Marine Ecosystem
Enclosed Experiments

Proceedings of a symposium held
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Editor: C.S. Wong and P.J. Harrison
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 phytoplankton 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.


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 Saanich 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.
# Contents

## Part I: Introduction  ......................................................... 1

Introduction to the MEEE Project

Summary
P.J. Harrison  ............................................................................ 7

## Part II: Applications of Marine and Freshwater Enclosures ................. 13

Use of rocky-shore mesocosms in pollution research
T. Bakke  .................................................................................. 14

Benthic mesocosms in the Netherlands
P.A.W.J. de Wilde  .................................................................... 26

Bremerhaven caissons — experience and results of experiments with dispersed crude oil in intertidal enclosures
H. Farke, C.-P. Guenther, and W. Arntz  .................................. 43

A subtidal soft-sediment mesocosm
J.S. Gray  .................................................................................. 57

Enclosed plankton ecosystems in harbours, fjords, and the North Sea — release and uptake of dissolved organic substances
U.H. Brockmann  ...................................................................... 66

Use of enclosures for assessing the effects of pesticides in freshwater aquatic ecosystems
K.R. Solomon, N.K. Kaushik, D. Herman, G.L. Stephenson,
P. Hamilton, K.E. Day, and G. Jackson  .................................. 87

Control of phytoplankton blooms in the Subarctic Pacific Ocean — experimental studies in microcosms
M.R. Landry and J.M. Lehner-Fournier  .................................. 106

Fate of petroleum hydrocarbons in marine ecosystem enclosures and relevance to marine oil spills
W.J. Cretney  ............................................................................ 122

Microbial degradation of petroleum in an intertidal beach environment — in situ sediment enclosure studies
K. Lee and E.M. Levy  .................................................................. 140
Part III: China–Canada MEEE Experiments .... 157

A. Sediments and Heavy Metals

Introduction to the Xiamen marine ecosystem enclosed experiments
Wu Jinping, F.A. Whitney, Hou Shumin, Chen Xiaolin, Zhuang Dongfa, and Wu Shengsan . 158

Application of different types of marine experimental enclosures to study the pathways and fate of chemical pollutants
C.S. Wong, F.A. Whitney, and W.K. Johnson .......................... 174

Effect of vertical mixing on ecosystem dynamics in large mesocosms
T.R. Parsons and A.H. Taylor ................................. 186

Phosphate limitation of phytoplankton growth in coastal estuarine waters of China and its potential interaction with marine pollutants
P.J. Harrison, Yang Y.P., and Hu M.H. ......................... 192

Effects of heavy metals and sediment pollutants on phytoplankton and primary productivity in an enclosed ecosystem
Qian Shuben, Chen Qihuan, Tang Senming, Wu Shengsan, Zhang Liangzhong, Hou Shumin, P.J. Harrison, and H. Dovey ............ 203

A Gray model for studying the effects of metals on phytoplankton growth in marine ecosystem enclosed experiments (abstract only)
Zeng Jiye and Wu Yuduan .............................................. 218

Use of enclosed experimental ecosystems to study the effects of suspended sediments on zooplankton communities
C.M. Lalli .............................................................. 219

Effects of heavy metals and sediment on zooplankton in marine ecosystem enclosed experiments
Chen Xiaolin, C.M. Lalli, and Lin Jinmei ........................ 224

Relationships between particle characteristics and biological activities in controlled ecosystems
Hong Huasheng, Guo Laodong, and Chen Jingqian ............ 230

Biological implications of organic carbon and nitrogen in the Xiamen enclosures
Fu Tianbao, Zhao Rongping, and Yang Yiping ...................... 244

Ecological impacts of pollutants on particulate organic carbon, nitrogen, and phosphorus in marine ecosystem enclosed experiments
Xia Zhongfong and Lu Xiankun .................. 252

Distribution of heavy metals in Xiamen seawater and in the MEEE enclosures
Li Jinxia, Zhang Gongxun, Du Ronggui, Chen Zexia, and Zheng Jihua . 263

Pathways and fates of heavy-metal mixtures in the Xiamen MEEE
Biogeochemical behaviours of heavy metals in marine enclosed ecosystems

Release of heavy metals from polluted sediment in the MEEE enclosures

$^{65}$Zn in the Xiamen MEEE
Zhou Hanyang, Xu Pian, Yao Jiadian, and Zhen Yunfei ............ 314

Biogeochemical processes of mercury in marine enclosures
Xu Kuncan, Wu Liqing, Zhen Changchun, and Zhan Xiumei ........ 323

B. Hydrocarbons

Response of bacterioplankton to Corexit 9527 and Corexit-dispersed Shengli crude oil: marine ecosystem enclosed experiments
Lin Rongcheng, Lin Yanshun, Wu Jinping, K. Lee, and Li Wenquan .... 332

Effects of chemically dispersed crude oil on marine phytoplankton: a comparison between two marine ecosystem enclosed experiments
Lin Yu, Zhuang Dongfa, and Wu Shengsan ................................. 343

Effect of chemically dispersed crude oil on the distribution of primary microfouling organisms
Lin Yanshun, Yao Ruimei, and Liang Ziyuan .............................. 353

Effects of Shengli crude oil and dispersant Corexit 9527 on zooplankton in marine ecosystem enclosed experiments
Chen Xiaolin .............................................................................. 360

Fate of chemically dispersed Shengli crude oil in a marine ecosystem enclosure
Zhuang Dongfa, Wu Shengsan, Lin Yu, Cai Ziping, W.J. Cretney, and F.A. McLaughlin ............................................................... 367

Fate of low-volatility alkanes from chemically dispersed crude oil in a marine ecosystem enclosure
Wu Shengsan, Cai Ziping, Zhuang Dongfa, Lin Yu, W.J. Cretney, and F.A. McLaughlin ............................................................... 378

Use of n-(1-14C) hexadecane to study the fate of dispersed crude oil in marine enclosed ecosystems
Li Wenquan, Wang Xian, Wu Jinping, Lin Rongcheng, and F.A. Whitney ............................................................... 388
Part IV: Other China–Canada Enclosure Experiments ........................................ 399

Enclosure study of metal release from dredged spoils and the effect of capping with alluvial materials
C.S. Wong and Vidas Stukas .......................................................... 400

Releasing experiment of mine tailings from Alice Arm, BC, Canada
Zhan Binqui, F.A. Whitney, W.K. Johnson, and C.S. Wong ................. 410

Effects of Liaohé crude oil and dispersant on marine phytoplankton in an enclosed ecosystem
Zhu Lin, Shen Liangfu, Huang Wenxiang, Zhang Youen,
Wang Hongyuan, and Zhao Zengchun ............................................ 425

Appendix

Participants list ................................................................. 436
Effect of Vertical Mixing on Ecosystem Dynamics in Large Mesocosms

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The effect of vertical mixing on ecosystem dynamics in a large mesocosm has been examined using an ecotrophic computer-simulation model accounting for turbulent diffusion within a Controlled Ecosystem Pollution Experiment (CEPEX)-type enclosure. Over a range of turbulent diffusivity in the thermocline from 0 to 1 cm²·s⁻¹, changes in the standing stock of plankton were followed for a simulated period of 60 d. Assuming initial conditions to be similar to those in large CEPEX enclosure experiments, the increased turbulent diffusion caused better phasing between primary, secondary, and tertiary producers, resulting in a higher standing stock of ctenophores in model simulations with the highest vertical diffusivity. Conversely, the highest initial standing stock (or "bloom") of phytoplankton occurred in simulations in which the vertical diffusivity was zero. These results have been compared with actual CEPEX experiments.

Enclosure of large volumes of seawater in plastic bags should ideally reduce the horizontal movement of water while maintaining vertical movement. However, because horizontal and vertical movements of water are physically coupled, exclusion of horizontal motion damps out much of the vertical transport in the water column. At the same time, vertical motion may be affected by temperature differences in the water inside and outside the bags. These problems were studied by Steele et al. (1977) who estimated average coefficients of turbulent diffusivity within Controlled Ecosystem Pollution Experiment (CEPEX) enclosures (60–1 300 m³) to be in the range of 0.05–0.26 cm²·s⁻¹ in the thermocline. Using a simulation model, the authors were able to account for the approximate distribution of chlorophyll and nutrients found in a 60-m³ CEPEX enclosure.

In another approach to the lack of vertical mixing within large plastic enclosures, Sonntag and Parsons (1979) attempted to increase vertical mixing experimentally through the sporadic release of bubbles at 15 m in a 1 300-m³ CEPEX enclosure. The purpose of this experiment was to study the effect of increased mixing on the trophodynamics of a food chain from phytoplankton to young fish and ctenophores. Although the results of these experiments were extensive, the authors had to conclude that "bubbling of the bags with compressed air did not serve as an
adequate simulator of upwelling." The reason for this was that bubbling created large convective cells with sporadic intense vertical circulation instead of a sustained gentle upwelling.

In the experiments reported here, an attempt has been made to combine the modeling approach of Steele et al. (1977) and the upwelling approach of Sonntag and Parsons (1979) by examining the effect of changes in turbulent diffusivity on an ecosystem trophodynamic model that includes all of the principal components measured in the CEPEX experiment conducted by the latter authors. The computer model was the mixed upper-layer ecosystem simulation (MULES) model (Parsons and Kessler 1986), which was extended into a two-layer system of mixed layer and thermocline in the manner discussed by Taylor et al. (1986).

Methods

The MULES model was applied to generate values of all of its state variables for each layer. A simplified flow design for the MULES system is illustrated in Fig. 1. The version employed differed from that of Parsons and Kessler (1986) in that autotrophic flagellates, heterotrophic flagellates, and microzooplankton are all included; the flagellates being grazed by the microzooplankton, which are, in turn, grazed by the macrozooplankton. Diatoms were grazed directly by the macrozooplankton. The flow design of the model as shown in Fig. 1 includes changes from the original model of Parsons and Kessler (1986), which are shaded in gray.

Fig. 1. Simplified diagram of the modified MULES model (Parsons and Kessler 1986). Shaded boxes are those that have been changed from the original model (DOC = dissolved organic carbon).
In the course of calculating primary production, the MULES model calculates a light profile down each layer. By applying the light intensity at the bottom of the mixed layer as the surface irradiance at the top of the thermocline, shading of phytoplankton in the thermocline by those in the mixed layer was included.

Following Taylor et al. (1986), rates of increase or decrease of any state variable $X$ were described by two equations:

$$
\frac{dX_M}{dt} = M_u(X_M) - vX_M/h_M + k(X_T - X_M)/h_M
$$

$$
\frac{dX_T}{dt} = M_u(X_T) - v(X_T - X_M)/h_T + k(X_0 - X_T)/h_T - k(X_T - X_M)h_M
$$

where $X_u$ and $X_T$ are the concentrations of $X$ in the mixed layers and thermocline, $M_u(X_M)$ and $M_u(X_T)$ are the increases and decreases of $X$ resulting from the MULES system, $v$ is the sinking speed appropriate for $X$, $k$ is a vertical mixing coefficient representing turbulent transfer between the layers, and $h_M$ and $h_T$ are the thicknesses of the two layers. $X_0$ is the concentration of $X$ below the thermocline; this was assumed to be zero for all variables except the concentration of dissolved nitrate.

For the purpose of the experiments described here, the depth of mixing within a CEPEX enclosure was assumed to be 15 m, with a thermocline of 5 m thickness beneath this. The ambient temperatures in the mixed layer and thermocline were taken to be 15 and 10°C respectively. The vertical mixing coefficient has the dimensions of speed. Its value was estimated by requiring that the time taken to cross the thermocline, whose thickness is $Z$ m, be the same as that taken by particles spreading within the thermocline under Fickian diffusion to reach a mean square displacement of $Z$, namely $Z^2/(2K)$. For typical thermocline values of the eddy diffusivity $K$ (i.e., 0.1–1 cm$^2$·s$^{-1}$), $k$ has values of 0.01–0.1 m·h$^{-1}$.

**Results**

Mixed layer starting values are listed in Table 1 for the three experiments in which mixing was varied from 0 to 0.01 to 0.1 m·h$^{-1}$; all other values are the same as in Parsons and Kessler (1986). These values were held constant and only the intensity of mixing was changed between each of the 70-d simulations during which the plankton community was followed. The results are shown in Fig. 2 as changes in the biomass of phytoplankton (chlorophyll $a$), zooplankton, and ctenophores.

| Table 1. Initial parameters used in the experiment. |
|---------------------------------|---|
| Depth of mixing                 | 15 m |
| Nitrate                         | 15 µM |
| Chlorophyll $a$                 | 1 mg·m$^{-3}$ |
| Zooplankton                     | 3 mg C·m$^{-3}$ |
| Ctenophores                     | 0.001 mg C·m$^{-3}$ |
| Surface radiation               | 1 000 µE·m$^{-2}$·s$^{-1}$ |
| Extinction coefficient          | 0.07 m$^{-1}$ |
| Temperature                     | 15°C |
| Nitrate below the mixed layer   | 20 µM |
Fig. 2. Changes in the mixed layer biomass of primary (chlorophyll a), secondary (zooplankton), and tertiary (ctenophores) producers as a result of different mixing rates.
The pattern of events generated by the model shows that the standing stock of tertiary producers (the ctenophores) is progressively increased by the degree of mixing. Although this may appear obvious, because more nitrate is supplied to the whole ecosystem by the greatly increased mixing, the mechanism by which the increased supply of nitrogen is transferred up the food chain is much less predictable. The peak zooplankton standing stock, for example, first increases in 0 to 0.01 m·h⁻¹ mixing regimes (i.e., from about 100 to 125 mg C·m⁻³) and then decreases to about 75 mg C·m⁻³ in the most severely mixed water column. Similarly, the chlorophyll concentration shows a maximum of more than 20 mg chlorophyll a·m⁻³ in the absence of mixing, but reaches <15 mg chlorophyll a·m⁻³ in the water column mixed at 0.1 m·h⁻¹.

These differences in the standing stock results at the first two trophic levels are not directly related to the standing stock of tertiary producers. What is related to the standing stock of tertiary producers is the extent of phasing between the various levels of production. This is illustrated in Fig. 2 by shading the phased portion of the primary and secondary standing stock curves. For 0 m·h⁻¹ mixing, the phased portion of these two curves covers a period of 20 d, whereas for 0.01 and 0.1 m·h⁻¹ mixing, the phased portions of the curves cover periods of 27 and 40 d, respectively.

What actually happens is that, under conditions of zero mixing, the phytoplankton use all available nitrate before the slower-growing zooplankton have a chance to graze much of the phytoplankton growth. The phytoplankton sink out and are then no longer available to the zooplankton. In the mixed-water columns, phytoplankton growth is sustained for a longer period by the mixing; zooplankton production is, consequently, better sustained; and more zooplankton are available for ctenophore grazing per unit of time. This results in a larger amount of the zooplankton being transferred to the ctenophore population. Thus, it is not so much a matter of increasing the nitrate supply as it is of sustaining the primary productivity and thereby, the phasing of the whole system with the result of higher tertiary production.

It is important to note, however, that in the absence of vertical mixing phytoplankton and zooplankton can only be lost from the mixed layer by sinking (i.e., sedimenting out). When there is mixing between the mixed layer and the thermocline, nutrients can be brought into the mixed layer from below, and at the same time phytoplankton and zooplankton can be transported out of the mixed layer by turbulent mixing. These turbulent losses are in addition to those resulting from grazing. As ctenophores are strong swimmers, it was assumed in the model that they were not subject to loss by sinking or turbulent transport. Because of turbulent losses, phytoplankton and zooplankton each increase more slowly with increased mixing.

These results are a partial explanation for some of the data reported by Sonntag and Parsons (1979) who simulated upwelling in controlled ecosystems. In their data, there was no obvious sequence of events in the standing stock levels of primary and secondary producers with upwelling. In fact, the standing stocks of chlorophyll and zooplankton were often lower in the upwelled containers than in the control (no mixing). However, primary productivity in the two mixed-water columns was up to 50% greater than in the control and in one container in which ctenophore grew, the standing stock of ctenophores was about 100% higher than in the unmixed control. These results are consistent with data illustrated in Fig. 2.
Conclusions

The effect of mixing on controlled ecosystems is shown in Fig. 2 to result in a larger standing stock of tertiary producers (ctenophores). In contrast, the standing stocks of phytoplankton and zooplankton do not show a progressive increase with mixing; this is attributed to the degree of phasing between the trophic levels. When these results are compared with experimental results reported earlier, a similar pattern is observed with respect to changes in standing stocks of primary, secondary, and tertiary producers. The results emphasize the importance of "trophic phasing dynamics" in marine ecosystems as described in earlier publications regarding salmon survival (Parsons and Kessler 1987).


