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The Composition and Functioning of Benthic Ecoystems in Relation to the Assessment of Long-Term Effects of Oil Pollution [and Discussion]

J. R. Lewis, K. Hiscock and A. J. Southward

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The composition and functioning of benthic ecosystems in relation to the assessment of long-term effects of oil pollution

By J. R. Lewis
Wellcome Marine Laboratory, University of Leeds, Robin Hood's Bay,
North Yorkshire YO22 4SL, U.K.

The assessment of long-term effects of oil pollution is ultimately a matter of field responses and ecological interpretation. Chronic conditions present much greater interpretative problems than the aftermath of a severe spill because the detection of subtle effects has to be made against the usually unknown scales of natural changes taking place.

Examples from various coastal benthic communities illustrate types of biological interactions, different types and degrees of biological stability and the sometimes unpredictable timescales involved. Special attention is drawn to the significance of natural fluctuations in recruitment and to the geographical scales on which these may occur.

Have such matters been taken into account in the past? For the future the extreme difficulty that may be involved in detecting subtle deterioration necessitates both a considerable increase in ecological awareness and the directing of work on sublethal effects to those species most amenable to ecological study.

INTRODUCTION

Long-term effects of pollution are ultimately matters for ecological judgement. This is not to deny the existence of biochemical, physiological and behavioural responses. Indeed the first effects of sublethal exposures will be at these levels, but the significance of any resulting loss of efficiency can only become manifest in the field. An experimentally demonstrated loss of perhaps 20% in feeding rate or locomotory activity may be a trivial or a vital issue depending entirely upon the types and abundance of prey, predators and competitors with which that species interacts in nature. Moreover, unless sublethal effects impair competitive efficiency sufficiently to have ecological repercussion at the population and community level, I find them of little concern, especially when set against the scales of naturally induced ecological events.

With oil there are two types of possible long-term effect to consider: the aftermath of acute incidents and the continuous consequences of chronic conditions. In the former case, obvious known damage has been done and we are merely observing the recovery phase. The duration of this will depend upon the types of organism and their methods of reproduction and dispersal, and especially upon their life spans, for it will clearly take many years to restore normal population age distributions in species living for one or two decades or longer. Only rarely, however, will one be able to say 'recovery is complete: there are now no discernible after-effects' because in most cases, and for reasons that will appear later, there can be little certainty about precisely what would have been naturally present after the lapse of 5, 10 or more years. All that can be expected is that an experienced naturalist will say, 'This community, in its general composition and age structures, is of a type that could occur naturally in similar habitats elsewhere.

When, however, our starting point is established complex communities with the possibility of slow deterioration or a slight but persistently abnormal bias, the scientific challenge is very much greater and therefore much more interesting. It is very easy in a pollution-charged era to ascribe all changes to pollution, but our task, if we are being fair and objective, is to identify those ecological changes for which no convincing natural explanation exists. Initially one will be expecting, and probably be able to discount quickly, the mortalites caused by storms and disturbance of bottom sediments (as reported by Eagle (1975), Rees *et al.* (1975) and Rachor & Gerlach (1978)) or by extreme temperature conditions (Crisp (ed.) 1964; Bowman 1978). Less obvious, perhaps, but surely in the mind of every watch-dog biologist are the recent unexpected revelations of shore-line deaths caused by red tides (Ottway *et al.* 1979; Cross & Southgate 1980). Those with long memories may recall that sea-grass (*Zostera*) was wiped out by disease in the 1930s (Tutin 1938), and others may know that pathogens may displace 'pollution' as the more likely cause of recent declines in Portuguese oysters. But when we have narrowed the field by elimination we shall still be left with changes that present serious problems of ecological interpretation. They arise from various characteristics of benthic communities.

Benthic communities and species interactions

The benthos, with its many attached or slow-moving species fairly simple to collect or count, seems easy to deal with by comparison with large mobile species or planktonic organisms in which even the habitat is moving. But it is precisely this abundance of sedentary forms that gives rise to the interpretational difficulties. To appreciate why it has first to be recognized that although species abundances are ultimately controlled by physical factors (e.g. sand grain size, wave action), many species have overlapping requirements or tolerances. Consequently, and except in physically difficult habitats, there are often several or many macrospecies capable of living in the same position. The resulting competition for space is usually most intense on rock, where the habitat is essentially two-dimensional. In sands and muds, burrowing to various depths introduces a third dimension and may reduce somewhat the competition for bodily space but not other aspects of competition.

The reality of such competition is very apparent after denudation, when the first occupiers of bare rock or mud are fine algae or small worms with high reproductive powers. Unless the cause of the initial denudation operates more or less continuously, these opportunistic colonizers are next replaced by longer-lived species, less fecund probably, but better competitors. In some habitats this process may culminate in a final, predictable dominant species with great powers of persistence, but more usually there are several potential dominants, and which one wins for a time depends upon chains of events and not a little on sheer chance.

The means by which species compete are various, and indeed there are other biological interactions of equal importance. To appreciate better what is going on in these deceptively static-seeming communities necessitates a brief survey of some of the more common types of organism.

Clearly, major differences of body form must exist between rock-living or sediment-living organisms, and very mobile sediments call for special adaptations, but nevertheless both types of habitat are usually dominated by space-occupying fixed, sedentary or slow-moving species. Among the plant life, familiar terrestrial types predominate in sediment (salt marshes, sea-grass meadows), but the marine algae of rock come in many sizes and forms (encrusting, shrubby, erect; calcareous, gelatinous, leathery, papery; filamentous, leafy, sheet-like). The fixed or sedentary animals feed by extracting particles in suspension in the water or deposited on the surface. They are typified on rock by barnacles, mussels, oysters and sea squirts (and many more subtidally) and in sediments by clams and fan-worms or tentaculate worms. Among the mobile animals, crawling on and between the sedentary forms, there are rasping grazers of the rock surface and algae (e.g. snails, limpets and sea urchins), engulfers of sediment detritus, and many types of slow-moving or active predators (starfish, sea slugs, whelks, crabs and other crustaceans). Predation also comes from non-benthic sources, e.g. fish and sea birds.

Two further general points about the benthos warrant attention: potential life spans ranging from a few months or a year to several decades; and the large proportion of organisms having a drifting, planktonic phase in their life cycles and in which recruitment is therefore often independent of the density of the immediately local breeding population.

The types of interactions among such species are many. Apart from the expected predation and grazing (this latter being directed mainly at the sporeling stages of the macro-algae), growth of sedentary forms can result in overcrowding and stunting, physical crushing, and overgrowth of one form upon another. Just occupying space denies it to others most effectively and in particular to settling larvae, but larvae may also be destroyed by the food-gathering activities of suspension or deposit feeders, or by the sweeping of algal fronds. The physical properties of sediments can be changed by feeding or burrowing, to the detriment or benefit of other species. But activities and interactions are not all destructive: massed tube-worms, sea-grass rhizomes and mussel beds stabilize sediments and gravels, and many species, by providing new attachment surfaces or creating novel microhabitats between their fronds, tubes or shells, greatly increase the diversity and numbers of smaller organisms.

The relative importance of the effects of these types of interaction upon the composition of communities and their rates of change is highly variable. At one extreme we find individual species or pairs of interacting species that virtually determine the overall biological character of a habitat. Because of their abundance or size, their form or the scale of their activities, they exercise a dominating or key ecological role. Thus the large, long-lived intertidal alga *Ascophyllum nodosum* appears immune to grazer control, and the associated subordinate species of shores where it is abundant comprise only those able to live on or beneath its fronds. Similar dominance and control of its own environment is demonstrated by the deposit feeding holothurian *Molpadia oolitica*, which by the scale of its ingestion and reworking of sediments prevents the establishment of possible competitors. But in some cases the dominance is less complete and the other or prey species may reassert themselves. Thus the fluctuating abundance of the relatively short-lived fucoid algae is largely determined by the intensity of grazing by limpets (*Patella* spp.) and other gastropods, and similar oscillating or stable balances occur subtidally, where the grazers are usually sea urchins. Mussels (*Mytilus* spp.), which are supremely efficient spatial competitors yet support a rich subfauna and can dominate extensively for long periods, are themselves destroyed by starfish (e.g. *Asterias* and *Pisaster*), which thereby close the circle by allowing the less efficient competitors to return for a time.

Persistent biological control usually requires potentially long life, to which may also be allied an adequate recruitment rate. Nevertheless, less well-endowed species still exert a strong influence but for short periods, so that 1–2 year reciprocating cycles or irregular fluctuations with alternative dominants are common (especially in sediment communities). The mortality of established individuals (from both physical and biological causes), which creates gaps or reduces the intensity of control, is often a chance event not only in space but also in time, and is therefore related to breeding cycles and availability of settling stages. Consequently the processes of destruction and reoccupation become out of phase and create patchy or gradient distribution patterns on various scales, often having no relation to constant physical conditions. The chance survival of individuals long enough for them to reach a size that confers immunity to predation creates further 'illogical' distribution patterns, especially when these are expressed as biomass rather than numbers of individuals.

Although biological interactions are an inevitable consequence of the fact that no species lives or can live in a biological vacuum, such interactions do not always play a conspicuous role. This is understandable in frequently disturbed habitats, especially sediments, and even after biologically caused denudation the re-establishment phase with low competitive pressures may be prolonged. It is also logical to find, even among dense, space-occupying populations, that competition is low and changes are slight where species are few and growth is slow, as they are in the upper half of exposed rocky shores (Lewis 1977). But there also appear to be stable sediment communities with little biological structuring in spite of their having large numbers of species. Such paradoxes may indicate an exceptionally high degree of niche specialization which minimizes competition, or simply the lack of an organism capable of exercising a key role *in situ*, or the periodic interference of mobile migratory species. Perhaps also the stable condition is, by chance, a pause between periods of change that could come to light only by longer observation; such speculation, whether relevant or not in these cases, nevertheless leads on to the vitally important subject matter of the next section.

Timescales of natural changes

While our objective is the detection of either a unidirectional trend or a persistent departure from normal, the cycles and fluctuations that constitute the normal make the task difficult. But at least they can be recognized for what they are – by an experienced field ecologist – and many can be discounted: the annual cycles of repopulation and mortality, especially in the shorter-lived species; the consequences among other species of an increase or decrease in a key organism, and so on. Indeed, the more dramatic and sudden a decline the greater the probability that it has natural causes, even if these have calmed down or crawled, swum or flown away before one arrives.

But are all changes abrupt? If we ignore the communities or habitats with the most dynamic features and concentrate only upon what appear to be the biologically stable areas, will a trend be significant in pollution terms, especially if it is downward? Our knowledge about long-term changes in benthic communities is unfortunately sparse (after all, publishable results do not come quickly enough to meet career needs), but what we have is not very encouraging in the present interpretational context.

A first example comes from a total community study of subtidal sediments. It is still being carried out by J. Buchanan of the Dove Marine Laboratory of the University of Newcastle, and I am indebted to him for information additional to that already published (Buchanan *et al.* 1978). For several years before 1974 there was a progressive change in the relative abundance of the species that he was studying, together with an increase in the total number of individuals. An initial hypothesis that these changes were caused by an increase in winter sea temperature has since been discarded, and an alternative suggests that the rapid decline of the principal and fast-growing polychaete *Ophelina acuminata* allowed the diversion of energy to other species. Whether or not correct, this leaves unanswered the questions: what caused *Ophelina* to decline, and when might it reappear? After 1974, lesser fluctuations resolved themselves into a regular biennial cycle of total abundance superimposed upon a basic community stability, which has lasted for 7 years. But now some major new changes appear to be taking place (J. Buchanan, personal communication).

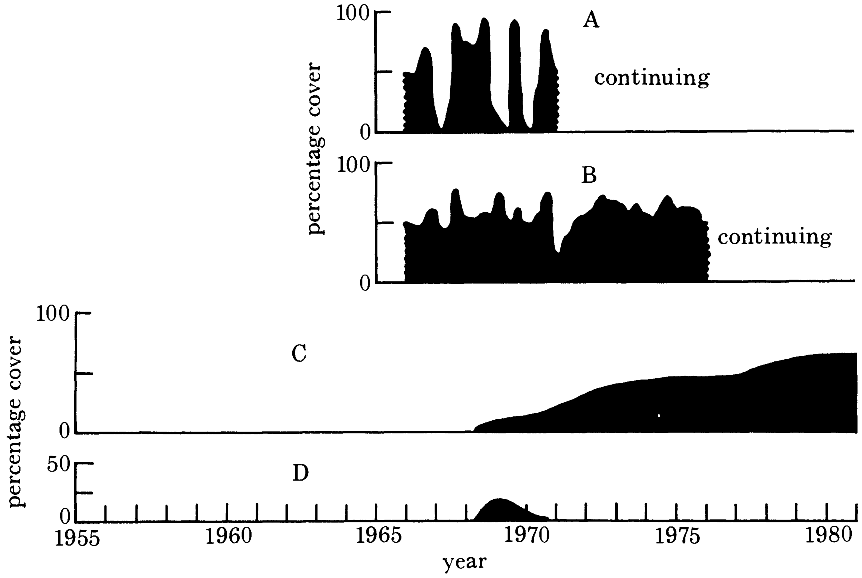


FIGURE 1. Long-term natural variation in the percentage cover of *Mytilus edulis* on four sites at Robin Hood's Bay, North Yorkshire. Site A is at low-tide level, and sites B, C and D are at mid-tide level. All are physically suitable for *Mytilus* occupation. A and B are approximately three-quarters of a mile from C and D.

An alternative approach, involving one or two species only, has been the careful recording of the fluctuating, partly reciprocating balance between the intertidal barnacles *Balanus* and *Chthamalus* over several decades (Southward & Crisp 1956; Southward 1967). Some original data on the amplitudes and timescales of change in *Mytilus edulis*, the common mussel, are given in figure 1. This species, which has been much favoured for studies of toxicology and uptake, and was proposed as suitable for a special 'Mussel watch' monitoring programme, is a key species of European coasts, but unfortunately it is a singularly difficult and unpredictable species to deal with ecologically. In the context of slow, long-term changes, site C is the most interesting of the four fairly adjacent localities in figure 1. Presumably numbers there will reach a maximum and then decline to the original condition of complete absence. How long will that take, and what conclusions about pollution might possibly be drawn then by those who observe only the declining phase?

A similar question must also arise from consideration of figure 2. *Patella vulgata* is another key species, the principal, intertidal grazer of northwest European coasts, and much more tractable to study than *Mytilus*. Here, too, we have an overall trend of increase resulting, after 14 years, in amazingly high densities of up to 1000 m^{-2}. If these observations had begun by chance not at a trough in numbers, but at the start of a decline of equivalent scale, it would probably have been obligatory to invent a source of local pollution.

In the event, the population changes in *Patella* are clearly related to the different levels of annual recruitment, and not only is there some understanding of the causes of the latter, but the above-average inputs of recent years (in figure 2) have their counterpart elsewhere around northern coasts of Britain. Thus we have a new source of population changes, recruitment variation, and a new spatial scale to take into account.

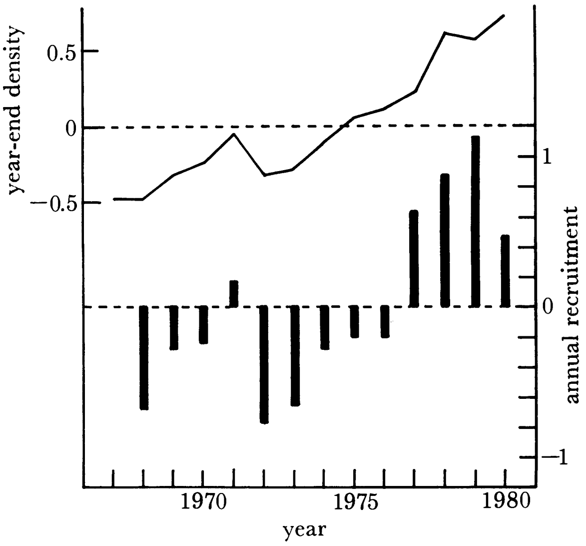


FIGURE 2. Year-end density (continuous line) and annual recruitment (columns) of *Patella vulgata* at Robin Hood's Bay for 1967–1980. Deviations astride each mean are expressed in units of 100%. (Note that each year's recruitment is derived from spawning in the previous autumn).

RECRUITMENT VARIATION

Recruitment is a matter of special importance because:

(1) it is fundamental to the maintenance of populations,

(2) the intensity of biological interactions is primarily dependent upon the numbers of individuals involved, and

(3) an extensive toxicological literature indicates that larval and juvenile stages are usually more sensitive than adults to pollutants.

The relations between settlement densities and eventual year-class strength varies among different species. In some it is very close, in others there are very high mortalities of immediately post-settlement stages. But even in the latter cases it is surely vital for interpretational purposes, and in view of the sensitivity to pollutants, to know what settlement actually took place. It is, after all, recruitment failure (and not great success) that would cause alarm, and failure is not usually apparent to the casual eye.

But if the abundance of early stages appears to be a suitable and sensitive indicator of water quality, its reliability depends upon the normal constancy of recruitment. Many studies (for example those by Coe (1953), Quayle (1964), Buchanan (1967) and Bowman & Lewis (1977)) show that recruitment, as opposed to reproduction, fluctuates considerably from year to year and may even fail. Fluctuations in one locality only could have local causes, but as more geographic data become available (Southward & Crisp 1956; Lewis *et al.* 1982) it is clear that some patterns of annual variation are synchronous over wide areas, and therefore can only be reflecting a sensitivity to entirely natural but broad-scale climatic–hydrographic factors. Such

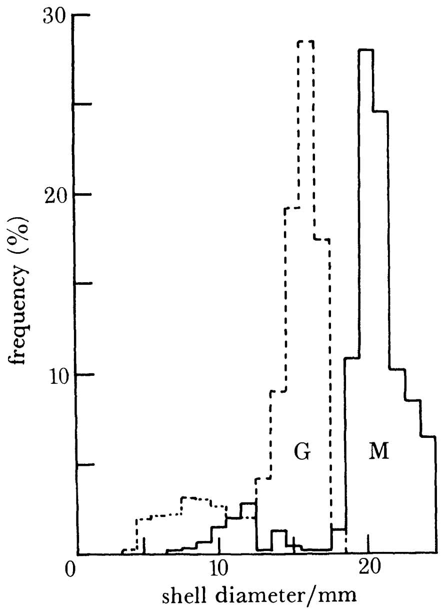
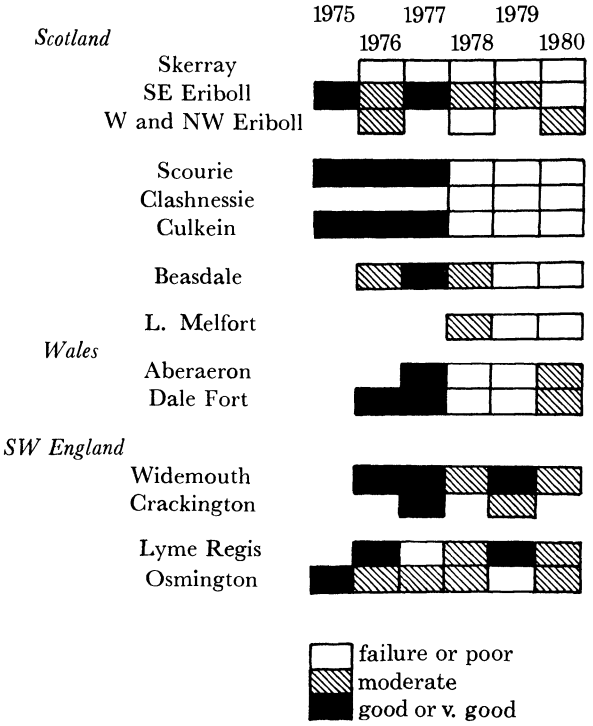


FIGURE 3. The size–frequency structure of populations of *Gibbula umbilicalis* (G) and *Monodonta lineata* (M) at Dale Fort, Milford Haven, in October 1981.



		1975	1976	1977	1978	1979	1980
Scotland	Skerray		□	□	□	□	□
	SE Eriboll	■	▨	■	▨	▨	□
	W and NW Eriboll		▨		□		▨
	Scourie	■	■	■	□	□	□
	Clashnessie				□	□	□
	Culkein	■	■	■	□	□	□
	Beasdale		▨	■	▨	□	□
	L. Melfort				▨	□	□
Wales	Aberaeron			■	□	□	▨
	Dale Fort		■	■	□	□	▨
SW England	Widemouth		■	■	▨	■	▨
	Crackington			■		▨	
	Lyme Regis		■	□	▨	■	▨
	Osmington	■	▨	▨	▨	□	▨

□ failure or poor
▨ moderate
■ good or v. good

FIGURE 4. Assessment of year-class success, 1975–80, in *Gibbula umbilicalis* at localities to the south of its northern limit in Scotland, and west of its Channel limit in Dorset.

latitudinal factors, inimical to successful reproduction or recruitment, or both, are likely to be felt most strongly towards species' geographical limits. How great a distance might be involved and with what frequency appear to be unpredictable, but any monitoring programme would do well to consider the geographical affinities and distribution of its species. This point is illustrated by reference to figures 3 and 4. From the former, depicting the size-structure of *Gibbula umbilicalis* and *Monodonta lineata*, two large and conspicuous littoral gastropods, it is reasonable to infer that there has been very low recruitment over the last 2–3 years. Since these data come from the major oil port of Milford Haven, the suspicion of a pollution effect must be strong. However, when set into a geographical framework (figure 4) it is clear that these poor recruitment years have extended for *Gibbula* over most of the west coast of Britain up to its northern limit. *Monodonta* similarly has failed up to its geographic limit in north Wales. This extensive scale of failure or near-failure points to the operation of natural factors, and the reasonable assumption must be that events in Milford Haven were only part of a larger event. The geographical scale of any biological pattern or trend is the first and most reliable clue to its cause, but this geographical perspective is lacking in most monitoring programmes.

CONCLUSION

In all cases of pollution effects, the worse they are the easier their detection; this leads to the apparent paradox that it is the unknown, the suspected but hard-to-detect chronic effects, that are the real cause for concern. In the present case, and because of the considerable but incompletely understood dynamic characteristics of many benthic communities, I anticipate that the unambiguous identification of subtle, chronic trends and persistent modest departures from normal will prove to be difficult, except perhaps in the immediate vicinity of a continuous or regular inflow.

Thus the reports of later speakers from areas of potentially high contamination will be of particular interest. If they contain convincing evidence of deterioration my pessimism will have been excessive, and we shall at least know something about long-term effects. But if they report little or no effect we shall still be left with uncertainty, for 'lack of effect' could mean either 'no effect' or 'no detectable effect'. This would leave us where we started, but may then lead to another obvious question. If it is so difficult to demonstrate an effect, does this not mean that whatever effects may be present are of no significance?

If we suppose that, for one reason or another, a case can be made for more scientific studies, what form should they take? Bearing in mind that after a decade of intensive studies of sublethal effects we are little nearer to the identification of field effects, I suggest that the balance of effort between sublethal studies and field ecology should be tipped heavily in favour of the latter, and that much closer collaboration between the two disciplines should be established. Moreover, since it is what happens at the population and community level which is of most importance, the toxicological studies should, whenever practicable, be primarily concerned with those species which are both important and manageable ecologically.

Secondly, and of much greater importance, it has to be acknowledged that if the long-term effects of man's activities are to be identified, this will necessitate a considerable increase in our knowledge of natural trends or cycles. Whether the emphasis should be spread over total community study or concentrated upon a few selected species is a matter of contention that may, in the end, depend on local circumstances, for the former approach fits well with the methods of sediment studies but not of rocky habitats. Nevertheless, in the absence of any single community attribute that can be taken as an infallible guide to an *adverse* change, I favour the selected species approach wherever this is possible and practicable. It allows greater depth of study into the interactive processes and recruitment, knowledge of which seems to me indispensible for correct interpretation. Selection of some species implies neglect of others, and clearly one may be unlucky, but the more a community is structured by key species, the more logical it is to concentrate upon these than to dissipate effort on dependent species.

But whatever one's view on that matter, there can be no doubting that the more we know about the changing composition of communities, about species interactions, and the causes and geographical extent of recruitment variations the more reliable our interpretation will be. Yet too much effort, often financed by industry, is still being given to uncritical routine recording of changes without in any way advancing our ability to interpret such changes. Ecology is not greatly advanced by effort given to studies of pollution, but pollution studies must be conducted against a wider background of ecological knowledge, so let us get our priorities right.

I acknoweldge the assistance of my colleagues of the N.E.R.C. Littoral Surveillance Group (Miss R. S. Bowman; Mr M. Kendall and Dr P. Williamson) in obtaining the data used in the figures.

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Discussion

K. Hiscock (*Field Studies Council Oil Pollution Research Unit*, *Pembroke*, *U.K.*). Dr Lewis has been rather pessimistic about separating natural fluctuations from pollution-induced effects. In long-term monitoring, we try to get around these problems in two main ways: (1) by the establishment of reference sites distant from the area of pollution or disturbance, sites that are similar in habitat and community to those near the source of pollution or disturbance, and (2) by establishing sites at increasing distances away from point sources of pollution or disturbance to detect gradients of change. Would Dr Lewis comment on these approaches?

J. R. Lewis. Reference or control sites are indeed a valuable and in some cases essential tool, provided that, in their use, one realizes that natural changes and especially those arising from the normal interactions of established organisms are frequently out of phase on various spatial scales. Clearly the ease of separating man-made effects from natural events depends upon their relative severities and scales. Given strong or constant pollutant gradients and biological changes around a point source input, the more confident is one's interpretation, as in the Fawley marshes. But with the more diffuse situation involving planktonic larvae and the area over which they may be expected to drift before settlement, a cluster of local control sites might well be of little use. If they all showed little or no recruitment one could not, or should not, assume a pollution effect without first ascertaining what had happened over a greater geographical area. Clearly one does not need to compare places as far apart as Milford Haven and northwest Scotland, as in my *Gibbula* example. That was primarily to illustrate the scale of recruitment events and to point the lesson. But on any occasion of poor recruitment throughout Milford Haven, data confined to the Haven would be regarded as inconclusive by me.

A. J. Southward (*Marine Biological Association*, *Plymouth*, *U.K.*). Has Dr Lewis considered the possibility that gastropods, including limpets and topshells, can somehow control their own population density, either through an effect on fecundity or gamete quality or through juvenile settlement and growth? I ask this because after the cold winter of 1962/3 and after the *Torrey Canyon* affair of 1967, when many adults were killed, there was very good settlement of juveniles for 2 or 3 years after, but not later. This applies particularly to the topshells at Lyme Regis and Osmington, two of the stations mentioned as having poor recent recruitment.

J. R. Lewis. I have no information about topshells, but in limpets there is certainly some degree of regulation in that the removal of adults before recruitment leads to rather higher juvenile densities than in adjacent non-experimental areas. Thus recovery of numbers after a severe decline might well be accelerated. On the other hand, the opposite process, i.e. progressively more destruction of spat or juveniles when adult density has increased, does not seem to play a significant role in regulation. As figure 2 shows, the highest recruitment rates have so far been recorded when the population density was also high and still rising. There could have been substantial spat destruction during the best recruitment years, but it has clearly not been on a sufficient scale to offset the effects of other and more fundamental factors that were especially favourable to recruitment during those years. Whatever density-dependent effects there are, density is determined by recruitment and not the reverse.

One general point, which should perhaps be borne in mind regarding possible adult–juvenile interactions in gastropods, is that the settling stages and juveniles do not necessarily occupy the same microhabitat as the larger animals. There is certainly a habitat difference in the topshells, and even in limpets, in which spat destruction can be demonstrated, many spat and juveniles remain in small cracks, among mussels, between barnacles and so on until they have reached a size that reduces or prevents destruction by adults.