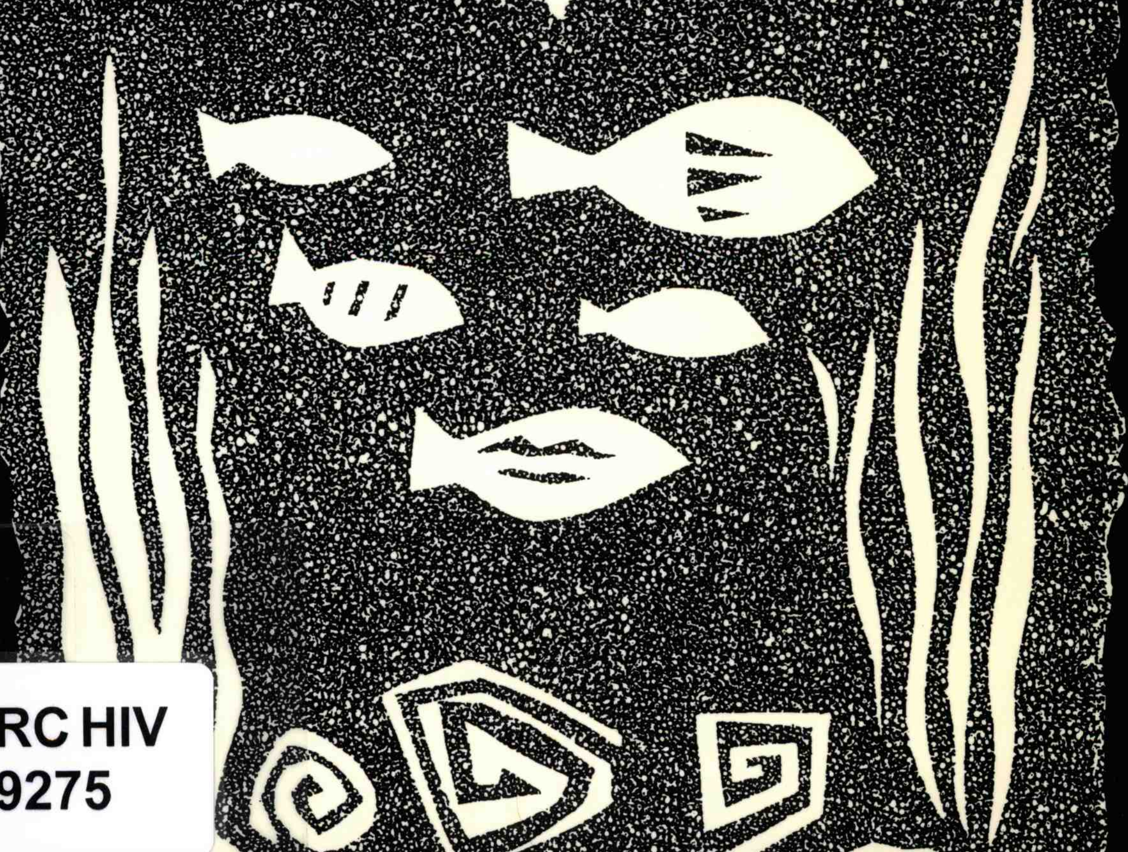
Marine Ecosystem Enclosed Experiments

Proceedings of a symposium held in Beijing, People's Republic of China, 9–14 May 1987



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Editor: C.S. Wong and P.J. Harrison

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Abstract

This symposium on marine ecosystem enclosed experiments (MEEE) consists of nine review papers that describe various types of ecosystem enclosures and a series of papers resulting from enclosure experiments in Xiamen, People's Republic of China, and Saanich Inlet, BC, Canada. The reviews on types of enclosures include benthic enclosures for rocky and sandy shores and the effects of pollutants (primarily hydrocarbons) on bacteria, macroalgae, and invertebrates. The pelagic enclosures were used to study the control of phytoplankton blooms, the uptake and release of dissolved organic substances, and the effects of pesticides on freshwater ecosystems.

Six enclosure experiments were conducted in China and Canada from 1986–87. Some of these experiments examined the effects of contaminated sediments, primarily heavy metals, on bacteria, phytoplankton, and zooplankton and the pathways and fates of these heavy metals in the seawater. Other experiments studied the chemistry and biological effects of chemically dispersed oil.

Résumé

Ce compte rendu du symposium sur les expériences faites en écosystèmes marins comprend neuf communications qui décrivent les écosystèmes retenus et les expériences faites à Xiamen en République populaire de Chine et à Saanich Inlet, C.-B., au Canada. Les communications portent, notamment, sur les écosystèmes benthiques des littoraux rocheux et sablonneux et sur les effets des polluants (surtout les hydrocarbures) sur les bactéries, les grandes algues et les invertébrés. Les expériences sur le contrôle des brutales pullulations ("blooms") du phytoplancton furent menées dans les écosystèmes pélagiques, ainsi que l'absorption et le dégagement des substances organiques dissoutes et les effets des pesticides sur les écosystèmes d'eau douce.

Six expériences ont été faites en Chine et au Canada entre 1983 et 1987. Certaines ont porté sur les effets des sédiments contaminés, principalement par des métaux lourds, sur les bactéries, le phytoplancton et le zooplancton et sur le cheminement et le sort de ces métaux lourds dans l'eau salée. D'autres expériences portaient sur la chimie et les effets biologiques du pétrole dispersé chimiquement.

Resumen

Este simposio sobre Experimentos Marinos en Ecosistemas Cerrados (MEEE) consistió en nueve trabajos de análisis que describen varios tipos de enclaustramientos ecosistémicos y una serie de trabajos derivados de experimentos con estos enclaustramientos en Xiamen, República Popular de China, y en Sannich Inlet, Canadá. Los estudios incluyen enclaustramientos bentónicos para costas rocosas y arenosas, y los efectos de los contaminantes (fundamentalmente hidrocarburos) sobre bacterias, macroalgas e invertebrados. Los enclaustramientos pelágicos se utilizaron para estudiar el control de la reproducción del fitoplancton, la ingestión y expulsión de substancias orgánicas disueltas y los efectos de pesticidas en los ecosistemas de agua dulce.

Se realizaron seis experimentos en ecosistemas cerrados en China y Canadá, de 1983 a 1987. Algunos de estos experimentos examinaron los efectos que ejercen los sedimentos contaminados, fundamentalmente los metales pesados, sobre bacterias, fitoplancton y zooplancton, y el ciclo y destino final de estos metales pesados en el agua de mar. Otros experimentos estudiaron los efectos químicos y biológicos de los aceites crudos dispersados por medios químicos.

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Use of Rocky-Shore Mesocosms in Pollution Research[1]

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Four 25-m^3 experimental, rocky-shore communities have been established at the Marine Research Station Solbergstrand, Norway. The communities are enclosed in concrete basins equipped with artificial wave and tide simulation and a water-exchange system to ensure an adequate supply of recruitment stages of algae and animals. The communities were established by transplantation and natural recruitment between 1979 and 1982. They have recently been used in a 3-year experiment on the effects of continuous exposure to low concentrations of diesel-oil hydrocarbons. The experiment has shown that rocky-shore mesocosms can be run successfully for several years, enabling complex studies of the effects of chronic perturbations, especially with respect to populations and individuals, to be carried out. The size of the model community is critical, particularly in relation to sampling requirements, but in hard-bottom communities, this can be minimized through the use of nondestructive sampling. The wave and tide system should have a built-in stochastic element because communities that have developed under the physical constancy of the present system are vulnerable to even slight maladjustment of, for example, the water level. A major problem encountered in interpreting results has been natural deviation among the communities over the years because of slight differences in community structure and recruitment. Deviation may, to some extent, be counteracted by manipulating the population sizes, but strict manipulation should be avoided because it represents an unnatural forcing factor on the system. Long-term benthic mesocosms must be regarded as a series of fairly similar and partly independent communities, not as experimental replicates in laboratory terms.

In the context of experimental model ecosystems, little attention has been paid to the hard-bottom benthos. Most mesocosm systems deal with the pelagic environment, subtidal soft bottoms, salt marshes, or other soft shorelines. The most comprehensive hard-bottom systems reported in the literature are the estuarine *Fucus vesiculosus* community mesocosms at Karlskrona in Sweden (Notini et al. 1977) and the marine rocky-shore mesocosms at the Marine Research Station Solbergstrand in eastern Norway (Bakke 1986; Gray 1986).

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[1] Marine Research Station Solbergstrand, Contribution 23.

The paucity of hard-substrate mesocosms available is, in a way, surprising as hard-bottom communities in both littoral and sublittoral zones should lend themselves to mesocosm experimentation. The physical structure is, in essence, two-dimensional. Artificial substrates can be created using concrete or rocks, or both, and, because most organisms are sessile, they can be moved into mesocosms without much disturbance by transplanting their substrate rocks. One of the reasons why only a few rocky-substrate mesocosms have been established could be that in-situ experiments can easily be performed in hard-bottom communities, especially in the littoral zone (e.g., Dayton 1975; Lein 1980; Bonsdorff and Nelson 1981). However, there are several situations where in situ experiments are not practical for logistic or other reasons and where mesocosms are the best alternative.

The purpose of this paper is to report on certain advantages and disadvantages of using the rock-littoral mesocosms established at the Marine Research Station Solbergstrand, and to assess this approach in comparison with in-situ experiments.

Rocky-shore mesocosm design

The Solbergstrand mesocosms were established in 1979. They consist of four outdoor concrete basins, each 8 m × 5 m × 1.5 m and containing 25 m^3 of seawater at midtide (Fig. 1). A wave generator, consisting of two heavy-duty polyvinyl chloride (PVC) pipes in a steel frame, runs along the entire side of each basin (Fig. 2). The wave generator moves up and down mechanically (18 strokes·min^{-1}), creating regular waves running across the basin to the other side where the main model community is established on a series of steps constructed to imitate a slanted shore.

The basins are supplied with running seawater pumped by impeller pumps from

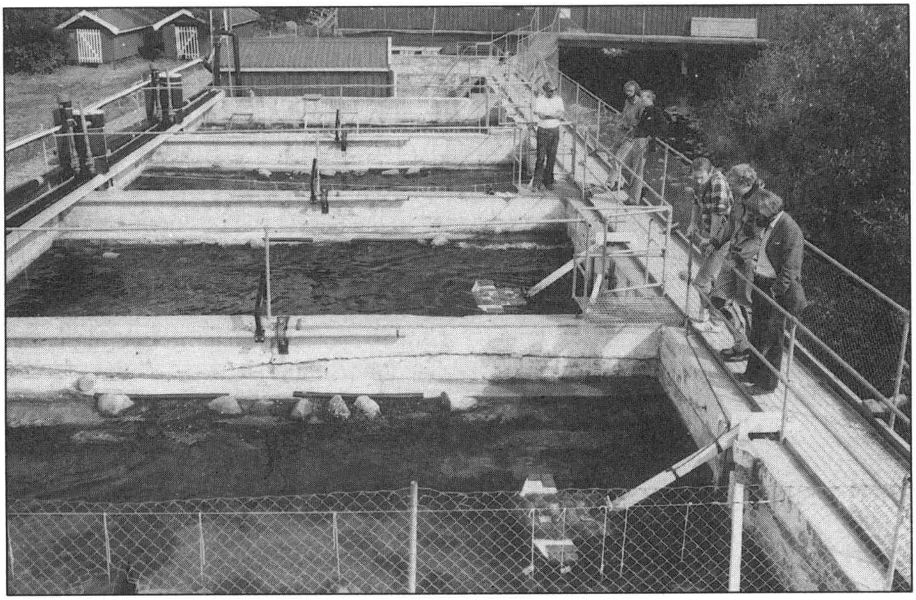

Fig. 1. Four concrete basins used to establish Solbergstrand mesocosms.

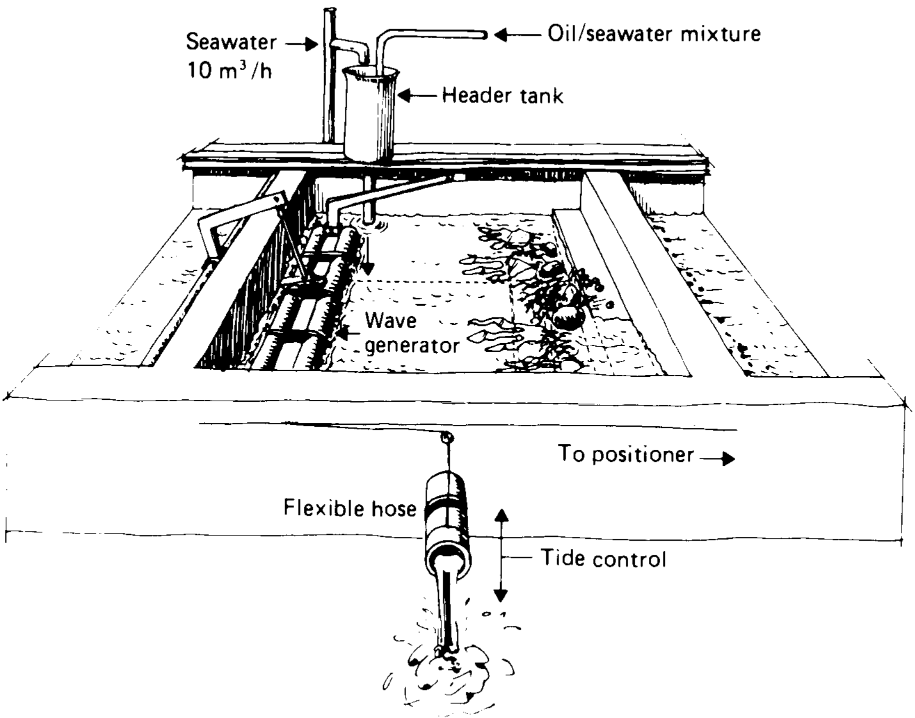

Fig. 2. Schematic of one of the basins.

a depth of 1 m in the fjord outside. The water enters the basins through a header tank, ensuring a stable flow rate of 10 m^3 per basin. The water exchange rate is normally in the range of 2–4 h. From each basin, a subsurface outlet leads to a flexible hose with a stiff nozzle that is raised and lowered automatically to regulate the basin water level in a 12-h sinusoidal cycle following the tidal rhythm and nominal amplitude (30 cm) on the shore. During extreme winter temperatures, water may be taken at 13 m depth to prevent ice formation in the basins.

The first community was established in October 1979. Rocks with algae and animals were transplanted from the littoral zone to the basins and positioned on the steps at a proper tidal level. The basins were then run without any manipulation for 3 years to let the communities develop and stabilize through self-propagation and through larvae and spores entering the basins with the water. At the end of this period, the basin communities contained about 50 species of macroscopic algae and animals. The community structure was typical for medium-sheltered shores of the middle and outer Oslofjord region.

Oil experiment

The mesocosms were established to perform long-term experiments on the effects of water-transported pollutants. Recently, the communities have been used in an experiment on the effects of chronic oil discharge. For 2 years, starting in September 1982, two of the communities were continuously exposed to a wateraccommodated fraction (WAF) of diesel oil in seawater, while the other two were run as controls. The WAF was produced by continuously mixing seawater and oil at a ratio of 1 800:1 in a 580-L mixing chamber. After removing excess oil through automatic surface skimming, the WAF was pumped into the header tank of the exposed basins at nominal dilutions of 75:1 and 300:1, giving average oil concentrations of 129.4 ± 33.3 (SD) and 30.1 ± 10.3 $\mu g \cdot L^{-1}$ in the water of the two basins. After the 2-year exposure period, the basins were observed for another year to study their recovery from the effects of the oil.

Overview of results

The studies performed during the exposure and recovery periods looked at the following:

- Hydrocarbon concentration in basin water, in primary growth on rock, and in tissues of *Ascophyllum nodosum*, *Fucus serratus*, *Mytilus edulis*, and *Littorina littorea*;
- Gross community structure and population size of macroscopic algae and animals;
- Colonization pattern, growth, metabolism, and the effects of grazing on primary rock communities;
- Individual growth of *A. nodosum*, *Laminaria digitata*, *Ulva lactuca*, and *L. littorea*;
- Population dynamics and genetics of *Balanus balanoides*, *L. littorea*, and *M. edulis*; and
- Energy conversion and utilization, and biochemical, cytochemical, and histological stress responses in *M. edulis* and *L. littorea.*

These subprojects were performed by individual researchers and students and are, at present, being published in various journals. Summaries of the results are given by Gray (1987) and Bakke (1986). Some of the main effects recorded include the following: a population collapse in *M. edulis* (Bokn and Moy 1985) and amphipods (Bakke, unpublished data); reduced growth in *M. edulis* (Thome and Walday 1984), *A. nodosum*, and *L. digitata* (Bokn 1985); reduced recruitment in *L. littorea* (Lystad and Moe 1985); reduced photosynthesis in the primary rock community (Pedersen 1985); increased cover of opportunistic green algae; reduced feeding and energy utilization in *M. edulis* (Widdows et al. 1985) and *L. littorea* (Bakke 1985); and clear signs of biochemical and cytological stress in *M. edulis* and *L. littorea* (Livingstone et al. 1985; Lowe and Pipe 1985; Moore et al. 1985).

Both algae and animals accumulated oil hydrocarbons in their tissues (Sporstol and Oreld 1985). The population genetics of *M. edulis* did not demonstrate any short-term selection due to the oil (Fevolden and Garner 1986). The severity of effects, in most cases, was dependent on the season, but was not always related to dosage. After the 1-year recovery period, most responses returned to normal.

How well do the mesocosms replicate nature?

A model ecosystem will never copy nature in all respects, but the better a mesocosm imitates natural conditions, the stronger the predictive value of any experimental conclusions. Certain requirements, regarding physical conditions and biological interactions, must be fulfilled in a good mesocosm design.

Physical condition

In a model ecosystem, the physical environmental conditions, with respect to substrate area and character, and water regime should be as natural as possible for the organisms and populations under investigation. This is a prerequisite if the organisms are to respond to a perturbation as they would in nature. The physical environmental constraint of the mesocosm should not in itself be a forcing factor interfering with experimental manipulation.

The model must be large enough to provide the populations under investigation necessary moving space. In rocky-shore mesocosms, this condition is easy to achieve as most of the organisms are sessile or show little migratory movement. Migratory fish demanding larger space were not part of the model community. The total hard-substrate area in each basin is 70 m^2, and the area of the main community space, the steps, is 20 m^2. The basin size is comparable to numerous smaller land-locked bays along the Norwegian coast and should, therefore, represent an adequate realm for the motile fauna of the community, mainly periwinkles, shore crabs, amphipods, isopods, and starfish. A disadvantage of the basins is that the shallow depth prevents motile animals from seeking deep-water shelter as they would normally do during periods of extreme temperatures, but this was counteracted by use of deep water during winter.

The substrate of the basins is a mixture of granite rock and concrete. Except for some of the macroalgae (e.g., *A. nodosum*), which are only found on the rocks on which they were transplanted, there was no obvious difference in the community pattern on neighbouring rock and concrete surfaces. Cracks in the concrete and crevices between the rocks represent shelter from predation for small and juvenile animals.

Hydrographic regime

The high water turnover ensured similar temperature and salinity in the basins as on the shore most of the time. Long-term seasonal change in the temperature followed the surface of the fjord closely, but the basins heated up slightly faster during spring and cooled slightly faster during autumn than the fjord. The mean monthly temperature for the period 1980–1985 ranged from 0.6°C in March to 18.9°C in August compared with 0.4°C and 18.3°C, respectively, in the fjord (Bakke 1986). Similarly, the mean salinity ranged from 30.5‰ in January to 17.8‰ in June in both the basins and the fjord. During extreme summer heat, the basin-water temperature exceeded that of the shore water by a maximum of 2.6°C over the years 1980–1986, but no mortality due to this raised temperature has been reported for any of the populations under investigation. Elevated surface temperature during the summer is also a common natural phenomenon in small shallow bays in the Oslofjord.

Switching to a water supply from 13 m depth during the winter not only prevented ice formation in the basins but also produced water conditions similar to those that the motile animals would experience if they had been able to migrate into deeper water. Still, a rapid decline in the population size of two species, *Asterias rubens* and *Carcinus maenas*, occurred during the winter of 1982–1983, and can be explained as resulting from a combination of low temperatures and a shortage of preferred food in the basins.

Waves and tide

The wave and tide fluctuations of the mesocosms lack the variability found on the shore. The influence of wind and hydrostatic pressure may create a real tidal amplitude in the Oslofjord of about 1 m compared with the regular 0.3 m in the basins. The waves in the fjord also change frequently, in contrast to the basins. The stability of the water regime in the basins created sharply defined borders between zones of total desiccation, periodic air exposure, and total immersion. Because this is the regime under which the organisms with different demands on immersion periods have been established, the sessile part of the community is vulnerable to even slight misadjustment of the water level. This occurred once during the oil experiment in July 1983. A slight lowering of the water level left several granite tiles dry for prolonged periods, causing problems with respect to interpreting data on primary community metabolism (Pedersen 1987).

In rocky-shore mesocosms, therefore, it would be an advantage if wave action and tide range were variable and if stochastic changes were built into the routine regulation of waves and tide.

Community development and deviation

A dominant succession of keystone organisms was demonstrated during the 3 years of community establishment. After the main transplantation in 1979, *M. edulis* settled densely on walls, wave generators, and algae in all basins in 1979 and 1980. This was followed by the appearance of predators *A. rubens* and, slightly later, *C. maenas*, which reduced the *M. edulis* population drastically during 1981–1982. These predators were themselves reduced in number after the summer of 1982, presumably due to a lack of food and low winter temperatures. *L. littorea* and many of the macroalgae (*Cladophora rupestris*, *Fucus distichus* ssp. *edentatus*, *Laminaria saccharina*, *L. digitata*, and *Phymatolithon lenormandii*) showed a gradual increase in density or cover during the community-establishment phase.

Although every effort was made to make the four basins as similar as possible at the time of transplantation, the communities gradually deviated in structure during subsequent years. The species composition and dominant pattern were the same in all basins, but population densities differed for several species, e.g., *F. distichus*, *M. edulis*, and *L. littorea* (Bokn and Moy 1985).

Grazing by *L. littorea* has a strong structuring effect on the algal community in the Oslofjord (Lein 1980). The difference in density of *L. littorea* among the basins was reflected in the densities of its favoured food organism, *Ulva lactuca* (Bokn and Moy 1985) and benthic diatoms (Follum 1985), but not in another potential food algae, *Entermorpha* sp. Moe et al. (1985) explained the differences in density and age structure of *L. littorea* as resulting from *C. maenas* praying on juvenile winkles. The basin with the highest number of crabs had the lowest number of winkles and a dominance of large individuals. Similarly, an inverse relationship between the densities of *M. edulis* and *A. rubens* was indicated in the two control basins (Bokn and Moy 1985). For the other species, basin differences had no observable repercussion on the rest of the community. It must also be stressed that although differences between the control basins made interpreting results difficult in many cases, the differences were not greater than the patchiness characteristic for rocky shores due to changes in topography, inclination, and aspect.

Deviation among replicate communities with time is a general disadvantage in long-term mesocosm experiments and, in most cases, it is unavoidable unless strong population management is executed. Such manipulation is undesirable primarily because it could, in itself, be a significant factor in structuring the community, thereby masking test–control differences of interest. Instead, one should try to prevent deviation through careful analysis of the possible causes in each case, which would then allow one to establish a design that would minimize these factors. In the present rocky-shore mesocosm system, there are several basin differences that might, a priori, cause deviation among communities:

- The structure of the community initially transplanted,
- Microhabitats of the substrate,
- The wave pattern due to slight differences in basin dimensions,
- The input of recruits with the water entering the basin, and
- Temperature differences between the outer and middle basins.

Of these, the differences in microhabitats and recruits have probably been the most significant. The concrete of one of the basins has been damaged more over time than in the other basins, creating a multitude of cracks and crevices. This basin had by far the highest densities of winkles (Bokn and Moy 1985; Lystad and Moe 1985), which has been explained as resulting from the increased shelter for juvenile winkles from predatory shore crabs.

Although self-propagation within the basins may have occurred, most recruits (eggs, larvae, and spores) were brought in with the water. The pump delivers 90 $m^3 \cdot h^{-1}$, of which 10 $m^3 \cdot h^{-1}$ is fed to each basin. The remaining 50 $m^3 \cdot h^{-1}$ goes straight through the pipeline system. Whether this ensures the same supply of organisms to each basin is uncertain. Follum (1985) detected a gradient in input of algal debris and mineral particles from the proximal to the distal basin and suggested that this indicated a difference in the supply of organisms. On the other hand, Lystad and Moe (1985) found no systematic difference in the number of egg capsules of *L. littorea* entering each basin.

Exclosure of organisms

Enclosure also means exclosure of organisms from the basins. The fjord end of the pipeline was equipped with a sieve with 5-mm mesh to prevent larger objects from damaging the pump. This also prevented larger organisms, such as fish, from entering the basins. In addition, the pump could also damage smaller, more delicate organisms. Another reduction in potential recruits was, at times, caused by filter feeders in the pipelines, even though the system was cleaned regularly to prevent fouling. The effect of excluding larger fish from the community is not known, but it is thought to be small, and the exclusion had no direct bearing on the experiment because larger fish were absent from all basins. Smaller flatfish and gobids were present in the basins, but in small numbers.

Plankton hauls at the basin inlet and around the water intake during the summer of 1982 demonstrated that although the water-intake system caused a significant reduction in the number of potential settlers, most species found outside were still present to the water entering the basins (Follum 1984) and in sufficient densities to ensure recruitment.

Indications of diminished recruitment were found, however. Bakke (unpublished data) recorded strong settlement of *M. edulis* on artificial substrates by the water intake during the summer of 1981, and nearly no settlement on the same type of substrate in the basins. Predation was excluded in both areas. Follum (1985) showed that the primary community in the basins was more diatom dominated than on a nearby shore, and concluded that the settling of macroscopic algae and animals was less successful in the basins. The cause for these differences was probably a lack of the stimuli necessary for settlement in the basins, primarily the reduced water movement, rather than a lack of potential settlers. In the header tanks above the basins, where water movement was vigorous, settlement of both mussels and barnacles was comparable to that on the shore, indicating that potential settlers of these and other species were also present in the basins.

Sampling stress

The main size constraint in rocky-shore mesocosms is not that of individual moving space, but that of allowing for population sizes large enough to be adequately sampled without changing the population structure significantly. This again is a function of the scope of the experiment. At Solbergstrand, nondestructive registration was used extensively. With the sessile and essentially two-dimensional structure of a rocky-shore community, this is relatively easy to achieve. Community structure was studied using fixed transects, which permitted recording percentage cover or exact numbers of individuals. Repeated fixed-site photography was used as a basis for establishing the population dynamics of barnacles. Growth was based on measurements of tagged individuals in situ (algae) or of individuals that were later returned to the basins after measurements had been taken (winkles and mussels). Community recruitment and metabolism was studied using replaceable granite tiles (Bokn 1985; Pedersen 1987). In general, destructive sampling was limited to the studies of physiology, biochemistry, population genetics, and the tissue burden of oil. Similar samples were generally removed from all basins to ensure comparability. Sampling loss of the inherent population of *M. edulis* was minimized by using transplanted and caged individuals for physiological and biochemical analyses. *Littorina littorea* suffered the most substantial sampling loss. During the oil experiment, a total of about 600 individuals were removed from each basin for various analytical purposes. This represented from 18 to 80% of the mean population size in each basin (3 358 and 742 individuals for the highest and lowest populated basins, respectively) (Lystad and Moe 1985) and might, therefore, represent a high toll in the basin with the smallest population. However, the population estimates did not suggest the sampling loss to be significant. A gradual reduction in total population of *L. littorea* was recorded in all basins from the summer of 1982 to the summer of 1983, but the least reduction occurred in the basin with the smallest population (Bokn and Moy 1985). Population analysis confirmed that this reduction was independent of sampling loss (Lystad and Moe 1985). The results indicated that sampling must have been balanced by recruitment.

Mesocosms versus field experiments

The cost of establishing and running rocky-shore mesocosms is high in terms of personnel and money. Therefore, one should consider carefully when choosing a mesocosm approach in preference to shore experiments. Such consideration may be based on several aspects: the purpose of the experiment, the type of manipulation involved, sampling and registration techniques to be applied, mesocosm realism, and the duration of community development required before the experiments.

To answer basic questions related to community structure and function, and species interaction, field experiments are preferable to mesocosms because there is no doubt about natural realism in the former. Although population management is more controlled in mesocosms (e.g., removal or introduction of species and population adjustment) and unexpected invasion by predators, such as starfish, fish, and birds, that may disturb field experiments is less likely, satisfactory control with field experiments can also be achieved, e.g., with sufficient personnel.

The problem of replication, i.e., obtaining a sufficient number of comparable experimental communities, is equal in the field and in mesocosms. Both systems will be characterized by short-term structural variability. Also, when using small neighbouring bays of comparable size, the possibility of time-zero differences and gradual deviation with time is similar to that of basins.

Most of the sampling and registration techniques applied in the present mesocosm experiment might, in principle, be applied to equally sheltered shores. For several of the subprojects, a shore reference site was, in fact, included in the investigations. Automatic recording of environmental conditions could also be arranged in situ if necessary. Still, some clear logistic advantages are associated with the use of mesocosms. For instance, experimental installations, such as settling panels, cages, electrodes, etc., are better protected against damage than on a shore with free access. As well, sampling is well controlled. Although a rocky-shore mesocosm is connected to the outside world through the water supply, there is no real exchange of individuals with the surroundings as in field experiments. This allows for excellent control of population sizes. Also, dead individuals with hard structures are usually retained within the mesocosms and can be recorded.

The primary advantage of mesocosms over field experiments remains the opportunity they afford to manipulate water conditions of the ecosystem and to introduce pollutants. In most pollution scenarios of the shoreline, the pollutants are mediated through the water, examples being industrial discharges, oil spills or seeps, cooling water, and freshwater runoff. In a mesocosm, these conditions can easily be replicated, and the pollutant level can be controlled and documented. This is not possible in the field, especially if long-term exposure is desired.

Conclusions

Rocky-shore mesocosms have proven to be a valuable experimental tool in pollution research, and are the only alternative to laboratory experiments if a chronic discharge into coastal water is to be imitated. Mesocosm experiments can also be valuable in basic ecological research on rocky shores, but only under special circumstances are they preferable over field experiments. Important ecological functions, such as competition, predation, recruitment, and seasonality, can be retained in basin communities for several years, and with careful management and advanced technical design, the physical environment can be satisfactorily copied.

The disadvantages of poor experimental replication and deviation of parallel communities over time exist in mesocosms as well as in field experiments, but they are more manageable in the former. However, moderate community deviation must be expected in rocky-shore units, and it should be interpreted as an indication that no strong artificial forcing function is being imposed on the community by the design or the researcher. Even well-designed rocky-shore mesocosms should not be regarded as replicates in laboratory terms, but as a series of reasonably similar and partly independent communities imitating shoreline conditions sufficiently to prevent the inherent organisms from reacting abnormally to the experimental perturbation.

The Solbergstrand mesocosm exercise has provided much experience in this sort of experimentation, and it has suggested several improvements for future development of hard-bottom mesocosms. Better imitation of stochastic events in the physical regime of waves and tides may be obtained through more flexible technology coupled with computer regulation. Community establishment time should be shortened by emphasizing careful transplantation more than water-mediated recruitment. This would also improve structural similarity in replicate communities. Efforts in enclosure techniques for littoral and sublittoral hard-bottom communities should also be pursued to obtain in-situ mesocosms. This would combine field experimental realism with the opportunity to manage the enclosed-water system.

Acknowledgments

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