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Pollution-Induced Changes in Populations [and Discussion]

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Pollution-induced changes in populations

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The effects of pollution by organic matter, oil or industrial waste on marine communities are remarkably similar. Diversity values fall, biomass and numbers of organisms initially rise and then fall as the pollution load is increased. Diversity indices are, however, insensitive to pollution-induced changes and have to be assessed subjectively. Departure from a log-normal distribution of individuals among species offers a sensitive and objective method of assessing perturbation effects on communities.

Under severe pollution stress, the dominant species are those which have a flexible life-history ranging from direct development to a planktonic larva and the ability to undergo short-term genetic selection. Species having a somewhat less flexible life-history strategy show increased abundance under conditions of slight pollution. The increase in abundance of seven or eight neither rare nor common species, which gives the departure from a log-normal distribution, is suggested as being the most significant and the earliest detectable change caused by pollution in a community. Thus the presence of a species in a polluted area may be more a question of life-history strategy than the tolerance of adverse environmental conditions. If this hypothesis is correct, considerable doubt must be placed on the ecological relevance of data from toxicity tests.

Introduction

The catastrophic effects of oil spills on marine populations and communities (*Torrey Canyon* (Smith 1970); Santa Barbara (Straughan 1971); West Falmouth (Sanders, Grassle & Hampson 1972)) are well documented, as are the effects produced by large inputs of organic matter such as sewage (Oslo fjord (Beyer 1968); Kiel Bay (Anger 1975); Marseilles (Bellan & Bellan-Santini 1972)) or paper-mill waste (Pearson 1975; Rosenberg 1972, 1973; Pearson & Rosenberg 1978). Surprisingly there are remarkably few data available in the official scientific literature on the effects of heavy industries on populations. Presumably the bulk of this information lies in confidential company files.

The most dramatic effects of pollutants on populations are, of course, a total elimination of all species from an area. Clearly no scientific competance is needed to assess such situations. However, detection of subtle effects leading to a gradual decline of a community requires a great deal of experience and detailed study. As a recent I.C.E.S. working party reported, 'The major problem of population/community monitoring, bearing in mind the non-specific nature of the response to pollutants, is to distinguish pollution induced changes from those due to other causes'. While the above problem is discussed fully in another paper (Cushing, this symposium), it also has relevance here.

Rather than attempt a comprehensive review, I shall use a limited number of thorough studies to extract some principles relating to effects of pollutants on marine populations. Since plankton and fisheries are dealt with in other papers, this study will be confined to benthic fauna. Most of the organisms considered are relatively sedentary and are much used in pollution studies since such organisms remain *in situ* and must therefore reflect the effects of pollution operating over long time periods.

CHANGES IN NUMBERS

Figure 1 shows data from sewage input (50×10^3 m^3 d^{-1}) into sand communities in Kiel Bay (Anger 1975). Moving from the unpolluted area (2000 m from outfall), effects are not observed until closer than 700 m. The community is enriched between 700 and 250 m of the outfall, giving a large increase in numbers of biomass, but within 200 m numbers and biomass are reduced.

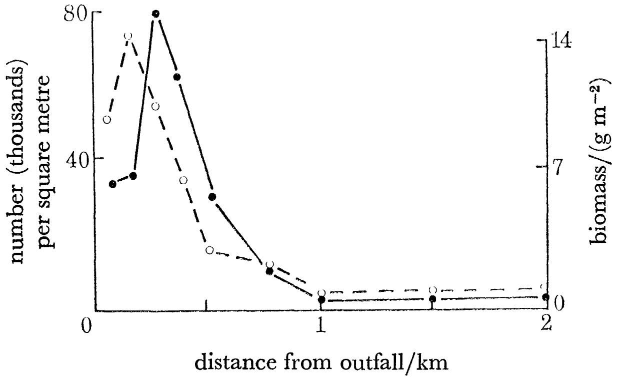

FIGURE 1. Effects of sewage on benthic fauna of Kiel Bay (data from Anger 1975). •, Numbers; o, biomass.

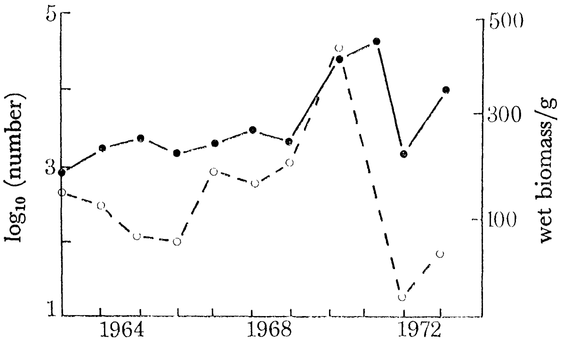

FIGURE 2. Effects of paper mill waste on benthic fauna of Loch Eil, Scotland (data from Pearson 1975). Pollution began in 1966. •, Numbers; o, biomass.

In Loch Eil, Scotland, Pearson (1975) has studied the benthic fauna from 1963, 3 years before a pulp mill came into operation, and followed changes in populations for a further 7 years. Figure 2 shows that significant increases in numbers and biomass were first evident in 1969, 3 years after discharge began. The addition of organic matter waste led to extremely high numbers and biomass, followed by a precipitous crash in 1972.

By a remarkable coincidence, in 1966, the year that the Scottish pulp mill started operations, at Saltkällefjord in Sweden the mill there stopped operating. Rosenberg (1972, 1973) followed the recovery stages of the benthic fauna and found the almost exact inverse of the decline found by Pearson in Scotland. Figure 3 shows the changes in numbers of individuals at the two areas. Thus, with large increases in organic matter both numbers and biomass show a rapid rise followed by a precipitous fall. The process is, however, reversible and with abatement of the organic matter the reverse trend occurs. Such spectacular changes did, however, only occur within a few hundred metres of the Kiel Bay outfall or only after three years of continuous discharge into Loch Eil and thus represent end-points in the decline of the communities. A key question is, therefore, could changes be detected at earlier points in a decline, for example by changes in community structure?

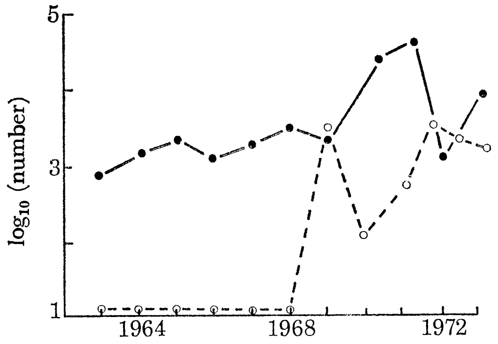

FIGURE 3. Comparison of Pearson's Scottish data (•) with recovery of benthic fauna in Saltkällefjord, Sweden (○) (data from Rosenberg 1972, 1973). Recovery began in 1966 on closure of the Swedish mill.

CHANGES IN COMMUNITY STRUCTURE

One of the major goals of pollution-orientated ecological surveys has been to try to find simple methods whereby the initial stages in the decline of a community can be measured. Many workers and in particular regulatory authorities have sought solace in the use of a simple index of community wellbeing. Diversity indices, which integrate the number of individuals per species and the number of species, have often been used. The theoretical background to such indices is, however, tenuous and based on the argument that diversity increases with time and that a highly diverse community is also highly stable (Margalef 1968; Odum 1969). It has been shown recently that diversity characteristically falls during the last stages of succession (Caswell 1976) and that there is no clear relation between diversity and stability (May 1975). Highly diverse communities may in fact be more susceptible to pollution than less diverse communities.

Of the many indices and methods available, the Shannon–Wiener index (Shannon & Weaver 1963) is probably the most widely used. In this index, species diversity

$$H = \sum_{i=1}^{s} p_i \log_2 p_i,$$

where $p_i = n_i/N$, n_i is the number of individuals of the ith species, N the total number of individuals and s the total number of species. An additional measure should also be calculated, that of evenness $J = H/H_{\max}$, where $H_{\max} = \log_2 s$ (Pielou 1966). Evenness is the inverse of dominance, so to estimate dominance I have used $(1-J)$ since J lies between 0 and 1.

Figure 4 shows diversity (H) and dominance values $(1-J)$, for the Kiel Bay data. Diversity reaches its maximum value at 700 m and changes little up to 2000 m; dominance which was almost 1, reaches a stable level of 0.4 at 200 m. Clearly diversity and dominance are inversely related. Thus pollution changes community structure in Kiel Bay only to a distance of 700 m from the outfall.

Figure 5 shows the changes in diversity and dominance for the Loch Eil station (from Pearson 1975). Diversity fell from the start of the survey in 1963 to 1973 and evenness rose. Figure 6 shows that the recovery of the Saltkällefjord in Sweden was the inverse of the fall in diversity at Loch Eil (Pearson & Rosenberg 1976). Thus, diversity falls with increasing pollution, and dominance increases, but it is hard to identify when the effect of pollution begins. In Loch Eil, diversity fell from 1963 to 1966, during which time there was no pollution, and thereafter showed a similar trend. Certainly number and biomass had increased dramatically by 1969, but the fall in the Shannon–Wiener index is difficult to interpret. Data from the river Tees (Gray 1976*b*) showed great variability in the Shannon–Wiener index within 1 km^2 of a relatively homogeneous mud flat (mean 1.08, range 0.06–2.25). Similar spatial variability in the diversity index can be found in surveys around the Ekofiskoil platform in the North Sea (Dicks 1976). Basedon these and other data, Gray (1976) said that in his experience a significant reduction in the mean diversity from marine benthic communities was equivalent to losing half the species. Under these circumstances, changes in the Shannon-Wiener index are insensitive as a measurement of changes in community structure.

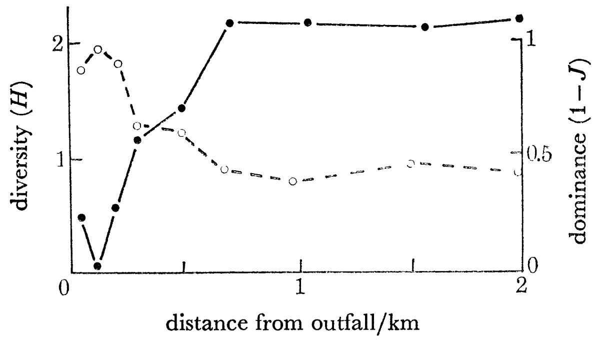

FIGURE 4. Effect of sewage on the diversity (•) and dominance (o) of benthic fauna in Kiel Bay (data from Anger 1975).

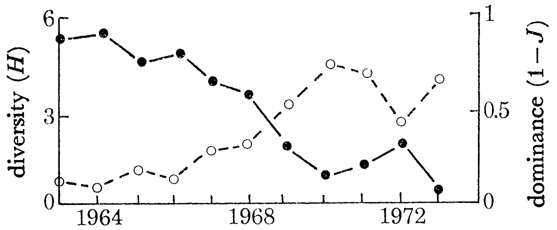

FIGURE 5. Effect of pulp mill waste on the diversity (•) and dominance (o) of benthic fauna of Loch Eil (data from Pearson 1975).

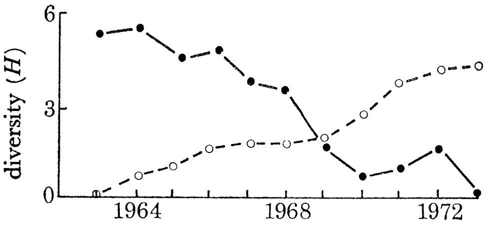

FIGURE 6. Comparison of effects on diversity of increased pollution in Scotland (•) (data from Pearson 1975) with recovery after cessation of pollution in Saltkällefjord, Sweden (o) (data from Rosenberg 1973).

Pearson (1975) used a graphical method of showing changes in diversity, the rarefaction method of Sanders (1968). Figure 7 shows these data from Loch Eil. Between 1966, when pollution began, and 1972 there was a clear change, but when did effects first begin? Thus the rarefaction method also seems insensitive to changes in community structure.

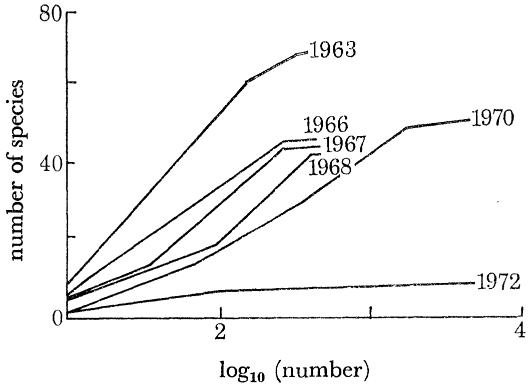

Figure 7. Rarefaction diversity curves from benthos of Loch Eil after pollution beginning in 1966 (data from Pearson 1975).

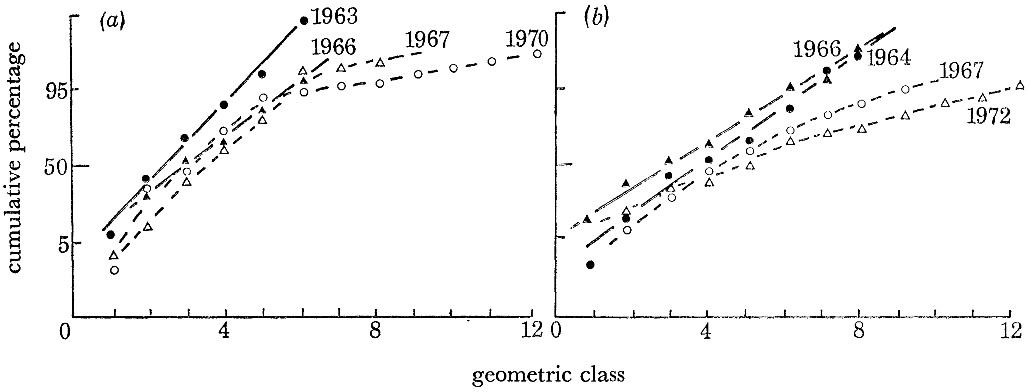

Figure 8. Log-normal plots of individuals per species before pollution (solid symbols) and after pollution (open symbols). (a) Loch Eil, station 2; (b) Loch Eil, station 34 (data from Pearson 1975).

Whenever a large sample is taken from a community the distribution of individuals among the species nearly always tends to give a log-normal distribution (May 1975). The log-normal results from the fact that populations tend to increase geometrically rather than arithmetically and that, following the central limit theorem, the interaction of many independent factors will act multiplicatively. Thus the log-normal distribution can be expected to give an adequate statistical description of any large sample. Gray (1978) has found that this indeed holds for a number of benthic communities.

Plots of cumulative percentage species on probability paper against species grouped in geometric classes gives a straight line if the distribution is log-normal (Bliss 1966). Departure from the log-normal can be tested statistically, whereas the Shannon–Wiener index has no expected distribution and cannot be tested. Pearson's data showed that from 1963 to 1966 the distribution was log-normal. From 1967 the plots diverged significantly from the expected pattern (figure 8a). Even at station 34, where Pearson found it difficult to detect clear effects, there was already in 1967 a departure from the log-normal distribution (figure 8b). Figure 9 illustrates the reverse trend for plots of the recovery stages of Saltkällefjord. Initially (1969, 1970), the data do not follow the log-normal expectation but by 1974 a 'normal' community has been produced.

Simple plots of the log-normal distribution do, therefore, seem to be sensitive to changes in community structure brought about by pollution, provided that the sample sizes are large and represent a heterogeneous species assemblage. Changes in the log-normal expectation cannot, however, categorically be related to effects of pollution since any environmental disturbance can alter the equilibrium community structure. The method utilizes changes in dominance patterns and is not based on species identity. Closer scrutiny of the changes in the log-normal plots brought about by pollution stress in the Scottish data shows that the significant changes are in the increased abundance of the 'middle-order' species, the neither rare nor common species (figure 8), in geometric classes 5, 6, 7 and 8, i.e. between 17 and 216 individuals per species.

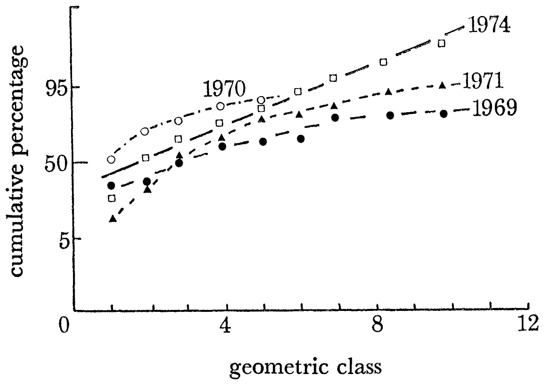

FIGURE 9. Log-normal plots of individuals per species during recovery from pollution in Saltkällefjord, Sweden (data from Rosenberg 1973).

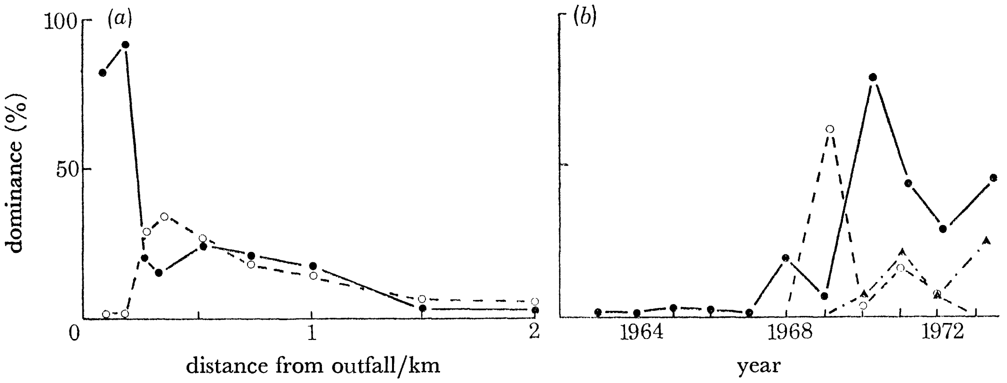

FIGURE 10. Species present in polluted areas. (a) Kiel Bay: ●, *Capitella capitata*; ○, *Pygospio elegans* (data from Anger 1975). (b) Loch Eil: ●, *Capitella capitata*; ○, *Peloscolex benendeni*; ▲, *Scolecolepis fuliginosus* (data from Pearson 1975).

CHANGES IN SPECIES COMPOSITION UNDER HEAVY POLLUTION

In the communities in Kiel Bay (figure 10*a*) and in Loch Eil (figure 10*b*) there is an extreme dominance of *Capitella capitata*. In Loch Eil the co-dominant with *C. capitata* was *Scolecolepis fuliginosus*. At less polluted levels in Kiel Bay, the dominant species was *Pygospio elegans*, whereas at Loch Eil it was *Peloscolex benendeni*. The changes in species during the recovery of Saltkällefjord paralleled the decline in the Loch Eil fauna and in 1969–70 both communities were dominated by *Capitella* and *Scolecolepis* (Pearson & Rosenberg 1978).

The river Tees estuary in England receives large amounts of mixed industrial wastes and is arguably Britain's most polluted estuary. The polychaetes *Capitella capitata*, *Polydora ciliata*, the oligochaetes *Peloscolex benendeni*, *Paranais littoralis*, the gastropod *Hydrobia ulvae* and the amphipod *Corophium volutator*, are extremely abundant in the mud flats at Seal Sands, within the estuary (Gray 1976*b*).

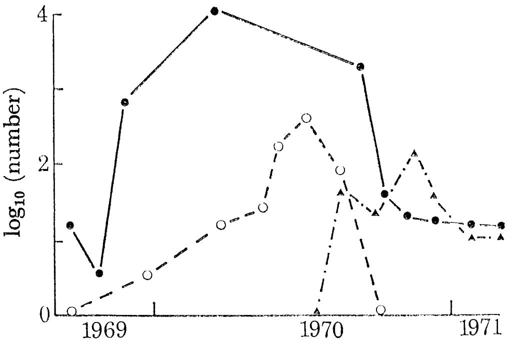

FIGURE 11. Species abundances in recovery stages after an oil spill in Massachusetts, U.S.A. ●, *Capitella*; ○, *Polydora*; ▲, *Prionospio* (data from Sanders *et al.* 1972).

TABLE 1. 'MIDDLE ORDER' SPECIES THAT INCREASE IN ABUNDANCE UNDER SLIGHT POLLUTION (FROM PEARSON 1975)

(Figures given are total numbers; see text for further explanation.)

	total numbers			
	station 2		station 34	
species	1966	1967	1966	1967
Polychaeta				
Cirratulus cirratus	7	30	66	181
Pholoe minuta	17	35	17	75
Prionospio cirrifera	40	290	63	349
Bivalvia				
Corbula gibba	20	35	2	23
Lucinoma borealis	11	38	22	58
Thyasira flexuosa	96	441	137	439
Echinodermata				
Labidoplax buski	193	226	173	600

Following a major spill of number 2 fuel oil at West Falmouth, U.S.A., a thorough study of population changes was made by Sanders *et al.* (1972). At their station VI the number of species fell from an average of 12–16 species per hundred individuals to 1 after the spill. Figure 11 shows the recovery stages. Initially *Capitella* increased dramatically and was followed by *Polydora ligni* and *Prionospio*. By placing azoic sediment in unpolluted areas, Grassle & Grassle (1974) were able to produce a similar colonization sequence to that shown in figure 11. They concluded that *Capitella* and *Polydora* are highly opportunistic, having high rates of increase, high mortality and high population size in the absence of competitors. Later in the successional phase, both *Capitella* and *Polydora* were displaced by other colonists, among which *Nereis succinea* and *Streblospio benedicti* were common.

It was shown earlier that under slight pollution due to organic matter the abundance of 'middle-order' species increased. Table 1 shows the numerical changes that occurred in Loch Eil (Pearson 1975) at two stations after one year of pollution. While the increase in abundance of a single species may not in itself be significant, the changes in all of these species lead to a departure from the log-normal distribution.

EFFECTS OF POLLUTION ON POPULATIONS AND COMMUNITIES

The effects of environmental factors acting on populations can be separated into two categories: first, physical disturbance whereby individuals are partly or totally destroyed (e.g. by storms, smothering, freezing, etc.) and secondly, stress where the productivity of the individual is reduced (e.g. by low salinity, low food concentration, desiccation, etc.). The effects of pollution can be separated similarly. Table 2 shows the adaptive strategies to pollution, based on the model proposed for plants by Grime (1977). K- and r-selection as adaptive strategies are well known (MacArthur & Wilson 1967; Pianka 1974); tolerance is suggested as a third strategy.

TABLE 2. ADAPTIVE STRATEGIES TO POLLUTION (ADAPTED FROM GRIME 1977)

	low stress	high stress
low disturbance	competitive (K)	tolerance (T)
high disturbance	reproductive (r)	none viable

It is commonly assumed that tolerance is the most widely adopted strategy to pollution stress. Surprisingly, the species that dominates under the heaviest pollution load, *C. capitata*, is not unusually tolerant of pollutants. Reish (1971) found that *Neanthes arenacedentata* and *Dorvillea articulata*, and Henricksson (1969) that *Nereis diversicolor* and *Scoloplos armiger*, were all more tolerant of low oxygen than *C. capitata*. *C. capitata* is not particularly tolerant of detergents (Bellan, Reish & Foret 1972) and is more sensitive to high concentrations of oil than *Nereis succinea* (Sanders *et al.* 1972). Little is known of the tolerance of the other species dominating under high pollution stress, but I believe that other factors will be found to be more important than tolerance.

Organic matter pollution can be regarded as primarily having a disturbing effect: suspension feeders are often eliminated by smothering (Rosenberg & Pearson 1978). Similarly, Grassle & Grassle (1974) regarded an oil spill as having a disturbing effect and that prediction of the species recolonizing areas depended on the degree of disturbance. The adaptive strategy to high disturbance is to have a high r value. *Capitella* and *Polydora* are highly opportunistic (Grassle & Grassle 1974), as assessed by their ability to find new areas, their rapid increase in numbers, large population size, early maturation and high mortality.

Species which have a direct development will have a greater ability to increase rapidly in an unexploited environment compared with species having planktonic larvae, yet the ability to colonize newly available substrata will be greater in species with a planktonic larvae. Thus, the best strategy for an opportunist species would be to find new areas by means of planktonic larvae and thereafter produce benthic larvae. Individuals of such a subpopulation will then be able to undergo rapid short-term selection for the genotype favouring benthic larvae, and achieve a rapid exploitation of the habitat. Clearly at maximal population densities, when mortality starts to increase rapidly, it will be advantageous to produce planktonic larvae again, thus ensuring the ability to colonize unexploited habitats. Thus the short-term selection is reversed to produce individuals having a high degree of polymorphism at low population densities. *Capitella* produces both planktonic larvae and benthic larvae and thus has the 'ideal' flexible life-history strategy to adapt to high disturbance. *Capitella* individuals settling immediately after an oil spill (Grassle & Grassle 1974) were highly polymorphic for malate dehydrogenase loci. As the population increased, individuals became increasingly monomorphic up to the maximal population density (30000 m^{-2}), but returned to a polymorphic state after high mortality, thus convincingly demonstrating short-term genetic selection.

Polydora ciliata (= *P. ligni* Rasmussen 1973) also has, like *C. capitata*, the ability to brood eggs within the adult tube or to produce larvae that live in the plankton for up to six weeks (Dorsett 1961). How short is the planktonic phase is, however, unknown. In the polluted Oslo fjord, Schram (1970) found not only that the larvae of *P. ciliata* were more abundant in the more polluted regions, but also that the larvae were available throughout the year in the most polluted areas. At the relatively unpolluted Drøbak station, few larvae were found except in June and July. The increased abundance of larvae in the polluted areas probably reflects the greater amount of food available here. In *C. capitata* the number of eggs produced is directly related to the amount of food available (Warren 1976). The variation in the seasonal availability of the larvae along the pollution gradient may reflect different temporal adaptations of subpopulations, as was found in *C. capitata* populations studied by Grassle & Grassle (1977).

Similarly, *Streblospio benedicti*, which occurred early in the succession following an oil spill (figure 11), has a variable type of development and can both brood eggs and have a larval period in the plankton from 4 days to 2 weeks (Dean 1965). *Scolecolepis fuliginosus* has large eggs and a long-lived planktonic larva. It is probable that this species is merely tolerant of polluted conditions rather than having any special life-history adaptation.

Two other species are frequently found in highly polluted areas: the polychaete *Heteromastus filiformis* (Bellan 1967; Leppakoski 1975; Wolff 1973 (in Europe); Holland *et al.* 1973; O'Connor 1972; Shorey 1973; Swartz 1972 (in the U.S.)) and the oligochaete *Peloscolex benendeni* (Anger 1975; Pearson 1975; Gray 1976; Smyth 1968; Stirn *et al.* 1975; Pearson & Rosenberg 1978 (review)). Not only are these species characteristic of highly polluted areas, but they are also among the first to colonize areas after an environmental disturbance such as a red tide (Simon & Dauer 1977), a new fish pond (Hanks 1968) or a tropical storm (Boesch, Diaz & Virnstein 1976). *H. filiformis* has lecithotrophic larvae and *P. benendeni* has direct development.

The ability to brood is a common attribute of the species found in highly polluted areas. Under the most severe pollution stress, the species present are also able to produce planktonic larvae at high population densities. Grassle & Grassle (1977), however, discovered from detailed electrophoretic studies of six enzyme systems that the *C. capitata* described in the 1974 experiments was in fact a group of at least six sibling species, among which crosses were infertile. Reexamination of the 1974 data showed that there was a successional sequence of species. Immediately after the oil spill (in November 1969) the population was composed entirely of a species with larvae that spend only a few hours in the plankton (species I). In April 1971, 46% of the population were of a species that had only benthic larvae (species III). Grassle & Grassle suggest that species III was prevented from colonizing the substrate by species I. Other members of the *Capitella* species complex had planktonic larvae that lived for several days to two weeks in the plankton. The breeding seasons of the species also varied: two species had very short breeding seasons but two (including species I) bred throughout the year. All the species could nevertheless be considered as opportunistic, and especially species I, which had the largest rate of increase, largest population size and highest mortality yet limited dispersion ability.

The taxonomic position of *P. ciliata* is also rather uncertain. Samples of a population of supposed *P. ciliata* taken on the coast of Yorkshire were sent to three polychaete specialists and each gave a different specific name! Thus it seems likely that, like *C. capitata*, *P. ciliata* is probably a species complex. The Oslo fjord data may indicate that spatial interpopulation adaptation has also occurred in this species. Both *Heteromastus filiformis* and *Peloscolex benendeni* are probably species complexes. *Streblospio benedicti* is common in polluted areas in the U.S. and *S. shrubsolii* occupies similar habitats in Europe. Further study may reveal that this genus too is a complex of species. The remaining species, *Scolecolepis fuliginosus*, occurring in highly polluted areas is not thought to be a complex and it has already been suggested that this species may be merely a tolerant species with no life-history adaptation.

Grassle & Grassle (1977) suggest that in opportunistic species 'the taxonomic unit that survives through evolutionary time may be a metaspecies in which species are continuously becoming extinct and being formed'. *P. ciliata*, *H. filiformis* and *P. benendeni* are probably similar to *C. capitata* in this respect. Åkesson (1973) has documented major differences in life-history strategies in sibling species of the dorvilleid polychaete genus *Ophryotrocha*. *Ophryotrocha* is typically present in highly organic (polluted) areas such as harbours.

In the highly polluted Tees estuary, a comparison of surveys done in 1935 (Alexander *et al.*) with others done in 1971 and 1973 (Gray 1976*b*) shows that there has been a dramatic reduction in the species of bivalves and polychaetes. *Scrobicularia plana* (da Costa), *Tellina tenuis* da Costa, *Venerupis pullastra* (Montagu), *Cerastoderma edule* (L.) and *Mya arenaria*, together with the polychaetes *Nereis virens* Sars, *N. pelagica* L., *Audounina tentaculata* (Montagu) and *A. johnstoni* Malmgren, are now absent. Undoubtedly reclamation of intertidal sediments and the resultant changes in hydrography have altered the environmental conditions for some of the above and their absence cannot be related exclusively to industrial discharges. All of the above species, however, have long-lived planktonic larvae whereas the species which were abundant in 1973 were brooders (*P. ciliata*, *C. capitata*, *P. benendeni*).

Adaptation to disturbance, from the examples quoted, is primarily by brooding which allows for short-term selection within a 'metaspecies'; such selection gives spatial and temporal adaptation of individuals within subpopulations.

After a disturbance of short duration (oil spill (Grassle & Grassle 1976), red tide (Simon & Dauer 1977) or excavation (Eagle & Rees 1973)), the initial dominants, *C. capitata* and *P. ciliata*, are displaced by later colonists (*K*-strategists) and the former species return to their normal low densities. With continuous disturbance, such as a permanent discharge of organic matter, *C. capitata* and *P. ciliata* dominate permanently since they are the species best adapted for such conditions. The continued presence of *C. capitata* can, therefore, indicate organically enriched sediments. However, the use of this species as a universal indicator of such pollution (Filice 1955; Reish 1960) seems unnecessary, since the pollution is usually more obvious than the presence of *Capitella*!

Leppakoski (1975), in a summary of data from the effects of organic matter on the benthic fauna in Sweden and in the Baltic, lists a number of 'progressive' species which show increased abundance under slight pollution, and Pearson & Rosenberg in their extensive review (1978) add to this list. Table 3 shows a summary of the species that are common in these lists and gives some of their characteristics. *Pygospio elegans* has a flexible life history and brooding is favoured by most species, whereas in unpolluted areas brooding is a relatively rare life-history strategy.

TABLE 3. LIFE-HISTORY STRATEGIES OF SPECIES THAT INCREASE IN ABUNDANCE UNDER SLIGHT POLLUTION

benthic larvae		pelagic larvae
	Polychaeta	
Cirratulus cirratus		*Nereis succinea*
Nereis diversicolor		*Pectinaria koreni*
Scolplos armiger		*Pholoe minuta*
Protodorvillea kefersteini		*Prionospio cirrifera*
Pygospio elegans		*Pygospio elegans*
	Gastropoda	
Hydrobia ulvae		
	Bivalvia	
Montacuta ferruginosa		*Corbula gibba*
Nucula tenuis		*Mya arenaria*
Thyasira flexuosa		
	Lucinoma borealis?	
	Echinodermata	
		Amphiura chiajei
		A. filiformis
	Labidoplax buski?	

Under slight pollution, individuals may be eliminated either by a direct toxic effect or as a result of reduced competitive ability or reduced avoidance of predators. Species which can utilize the vacant niches will increase in abundance. While brooding species will clearly be able to exploit such situations rapidly, species with larvae available to colonize will also be at an advantage. Thus either strategy can be successful, but as the disturbance increases brooding species will be at a selective advantage.

Adaptation to stress pollution (T (tolerance) strategy) in populations is harder to document. Individuals of *N. diversicolor* are known to be highly tolerant to heavy metals (Bryan & Hummerstone 1973 *a*, *b*), and to low oxygen concentration, (Henricksson 1969). *N. succinea* is probably as tolerant (Grassle & Grassle 1974). In the Tees estuary, *N. diversicolor* occurs in salinities higher than its normal range, probably owing to the absence of *N. virens* which normally outcompetes *N. diversicolor* (Gray 1977). It is likely that *N. virens* is less tolerant of the high pollution stress than *N. diversicolor*.

This paper has been concerned with pollutants which primarily cause disturbance (organic matter and oil), but high organic matter loads produce anoxic conditions and H_2S. Most pollutants therefore will be a mixture of disturbance and stress. However, from the data presented, it seems probable that mere tolerance is a relatively uncommon adaptive strategy; the species that occur in the most polluted areas have life-history strategies that enable them to combat continuous disturbance.

Where disturbance is slight, a group of 7–10 species characteristically increase in abundance and produce a departure from the log-normal distribution of individuals among species. Lack of fit to the log-normal may therefore be the simplest detectable effect of disturbance or stress on communities. The impressive data on the measurement of physiological stress in bivalves (Bayne, Widdows & Thompson 1976; Widdows 1978) could clearly be used to detect pollution-induced stress on individuals.

Clearly life-history strategies are more varied than merely brooding or having planktonic larvae. The period of availability of the larvae and length of larval life will also be important aspects. The view presented here is undoubtedly oversimplified. I do, however, suggest that life-history strategies are a neglected aspect of pollution biology.

If life-history adaptation is in fact more important than tolerance as a mechanism for coping with pollution, then the emphasis on toxicity testing seems doubtful since it will not be possible to predict ecological consequences from such tests.

REFERENCES (Gray)

Åkesson, B. 1973 Reproduction and larval biology of five *Ophryotrocha* species (Polychaeta, Dorvilleidae). *Zool. Scripta* **2**, 145–155.

Alexander, W. B., Southgate, B. A. & Bassindale, R. 1935. *Survey of the River Tees Estuary. II. The estuary chemical and biological.* Technical Paper on Water Pollution Research no. 5 (71 pages). London: Her Majesty's Stationery Office.

Anger, K. 1975 On the influence of sewage pollution on inshore benthic communities in the south of Kiel Bay: 2. Quantitative studies on community structure. *Helgoländer. wiss. Meeresunters.* **27**, 408–438.

Bayne, B. L., Widdows, J. & Thompson, R. J. 1976 Physiological integrations. In *Marine mussels: their ecology and physiology* (ed. B. L. Bayne), pp. 261–291. Cambridge University Press.

Bellan, G. 1967 Pollution et peuplements benthiques sur substrate meuble dans la région Marseille. 2. L'ensemble portuaire Marseillais. *Revue int. Océanogr. méd.* **8**, 51–95.

Bellan, G. & Bellan-Santini, D. 1972 Influence de la pollution sur les peuplements marins de la région de Marseille. In *Marine pollution and sea life* (ed. M. Ruivo), pp. 396–401. London: Fishing News (Books) Ltd.

Bellan, G., Reish, D. J. & Foret, J. P. 1972 The sublethal effects of a detergent on the reproduction, development and settlement of the polychaetous annelid *Capitella capitata*. *Mar. Biol.* **14**, 183–188.

Beyer, F. 1968 Zooplankton, zoobenthos and bottom sediments as related to pollution and water exchange in the Oslo fjord. *Helgoländer wiss. Meeresunters.* **17**, 496–509.

Bliss, C. I. 1966 An analysis of some insect trap records. In *Proceedings of the International Symposium on Classical and Contagious Discrete Distributions*, Montreal 1963 (ed. G. P. Patel), pp. 385–397. Calcutta: Statistical Publishing Co.

Boesch, D. F., Diaz, R. J. & Virnstein, R. W. 1976 Effects of the tropical storm Agnes on soft-bottom macrobenthic communities of the James and York river estuaries and lower Chesapeake Bay. *Chesapeake Sci.* **17**, 246–259.

Bryan, G. W. & Hummerstone, L. G. 1973*a* Adaptation of the polychaete *Nereis diversicolor* to estuarine sediments containing high concentrations of zinc and cadmium. *J. mar. biol. Ass. U.K.* **53**, 839–857.

Bryan, G. W. & Hummerstone, L. G. 1973*b* Adaptation of the polychaete *Nereis diversicolor* to manganese in estuarine sediments. *J. mar. biol. Ass. U.K.* **53**, 859–872.

Caswell, H. 1976 Community structure: A neutral model analysis. *Ecol. Monogr.* **46**, 327–354.

Dean, D. 1965 On the reproduction and larval development of *Streblospio benedicti* Webster. *Biol. Bull.* **128**, 67–76.

Dicks, B. 1976 Offshore biological monitoring. In *Marine ecology and oil pollution* (ed. J. M. Baker), pp. 325–440. London: Applied Science Publishers.

Dorsett, D. A. 1961 The reproduction and maintenance of *Polydora ciliata* (Johnst.) at Whitstable. *J. mar. biol. Ass. U.K.* **41**, 383–396.

Eagle, R. A. & Rees, E. I. S. 1973 Indicator species – a case for caution. *Mar. Pollut. Bull.* **4** (2), 25.

Filice, F. D. 1958 Invertebrates from the estuarine portion of San Francisco Bay and some factors influencing their distribution. *Wasmann J. Biol.* **16**, 109–124.

Grassle, J. F. & Grassle, J. P. 1974 Opportunistic life histories and genetic systems in marine benthic polychaetes. *J. mar. Res.* **32**, 253–284.

Grassle, J. F. & Grassle, J. P. 1977 Temporal adaptations in sibling species of *Capitella*. In *Ecology of marine benthos* (ed. B. C. Coull), pp. 177–190. (*Belle W. Baruch Library in Marine Science* no. 6.) Columbia: University of S. Carolina Press.

Gray, J. S. 1976*a* Are base-line surveys worthwhile? *New Scient.* **70**, 219–221.

Gray, J. S. 1976*b* The fauna of the polluted river Tees estuary. *Estuar. coast. mar. Sci.* **4**, 653–676.

Gray, J. S. 1978 The structure of meiofauna communities. *Sarsia* **63**, 265–272.

Grime, J. P. 1977 Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* **111,** 1169–1194.

Hanks, R. W. 1968 Benthic community formation in a 'new' marine environment. *Chesapeake Sci.* **9**, 161–172.

Henricksson, R. 1969 Influence of pollution on the bottom fauna of the Sound (Öresund). *Oikos* **19**, 111–125.

Holland, J. S., Maciolek, N. J. & Oppenheimer, C. H. 1973 Galveston Bay benthic community structure as an indicator of water quality. *Contr. mar. Sci. Univ. Texas* **17**, 169–188.

Leppakoski, E. 1975 Assessment of degree of pollution on the basis of macrozoobenthos in marine and brackish-water environments. *Acta Acad. åbo.* B **35**, 1–90.

MacArthur, R. H. & Wilson, E. O. 1967 *The theory of island biogeography*. Princeton: Princeton University Press.

Margalef, R. 1968 *Perspectives in ecological theory*. Chicago: Chicago University Press.

May, R. M. 1975 Patterns of species abundance and diversity. In *Ecology and evolution of communities* (ed. M. L. Cody & J. M. Diamond), pp. 81–120. Cambridge, Mass.: Bellknap Press.

O'Connor, J. S. 1972 The benthic macrofauna of Moriches Bay, New York. *Biol. Bull.* **142**, 84–103.

Odum, E. P. 1969 The strategy of ecosystem development. *Science, N.Y.* **164**, 262–70.

Pearson, T. H. 1975 The benthic ecology of Loch Linnhe and Loch Eil, a sea-loch system on the westcoast of Scotland. IV. Changes in the benthic fauna attributable to organic enrichment. *J. exp. mar. Biol. Ecol.* **20,** 1–41.

Pearson, T. H. & Rosenberg, R. 1976 A comparative study of the effects on the marine environment of wastes from cellulose industries in Scotland and Sweden. *Ambio* **5**, 77–79.

Pearson, T. H. & Rosenberg, R. 1978 Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. mar. Biol. A. Rev.* **16**, 229–311.

Pianka, E. R. 1974 *Evolutionary ecology*. New York: Harper & Row.

Pielou, E. 1966 Species-diversity and pattern diversity in the study of ecological succession. *J. theor. Biol.* **10**, 370–383.

Rasmussen, E. 1973 Systematics and ecology of the Isefjord marine fauna (Denmark). *Ophelia* **11**, 1–507.

Reish, D. J. 1960 The use of marine invertebrates as indicators of water quality. In *Waste disposal in the marine environment* (ed. E. A. Pearson), pp. 92–103. (Proc. First Int. Water Poll. Conf., New York.) Pergamon Press.

Reish, D.J. 1971 Seasonal settlement of polychaetous annelids on test panels in Los Angeles – Long Beach harbors, 1950–51. *J. Fish. Res. Bd Can.* **28**, 1459–1467.

Rosenberg, R. 1972 Benthic journal recovery in a Swedish fjord following closure of a sulphite pulp mill. *Oikos* **23**, 92–108.

Rosenberg, R. 1973 Succession in benthic macrofauna in a Swedish fjord subsequent to the closure of a sulphate pulp mill. *Oikos* **24**, 1–16.

Sanders, H. L. 1968 Marine benthic diversity: a comparative study. *Am. Nat.* **102**, 243–282.

Sanders, H. L., Grassle, J. F. & Hampson, G. R. 1972 The West Falmouth Oil Spill. I. Biology. *Woods Hole oceanogr. Inst. tech. Rep.* 72–20.

Schram, T. 1970 Studies on the meroplankton in the Inner Oslofjord. II. Regional differences and seasonal changes in the specific composition of larvae. *Nytt Mag. Zool.* **18**, 1–22.

Shannon, C. E. & Weaver, W. W. 1963 *The mathematical theory of communications*. (117 pages.) Urbana, Illinois: University of Illinois Press.

Shorey, W. K. 1973 Macrobenthic ecology of sawdust bearing substrate in the Penobscot River estuary (Maine). *J. Fish. Res. Bd Can.* **30**, 193–297.

Simon, J. L. & Dauer, D. M. 1977 Reestablishment of a benthic community following natural defaunation. In *Ecology of marine benthos* (ed. B. C. Coull), pp. 139–154. (*Belle W. Baruch Library in Marine Science* no. 6.) Columbia University of S. Carolina Press.

Smith, J. E. (ed.) 1970 *'Torrey Canyon' – pollution and marine life*. Cambridge University Press.

Smyth, J. C. 1968 The fauna of a polluted shore in the Firth of Forth. *Helgoländer wiss. Meeresunters.* **17**, 216–223.

Stirn, J., Avcin, A., Kerzan, I., Marcotte, B. M., Meith-Avcin, N., Vriser, B. & Vukovic, S. 1975 Selected biological methods for assessment of pollution. In *Marine pollution and waste disposal* (ed. E. A. Pearson & E. Defraja Frangipane), pp. 307–328. Oxford: Pergamon Press.

Straughan, D. 1971 *Biological and oceanographical survey of the Santa Barbara Channel oil spill, 1969–70*, vol. 1: *Biology and bacteriology*. Los Angeles: Allan Hancock Foundation, University of Southern California.

Swartz, R. C. 1972 Biological criteria of environmental change in the Chesapeake Bay. *Chesapeake Sci.* **13**, 17–41.

Warren, L. M. 1976 A population study of the polychaete *Capitella capitata* at Plymouth. *Mar. Biol.* **38**, 209–216.

Widdows, J. 1978 Physiological indices of stress in *Mytilus edulis*. *J. mar. biol. Ass. U.K.* **58**, 125–142.

Wolff, W. J. 1973 The estuary as a habitat. An analysis of data on soft bottom macrofauna of the estuarine area of the rivers Rhine, Meuse and Scheldt. *Zool. Verh., Leiden* **126**, 1–242.

Discussion

M. Waldichuk (*Pacific Environment Institute, West Vancouver, B.C., Canada*). Let me congratulate Professor Gray on an excellent paper. It is one of the few papers where a trend has been demonstrated in benthos as a result of pollution. Perhaps this is related to the large amount of work done by Dr Pearson in Loch Eil and by others in the Swedish pulp mill case cited.

Could Professor Gray say something about the general level of effort and the time required to demonstrate the trends, for example through deviations from the log-normal distribution in benthos as a result of pollution.

J. S. Gray. A log-normal distribution can only be fitted to large samples from a heterogeneous assembly of species and obviously all species have to be accurately determined. The technique will show if the environment is disturbed and will produce a list of 5–8 species that are sensitive to disturbance.

As to the time interval, with Pearson's data a 1 year period between samples gave an effect. In Oslofjord we have also been able to monitor spatial effects of disturbance.

A. J. Newton (*Clyde River Purification Board*). In order to produce a log-normal distribution curve for the sample population, each component specimen must be identified to species level. Such a procedure can, of course, be extremely time consuming and imposes a heavy burden on 'pollution assessment organizations' such as my own. The author has suggested that some of the dominant species in polluted situations may in fact be species complexes and I wonder how fine 'splitting' of these complexes might influence the slope of the log-normal distribution curve?

J. S. Gray. In general, the fitting of the log-normal is fairly robust to possible misidentifications provided the sample is a large one and from a heterogeneous community. Problems usually lie in the number of species with one individual and with two or three individuals (geometric classes 1 and 2). One often finds that these two points do not lie along a straight line with the other points of the cumulative curve. The explanation is that owing to some misidentification problems there may be too many species with one individual and too few with two or three individuals or vice versa. At the other extreme, with the highest geometric classes with numbers of individuals of 4000–8000 and 8000–16000 it clearly does not matter if *Capitella* and *Polydora* are only counted approximately. So I would doubt that the splitting of *Capitella* into four or five species by electrophoretic methods would be worthwhile.

R. J. Berry (*Royal Free Hospital School of Medicine*). Professor Gray's comments on short-term genetic effects following an environmental change could be very important for techniques of surveillance in the future. There is now considerable evidence for rapid and sensitive genetic adjustment to environmental pressures in many organisms, and monitoring such responses could lead to new methods for detecting the *biological* effects of pollution (and it is, after all, the biological consequences that are most relevant in setting acceptable limits) (Berry 1971, 1977; Luoma 1977). For example, the proportions of the different sibling species of *Capitella capitata* described by Grassle & Grassle (1976) could be determined simply by electrophoresis, and may indicate the state of disturbance of the site whence they came. This would be much cheaper and easier than investigating the population state of 'moderately common' groups as advocated by Professor Gray. Furthermore, it may turn out that some general relations between environmental disturbance and species proportions in *Capitella* (or other groups such as *Polydora*) may emerge, whereas the data for 'moderately common' species will have to be determined for every area monitored.

There seem good grounds, therefore, for exploring the genetic dynamics of some of the common species which have been suggested as useful pollution indicators, and perhaps following up Professor Gray's interesting distinctions between disturbance, stress, and tolerance. On the academic level it will be interesting to discover if these marker species are often species groups: and on the more practical level, allozymic variation will be a useful tool for investigation because the behaviour of many chromosomal segments can be detected, and the function of any changing alleles can be investigated under laboratory conditions (probably most of them may be mere markers of important linked loci, but some could be important in themselves, as is the esterase which serves as an indicator of organophosphorus resistance in the aphid *Myzus persicae* (Beranek & Oppenoorth 1977)).

References

Beranek, A. P. & Oppenoorth, F. J. 1977 Evidence that the elevated carboxylesterase (esterase 2) in OP resistant *M. persicae* (Sulz.) is identical with the organophosphate-hydrolyzing enzyme. *Pestic. Biochem. Physiol.* **7**, 16–20.

Berry, R. J. 1971 Conservation aspects of the genetical constitution of populations. In *The scientific management of animal and plant communities for conservation* (ed. E. Duffey & A. S. Watt), pp. 177–206. Oxford: Blackwell.

Berry, R. J. 1977 Genetical factors in animal population dynamics. In *Population dynamics* (ed. R. M. Anderson & B. D. Turner). Oxford: Blackwell. (In the press.)

Grassle, J. P. & Grassle, J. F. 1976 Sibling species in the marine pollution indicator *Capitella* (Polychaeta). *Science, N.Y.* **192**, 576–569.

Luoma, S. N. 1977 Detection of trace contaminant effects in aquatic ecosystems. *J. Fish. Res. Bd Can.* **34**, 436–439.

J. S. GRAY. First, I would not advocate the short-cut method of detecting disturbance by separating the proportions of the different species of *Capitella* with the use of electrophoresis since I believe that the dominance by *Capitella* and *Polydora* represents end-points of gross pollution. What we need are methods for detecting the initial stages of disturbance of an ecosystem, which the departure from the log-normal appears to provide. Furthermore, the method should apply to any community, not just to sediment-living species.

Secondly, I would completely agree about the need for genetic work on the species groups which I have suggested as being characteristic of grossly polluted areas. It is the common patterns that will help to elucidate the effects that pollutants have on organisms and this type of research should elevate pollution studies to a higher academic level.

A. V. HOLDEN (*D.A.F.S., Pitlochry, U.K.*). In one of the earlier graphs of Pearson's data from the Scottish pulp mill area, with the use of Sanders's method, very large changes between years were shown which could not always have been due to pollution. This seems to suggest that the method can reflect natural changes to the same degree as those which might be due to pollution.

The assumption that any further addition of a naturally occurring substance produces an adverse change raises the question of the situation in unpolluted sea water. Is this an optimum situation, or would a decrease in the natural level, if this were possible, be likely to increase diversity and biomass still further? It seems unlikely that the equilibrium between species in unpolluted sea water could be intolerant of any degree of change in the concentrations of naturally occurring substances.

J. S. Gray. In an unpolluted environment the values of any diversity measure will fluctuate from time to time at a given place, reflecting changes in the equilibrium set of species and in fluctuations in species abundance. Diversity does not always increase with time; for example, at the end of successional sequences diversity often falls. So a mild disturbance may increase diversity. My figure of Sanders's rarefaction method applied to Pearson's data showed that a wide range of diversity occurred when no pollution existed and my point was that even after 3 years of pollution the curves could not be distinguished from those for unpolluted years. Data from the use of the Shannon–Wiener index showed similar findings. Yet by using the log-normal test a change was detected after only 1 year of pollution and the same effect can be demonstrated in many different communities. The departure from the log-normal after 1 year of pollution represents a departure from an equilibrium community.

T. H. Pearson (*Dunstaffnage Marine Research Laboratory, P.O. Box* 3, *Oban, Argyll, U.K.*). I do not think that the problem of speciation in polymorphic groups such as *Capitella* and *Polydora* is one that should worry workers concerned with pollution effects in the field too greatly. In so far as *Capitella* occupies a particular niche related to high organic inputs to the sediments it may be regarded as a monotypic ecological species despite its apparent inherent genetic variability. The fact that part of its response to environmental perturbations is genetic selection within a broad scale genotype does not invalidate the ecological relevance of its domination of highly organic situations in marine sediments, even if we behave as 'splitters' in the classical taxonomic sense and start talking about a species 'group' or species 'complex'. Professor Gray's designation of *Scolelepis* as being an example of a species following a 'tolerance' strategy rather than being an *r*-strategist is interesting. The fact that it lacks a benthic larva does not appear to inhibit its explosive population growth under the right conditions. It seems possible that such conditions are in part created by the presence of *Capitella*. We have recently completed a review of species succession in organically enriched marine sediments (Pearson & Rosenberg 1978) in which we list twelve areas in northwest Europe and the Mediterranean where *Scolelepis* has been reported as being codominant with *Capitella* in highly organic sediments. However, we note a further 28 reports from various areas round the World where *Capitella* is dominant in such situations without *Scolelepis* or with another codominant present. Recent observations on cultured populations in our laboratory have suggested that there is biological interaction between the two species with *Scolelepis* populations being enhanced by the presence of *Capitella*. In North American waters, another spionid species *Streblospio* takes the place of *Scolelepis* as a codominant with *Capitella*. It is possible that the adaptive strategy of such spionid species in highly organic situations is dependant on the co-occurrence of *Capitella*.

In the review mentioned above, we have distinguished two groups of *r*-strategists among the marine macrobenthos, i.e. general opportunists, which appear to take advantage of unexploited space to breed explosively after any environmental disturbance which has created such ecological space, and enrichment opportunists, which dominate high organic sediments and are the initial exploiters of rich food sources. The capitellid and spionid polychaetes are prominent among the latter group.

J. S. Gray. I thank Dr Pearson for his interesting and important comments. I agree that using the *Capitella* complex as an 'ecological species' may be a practical expedient. My main purpose in this paper was to try to extract principles appertaining to effects of pollutants and I believe that in the most polluted areas the dominant species are complexes. We are beginning a project to follow allozymic variations in *Polydora* populations in Oslofjord in a spatial and temporal context, since this species is abundant in the most polluted areas and seems to show some form of life-history adaptation, as I indicated in my paper.

Referring to the *r*-strategists, I would repeat that it is my belief that if one separates pollutants into two categories, disturbance and stress, then adaptive strategies to high disturbance will have a high *r*. That is why *Capitella*, which has a high *r*, can occur immediately after an oil spill or in organically enriched areas where there is a continuous disturbance in the form of sedimenting material. The adaptive strategy is to disturbance and I am therefore not sure that I would agree with Dr Pearson in separating those species adapting to available space from those adapting to high amounts of organic matter.