

## International Helgoland Symposium "Ecosystem research": Summary, conclusions and closing

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**ABSTRACT:** This final contribution to the International Helgoland Symposium 1976 summarizes important information presented during the meeting, discusses some concepts and principles of ecosystem research, draws a few conclusions and offers some theories and speculations. It is suggested that, in the future, more attention be paid to: the role of micro-organisms for overall system dynamics and for providing trophic and biochemical linkages; behaviour as a regulating factor, especially at higher trophic levels; development of new techniques for operating experimental ecosystems; and critical application of mathematical models. Various functional states of ecosystems are considered in some detail, as are the food-web concept and system integration. The forces which could contribute to ecosystem integration appear to include non-genetic nutritional adaptation, non-genetic behavioural adaptation, social dynamics and biochemical interactions.

### INTRODUCTION

Based on the concept of the symposium and on the papers received, the formal sessions focussed on 7 topics: General aspects, Experimental ecosystems, Tidal ecosystems, Coral-reef ecosystems, Benthic ecosystems, Pelagic ecosystems, and Pollution effects on ecosystems.

None of these topics could be considered exhaustively. However, much new information was presented on ecosystems, both in the sea and in the laboratory. This, as well as methodological considerations, the hypotheses offered and the attempts at modelling complex multispecies dynamics, document rapidly increasing interest in ecosystem research – emphasizing, at the same time, the tremendous difficulties encountered by investigators who strive for analysis, comprehension and prediction of ecological processes in oceans and coastal waters.

Not all of the papers read during the symposium have been included in this volume. The editors rejected a number of contributions for various reasons, e.g. failure to adhere to submission dates, lack of relevance, or insufficient quality.

## SUMMARY

This summary is restricted to the formal papers presented. A summarizing report on the informal session 'Biomass and productivity of microorganisms in planktonic ecosystems' was provided by John McN. Sieburth (pp. 697–704); a report on 'Marine ecosystem research and man's dependence on the sea', by Joel W. Hedgpeth (pp. 705–706).

## General aspects

The major themes of the introductory session – chaired by R. Riedl, Vienna, Austria – deal with the dynamics of marine ecosystems, aspects of system analysis, and mathematical modelling of ecosystems.

Concentrating on the trophic organization of pelagic ecosystems, Landry (pp. 8–17) emphasizes the partitioning of the nutritional resources available on the basis of body size (see also p. 575). Consideration of body-size effects must take into account the fact that prey species of a given size may differ in their behaviour; similarly, predators of a given body size may differ in their strategies of predation. Nevertheless, Landry comes to the conclusion that the physical environment exerts significant influence on the body-size composition of planktonic primary producers, and that this influence is perpetuated via size-selective feeding at each successive trophic level. There seem to be energetic benefits for preferential feeding on large prey, e. g. by fishes, but size preference must also be seen in context with the feeding apparatus available and with morphological and physiological changes occurring as the predator grows. In the trophic organization of pelagic ecosystems alternate pathways may play a more important role than frequently expected. The effect of fish removal (fishing activities) is considered to be less dramatic than has often been assumed.

The predictable evolution of ecosystem components, leading to climax communities, constitutes the main theme selected by Fishelson (pp. 18–29). Two stages of ecosystem development are distinguished: the *s u c c e s s i v e* *s t a g e*, during which colonization and competition gradually result in a climax condition characterized by maximum resistance to change (stability; see also p. 721); and the *e n r i c h m e n t* *s t a g e*, which occurs in a climax system by means of evolution (genetic speciation) and by invasion of rare species – usually extreme specialists which are capable of utilizing specific microhabitats. Fishelson postulates that, in shallow waters, man-made perturbations will lead to modified ecosystems, dominated by opportunistic species, and will produce physically controlled ecosystems, instead of biologically controlled ones. Tropical marine ecosystems subjected to environmental stress change from well-balanced to unbalanced. They lose their climax condition and remain at some stage of successive development; their final structure is unpredictable.

Oviatt et al. (pp. 30–46), Matthews & Bakke (pp. 47–61), Hameedi (pp. 62–75), and Greve (pp. 83–91) emphasize dynamic and analytical aspects. According to Oviatt et al., multivariate statistical techniques may provide a powerful tool for analyzing dynamic aspects of experimental ecosystems. However, lack of spatial heterogeneity and the small size of the microcosm studied, as well as the 'wall effect' tend to in-

roduce critical artifacts. Microcosm research is still confronted with severe methodological and conceptual problems, and the criteria applied for evaluating the performance of a model system with that of the 'real' system suffer from lack of agreement among researchers. Studies in a Norwegian deep-water pelagic community indicate that there can be considerable flexibility in the species composition of a planktonic community without correspondingly marked effects on its trophic structure (Matthews & Bakke). Experiments concerned with light effects on photosynthetic rates of oceanic phytoplankton (Hameedi) have revealed that both experiment duration and light quality can considerably affect primary productivity. Greve has analyzed ctenophore (predator)-copepod (prey) interrelationships and stresses that the feeding of prey adults on predator-juveniles may be important for the survival of the copepod population involved. He further presents and discusses graphic models of population interactions.

The pros and cons of mathematical modelling of ecosystems receive detailed attention from Dubois (pp. 76-82) and Hedgpeth (pp. 92-104). The large number of components of an ecosystem and of the numerous potential interrelationships between such components make modelling a very difficult procedure. Conceptual subdivision is necessary in interacting subsystems. However, such subdivision is subjective and may create additional problems because of the ambiguity of the criteria employed. Dubois focusses his attention on mathematical modelling of the mechanism of patch-emergence in planktonic ecosystems. He concedes that many models lead to unrealistic conclusions about the biological mechanism involved and that the most sophisticated models can produce 'practically any solution by adjusting the parameters' (p. 81). Consequently, essential requirements for mathematical modelling are simplicity and compatibility with available data.

Hedgpeth puts the pros and cons of modelling in a nutshell: "The model itself is considered an excellent effort; the muddle comes from assuming it is a factual rather than theoretical contribution" (p. 101). He rightly emphasizes that the old-fashioned naturalist is still not obsolete, but more needed than ever. Models have been particularly successful in fisheries management, where the production of resources useful to man, fish-population structure and environmental influences on one or a few species have dominated the perspectives of the investigator. Attempts to apply comparable models to reconstruct essential functions and structures of complex ecosystems have thus far largely failed. Our present knowledge regarding essential data and processes is inadequate. What is needed here more than anything else is sound, basic ecological research.

### Experimental ecosystems

The session on experimental ecosystems (chairmen: K.-G. Nyholm, Uppsala, Sweden, and J. J. Zijlstra, Texel, The Netherlands) concentrates on the description and performance of new culture technology, on methodological aspects and on inter-system dynamics.

Conover & Paranjape (pp. 105-117) describe their Aquatron facility, a large tower tank with viewing ports and programmable illumination, designed for plank-

tological research (main drawbacks: lack of adequate control; irradiance with too much directionality; main advantages: useful for short-term studies of behaviour and community interaction). An account of the Controlled Ecosystem Pollution Experiment (CEPEX) by Grice et al. (pp. 118–133) discusses the predictive and analytical potential of enclosed water columns for studying stress on plankton ecosystems. The large, transparent, closed-ended polyethylene bags lead to a mechanical separation of the enclosed water from the sea outside (reduction of mixing forces affects behaviour and survival of some of the organisms studied). Usually the population dynamics inside the bag do not closely duplicate those outside. However, the enclosures can replicate each other when manipulated identically. This fact facilitates experimentation. Comparable experiments with smaller plastic tanks (Brockmann et al. pp. 201–216) employed cultures of *Thalassiosira rotula* and *Skeletonema costatum*. The results presented indicate “acceptable” experimental reproducibility in regard to algal development (see also p. 652).

Laboratory micro-ecosystems have been designed and tested by Ringelberg (pp. 134–143). The culture system employed is based on spatial separation of the three trophic elements (autotrophs, heterotrophs, decomposers) in individual aquaria connected by tubing, thus facilitating controlled medium recirculation. Although methodological improvements are necessary, the principle of this technique can be expected to yield much useful information on intertrophic relationships. Studies on other experimental ecosystems focus on: interactions between pelagic and benthic components (Perez et al., pp. 144–162; see also p. 598); development of bacteria and meiofauna populations in a sand ecosystem (Chamroux et al., pp. 163–177); microcosm responses to environmental perturbants in a newly constructed facility (Evans III, pp. 178–191); and population interactions of diatoms and dinoflagellates (Elbrächter, pp. 192–200).

Dynamic aspects in mariculture ecosystems constitute the main theme of the remaining two papers devoted to experimental ecosystems. Langton et al. (pp. 217–229), consider the production of ammonia-N by the bivalve *Tapes japonica* and ammonia-N recovery by the seaweed *Hypnea musciformis*. Hirata (pp. 230–242) who studied zooplankton cultivation and prawn seed-production suggests that mariculture systems should preferably be maintained in the form of a balanced ecosystem consisting of producers, consumers and decomposers. Such an approach leads to an increased continuity of culture-system parameters as well as to increased system homeostasis and resistance to deformation.

## Tidal ecosystems

Chaired by M. Bernhard (Fiascherino, Italy) and M. Bilio (Comacchio, Italy), the session on tidal ecosystems was introduced by Kussakin (pp. 243–262) who reported on the composition and distribution of intertidal ecosystems in the White, Barents, Bering, Okhotsk and Japan Seas. Within almost a quarter of a century, a wealth of information has been accumulated by Soviet hydrobiologists. Kussakin's review describes and analyzes essential facts and problems that have emerged, especially with

regard to structural differences of the communities examined. It is emphasized that intertidal communities and their abiotic environment should not be visualized as independent ecosystems, but as components of ecosystems – such as those of estuaries, lagoons, bays or the open seashore.

An important means of analytical in-situ research are predator-exclusion experiments. Reise (pp. 263–271) studied the intensity of predation pressure exerted on the macrofauna in shallow-water muddy sediments. Continuous removal or introduction of predators and translocation of prey organisms into areas of varying predator abundance have shown predation pressure to be an essential force in biological interactions. Predation determines, to a large extent, the structure and dynamics of the macrofaunal assemblages investigated. The protective effects of predator exclosures were remarkable, resulting in prey densities unparalleled in related macrofauna habitats.

In salt-marshes, Lee et al. (pp. 272–282) found food quality to influence meiofauna distribution, thus accounting for some of the spatial heterogeneity often observed under natural conditions. Carbon-budget studies in the Ems estuary revealed allochthonous detritus as main energy source (van Es, pp. 283–294). Por et al. (pp. 295–314) report on hydrography, flora and fauna of mangrove forests of the Red Sea; Dame et al. (pp. 343–356), on a conceptual approach employed in the investigation of a marsh-estuarine ecosystem. In temperate seas, the rocky intertidal benthos exhibits high productivity values (Niell, pp. 315–333). These are attributed, in part, to extra (non-solar) energy input in terms of water movement (e. g. waves, tides). The potential significance of such extra energy is discussed; it requires further investigation. De Wilde & Kuipers (pp. 334–342) studied dynamic processes in a large indoor tidal mud-flat ecosystem. The system revealed predictable trends and development towards a steady-state condition. There was heavy bioturbation and acceleration of remineralization processes due to high infauna activities. Artificial tidal mud-flats are likely to become important tools for experimental ecologists.

### Coral-reef ecosystems

Coral-reef ecosystems have attracted considerable attention from marine ecologists. The few papers presented at this session (Chairman: H.-P. Bulnheim, Hamburg, FRG) convey only a very restricted overview. Preobrazhensky (pp. 357–361) formulates main problems related to the study of coral reefs, and Benayahu & Loya (pp. 362–382) report on space partitioning. According to the last named authors, colonization of soft corals in shallow waters appears to be favoured by lack of predators, high tolerance against abiotic factors and the coral's capacity to form large colonial aggregates. As the succession advances, space partitioning seems to be increasingly controlled by biotic factors (competition, predation, grazing). In all areas studied, the coexistence of stony corals, soft corals and algae indicates a lack of competitive dominance by any one of these faunal components. Mergner & Svoboda (pp. 383–399) studied reef productivity and seasonal dynamics in the Gulf of Aqaba; Schuhmacher (pp. 400–411), the initial phases in reef development near Eilat. He

distinguished start-phase, preparation-phase, phase of pioneer frame-building, and phase of frame-binding; as the coral dies there is a complete change in associated organisms with a tendency towards a less specific but more diverse community.

Fricke (pp. 412–426) emphasizes, and rightly so, that the functioning of an ecosystem cannot be fully appreciated without taking into account behaviour. He demonstrates interrelationships between environmental factors and social structures. After examining the behaviour of 25 species of damselfish (Pomacentridae) Fricke concludes that species with the same social structures are similarly specialized ecologically. Damselfish respond flexibly to environmental change, revealing intraspecific variation in group structure, feeding habit and reproductive strategy.

### Benthic ecosystems

Under the chairmanship of S. Gerlach (Helsingør, Denmark; now: Bremerhaven, F. R. Germany), ecosystems in benthic areas received attention in 8 papers. Considering the stability of benthic ecosystems, Gray (pp. 427–444) stresses the need for more natural-history-type studies and the importance of biological interactions. He discusses a variety of stability models. Most of the benthic-ecology studies presented thus far have dealt with the relations between physical properties of the environment and species distribution. There is a deplorable lack of dynamic, theoretical interpretation and of information on niche proportions, competition, predation and interference (including the re-working of sediments; see also p. 342). According to Wildish (pp. 445–454), our knowledge on marine and estuarine sublittoral benthic synecology is still in a descriptive stage of study. Much of the literature contains either qualitative and quantitative descriptions of communities or associations, or concepts of such aggregations including diversity, stability and succession. Wildish presents a theory, based on a hierarchy of multiple abiotic and biotic (food supply, supply of colonizing larvae, interspecific competition) limiting factors, for studying control mechanisms governing community composition, biomass and productivity. The usefulness of his hypothesis remains to be examined.

For a kelp-bed ecosystem off Nova Scotia, Mann (pp. 455–467), reports increasing loss of stability due to overgrazing by sea urchins. Almost all kelp-beds in St. Margarets Bay have now been destroyed. Mann hypothesizes that the decrease in the local lobster population, and hence the reduction in predation, allowed sea urchin abundance to increase to an extent where the food algae are practically destroyed. According to Mann, the urchin-dominated barren grounds seem to represent a new, stable configuration of the local ecosystem. He expects a long-term decrease in primary and secondary productivity. Sea-urchin grazing on the benthic macrophyte community and community recovery indicated to Foreman (pp. 468–484) that populations of *Strongylocentrotus droebachiensis* in the Strait of Georgia undergo periodic, environmentally controlled, outbreaks. These outbreaks are held responsible for localized perturbation of the macrophyte community. The community requires 2 to 3 years to regain, or exceed, pre-grazing biomass levels; an estimated period of 4 to 6 years is needed to achieve "ecological climax" (see also p. 20). In kelp beds of the

Benguala upwelling system, Velimirov et al. (pp. 495–518) have determined faunal and algal boundaries and biomasses. The authors discuss mechanisms regulating the kelp-bed structure, as well as a descriptive model of the food web. In a Scottish sea-loch, seasonal carbon-budget studies on *Laminaria saccharina* revealed to Johnston et al. (pp. 527–545) net annual production rates exceeding  $120 \text{ g C m}^{-2} \text{ yr}^{-1}$ . Over 13 % of the gross carbon input is lost in the form of extracellular releases, and 40 to 50 % by peripheral decay.

Benthic-fauna dynamics have been studied by Gulliksen (pp. 519–526) and Ott & Fedra (pp. 485–494). Employing the services of UWL "Helgoland", Gulliksen reports on his second investigation on the benthic fauna of rocks and boulders in Lübeck Bay (western Baltic Sea). He concentrates on faunal composition, relative abundances of some invertebrates and on swarming activities of *Idothea baltica*. Ott & Fedra found the shallow Northern Adriatic Sea to support a high-biomass benthic epifauna community with biomass values of  $370 \pm 73 \text{ g wet weight m}^{-2}$ . Consisting of almost 90 % filter feeders, the fauna comprises a stabilizing storage compartment. The ecological significance of such a storage compartment is seen in its regulatory effect on ecosystem metabolism through controlling water-column biomass and converting it into macrofauna biomass with a reduced ratio respiration: biomass.

### Pelagic ecosystems

In terms of overall oceanic dynamics, pelagic ecosystems are of basic importance. Chaired by T. Levring (Göteborg, Sweden), the session on pelagic ecosystems focussed on the role of particulate and dissolved organic matter, the importance of body weight for ecosystem organization, structural aspects of plankton communities, the activities of heterotrophic bacteria, and exchange processes at ecosystem boundaries.

In pelagic ecosystems, a general correlation appears to exist between the productivity of a water mass and its content of particular matter (Riley, 1963). Hence, Wangersky (pp. 546–564) has devoted his attention to assessing the role of particulate matter in the oceans, both in regard to time and space. Except for the special situations of upwelled water and spring blooms in temperate and boreal waters, the productivity of the oceans is largely governed by the rate of nutrient regeneration in surface waters. The rate of nutrient regeneration is a function of the number of actively metabolizing bacteria which, in turn, appears to depend on the water's content of particles. Consequently, particle content seems indeed to exert basic control on the rate of productivity in the open oceans. Finally, Wangersky investigates the implications of the oceanic distribution of particulate matter.

Sieburth et al. (pp. 565–574) developed a scheme for observing diurnal changes in dissolved organic matter in the photic zone and for correlating the changes recorded with specific microbial fractions and their rates of growth and uptake. Although more work is required for evaluating their procedures in detail, the results obtained are encouraging. The authors plan to revise their techniques, to eliminate contamination effects of the research vessel and to position the latter in a particular water body. Ultimately, they hope to verify the rates of dissolved organic-matter release and up-

take and to determine how these occur – a goal as important for marine ecosystem research as it may be difficult to attain.

Based on accepted relations between body weight and rates of metabolism and growth, Platt & Denman (pp. 575–581) present a steady-state theory accounting for organismic abundance in pelagic ecosystems as a function of body weight (see also p. 8). They conclude that, in the steady state, the total biomass of any given size-group decreases in a regular manner with increasing size. The new theory is applied for assessing rates of energy flow through the system and total community metabolism. Since data on organismic size distributions (1–100  $\mu\text{m}$ ) can be recorded automatically, the theory may attract general interest and assist in analyzing organizational principles in pelagic ecosystems.

Structural aspects of plankton communities are considered by Eriksson et al. (pp. 582–597) on the basis of long-term intensive sampling, analysis of taxonomic components comprising the biocoenosis examined and seasonal variability. Attempting to elucidate the relative importance of micro- and mesozooplankton, the authors assume that microzooplankton, especially the ciliates, play a decisive role in the pelagic biocoenosis. Data on consumer activities of heterotrophic bacteria (Joiris, pp. 611–621) are consistent with literature data, but fail to resolve the discrepancy between rates of production and consumption (see also the report on the Informal Session convened by Sieburth, pp. 697–704). In a near-shore ecosystem, Propp (pp. 598–610) focussed his attention on ecosystem boundaries (see also p. 144). He presents estimates on direction and rate of energy flow and on chemical dynamics. At a permanent station in Vostok Bay (Sea of Japan), turnover rates of nitrogen and phosphorus between water and sediment were about 2 to 4 months. In coastal regions, higher production data prevail; these are explained, in part, by the proximity of photic and sediment layers, and by increased regeneration rates of biogenous elements.

## Pollution effects on ecosystems

Oceans and coastal waters are subject to increasing man-made pollution. Recently, the pollution of marine environments, especially due to industrial activities, has attained dimensions which may cause irreversible damage, unless world-wide conditions of control and restriction are formulated, accepted and enforced. A continuation of present trends must be expected to lead to the elimination of sensitive species, to changes in ecosystem dynamics and, ultimately, to failure of ecosystems to sustain human life. Basic studies on the resistance of ecosystems to man-made deformation should be given top priority in research planning and funding.

While a number of papers and discussions have dealt with the problem, the session on pollution effects on marine ecosystems (chairman: M. J. Hameedi, Boulder, USA) covered only a very restricted area of this broad field. For shallow waters, Poole et al. (pp. 622–632) demonstrate that effluent from the pulp and paper industry modifies the balance between the supply of, and the demand for, oxygen. The ligno-sulphonate component of pulp-mill effluent greatly reduces illuminance and hence the transmission of radiant energy to autotrophs. A major consequence is the diminution



in oxygen supply. At the same time, oxygen demand increases due to microbial degradation of the additional amounts of organic matter entering the ecosystem. Water temperature controls the release of sulphide from the sediment and can be expected to affect the ecosystem's resistance to deformation due to effluent release. Studies in a sublittoral muddy-bottom biocoenosis near Helgoland revealed to Rachor (pp. 633–651) a long-term trend of faunal impoverishment. The trend is attributed to the development of anaerobic conditions in the sediment. These conditions are favoured by thermohaline stratification and sewage pollution.

For analysing mercury effects on a plankton community, Kuiper (pp. 652–665) employed plastic bags (see also p. 118 and p. 201). A single dose of 5 ppb mercuric chloride added to a North Sea coastal plankton community enclosed in a plastic bag resulted, among other things, in (1) adsorption of free-water mercury within 5 days; (2) reduced phytoplankton growth at mercury concentrations exceeding 1.5 ppb; (3) delay in the onset of the second phytoplankton bloom; and (4) changes in community structure. Effects of zinc sulphate on dinoflagellates and diatoms have been examined in mono- and multispecies cultures by Kayser (pp. 682–696). Interestingly, algal sensitivity to zinc pollution increased with the number of species combined in the test medium. Multispecies cultures are considered more adequate for investigating ecological consequences of pollutants than are monospecies cultures. In natural plankton communities, heavy-metal toxicity may manifest itself – especially over extended periods of time – at limiting concentrations considerably below those established in short-term laboratory experiments.

Responses of marine organisms to low-level pollution under natural conditions of temperature, weather, season etc., have been examined by Davis et al. (pp. 673–681) in newly designed "Marine Ecosystem Testing Units". The basic layout of the units consists of 96 rectangular containers, each of 37.5-l capacity into which unfiltered sea water is pumped at the rate of 40 l h<sup>-1</sup> container<sup>-1</sup>. The first year of operation has demonstrated responses to chlorination at levels below chemical detectability and has indicated a "holistic" ecosystem response to sodium hypochlorite pollution.

Considering effects of climate and pollution, Greve & Parsons (pp. 666–672) offer and discuss the following hypothesis: Increase in flagellate populations due to climate or pollution may (1) increase the number of trophic levels and, thereby, decrease fish production; (2) cause changes in biomass flow from fish to ctenophores and other planktonic predators, thereby again decreasing fish availability for human consumption. The hypothesis is based on literature information. It requires verification.

### General consensus

The general consensus among the symposium participants can, perhaps, be conveyed to some extent by the following statements:

- (1) Our subject is extraordinary in several respects – particularly in regard to its actuality, its complexity and breadth, and its methodological and conceptual difficulties.

- (2) Ecosystems can be viewed from many different perspectives. Several perspectives were represented adequately at the meeting.
- (3) There is a common base line among those who study ecosystems, but the base line is short. Practically all investigators are in agreement about the basic components making up an ecosystem: environment and organisms representing different, integrated nutritional categories. There is further agreement regarding the interdependence of components and the fact that ecosystems are open systems. Size and delimitation of the ecosystem are usually a matter of convenience, perspective or methodological considerations. In most cases, the ecosystems considered represent subsystems (communities) of larger aquatic ecosystems. Ultimately, all ecosystems must be visualized as components of the overall global ecosystem (biosphere).
- (4) Some of the discussions suffered from verbosity and from lack of constructiveness. Nevertheless, the Evening Discussion and the two Informal Sessions were considered useful by most participants. They provided a means for considering a few aspects in more depth and for drawing from additional sources and talents.
- (5) A major controversy of data and ideas was related to the rate of production of organic matter in oceans and coastal waters. It seems that a much higher percentage of marine plankton consists of microorganisms than hitherto assumed. We must consider and thoroughly examine the possibility that bacterioplankters and related microorganisms play a decisive role in the dynamics of oceanic ecosystems.

## CONCLUSIONS

Life on earth has evolved and exists in the form of ecosystems (p. 5). Man's future depends on his capacity to analyse, comprehend and protect ecosystems so that they remain capable of supporting him. Analysis and comprehension of ecosystems is extremely difficult. In fact, ecosystem research has become the greatest challenge to modern natural sciences. The protection of ecosystems from the exponentially increasing human impact requires rigid control and restriction in terms of total human population size and impact per capita. The present trend is deadly. Is there a chance for change? Can we master human egocentricity in time? I cannot see any circumstances that would justify optimism.

## General points

The symposium revealed great need for gaining more knowledge on the essential functions and structures of natural marine ecosystems and for taking a critical look at some of the "firmly established" textbook wisdom regarding the dynamics of biological processes in the seas. Only if we learn much more about the basic properties of ecosystems and their capacities to endure, and to compensate for, stress – including man-made deformation – can we hope to work out practicable guidelines for the system's control and for its long-term protection.

It appears that there are four major aspects which deserve special attention in future research:

(1) The role of microorganisms, both planktonic and benthic for overall system dynamics, especially production and remineralization, and for providing trophic and biochemical linkage and bondage.

(2) The importance of behaviour as a regulating factor, especially at the higher and highest trophic levels. Most species seem to possess a considerable genetic reservoir of different behavioural traits which become activated and realized only in specific situations. Behaviour may thus contribute to the directionality of events and to homeostasis in ecosystems, and to initiating and controlling alternative flow routes of energy and matter. Such alternatives may, to a large extent, remain unpredictable and hence not fully accommodatable in mathematical models.

(3) The development of new techniques for operating experimental ecosystems, both in the sea and in the laboratory. Experimental ecosystems are the most difficult to operate, but also the potentially most powerful, tools for analysing natural ecosystem dynamics.

(4) More critical application of ecosystem modelling, i. e. of empirical statistical techniques for simulating or defining essential system components and processes, and their interrelationships. We are presently facing an explosion of "model studies", which are insufficiently backed up by hardware, i. e. ecologically valid data on metabolic performance, behaviour and intra- and interpopulational dynamics. Models are tools aimed at simulating, comprehending, predicting or controlling ecosystem dynamics. They are theoretical concepts that require permanent verification and improvement by reference to the 'real' system. In addition to the lack of valid data, our present models suffer, for example, from uncertainty about which data to use, failure to allow for alternative component relationships, and coupling of submodels with different scales. Most models are concerned with rather limited portions of small ecosystems; whole-scale ecosystem modelling seems still far away.

## Principles, theories and speculations

### *Functional states of ecosystems*

The major functions of an ecosystem seem to be based on: (1) exploitation by living organisms of every possible circumstance which can support them; (2) competition, resulting in diversification, specialization and progressive functional and structural complexity; (3) increasing interspecific interdependence and coordination; (4) the tendency of living organisms – and of the interrelationships between them and their environments – to evolve, i. e. to undergo irreversible changes with time; (5) system survival: counteraction of conditions potentially detrimental to the ecosystem, such as the critical accumulation of toxic materials or the evolution of abnormally behaving system components.

In the papers presented during the symposium and in the relevant scientific literature, attempts towards providing qualitative criteria for assessing different func-

tional states of ecosystems have led to the introduction of terms such as efficiency, maturity, resistance to deformation, stability, healthiness and diversity. It seems desirably here to briefly discuss these and some related terms and their biological basis.

In biology, the term "efficiency" denotes the capacity of organisms – or of their structures and functions – to attain a certain effect with minimum expenses (energy, material, waste). This concept is useful for assessing properties and capacities of individuals or populations, such as rates of growth and reproduction, ability to catch prey, or utilization of energy and matter. In ecosystems, the effect to be attained has often been seen in its productivity. However, we seem to visualize ecosystem dynamics too much from the perspectives of agriculture or fisheries. There is a tendency to overemphasize those processes in the system which build up organic matter, especially materials immediately useful to man. In reality, nothing is "produced" in ecosystems. On the contrary, it seems to be characteristic of intact ecosystems that the organic matter formed by autotrophs is transformed and utilized as completely as possible by heterotrophs – in other words, that anabolic and catabolic events are balanced.

Ecosystem evolution appears to involve a tendency of achieving the maximum diversity and amount of life supportable by prevailing environmental conditions. Such tendency should, among other things, lead to a more and more complete transformation and decomposition of the material synthesized by autotrophs. In the light of these considerations, the efficiency of an ecosystem could, perhaps, best be interpreted as the capacity of the system to fully integrate all components involved in the synthesis, resynthesis and desynthesis (decomposition) of organic matter, with the result of avoiding critical accumulation of material potentially detrimental to the system (self-regulation, self-cleaning).

Adequate integration and regulation of anabolic and catabolic events appear to be a prerequisite for long-term system survival. Where full niche exploitation prevails and where full integration and regulation are achieved, the ecosystem could be said to have attained maturity or – in terms of its living components – to be saturated. Immature or unsaturated systems are characterized by incomplete exploitation of the trophic or spatial niches available and hence by a submaximal number of different forms of life.

The terms "resistance to deformation" or the "tolerance" of an ecosystem are expressions of the degree of stress endurance, i. e. of the system's capacity to endure biotic or abiotic changes or unusual inputs – natural or man-made (pollution; removal, translocation or alteration of system components). The degree of resistance seems to be primarily related to the degree of euryplasticity of the dominating living system components and to the elasticity of their interrelationships. Based on my studies on a number of brackish-water and marine animals, I postulated (Kinne, 1956a) that species which exhibit high resistance (are euryplastic) to variations in abiotic factors (e. g. temperature, salinity), tend to exhibit low resistance (are stenoplastic) in regard to biotic factors (competition, predation, biochemical interactions) and vice versa. Physically euryplastic populations tend to occupy habitats in which abiotic factors attain critical intensities and thus assume control of organismic

distributions (e. g. estuaries); in contrast, stenoplastic populations are restricted to habitats with physically more stable conditions; here population dynamics are controlled primarily by biological interrelationships. In their essay on genetic adaptive strategies, Brestky & Lorenz (1970) found populations primarily controlled by abiotic factors to be genetically heterocygote, those primarily controlled by biotic factors, to be homocygote (low stress resistance due to low genetical variation).

The term *stability*, in its usual meaning, includes (1) aspects of resistance to deformation (plasticity, elasticity), i. e. the capacity of maintaining essential system characteristics in the presence of stress or of returning to the original state after disturbance; (2) the constancy, persistence or continuity of system characteristics such as species composition or environmental conditions, irrespective of stress. A frequently employed measure characterizing the degree of stability are abundance fluctuations of populations around the equilibrium density. Holling (1973) has termed the bounce-back characteristics (resistance to deformation) of a system "true stability" and its persistence through time "resilience". Stability and resilience are not necessarily directly related: an ecosystem may be stable and yet exhibit low resilience and vice versa. A few authors, especially Orians (1975), have provided detailed descriptions or interpretations of different aspects of stability. Nevertheless, the concept of stability remains ambiguous and controversial: What is unstable in a small system may become stable in a large system. Ultimately, a large system may be stable because its subsystems are unstable (Margalef, in press).

The *healthiness* of an ecosystem appears to be seen primarily as a measure of the system's capacity to support human life. Criteria other than the hypothetically assumed capability of the system to sustain long-term civilized human existence remain to be established.

The term "diversity" refers to three different ecological parameters: the number, abundance and response potential of different species or populations in an ecosystem. The concept of diversity in aquatic ecosystems and the relation between system diversity and system change was pioneered by Thienemann. Based, in part, on his 1913 paper, Thienemann (1920, 1939) has elaborated general ecological principles or laws ("Grundprinzipien oder Grundgesetze der Biocoenotik"). Thienemann's first biocoenotic principle states: The more variable (within limited and regular, i. e. predictable, oscillations) the living conditions in a biotope, the larger the number of species present – in other words, the higher the diversity of the community or ecosystem concerned. The second biocoenotic principle states: The more the living conditions of a biotope diverge from the norm – and for most of the organisms present from their optimum – the smaller the number of species comprising the biocoenosis, the more characteristic the biocoenosis, and the higher the number of individuals per species. These two principles have been amended by Franz (1952–1953) who formulated the third biocoenotic principle which takes into consideration the historical factor (time): The more continuously the milieu conditions in a biotope have developed, the longer the same (similar) environmental conditions have prevailed, the higher the number of species comprising the biocoenosis, and the more balanced and stable the biocoenosis.

These general principles have later found support in a number of studies con-

ducted on land, in lakes, in brackish and in marine waters. It is well known, for example, that low latitudes (tropical waters) offer optimal temperature conditions for numerous species and tend to entertain a greater diversity of different organisms than do higher latitudes (temperate or arctic waters; e. g. Gunter, 1957; Kinne, 1970). Similarly, marine waters entertain a greater variety of species than do brackish waters (Remane, 1934, 1940; see also Kinne, 1956b, 1971, and Khlebovich, 1962). Sanders (1969) studied marine benthic communities and concludes that communities with a high degree of diversity are found where predictable (stable) environmental conditions have prevailed for extended periods of time. In another study, Sanders (1968) distinguishes communities which are controlled by abiotic factors ("physically controlled systems") and those which are controlled by biotic factors ("biologically controlled systems") (see also p. 720).

A number of investigators have related ecosystem diversity to the system's stability (mainly its resistance to deformation). They assumed, and in a few instances claim to have provided evidence, that stability increases as a function of increasing diversity (e. g. McArthur, 1955, 1957; see also Steele, 1974, and Orians, 1975). However, diversity-stability relations are not as simple as that: The expectations of the diversity-stability hypothesis are born out neither by experiments, by observations, nor by models (Goodman, 1975).

Increased diversity increases the number of possible interrelations among co-existing organisms and thus the number of alternative routes in the flow of energy and matter, thereby augmenting the total quantity and quality of the system's responses to a potentially deforming stress. The ecosystem's stability (its resistance to deformation) appears to be based to a considerable extent on the capacity of its ecologically dominant forms for (1) escaping or enduring the stressor (the agent which causes the stress); (2) regulation; and (3) adaptation. However, in ecosystems which have not yet attained maturity, the degree of balanced integration achieved among essential components may, conceivably, affect system stability.

In analogy to the situation observed at the individual level, it may be postulated that ecosystems characterized by high rates of energy flow and material cycling, i. e. by high metabolic rates, are less resistant to stress (deformation) than ecosystems with lower metabolic rates.

### *The food-web concept*

The food-web concept emphasizes potentially multidimensional nutritional interrelations among coexisting organisms with built-in alternative routes. It is based on the phenomenon of progressive energy degradation along successive food links. A food link comprises the nutritional relations between members of two species. As the material made available by autotrophs is processed, the amount of biologically usable energy decreases at each successive food link. In general, the efficiencies with which food is converted into biologically useful energy and material at each food link ranges from about 5 to 25 %. However, the conversion efficiency depends on a variety of factors, especially environment and age, physiological condition and type of the animal concerned. For example, sub- or supranormal temperatures or salinities tend to

reduce conversion efficiency (Kinne, 1960, 1970, 1971); young, fast growing animals exhibit increased efficiencies, especially in terms of material incorporation into body-own substances (25–40 %); small-sized organisms tend to exhibit lower efficiencies than large-sized ones.

Regarding the significance of the food-web concept for the organization of marine ecosystems, four aspects require brief attention in the present context.

(1) In most cases, food webs have been visualized in terms of nutritional relations between adult life-cycle stages. However, larvae or juveniles may often entertain quite different nutritional relationships than their adult counterparts. Several molluscs and crustaceans, for example, change their feeding behaviour and their food source drastically and repeatedly during their life cycle. The text-book version 'fishes eat copepods' is far too general. We now know that juvenile fishes may be preyed upon by adult copepods. In fact, most interactions among coexisting species have a reciprocal component.

(2) Disease agents such as microorganisms or parasites can affect food-web dynamics. There is evidence that microbial infections or parasitical infestations may significantly modify the flow of energy and matter in marine ecosystems (Kinne, in press). In fact, distributions of organisms in space and time, fluctuations in population strength, and variations in performance (rates of growth and reproduction, resistance to stress) may depend much more on disease agents than hitherto assumed (Lauckner, in press). Disease agents can invert the generally prevailing size trend in the system, i. e. when small parasites stand at the top (Margalef, in press), and change food-web interrelations in thus far unknown ways.

(3) While switching (changes in food-source selection) may occur less often under natural conditions than is often assumed, it does occur and may affect food-web dynamics. Hence, the circumstances which induce switching and the capacity of an animal for switching require more attention. It seems likely that switching involves a period of reduced efficiency in terms of prey catching and food conversion prior to reattaining pre-switching efficiencies (readaptation).

(4) The concept of *food chains* emphasizes unidirectional, parallel nutritional relationships. These are rare in nature. We agree with Margalef (in press) who considers a food chain an extreme type of a degenerated food web, in which food links are neither convergent nor divergent, but only parallel.

### *Integration in ecosystems*

In biology, a system may be defined as an organized, coherent entity which is composed of diverse, interdependent and interacting parts, and which exhibits regulative, homeostatic properties. Biological systems are open in the sense that they require a continuous flow-through of energy and matter. The problems involved in investigating a highly integrated system rest in the fact that analysis requires separation and dissection and hence may lead to change or even destruction of the system characteristics to be studied. The difficulties of studying biological systems culminate

in ecosystems – the most complex, diverse and dynamic systems nature has produced. Compared to the increasing effort invested in the field of ecosystem research, progress has remained slow. Our restricted ability to comprehend the interrelated complexities becomes more and more evident. This has often resulted in discouragement and frustration.

Attempts to define, analyse and comprehend organizational principles of ecosystems in detail have largely failed. We have thus far focussed our attention almost exclusively on the dynamics of energy flow, food-webs, cycles of nutrient and non-nutrient materials, the overall metabolism of selected water bodies, and general balance sheets. A major aspect has remained largely untackled: the search for, and the definition of, integrative forces. What exactly turns organisms which live together in a given space into a system? What is the basis of the much-referred-to homeostasis of an ecosystem?

In order to shed more light on the phenomena which affects integration in ecosystems, it is necessary to look for the “cement“ which binds together or relates between the separate building blocks recognized. I would like to draw attention here to four phenomena which could, conceivably, constitute significant aspects in the organizational integration of ecosystems: non-genetic nutritional adaptation, non-genetic behavioural adaptation (imprinting), social dynamics, and biochemical interactions. I shall briefly explain this view.

The term “non-genetic nutritional adaptation“ (or nutritional acclimation) is introduced here to designate individual adjustments of organisms to a certain food source. It is assumed that such adjustments occur relatively early in the life-history of an organism, involve a variety of physiological and enzymatic processes, and tend to perpetuate a given nutritional relationship beyond the circumstances that originally induced the adaptation. In contrast to genetic nutritional adaptation, which involves genetically fixed structures and functions related to food uptake and food conversion, non-genetic nutritional adaptation is reversible and based on the history of the individual involved. In a sense, I visualize non-genetic nutritional adaptation as a phenomenon which parallels non-genetic adaptation (acclimation) to environmental factors, e. g. to temperature or salinity. The ecological significance of the non-genetic nutritional adaptation postulated here is seen in efficiency maximization related to energy procurement, as well as in the establishment of a certain amount of directionality in regard to the flow routes of energy and material.

In microorganisms – such as bacteria, protozoans, nanoplankters and other minute mass organisms – non-genetic nutritional adaptation is visualized to involve specific enzymatic and physiological adjustments of the consumer to a given nutrient source. Hypothetically, one and the same species of microorganism could adapt to quite different food sources in different parts of its distributional area. Conceivably, non-genetic nutritional adaptation may constitute the first step of those evolutionary processes which have ultimately led to the genetically-fixed nutritional interrelationship which we now witness between several hosts and symbionts, e. g. in some cnidarians and turbellarians, or in hosts and parasites. Non-genetic nutritional adaptations of microorganisms could influence and stabilize to a certain degree the flow routes of energy and matter in a given body of water and thus provide a basis for system integration and homeostasis.

Similarly, non-genetic nutritional adaptation may be of significance in multi-



cellular, more complex forms of life. For example, a variety of marine animals newly caught and exposed to culture conditions in the laboratory refuse to accept food which they are not accustomed to. In such cases, nutritional readaptation may be difficult and sometimes require a period of force feeding (e. g. in fishes or marine mammals), or a situation in which conspecifics – already trained to accept the food offered – induce feeding in the newcomers (copying). Such conditioning is likely to introduce increased directionality, and regulative capacities into nutritional relations between coexisting organisms.

Non-genetic behavioural adaptation or imprinting has been reported and analyzed in several “higher” marine animals, especially fishes, mammals and birds. Although non-genetic behavioural adaptation and non-genetic nutritional adaptation must be assumed to have a common basis, nutritional adaptation is seen here as a phenomenon exclusively related to feeding dynamics, whereas the term “behavioural adaptation” is used in referring to such aspects as orientation in space and time; the strategy of escape from predators or from potentially detrimental environmental conditions; the selection of sites, e. g. for settlement; as well as reproductive behaviour, territorial behaviour and construction activities such as tube building. The behavioural pattern induced selects and directs the activities of the imprinted individual, i. e. it introduces a hierarchy within the total amount of responses theoretically possible on the basis of the individual’s genetic constitution. Such directionality in the responses may, again, introduce elements of integration and homeostasis into the pattern of organismic coexistence.

Social dynamics are closely related to, and may be considered a special form of, non-genetic behavioural adaptation. Social relations are a basic denominator of animal life. In nature, practically all animals exist as members of some social unit. Within closely-knit social units, such as a school of fish or a herd of odontocetes, a behaviour response pool is built up and stored; it contains specific information, for example, on social structures, hierarchical dynamics, migration, manoeuvring, cooperative hunting tactics, escape techniques, etc. The response pool serves as source of reinforcement, thus perpetuating the specific social dynamics developed. Social imprinting and its perpetuation via conditioning mechanisms introduce directionality and regulative capacity into social activities. In a predator, imprinted social dynamics may affect prey organisms and a variety of integrative ecosystem parameters.

Biochemical interactions among coexisting organisms can be expected to play a decisive role in aquatic ecosystems. Organisms release into, and take up from, the surrounding water chemical compounds. Some of these may affect metabolism, growth and reproduction, and act as messenger substances. Known for decades and investigated especially in protozoans and a few multicellular organisms, the substances involved have been collectively referred to as conditioners, allelocatalyzers, pheromones, ectohormones, probiotics, growth factors, telemediateurs, or allelochemicals (for pertinent literature consult Kinne, 1977, p. 616). It is very likely that biochemical interactions, mediated via the ambient water – and transportable over considerable distances by water currents – constitute important means of system integration. Intensive research into the ecological role of chemical messenger substances could revolutionize marine

ecosystem research. In terms of modelling, biochemical interactions may provide striking examples of non-linearity: small causes can have increasingly large effects.

It seems worthwhile to critically examine the views and hypotheses outlined above and to assess in detail the potential of the phenomena mentioned for providing homeostatic properties and integration in ecosystems.

### CLOSING

The International Helgoland Symposium 1976 on 'Ecosystem research' was formally closed by Professor Kinne on October 1, 1977. In his closing address, he thanked all participants for coming to Helgoland and for contributing to the meeting, as well as Professor Riedl, for his kind words (pp. 707–708). In particular, Kinne acknowledged the financial assistance received from the Minister for Research and Technology, Bonn; the activities of the chairmen and of the conveners Drs Wulf Greve, Joel W. Hedgpeth, and John McN. Sieburth; the help of his associates who contributed enthusiastically, both during the preparation period of the meeting and while on Helgoland: Helga Witt, Agnes Heinemann, Sieglinde Bahns, Monica Blake, Nicole Dubilier, Betty Edel and Uwe Kersten.

Regarding the organization on Helgoland, the local coordinator, Dr. W. Greve had asked not to mention any names, since practically all members of the "Meeresstation" have generously offered extra time, energy and ideas. A most laudible aspect of marine ecosystem productivity was the seafood collected and served by our sailors. The "Institut für Meereskunde" (Bremerhaven) placed its new research vessel at our disposal during the meeting. Finally, the community of Helgoland, through Town-councillor Botter and Mayor Rickmers, supported the symposium in many ways. Thanks for all this help and assistance!

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