored barnacles after the Santa Barbara accident and found that they released normal nauplii; release and subsequent cyprid settlement were normal in all affected localities except the badly polluted Santa Barbara harbour. Similarly, George (1970) found that the success of cirratulid polychaete spawning and meroplanktonic development was unaffected by a refinery oil spill in the Solent during 1960. Returning to the *Dentalium* results: it would appear that the damage to tusk shell development caused by the oil resulted not from direct toxic effects (levels at Roscoff in the laboratory sea water supply were no higher than 20 ng g^{-1}), but from the accumulation (less than 1000-fold) of hydrocarbons in the neutral lipids of the oocytes. This accumulation factor was also believed to be responsible for the abortion of lobster eggs reported by Laubier (1978).

Discussion

The information reviewed in this paper strongly suggests that lasting damage to the bulk of the plankton of the open sea is unlikely to be produced by chronic low-level oil input or by most sorts of acute oil spill. Local damage by oil industry accidents may produce short-term local deterioration, but the great volume of the oceanic water masses serves to dilute the hydrocarbon input. Microbial degradation, zooplankton metabolism and physical sedimentation rapidly cleanse the water column, while open water planktonic organisms are so widely distributed that locally damaged ecosystems will be gradually regenerated or replaced by plankton from unaffected areas. During the first few days after a spill it is usual to see an upsurge in microbial and plant biomass (the latter often caused by increased flagellate numbers) later followed by a burst of small zooplankton. These effects are analogous to those occurring in water bodies exposed to sewage pollution, but on a much shorter timescale. There have to be some reservations about this picture, however. Productive inshore benthic communities supply much of the open sea meroplankton (animal eggs and larvae, plant spores). Since oil pollution damage to the benthos appears to last longer than that caused directly to plankton, it may be that subsequent recruitment to the meroplankton is adversely affected. Unfortunately most investigators have concentrated upon holoplanktonic organisms (e.g. copepods and diatoms) in the weeks and months after oil spill incidents and studies of meroplankton numbers and composition in subsequent years are lacking and would probably be statistically very difficult. However, the *Dentalium* results described above support the idea that damage to meroplankton recruitment is unlikely to be important unless the breeding season of the parent organism is very short and happens to coincide with a spill. Even in such an extreme case the localized loss of a year class will rarely be of significance and is the sort of event which may well be induced by natural factors (e.g. harsh winters).

In more two-dimensional or enclosed habitats the potential for damage to planktonic organisms by oil products becomes greater because of the reduced dilution capacity and low-energy nature of the environment. Planktonic ecosystems in such situations (lakes, rivers, enclosed shallow seas, lagoons or estuaries) are exposed to higher concentrations for longer periods and noticeable effects may persist for months (or even years in tundra ponds (Federle *et al.* 1979)) rather than disappearing after a few days as they usually do in the open sea. More insidiously, it seems possible that the presence of healthy plankton in low-energy environments that have been chronically polluted or exposed to a spill may be misleading; the water column may be relatively clean but contaminated sediments may prevent effective settlement or metamorphosis of the dispersive planktonic stages of benthic or nektonic organisms. However, it must be admitted that despite the existence of seriously polluted sheltered bodies of water containing severely damaged benthic communities and which are not expected to recover for decades at best (e.g. the Wild Harbor River estuary, affected by the 1969 *Florida* no. 2 fuel oil spill (Sanders *et al.* 1980)), there has been no evidence of long-term damage sustained by any planktonic ecosystem (except in the smallest of water bodies) reported in the literature. Part of the problem as far as sheltered marine areas or estuaries is concerned lies in the lack of quantitative study of their planktonic communities. Paradoxically there is usually more knowledge about the plankton of seas and oceans, perhaps because of the long-established Continuous Plankton Recorder Survey and the numerous large research vessels operating from many countries, than there is about the theoretically more accessible plankton of lakes, estuaries and lagoons.

One particular, almost two-dimensional, habitat that has received little attention, except perhaps by Russian workers, is that occupied by the neuston, the planktonic organisms living within a few centimetres of the sea surface. The neustonic ecosystem is poorly studied (only a handful of largely taxonomic papers are published each year) despite containing the eggs and larvae of many commercially important fish and crustacean species. Beneath any oil slick the organisms of the neuston (including bacteria, blue-green algae and amoebae) will be in intimate contact with relatively high concentrations of hydrocarbons. Indeed, this may be the one group of planktonic organisms for which laboratory experiments in the microgram per gram total hydrocarbons range are realistic. However, oil spills, even at their worst, occupy exceedingly small proportions of the area of the world's oceans for short periods and the resultant local damage to neuston ought to be rapidly repaired by influx from surrounding unaffected populations. Perhaps more worrying are the possible consequences of eutrophication of the neuston by oil products (e.g. tar balls), at least in enclosed seas associated with oil exploitation (e.g. Red Sea, Arabian Gulf and Mediterranean). Tar balls have undoubtedly caused eutrophication of the Mediterranean neuston and this process was increasing rapidly in the early 1970s. The current situation is impossible to predict, but the assessment of tar ball densities is such a simple procedure that it would seem prudent to monitor their quantities in susceptible areas, particularly since we have no idea of what might constitute a dangerous level of hydrocarbon input in this form. A degree of eutrophication can of course be beneficial to communities, at least from a human viewpoint. Increased productivity of seas exposed to sewage input has been observed, but there is also a case reported in the literature devoted to oil. Thomson *et al.* (1977) reported heightened populations of the commercially important scarlet prawn *Plesiopenaeus edwardsianus* (and presumably their planktonic larvae) associated with a natural benthic oil seep near the Dutch West Indies.

Finally there are two other habitats that may be especially vulnerable to the influence of oil. First there are the polar marine ecosystems, both north and south, which are currently threatened with the possibility of exploitation by the oil industry. Much concern has been expressed over benthic populations that tend not to have dispersive stages, and a major worry is the likely slowness of biochemical depuration and microbial breakdown processes in cold, dark waters (Varanasi & Malins 1977). Field or experimental studies on Arctic plankton in relation to oil are unfortunately virtually absent. Coral reef ecosystems have also been regarded as particularly susceptible to oil pollution, though it can be argued that their subtidal nature and presence in high-energy oceanic areas makes serious damage from oil spills unlikely. However, chronic low-level pollution in more sheltered areas may be more dangerous because there is evidence that the premature release of the planktonic planula larvae of some corals can be induced by hydrocarbon levels that do not otherwise trouble the parent organism (Loya & Rinkevich 1979). The aborted larvae have a much reduced viability, and new colonies of corals are difficult to find in some polluted areas (e.g. the Red Sea near Eilat) even though old colonies appear unaffected.

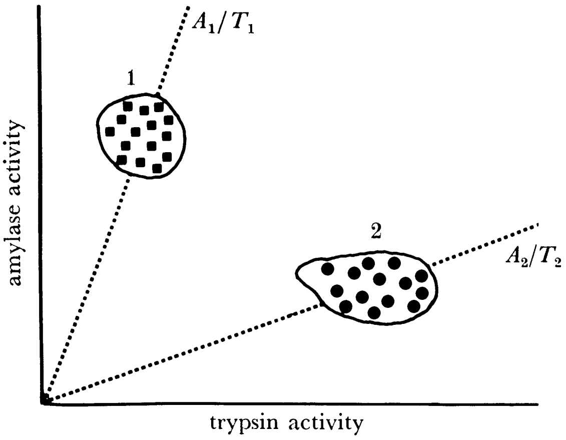

FIGURE 2. Two theoretical populations (or species) with differing feeding preferences. Population 1 (squares) tends towards a herbivorous habit; population 2 (circles) are more carnivorous. (After Samain *et al.* (1980).)

Many of the problems of interpretation of planktonic data stem from the variability and complexity of the planktonic ecosystem in any single area. It is to be hoped that our understanding of plankton ecology will improve to obviate this problem to some extent, but in the mean time a possible alternative approach to assessing the 'health' of plankton appears to lie in the measurement of certain biochemical indices on whole plankton samples. The most promising of these was described by Samain *et al.* (1980). These workers determined amylase and trypsin concentrations and ratios for whole zooplankton samples after the *Amoco Cadiz* incident (see figure 2). Concentrations of amylase and trypsin give information about the physiological state of organisms, while the ratios between the enzyme concentrations give data about the general tendency of a zooplankton population towards a herbivorous, omnivorous or carnivorous diet (Boucher *et al.* 1975), and therefore about trophic relationships. Depressed amylase and trypsin concentrations were found after the *Amoco Cadiz* wreck and this novel type of ecophysiological survey allowed oil-induced disturbances of the zooplankton to be detected for several months in inshore areas (e.g. Aber Benoît).

Another index measurement, as yet unproven on plankton, is the assessment of the adenylate or energy charge of an organism's cells:

$$\text{energy charge} = \frac{[\text{ATP}] + 0.5\,[\text{ADP}]}{[\text{ATP}] + [\text{ADP}] + [\text{AMP}]}.$$

Growth occurs at energy charges above 0.8; viability persists at energy charges above 0.5; death occurs at energy charges below 0.5.

Energy charge measurements were first performed upon bacteria such as *Escherichia coli* (see, for example, Chapman *et al.* 1971), and can now be carried out fairly easily on the freeze-clamped tissues of moderate sized marine animals (e.g. adult molluscs (Ivanovici 1980*a*)). Ivanovici (1980*b*) has suggested that adenylate charge measurements will be useful in future environmental impact studies, but two factors militate against their usefulness with plankton at present. First, from the critique of Atkinson (1977) it would appear that past energy charge measurements have often been of dubious accuracy and that claims about the precision of the techniques used have been rather premature. Secondly, the extremely short life of adenylate compounds means that it is probable that the energy charge of plankton samples would be altered significantly by the stress of handling (e.g. tow net collection). Certainly the values of euphausids obtained by Skjoldal & Bamstedt (1976) appear suspiciously low (0.4 in winter) for supposedly healthy organisms. However, despite these reservations, the concept of an easily measured biochemical index of 'condition' or 'health' in plankton appears to be a goal worth further pursuit.

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Discussion

M. V. ANGEL (*Institute of Oceanographic Sciences, Wormley, Surrey, U.K.*). There are three points that I wish to make. Firstly, tar balls are caught in every neuston net haul taken in the northeast Atlantic. Large tar balls act as settlement sites for goose barnacles (*Lepas* spp.), which will bend over and scrape away at the tar and eat it. Examination of fish stomach contents including myctophids (*Gonichthys cocco* and *Myctophum punctatum*) and sauries (*Scomberesox* sp.) shows that they too eat floating weathered oil.

Secondly, in the open ocean there are well known time–space scale relations. Hence a space scale of 1 km as observed around the Buccaneer platform will represent a response time of only 1 or 2 days. Any longer responses are being rendered indistinguishable from the background variability because of turbulent mixing. In the study of plankton it is important to design the sampling so that a large enough area is covered to recognize the response; also there are real limitations to what we are ever likely to detect.

Thirdly, is there any evidence of oil floating on the surface acting as a neutral density filter that causes significant reduction in primary production? It could be a locally important effect over stratified water columns where there is a subsurface chlorophyll and productivity maximum?

J. Davenport. There is evidence that oil layers on the sea can reduce the transmission of light and also alter its spectral quality (see, for example, Holmes 1969; Garrett 1971; Green 1974). However, although this might theoretically affect primary production, it seems probable that oil concentrations high enough to produce effects on phytoplankton by this means would also have direct inhibitory or toxic effects. Certainly field measurements showing reduced light transmission after spills have been carried out in water columns sufficiently contaminated to smother organisms.

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J. S. Gray (*University of Oslo*, *Department of Marine Biology and Limnology*, *Oslo*, *Norway*). In adding to Dr Davenport's comments on ecosystem manipulation experiments, I believe there is a problem of scaling. In a relatively small area a predator (or herbivore) can crop the whole of the prey (plant) population. This is analogous to rocky shores where starfish control mussel populations or limpets algal populations. Yet in the large areas with known phyto- and zooplankton patchiness and zooplankton vertical migration, complete control of prey or plant density is not possible. The same analogy can apply to the subtidal benthos, where predators rarely control prey density. Thus the conclusion from Cepex and M.E.R.L. type experiments of strong trophic structure in the plankton is not necessarily applicable to open systems. Effects of oil in the sea may not therefore give effects such as those shown in these experiments. I believe it is important to test hypotheses on strong trophic links implying structured food webs against weak links and unstructured webs as this has important consequences on expectations of biomagnification up food webs.

In the same vein I should also mention an unpublished Norwegian experiment on a planktonic system with added oil. It has been shown that oil-degrading bacteria compete with phytoplankton for the available nutrients. Yet the bacteria are grazed by ciliates so the dynamic balance between predators, ciliates and bacteria may be highly important in predicting effects of oil on planktonic systems.

D. J. Crisp, F.R.S. (*Marine Science Laboratories*, *Menai Bridge*, *U.K.*). Dr Davenport emphasized a number of defects in the large-scale and medium-scale ecological experiments. It occurs to me that the wide differences between the results of this type on investigation may also lie in the use of various complex petroleum mixtures of hydrocarbons, which make interpretation unnecessarily difficult. Not only are such mixtures imperfectly defined, but since the various fractions dissolve or volatilize differentially, their activity is changing throughout the experiment. Expressing concentrations as micrograms of oil per gram has little bearing on either chemical or biological activity, which is what the experiment is all about. For a defined substance it has significant meaning.

With accidental spills, one must make the most of the opportunity to examine its effects, notwithstanding that the occasion is messy scientifically as well as ecologically. But in controlled experiments we surely ought to make interpretation and understanding the predominant consideration by using defined substances. Does Dr Davenport know of any such experiments on restricted ecosystems?

J. Davenport. None to my knowledge.

Author's addition. Since the Discussion Meeting it has been brought to my notice that some Cepex-type experiments have been carried out with defined substances (ignoring of course the many experiments in which ^{14}C-labelled defined substances have been added to microcosms already contaminated with oil or oil products for the purposes of measuring degradation rates). Lee & Anderson (1977) studied the fate and effect of naphthalenes in a 68000 l enclosure, but even in that case a mixture of naphthalene and methylated naphthalenes rather than a single defined substance was used, thus still falling into the scientifically 'messy' category mentioned by Professor Crisp. More recently, Hinga *et al.* (1980) have performed what appears to be the only controlled ecosystem experiment that meets Professor Crisp's criterion that investigations should be carried out with single defined substances. These workers used ^{14}C-labelled benz[*a*]anthracene in a microcosm at M.E.R.L. and followed the substance's fate in the water column, sediments and plankton for 230 days. I am grateful to Dr K. J. Whittle and Dr J. M. Davies (Torrey and D.A.F.S. laboratories, Aberdeen, respectively) for bringing this information to my attention.

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