CHAPTER 1: Introduction

1.1. Concepts of experimental ecology

Every field of knowledge advances from a description and systematization of facts to their generalization, from revealing the mechanisms of phenomena to establishing the governing laws integrated in a coherent system. Such development enables one to proceed from a description to the comprehension of a phenomenon, from comprehension to a prediction of its probable changes and on to control or rational use of the object under study. The ecology of the hydrosphere or hydrobiology has also passed certain stages in its development.

The formation of hydrobiology as a science started with a description of the fauna and flora of basins, measurement of the water temperature, the contents of oxygen in it and numerous other parameters characterizing the features of environmental conditions which are the main factors determining the species diversity and seasonal dynamics as well as the quantitative development of the populations of natural waters. The study of a great number of bodies of water yielded a large quantity of material evidence on the species composition, number and biomass of hydrobionts. Typical species were singled out for different conditions, and systematic observations of the seasonal changes in the main abiotic factors were carried out.

The further development of hydrobiology is associated with the study of the production processes and the transformation of matter and energy in ecological systems. Sampling for chemical analysis or determination of the species composition, number and biomass of plants and animals proved to be insufficient for the characterization of the rates and direction of biotic processes or for an understanding of the mechanisms of phenomena. Special experimental studies became necessary; for instance, for the measurement of respiration rates of organisms, as the oxygen balance of a water body consists of oxygen release by autotrophs and oxygen consumption by heterotrophs. The study of hydrobionts' feeding became one of the most important parts of experimental works, as the transformation of matter and energy is effected through trophic interactions. A gradual accumulation of experimental results occurred characterizing different aspects of the vital activity of algae, bacteria and animals. The results of these experiments and regularities established on the basis of these results were often able to account for the species structure and quantitative development of organisms. The biotic interactions differed from abiotic ones, the former being the main factors in the majority of the following examples. A gradual transition from an autoecological to a synecological explanation of processes and phenomena occurring in the ecosystems has developed. The synecological trend in recent studies has resulted in the exploration of various interactions among organisms becoming the main experimental approach.

Here are a few examples. For instance, the species composition of the periphyton on the boulders in a small arctic lake is characterized by the domination of a gastropod *Limneaea eloides* in the littoral. The mechanism of the algae assemblage formation on the boulders implies that when the algae are consumed, animals assimilate mostly the large cells of diatomes whereas the rest of the cells pass through the gut without being assimilated. The photosynthetic activity of mollusks' faeces is lower by one fourth than in natural periphyton (Guker, 1983). Lampert (1978) observed a mass development of phytoplankton in spring ceasing at the beginning of summer in Lake Constance as well as in other lakes of the moderate climate zone. He explained this phenomenon after studying trophic interrelationships among mineral phosphorus, algae, *Daphnia* and *Cyclops*. In the middle of spring (prior to the temperature stratification, the phosphate phosphorus contents in water being about 50 µg/l), phytoplankton consisting of small cells start to grow. The amount of chlorophyll increases to 35 µg/l whereas the transparence and mineral phosphorus content decrease to 1 m and 2 - 3 µg/l respectively. Fully-grown *Cyclops vicinus* dominate in the zooplankton amounting to 15 ind./l. Predators control the number of Daphnia, their high specific birth rate (0.3 day^{-1}) supporting a possible increase in their quantity. The number of *Daphnia* is ten-fold lower than the number of *Cyclops*. *C. vicinus* brings forth a new generation in May, and nauplii and copepodites appear in plankton which does not feed on *Daphnia. Daphnia* reach the peak of their development during this period: 60 ind./l. Calculation of the energy demands for *Daphnia* and young stages of *Cyclops* shows the demands to be equal to or even to exceed the amount of primary production. Therefore the chlorophyll content decreases to 5 µg/l at the beginning of summer; the transparence grows up to 6 - 8 m and mineral phosphorus up to 20 - 30 µg/l. Then, after a diapause, elder copepoides and fully-grown *Cyclops* appear in the plankton and again reduce the quantity of Daphnia in July. The mechanism of the "clear water" phenomenon at the beginning of summer has been comprehended as a result of study of the interactions among algae, *Daphnia* and *Cyclops*.

Consequently, the species structure of populations, the number and the biomass of certain species are often a result of the biotic interactions. The latter can be comprehended through experiments carried out in order to reveal the peculiarities of growth, feeding and energy demands of the organisms. The animals are thereby the main regulators of processes occurring in water bodies. A large amount of quantitative evidence has been obtained characterizing the respiration, growth and feeding of animals, evidence which in particular enables one to generalize the data and to obtain common regularities of main vital processes both for different species and for large systematic groups. As the majority of species spend their whole life cycle in a basin, the quantitative approach to the growth, respiration and feeding of animals provides the main data necessary for revealing their role in the processes of aquatic ecosystems and mechanisms of biotic interactions. This represents the set of problems involved in the experimental ecology of water animals.

Further development of this field of knowledge will likely contribute to the general understanding of ecology in the same way as the study of basins introduced the ideas of "biocoenosis" and "microcosm”. The former was suggested by Moebius in 1877 when studying the oyster-banks of the North Sea; in 1887 he published his classic work in which a lake was regarded as a "microcosm". These ideas have only recently been accepted as a result of experimental approaches to investigation of interactions between organisms.

It is quite evident that experimental ecology is not an independent science but a part of the field of ecology or, in this particular case, of hydrobiology, in the way that experimental physics is a part of general physics. Experimental ecology is most closely associated with zoology and physiology. When, for instance, the respiration of fish is studied, the data is related to the “physiology of fish" but, if it is possible to use it for the estimation of the significance of a given organism for the reduction of the oxygen content of a lake or pond, it can also be used for hydrobiological purposes. The same is true for feeding. The morphological structure of the mouth of an animal and the way it operates are known in zoology. If this knowledge enables one to understand what kind of food the animal would select from the available natural selection, it also helps to explain the observed concentrations of these or other kinds of food. In those cases where certain studies provide data which help to understand the place and the role of species or uniformly functioning groups of organisms in ecosystems, these studies naturally become part of experimental ecology.

The above examples have already shown that, to understand the mechanisms of phenomena, it is necessary to know what the animal feeds on, how high its demands are, and how the energy of consumed food is used for respiration and growth. The unity of the main functions of living organisms countervails the morphological diversity of the organisms. The quantitative characteristics of the respiration, growth and feeding of organisms allow a comparison of the values obtained.

Matter and energy transformation in water bodies depends upon the values representing rates of feeding, respiration and growth of aquatic animals. Of course, if it were possible to obtain the necessary regularities even for the mass species of algae, animals and bacteria, this would enable the quantification of biotic interactions in the whole ecosystem. Presently, however, we only have data for aquatic animals. For the rest of the components of aquatic ecosystems data has just started to be accumulated (s. Respiration in Aquatic Ecosystem). This is why the present manual is dedicated to the experimental ecology of animals. However, data on other components of aquatic communities will also be used as required.

The essence of experimental ecology of animals consists of finding out the quantitative regularities of the balance equality components and of their application to concrete ecosystems. This means, of course, that the point involves not the results of separate measurements performed, under inevitably artificial conditions of experiments, but the regularities which characterize animals in natural conditions or in a maximal approximation of natural conditions.

Each particular experiment is valuable because the separate results of the experiments are subsequently integrated into general regularities and ideas. Since experimental ecology is based on experiments, the data obtained needs statistical processing to obtain confidence intervals of the parameters measured. Accordingly, each chapter starts with a short introduction, a description of frequently used techniques of the study with the aid of which the main results have been obtained, presentation of the main results and a deduction of the main conclusive regularities. The last chapter considers them all in a complex and suggests their application to concrete natural objects.

Certain ambient factors obviously affect the rates of the processes. Out of the great variety of factors, temperature has been singled out, because all of the invertebrates and the major part of the aquatic vertebrates are poikilotherms whose rate of metabolism depends upon temperature. The effect of other abiotic factors upon natural populations of aquatic organisms was clearly and unequivocally postulated by Winberg (1936): "Most (if not all) ambient conditions except, of course, the temperature, within a wide range affect very weakly if at all the intensity of the organism vital activity which becomes considerably upset only with approach of the ambient factor to a value extreme for a given organism. When the tension of some ambient abiotic factor approaches the extreme value and starts adversely affecting the organism, this creates such unfavourable conditions for competition of a given species with other forms better adapted to the given ambient factor that the species must inevitably yield to the other forms and either temporarily (seasonal changes) or permanently fall out of the population of the given biotope."

It is unnecessary here to emphasize the effect of, for instance, light, salinity or active reaction of water upon the vital activity of aquatic organisms. These questions are usually considered in "General Hydrobiology". It is quite obvious that a change of one or another factor forms a different species composition of the community which can affect the whole ecosystem. Convincing evidence to support this statement is the acid reaction of water and the change of hydrobiotic composition in numerous lakes of North-Western Europe as a result of acid rains.

The effect of an ambient factor on the process is studied only within the tolerance range when a long-term influence does not reduce, for instance, the survival of animals under study (Fig.1-1). Therefore, for ecological purposes, the experiments are performed with acclimated organisms. The acclimation involves a compensatory change occurring in the organism after a long-term deviation of some ambient factor from the initial level (Prosser, Brown, 1962). Since the regularities of experimental ecology of aquatic animals are necessary for understanding the functioning of natural objects, one usually strives to maximally approximate experimental conditions to natural ones and to study the object with all of the inherent and specific aspects of the natural environment. Following this rule, in future one can use the results of the experiments for understanding the functioning of natural ecosystems.

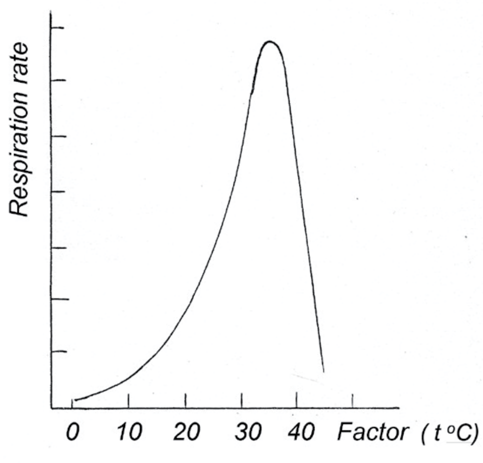

Fig. 1-1. Effect of temperature on the rate of the biological process.

The experimental ecology of aquatic animals is a field of knowledge quantitatively characterizing such main functions as respiration, growth and feeding of aquatic animals, clarifying their role in biotic processes and the mechanisms of interaction between organisms determining the productivity and quality of natural waters.