PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Uses of Experimental Ecosystems [and Discussion]

J. H. Steele, R. J. Morris and M. Waldichuk

Phil. Trans. R. Soc. Lond. B 1979 **286**, 583-595
doi: 10.1098/rstb.1979.0047

Phil. Trans. R. Soc. Lond. B. **286**, 583–595 (1979)
Printed in Great Britain

The uses of experimental ecosystems

By J. H. Steele, F.R.S.
Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543, *U.S.A.*

The experiments conducted so far with large experimental ecosystems have probably taught us more about the general ecological interactions in such systems than about subtle long-term effects of pollutants. This knowledge is not only valuable in its own right but may be more useful in an indirect rather than a direct way, in understanding the robustness of these systems and so evaluating the general effects of stresses.

Introduction

The experimental study of the interactions within communities is a standard part of ecological method providing a bridge between laboratory work on individual organisms or species, and field surveys of natural ecosystems. The complexity of the experimental ecosystem can range from a two species relation up to a set of lakes used as experimental units. The general ideal should be to combine some degree of natural interaction with advantages of experimental control. In reality, it is possible that the system might be highly unnatural and relatively uncontrolled. Thus great care is needed in the design and, in turn, this requires a fairly explicit statement of the purposes of the experiment.

We are concerned with the longer-term effects of relatively low levels of pollutants. Especially, we wish to consider the ways in which such contaminants act by altering population levels and so changing community structure. These various aspects necessarily imply that the concern is with relatively large areas of the open sea or long stretches of coastal waters, rather than with effects in the immediate vicinity of an outfall, or a dumping ground. In turn, this introduces other complications. For the study of local disposals one usually has a knowledge of the contaminants likely to have an effect. Further, for existing disposals, neighbouring areas can be used as a control so that direct comparisons of field data can be used. For the evaluation of larger-scale effects no such natural control is usually available, nor is it often possible to isolate one or two potentially dangerous contaminants since the source may be from a variety of industries in the general area, from advection of water into the area, or via atmospheric input from distant sources.

The problems can arise from two sources; observed changes in chemical concentration or population levels. Evidence of new or enhanced levels of contaminants in the water or in organisms may cause concern. Equally, evidence of changes in community structure or population levels may raise questions of possible man-made impacts. In some areas or organisms the higher chemical levels may be of natural origin, and population changes may result from long-term climatic trends or from other man-induced effects such as commercial fishing. Thus such problems require general ecological knowledge of various types of stress exerted on ecosystems and the way in which these systems respond. Toxic chemicals can be regarded as providing one set of stresses. We need to know the response of systems to these but also to know how these responses compare qualitatively and quantitatively with naturally occurring stress. The effect of pollutants at the population and community level must be considered in the context of the resilience of systems to perturbation in general (Holling 1973).

Experimental design

Single species studies

To estimate the resilience of a system, one can select critical stages in the life cycle of organisms which are ecologically or commercially important. Many such organisms have been proposed and several used. Eggs and larvae of commercial fish species are a frequent choice because such fish populations are already less ecologically robust due to fishing stress. For herring, the rate of egg development and subsequent larval mortality is sensitive to water quality and to certain pollutants (Steele *et al.* 1973; Westernhagen *et al.* 1974). Such experiments can be carried out under carefully controlled laboratory conditions but any effects observed, when considered in relation to open sea conditions, may be dependent on other environmental stresses. Thus pollutant effects on larvae may be negligible in comparison with the very high mortality, 5–10 % per day, which occurs in the natural environment.

On the other hand, an enclosed environment may be more equable than natural conditions. No significant effects of an organophosphorous insecticide on fiddler crabs were observed when the crabs were in cages but there was a significant extra mortality compared with controls when the treated crabs were exposed to natural predators (Ward *et al.* 1976).

Food chain studies

The next stage in complexity is to take some particular link in a food chain and examine effects under relatively natural circumstances. One food chain occurring on sandy beaches in northern Europe involves the predation by juvenile (O-group) plaice on the siphons of the bivalve *Tellina tenuis*. A detailed study in one location, L. Ewe, West Scotland, showed that the plaice population surviving this nursery stage was dependent on the quantity of in-faunal food of which *Tellina* was typical and sometimes dominant (Steele & Edwards 1970). Conversely, the rate of predation on the siphons, which are renewed by *Tellina*, is a drain on energy reserves from the *Tellina* which otherwise would be used for reproduction (Trevallion *et al.* 1970). Thus metabolic effects of a pollutant on plaice or *Tellina* could be expected to have consequences for the population level of both. Part of this general ecological study involved large outdoor tanks 1.8 m × 3.7 m × 1.2 m deep with a sandy bottom containing different population densities of *Tellina* and plaice. By exchanging 30 % of the water daily with water from the sandy bay, natural phytoplankton food was provided for the *Tellina*. The good reproducibility of data from such tanks made them ideal for experimental study of the effects of pollutants on a commercially significant and ecologically interesting nearshore system.

In various experiments with these tanks, copper concentrations were maintained at 3, 10, 30 and 100 μg/l above the natural levels by addition after the daily water exchange (Saward *et al.* 1975). Effects on the phytoplankton were noted for all copper additions. In particular, at 3 μg Cu/l, average chlorophyll concentrations and ^{14}C uptake were two-thirds of the control and the differences were statistically significant. Also, at 10 μg Cu/l, microscopic examination indicated a notable lack of healthy diatoms (Stirling 1974). A major feature of the results was that copper continued to accumulate in the *Tellina* throughout the 100 days of the experiment.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

At all concentrations, copper had a significant effect on *Tellina* as shown by a reduction in carbohydrate reserves and nitrogen levels. These changes may be in part the result of decreased food concentrations indicated by lower chlorophyll levels. Also, in the absence of plaice, there was a reduction in siphon mass and this, as much as a direct effect of copper on the plaice, could have been responsible for the reduced growth rate of the latter in the presence of copper. Thus food chain interactions appear to have reinforced the direct deleterious effects of copper on each component.

Similar experiments were carried out with mercury (Stirling 1974) at concentrations of 0.1, 1.0 and 10 μg Hg/l. Although there were reductions in chlorophyll in mercury-treated tanks, there was an enhancement in ^{14}C uptake at 0.1 and 1.0 μg Hg/l. In these experiments, accumulations in *Tellina* reached a plateau after 40 days. A curious feature was that at all levels of added mercury there was a decrease in growth rate of the plaice compared with controls, but these lower growth rates did not differ significantly over the range of added mercury concentrations (Saward, personal communication). The overall consequence for *Tellina* in the presence of plaice was a reduced growth rate at 10 μg/l, increased growth at 0.1 μg/l and no significant difference between treated and control tanks for the 1.0 μg/l dose (Stirling 1974).

It appears that for copper the direct adverse effects on *Tellina* were reinforced by other factors. For mercury, however, although there was a slight algicidal effect and consequent reduction in food supply, this was offset by a reduced predation pressure on *Tellina* due to a direct effect of mercury on the plaice.

These tank experiments illustrate the complexities of plant–herbivore–predator changes under stress where the observed changes can result both from a direct effect of the pollutant on each trophic level and from indirect effects through trophic interactions. In these examples, because we are dealing with a simplified food chain, rather than a full community web, it is just possible to disentangle the different effects and so describe, albeit circumstantially, the consequences of their combined actions.

Experimental ecosystems

The disadvantage of such a selected food chain is that it excludes interactions between species *within* the same trophic level. We know that in many natural situations the effects of stress usually result in a shift in species composition; this aspect should therefore be included in experimental studies. At this level of complexity it is obvious that many factors will be involved beyond the actual pollutant effect. The enclosure of a body of water will necessarily impose artificialities compared with the larger system from which it has been abstracted. These artificialities will occur both in the physical environment created and in some unavoidable exclusions such as very large fish or mammals. Thus the system is bound to be stressed and the effective stress will depend on the degree of scaling down from the natural to the experimental system. For this reason a study of these 'natural' stresses is an essential preliminary to the consideration of the added effects of chemical pollutants.

Because of the technical problems of experimental work in the open sea, many of the earlier studies with experimental ecosystems have been done in fresh water, including the largest so far used (Lund 1972). A major study by Hall *et al.* (1970) is of special interest since, using 20 ponds, they studied the effects of variable nutrient addition and predator concentration on both production and community structure. 'Nutrients generally increased production of the

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

zooplankton but had little effect on community composition. Fish predation had profound effects on the size distribution of the zooplankton but only affected production at lower nutrient levels.' In particular, the fish predation increased the diversity of the zooplankton in comparison with ponds where such predation was absent. In the experimental system of Hall *et al.* there appeared to be a relatively stable prey selection system based on particle size. In terms of experimental technique, Hall *et al.* point out that the initial stress of changing the baseline nutrient level upsets the community structure.

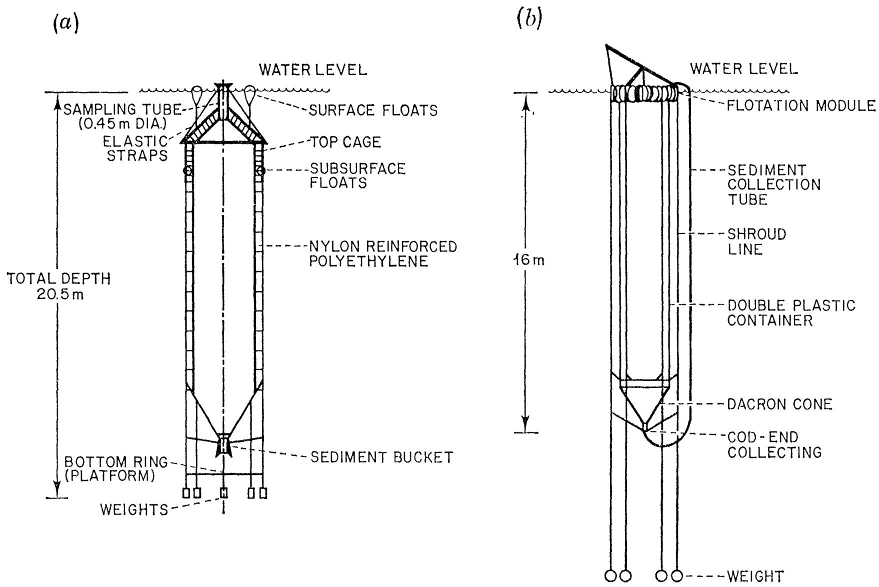

FIGURE 1. The main features of the enclosures used at (*a*) L. Ewe and (*b*) Saanich Inlet.

These freshwater experiments have certain technical similarities to the plaice–*Tellina* tanks but display the complexities of containing whole communities including plankton and benthos. Considering the needs of marine studies for relative simplicity in both logistic and ecological features, it was decided to contain planktonic ecosystems only. The basic idea of large flexible enclosures has been used before to study natural phytoplankton populations (McAllister *et al.* 1961) and the effects of oil on phytoplankton communities (Lacaze 1974). As a result of discussions between British, American and Canadian marine ecologists, it was decided to try to 'capture' communities from at least three trophic levels; plants–herbivores–small carnivores (see Menzel & Steele (1978) for review). This appeared to require enclosures containing approximately 100 m^3 and possibly very much more if, say, young fish were to be included.

Details of the design and first major experiments with copper in Saanich Inlet, Vancouver Island, Canada, and L. Ewe, Scotland, are given in *Bull. mar. Sci.* (1977, **27** (1)). Slight differences in design (figure 1) led to different methods of filling. The Saanich Inlet bags were hauled up like an expanding concertina to capture undisturbed stratified water columns. The L. Ewe systems required pumping to fill, thus creating an initially mixed and so less natural physical system.

Two copper experiments were done at Saanich, in spring and autumn 1974, with the copper added at 10 μg/l to certain bags a few days after water capture and maintained at this level by further addition when necessary. One experiment was done at L. Ewe with the use of four bags, two with a relatively high rate of nutrient addition and two with a low rate. Nutrients were added to replace those lost in detrital material which sank to the bottom of the cone and was removed for measurement. Copper was added at 10 μg/l about 40 days after the start of the experiment and no further additions were made so that there was a decrease in copper concentration with time. (There are certain other detailed differences between the two experiments for which the original papers in *Bull. mar. Sci.* should be consulted.) A comparison will be made between the second Saanich experiment and the two containers at L. Ewe with low nutrient additions.

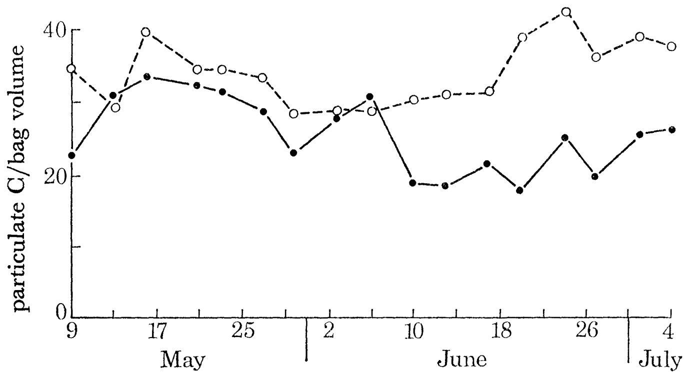

Figure 2. Total particulate organic carbon in two enclosures, C (•) and D (o), at L. Ewe (from Gamble *et al* 1977).

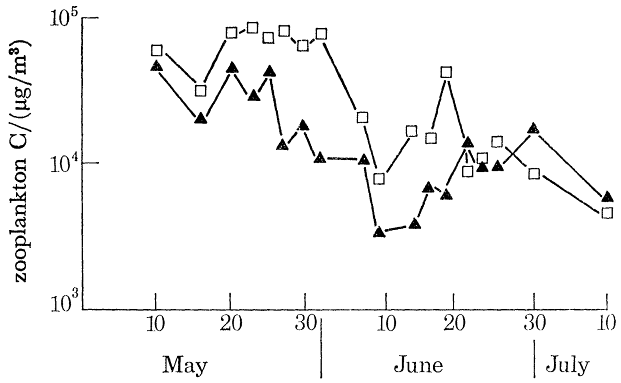

Figure 3. Total herbivorous zooplankton expressed as carbon in two enclosures, C (▲) and D (□), at L. Ewe (see Gamble *et al.* (1977) for details).

Comparison of the two systems

At L. Ewe there did not appear to be any immediate stress resulting from enclosure. Chlorophyll and particulate carbon levels (figure 2) were relatively constant. There was, however, a gradual divergence in the herbivorous zooplankton of the two bags (figure 3) and this has been explained by differences in the predator populations of the ctenophore *Bolinopsis infundibulum* which developed in the bags (figure 4). The possible effects of the divergence in herbivores was not apparent in the chlorophyll data but differences in phytoplankton species composition occurred and these differences are illustrated by the changes in the size composition of the particulate material at 10 m depth (figure 5). These changes occurred before copper was added to bag D on 14 June.

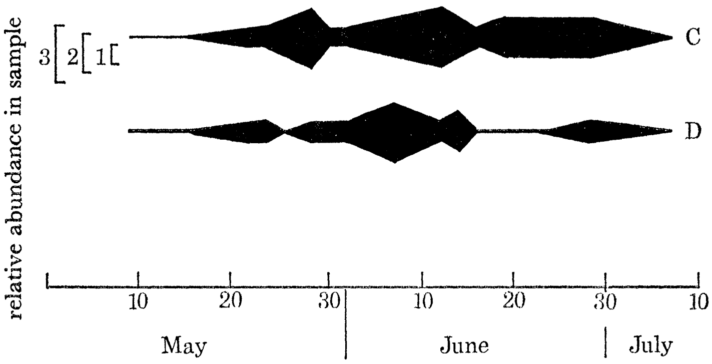

FIGURE 4. Abundance of *Bolinopsis infundibulum* in bags C and D at L. Ewe on a relative scale of 0–4 (because of difficulties with preservation of *B. infundibulum*, the earlier results are based only on disintegrated remains while the later values were confirmed by counts on fresh samples).

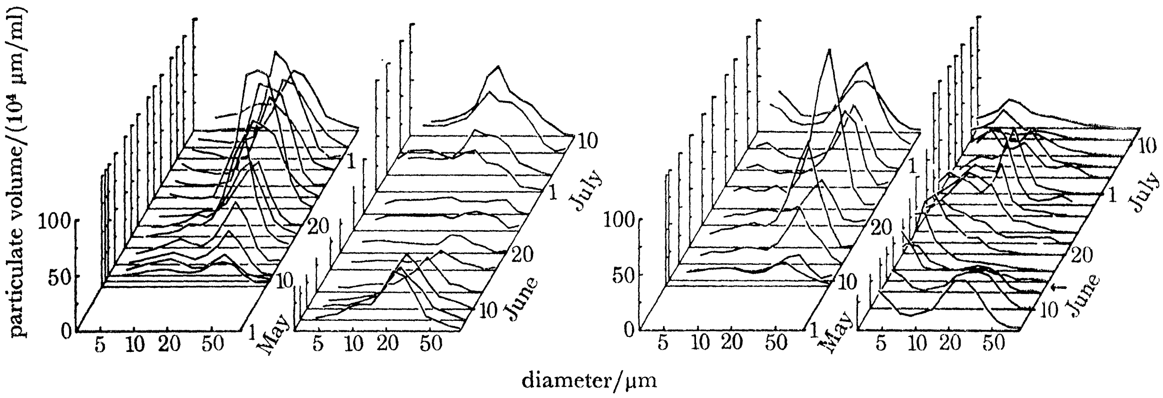

FIGURE 5. Size spectra of particulate matter at 10 m in bags C (left) and D (right) at L. Ewe.

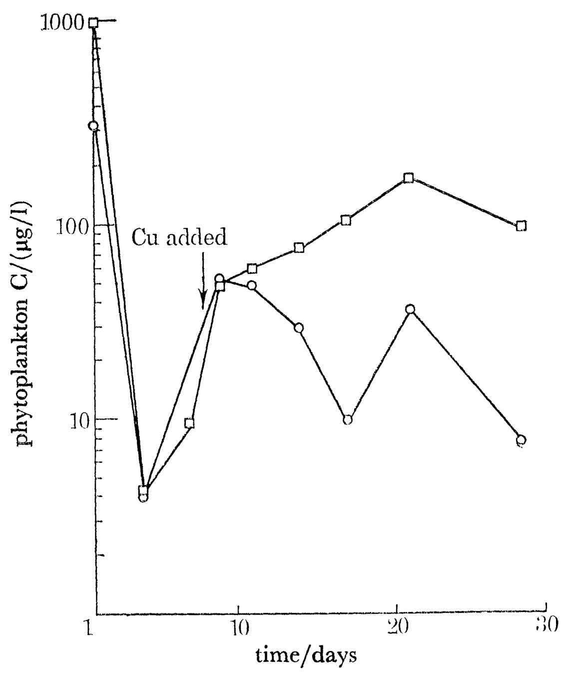

FIGURE 6. Changes in phytoplankton carbon (averaged between 0 and 10 m depth) in control (o) and 10 µg/l copper (□) enclosure at Saanich Inlet (from Thomas *et al.* 1977).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

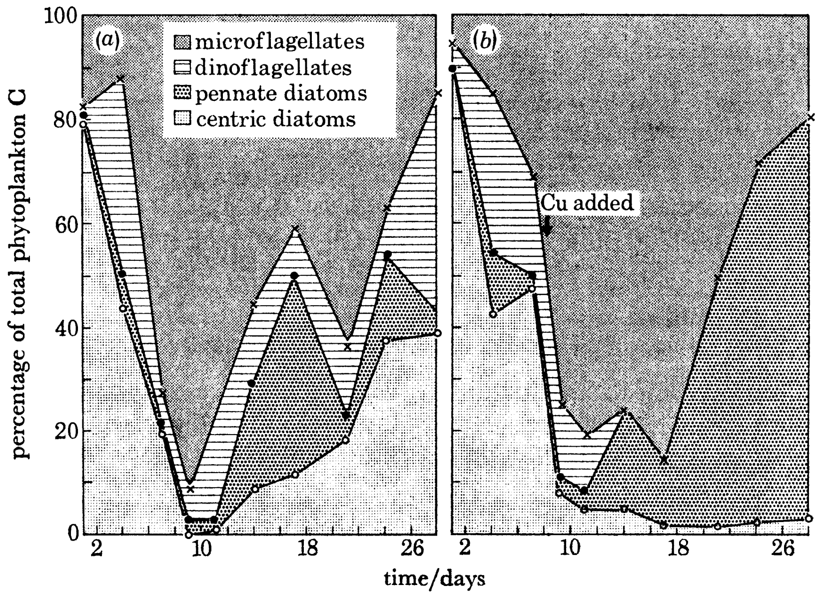

FIGURE 7. Proportions of carbon in different phytoplankton groups in (*a*) control and (*b*) 10 μg/l copper enclosures at Saanich Inlet (Thomas & Seibert 1977).

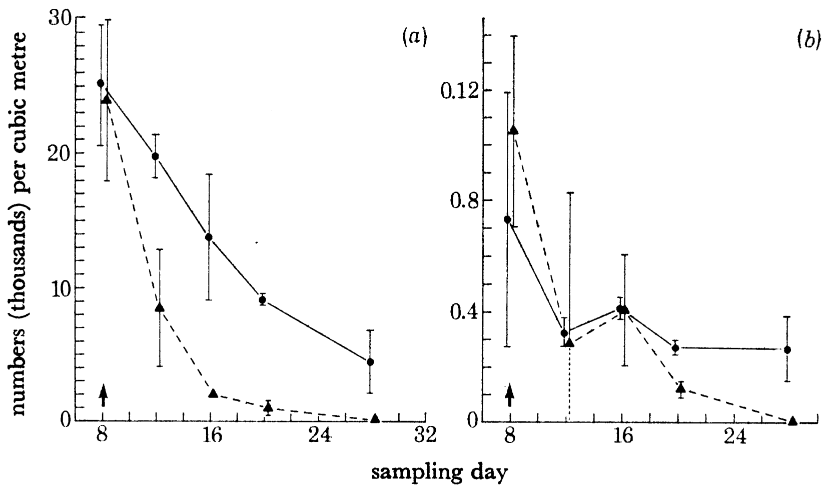

FIGURE 8. (*a*) Total number of zooplankton excluding ctenophores and medusae, and (*b*) total numbers of ctenophores and medusae, in control (•) and 10 μg/l (▲) copper enclosures at Saanich Inlet. Vertical bars represent ±s.d. Copper was added at day 8 (arrow).

At Saanich the copper was added 8 days after the capture of the water columns but the control enclosure shows that there was a dramatic decrease in carbon over the first three days, followed by some recovery (figure 6). These fluctuations were associated with marked changes in species composition during the period that copper was added and corresponded to a fallout of centric diatoms from the system (figure 7). Sampling of the zooplankton at the start of the experiment revealed rapidly declining populations and so plankton collections from outside the bags were added in an attempt to increase the density in the enclosures (G. D. Grice, personal communication). Sampling after these additions (figure 8*a*) shows a continuing marked decline both in the control and the treated enclosures. In these enclosures, as at L. Ewe, *Bolinopsis* spp. were dominant predators but no data are available on their densities. However, other predators showed a decline (figure 8*b*).

Events before addition of copper, or in controls without copper, are very different for the two locations. Some of these differences may be related to the different physical conditions in the two environments. Vertical mixing rates are considered to be lower in the enclosures than outside but this is accentuated at Saanich Inlet where rates measured in short-term dye experiments were one-third of those at L. Ewe (Steele *et al.* 1977). This is due in part to greater density gradients occurring naturally at Saanich Inlet but the difference was enhanced by the methods used for filling which, at L. Ewe, resulted in an initial complete mixing of the enclosed waters. Also, the rate of production at Saanich Inlet is generally higher than at L. Ewe and this, combined with low mixing at Saanich Inlet, can explain the rapid fallout of the larger diatoms (Eppley *et al.* 1978).

We can regard the Saanich Inlet ecosystem as controlled predominantly by physical processes and one main ecological parameter, phytoplankton sinking rate. In the outside water, grazing may become a significant factor later in the summer. In the bags the rapid drop in herbivore numbers can decrease this effect. The reasons for the drop in copepod numbers is not clear. There are three possibilities: (i) vertical migration of the copepods to the bottom of the bags occurs in L. Ewe and Saanich Inlet, at Saanich Inlet there are, on occasions, extremely high phytoplankton densities in the bottom cone and these might be a very unsuitable environment for the copepods; (ii) the change in size structure of the phytoplankton could provide the herbivores with a less suitable food, but this seems unlikely to account for the rapid mortality of the copepods; (iii) the numbers of carnivores, or their ability to catch the copepods, may be enhanced within an enclosure. The first and third seem likely explanations but the end result is that the phytoplankton–copepod interactions are probably less significant for the overall system than they are in L. Ewe. A probable conclusion is that the design of the Saanich bags and of the experiments emphasizes rather than alters the major features of the external environment.

Whereas at Saanich phytoplankton populations are determined by mixing and sinking, in L. Ewe the major factor is probably grazing which will play a dominant rôle in determining not only total phytoplankton carbon but also the size composition of the phytoplankton. From experiments at L. Ewe in 1973 (Davies *et al.* 1975) and 1974 (Gamble *et al.* 1977) it is possible that the method of filling may exclude (or damage) some predators thus tending to increase the grazers. Also, the near surface constriction of the bag decreases the plant production rate per unit surface area. In consequence, the limitation of phytoplankton by grazing may be greater than outside. Thus again the bag design and experimental technique may emphasize certain features of the interactions in the natural environment.

Combining these deductions, one has the conclusion that there are significant differences between the natural system in L. Ewe and Saanich Inlet and these differences are exaggerated in the respective enclosures.

There is, however, one common feature that has been observed and commented on in both experiments. The effects of stress resulting from enclosure are seen not so much in total biomass changes as in alterations in the size structure of the populations, especially the phytoplankton. This effect occurs rapidly at Saanich Inlet and more slowly at L. Ewe because of the different mechanisms, but it provides the major common conclusion from the joint work and gives a basis for the development of conceptual models as well as further environmental work. Additional stresses due to pollutants can be viewed in terms of these aspects of size structure but must be put in the context of the very different control mechanisms operating in the two areas.

The general picture of the effects of copper addition in 1974 at 10 μg/l is of (*a*) marked effects on the phytoplankton in Saanich and probable effects on the zooplankton; and (*b*) negligible observable effects on the phytoplankton in L. Ewe with possible effects on the zooplankton. The reasons for these differences need to be considered in the context of the factors controlling the populations.

One divergence between the experimental designs in the two areas should be noted. In Saanich, copper was added to recently filled bags after an interval of 8 days. In L. Ewe the copper was added 35 days after the bags were filled. The timing of the additions in Saanich meant that copper was added during, or towards the end of, the period of rapid decline in the phytoplankton and copepods. If we regard these declines as the consequence of stress, then the copper will have a synergistic effect. Laboratory experimental data suggest that larger diatom cells may be more sensitive to metal pollutants, partly through a decrease in growth rate, but particularly by an increase in sinking rate. The latter effect appears to have occurred in the September Saanich experiment, as shown by a comparison of sedimented material from control and 10 μg Cu/l enclosures (J. M. Davies & W. G. Harrison, personal communication).

For the zooplankton in Saanich, Gibson & Grice (1977) have pointed out the difficulty of determining any effect because of the large rates of decrease of the copepods in the controls. They suggest that this is mainly due to predation. Further, there is a decrease in predator numbers in the treated bags relative to the controls (which may be attributed to copper). Combining these two factors implies that the more rapid decrease in the copper-treated bags may be attributed to the effects of copper.

With the use of the control to correct for the mortality rate in the copper-treated bag, there is still a relative reduction over 4 days to 40 % of the initial numbers. Laboratory 96 h l.c.$_{50}$ experiments show a remarkable similarity between the populations at L. Ewe and Saanich Inlet and give a copper concentration of 50 μg/l, which is five times the dose in the enclosures. Thus there would appear to be a very large synergistic effect between the enclosure and the copper stress. This is confirmed by a short experiment in 1976 (Eppley *et al.* 1978) when 15 μg/l copper was added to an enclosure at Saanich which had been in place for 25 days. Because the phytoplankton species structure had already adapted to the enclosed environment, there were no significant alterations. Also, in turn, the zooplankton showed only minor and very short term response to a copper level considerably higher than that which produced marked alteration in the earlier experiments. This experiment was closer in design to those carried out at L. Ewe.

In L. Ewe there was no overall decrease in herbivore numbers after the copper addition but otherwise the same features were observed: (*a*) a relative decrease in predators (*Bolinopsis*) in the polluted bags, and (*b*) a relative decrease also in numbers of copepods in the polluted bags. From these *relative* changes in L. Ewe the same tentative conclusions have been drawn (Gamble *et al.* 1977) about a possible effect of copper at the herbivore–predator level. The correspondence between the patterns in the two very different environments enhances this conclusion.

For the phytoplankton in the L. Ewe bags in 1974 there is no correspondence with the marked changes at Saanich in 1974. There are various explanations for this divergence but the most likely is based on the evidence of differences in the ecosystem structure. In the simplest terms, differences in phytoplankton in L. Ewe do not get an opportunity to appear because of grazing pressure. The evidence of Reeve *et al.* (1977) that grazing rates can be affected by 10 μg Cu/l will complicate the situation more at L. Ewe than at Saanich. This complication is increased by the size selective nature of zooplankton grazing on phytoplankton. These factors might tend to obscure observable effects of copper on phytoplankton at L. Ewe.

Discussion

In experimental ecosystems, we are concerned with two categories of effect of a pollutant: that arising from a direct impact on a species or a trophic level, and that from the interaction between species either within or across trophic levels. Laboratory studies with single species indicate that many of the common pollutants such as copper and mercury will have effects on organisms in all the main trophic levels although the degree of this effect can vary, for example with species of phytoplankton or size of herbivore (Thomas & Seibert 1977; Reeve *et al.* 1977). The invertebrate predators appear to be particularly sensitive to metals such as copper and mercury. Thus we can expect such pollutants to exert a broad but variable spectrum of stresses on ecosystems, natural or experimental.

On the other hand, certain 'natural' stresses may be much narrower in their impact. Thus rates of nutrient addition should affect only the phytoplankton. Deliberate or inadvertent variations in certain predators will alter only the herbivore populations. From the detailed experiments of Hall *et al.* (1970) and from the first 30 days of the L. Ewe 1974 studies, it appears that an increase in nutrients (as expected) increases the productivity and can increase herbivores and predators (in the experiments of Hall *et al.*) without significant alterations in the species composition. On the other hand, changes in predator numbers may have only slight effects on the general productivity but can produce very marked changes in species composition, not only in herbivores but possibly in phytoplankton. The nature and extent of such changes, in both directions, depends on the degree of coupling between different trophic levels.

General hypotheses about these interactions can help in the interpretation of experiments with added pollutants and, especially, in relation to results obtained with different experimental ecosystems. One tentative conclusion is that, where most of the energy produced by phytoplankton passes up the food chain, the grazing process may ameliorate any effect of pollution on the phytoplankton. This contrasts with a situation where much of the energy may go downwards, physically, to deeper anaerobic layers. Theoretical work (Steele & Frost 1977) would support this hypothesis. Because of these differences in response, generalizations about the effect of a particular pollutant are not acceptable. Recent results from mercury-treated bags (*Mar. Sci. Commun.* 1977, **3** (4)) showed that relatively high mercury levels (5 μg/l) produced a decline in zooplankton combined with an increase in cell size of the phytoplankton. These results indicate that we are not likely to be able to present simple generalizations about pollutant stress within an ecosystem.

It would appear that the pelagic ecosystem is itself a critical variable and the response to enclosure is very different in different areas. As a consequence of the natural differences which can be enhanced by enclosure, the response to pollutants can be very different. The Saanich results illustrate the marked synergistic effects of physical stress and pollutant addition. The L. Ewe data show that, at the population level, there is great qualitative similarity between the effects of natural ecological changes and pollutant additions. These results lead to the assumption that, at the population level, the observable consequences of copper (and of other pollutants) are similar to the natural stresses imposed on these communities. Stresses can be synergistic, as at Saanich, or they may alleviate each other, as in the mercury tanks at L. Ewe.

This similarity in response and possible synergism of combined effects also imposes problems in the analysis of such experiments. Because of the similarity, it becomes very difficult to separate the sublethal effects due to the pollutant. For this reason, only the relatively catastrophic changes may be apparent to the experimenter. These problems raise questions about the relative value for pollution studies of (i) captured ecosystems which are as natural as possible in the sense that the ecosystem survives with minimal management, and (ii) food chains composed of selected organisms where there is also significant continuing control.

Table 1. A summary of the advantages and drawbacks of different types of experiments

	laboratory		outdoors	
number of species	1	2	3	many
advantages	increasing container size increasing exposure duration increasing sensitivity to stress			
problems	decreasing cheapness decreasing replication decreasing operator control decreasing isolation of cause and effect			

The plaice–*Tellina* food chain in shore-based tanks is an example of type (ii) where only selected species of herbivore and predator are used and where there is a controlled, and large, rate of water exchange. Such techniques provide more information on the effect of a pollutant on the dynamics of a particular prey–predator interaction but less idea of how this will affect the larger system of which this is a part. Comparison of the tank and bag experiments at L. Ewe indicated that the tanks provided a more sensitive index of effect because of the relative simplicity of the tank ecosystem.

It is necessary to consider the use of each system for pollution studies in the context of other experimental approaches. Table 1 shows the consequences of going from one-species laboratory studies to large-scale experimental ecosystems. Increasing container size should be more natural and should permit longer-term experiments which are generally considered to give more sensitive responses to pollutant stress. On the other hand, such very large systems can be extremely expensive, making the normal scientific requirement for adequate replication difficult to achieve. Further, the apparent advantage of having a semi-natural system which requires minimal interference of the experimenter also implies that, without this control, one will have much less understanding of the nature of interactions within the system. Cumulatively, these difficulties mean that, as Menzel (1977) has indicated, subtle differences are very difficult to detect and to explain. In consequence, although the system may be inherently very sensitive to stress, only large, almost catastrophic, differences between two enclosures can be explained with any assurance. The systems are, however, useful in observing transfers of pollutants, physically through vertical downward movement, through changes in chemical speciation, and through the existence, or non-existence, of transfers into organisms.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The experiments conducted so far with large experimental ecosystems have probably taught us more about the general ecological interactions in such systems than about subtle long-term effects of pollutants. This knowledge is not only valuable in its own right but may be more useful in an indirect rather than a direct way. Our understanding of the factors determining the robustness of these systems is essential before we can interpret the consequences of a pollutant. Thus an extension and elaboration of these studies as part of general marine ecosystem research may be most desirable.

Similarly, the plaice–*Tellina* experiments were originally started as part of an ecological program but have proved of value in assessing environmental quality standards for a range of pollutants and in providing data to link pollutant load with specific effects. It is possible that simple food *chains* of this type derived from a more general and complex ecosystem may be the best combination of naturalness and experimental control for certain types of pollution study.

Lastly, it is essential to emphasize that both need to be supported by laboratory experiments on one or two species so that, for example, the work with herring larvae mentioned earlier can be extended to large-scale studies of both the ecological problems of growth and mortality and to studies of the effects of pollutants under more natural conditions.

References (Steele)

Davies, J. M., Gamble, J. C. & Steele, J. H. 1975 Preliminary observations with a large plastic enclosure. In *Estuarine research*, vol. I (ed. L. E. Cronin), pp. 251–264. Academic Press.

Eppley, R. W., Koeller, P. & Wallace, Jr, G. T. 1978 Stirring influences the phytoplankton species composition within enclosed columns of coastal seawater. *J. exp. mar. Biol. Ecol.* (In the press.)

Gamble, J. C., Davies, J. M. & Steele, J. H. 1977 Loch Ewe bag experiment, 1974. *Bull. mar. Sci.* **27**, 146–175.

Gibson, V. R. & Grice, G. D. 1977 Response of macro-zooplankton populations to copper: controlled ecosystem pollution experiment. *Bull. mar. Sci.* **27**, 85–104.

Hall, D. J., Cooper, W. E. & Werner, E. E. 1970 An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnol. Oceanogr.* **15**, 839–928.

Holling, C. S. 1973 Resilience and stability of ecological systems. *A. Rev. Ecol. Syst.* **4**, 1–23.

Lacaze, J. C. 1974 Ecotoxicology of crude oils and the use of experimental marine ecosystems. *Mar. Pollut. Bull.* **5**, 153–156.

Lund, J. W. G. 1972 Preliminary observations on the use of large experimental tubes in lakes. *Verh. int. Verein. theor. angew. Limnol.* **18**, 71–77.

McAllister, C. D., Parsons, T. R., Stevens, K. & Strickland, J. D. H. 1961 Measurements of primary production in coastal sea water using a large volume plastic sphere. *Limnol. Oceanogr.* **6**, 237–258.

Menzel, D. W. 1977 Summary of experimental results: controlled ecosystem pollution experiment. *Bull. mar. Sci.* **27**, 142–145.

Menzel, D. W. & Steele, J. H. 1978 The application of plastic enclosures to the study of pelagic marine biota. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* (In the press.)

Reeve, M. R., Gamble, J. C. & Walter, M. A. 1977 Experimental observations on the effects of copper on copepods and other zooplankton: controlled ecosystem pollution experiment. *Bull. mar. Sci.* **27**, 92–104.

Saward, D., Stirling, A. & Topping, G. 1975 Experimental studies on the effect of copper on a marine food chain. *Mar. Biol.* **29**, 351–361.

Steele, J. H., Farmer, D. M. & Henderson, E. W. 1977 Circulation and temperature structure in large marine enclosures. *J. Fish. Res. Bd Can.* **34**, 1095–1104.

Steele, J. H., McIntyre, A. D., Johnston, R., Baxter, I. G., Topping, G. & Dooley, H. D. 1973 Pollution studies in the Clyde Sea Area. *Mar. Pollut. Bull.* **4**, 153–157.

Steele, J. H. & Edwards, R. R. C. 1970 The ecology of O-group plaice and common dabs in Loch Ewe. IV. Dynamics of the plaice and dab populations. *J. exp. mar. Biol. Ecol.* **4**, 174–187.

Steele, J. H. & Frost, B. W. 1977 The structure of plankton communities, *Phil. Trans. R. Soc. Lond.* B **280**, 485 534.

Stirling, E. A. 1974 Some effects of heavy metal pollutants on the marine bivalve mollusc *Tellina tenuis* Da Costa. Ph.D. Thesis. University of Aberdeen.

Thomas, W. H., Holm-Hansen, O., Seibert, D. L. R., Azam, F., Hodson, R. & Takahashi, M. 1977 Effects of copper on phytoplankton standing crop and productivity: controlled ecosystem pollution experiment. *Bull. mar. Sci.* **27**, 34–43.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Thomas, W. H. & Seibert, D. L. R. 1977 Effects of copper on the dominance and the diversity of algae: controlled ecosystem pollution experiment. *Bull. mar. Sci.* **27**, 23–33.
Trevallion, A., Edwards, R. R. C. & Steele, J. H. 1970 Dynamics of a benthic bivalve. In *Marine food chains* (ed. J. H. Steele), pp. 285–295. Edinburgh: Oliver & Boyd.
Ward, D. V., Howes, B. L. & Ludwig, D. F. 1976 Interactive effects of predation pressure and insecticide (Temefos) toxicity on populations of the marsh fiddler crab *Uca pugnax*. *Mar. Biol.* **35**, 119–126.
Westernhagen, H. V., Rosenthal, H. & Sperling, K.-R. 1974 Combined effects of cadmium and salinity on development and survival of herring eggs. *Helgoländer wiss. Meeresunters.* **26**, 416–433.

Discussion

R. J. MORRIS (C.U.E.P., *Department of the Environment*, *London*, *U.K.*).

First, surely it is difficult to compare the Saanich Bay and L. Ewe experiments without adequate data on changes in the chemical speciation of the metals (Cu, Hg) during the course of each of the experiments? Will the fate and behaviour of Cu and Hg not be controlled by the separate water chemistries of the two locations?

Secondly, can Dr Steele properly compare the results of the L. Ewe bag Cu experiment with those from Dr Stebbing's Cu experiments? The L. Ewe experiment was based on the addition of a single pulse of Cu^{2+}, whereas the I.M.E.R. experiment was based on a daily addition of fresh Cu^{2+}.

J. H. STEELE.

1. I agree that more information is needed from both areas on long-term changes in water chemistry. However, small-scale experiments in the different waters with plankton from each area gave similar short-term effects suggesting that some of the differences were ecological rather than chemical.

2. The proper comparison is between Dr Stebbing's results and the tank experiments with copper and small flat fish at L. Ewe where there was daily addition of fresh copper (Saward *et al.* 1975).

M. WALDICHUK (*Pacific Environment Institute*, *West Vancouver*, *B.C.*, *Canada*). From what has been said in the two papers on enclosed ecosystems, I should presume that there are two problems of comparability of data acquired in enclosures with those from natural marine situations: (1) lack of lateral exchange by advection and diffusion as occurs in nature; and (2) wall effects. It would seem that there is no known way of overcoming (1), but it may be possible to minimize (2) by increasing the size of the enclosure. Increasing the size, of course, leads to greater cost. In Saanich Inlet, the full-scale bags were used as well as units one-quarter the size. Does Dr Steele now have an idea of the optimum size of enclosure, bearing in mind the minimization of wall effects, logistics of transportation and installation of units and costs?

J. H. STEELE. The appropriate size of the container depends on the experiment, particularly the length of time involved. Thus quarter-scale enclosures are still useful for certain experiments on phytoplankton and on chemical speciation while the full scale model is necessary for work with young fish. In L. Ewe, Scotland, approximately half-scale containers, holding 350 m^3, are being used for study of fish larval growth and mortality.