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Project Summary

The Molluscan Shell: Biological Record of Environmental Change

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The responses of benthic organisms to temporal and spatial changes in environmental quality cannot always be directly measured. For instance, the effect of a storm, pollution event, change in salinity, temperature, sediment type, etc., may be assessed with a species population after the change (or event) has taken place. In the absence of data about pre-disturbance rates of reproduction, recruitment, growth and mortality, the biologist must depend on an indirect or deductive approach. This kind of after-the-fact problem is common in paleoecology and is an increasingly important one in pollution biology.

This manual of molluscan shell growth has been prepared so that the pollution biologist, confronted with these after-the-fact monitoring problems, can extract information about recruitment, growth, and mortality responses of molluscs to past and present changes in environmental quality. Information is stored within individual molluscan shells in the form of ontogenetic records of growth and development: larval top shells, internal microgrowth increments, and changes in shell microstructures (Chapters 1-4).

Environmental change is also manifested at the population level in the form of temporal or spatial changes in the structure of whole-shell, size-frequency distributions of both living and death assemblages. An example of this approach is given for two bivalve life assemblages, *Nucula annulata* and *Mulinea lateralis* from central Long Island Sound. Populations living on a dredge-spoil dump site show very different survival curves than those populations living on the ambient seafloor (Chapter 5).

Appendices are included which provide practical information in preparing the molluscan shells for microscopical and ultrastructural study of ontogenetic growth patterns.

The purpose of this grant was to produce the handbook referred to above. However, Rhoads and Lutz, in a parallel effort, expanded on the theme of this grant to produce a book entitled *Skeletal Growth of Aquatic Organisms, Biological Records of Environmental Change* edited by Donald C. Rhoads and Richard A. Lutz, published by Plenum Press, New York, in 1980. The book provides broader coverage of skeletal growth studies including other phyla in addition to molluscs. Details of appropriate techniques are contained in an extensive appendix. This book is recommended as a reference for those interested in this topic.

This Project Summary was developed by EPA's Environmental Research Laboratory, Narragansett, RI, to announce key findings of the research project that is fully documented in a separate report of the same title (see Project Report ordering information at back).

Introduction

A wealth of information about past and present-day environments is contained within the shells of fossil and living molluscs. Information about an organism's dynamic environment can be preserved as a structural, morphological, or chemical change in the shells of individuals. The demographic[1] structure of a species population also contains much environmental information. Research into these relationships has been largely for the purpose of reconstructing paleoenvironments. The implications of this approach for ecological work has recently interested many neontologists. The ecologist is frequently concerned with reconstructing environmental events after they have taken place. For instance, it may be desirable to assess the effects of major storms, salinity fluctuations, temperature changes, or pollution events on organisms after the event or change has taken place. In the absence of information about pre-disturbance rates of reproduction, recruitment, growth, and mortality, the ecologist, like the paleoecologist, is confronted with a problem of after-the-fact data acquisition. Shell growth records can address this kind of problem.

The molluscan mantle and pallial fluid are responsible for the formation of the shell and its microstructures. Until the physiological basis of shell deposition and dissolution are well understood, interpretation of how environmental changes may be recorded in shell growth remain indeterminate. Under certain physiological conditions, part of the interior shell surface may be dissolved. In the process of shell dissolution and subsequent redeposition, primary shell architecture is sometimes reworked into distinctive secondary structures. These reworked shell layers provide an important datum for reconstructing an organism's physiologic history.

The earliest growth stages of molluscs are often preserved in the umbonal or apical top shell of post-metamorphosed individuals. The size, shape and ornamentation of the top shell can be related to larval developmental type. The larval developmental type, in turn, strongly influences the dispersal potential of a species and allows inferences to be made about a species' adaptive characteristics.

[1]Demography is used here in a broader sense; the statistical description of populations of any taxonomic group.

Methodology

How Environmental Change is Recorded by Shell Growth

A species is able to grow and reproduce as long as its functional range (biospace) is not exceeded by the ambient environment. Not all parts of the realized biospace promote equal growth or fecundity. Different combinations of niche parameters will be expressed as change rates of growth, survival, or reproductive success. Suboptimal conditions can lead to ecological stress. This stress, broadly defined, is probably responsible for many ontogenetic and demographic patterns.

Ontogenetic Growth Records

In the context of this book, ontogenetic growth is defined as the life history of an individual as it is preserved in mineralized or refractory tissues. The ontogenetic history of an organism can be preserved in the shell in several forms. In order for a change in the external environment to be recorded in the molluscan shell, the physiology of the organism must be altered. A metabolic response to an environmental change may, in turn, promote a biochemical response in the mantle and its associated pallial fluid (Chapter 2). Many physiologic changes are preserved in the shell as growth increments, growth discontinuities, changes in shell allometry, structure and mineralogy. These shell features can be observed on the whole shell or studied from specially prepared shells (see Appendices).

One of the features of the shell most frequently used in the study of ontogenetic growth is internal growth increments and patterns of increments. In molluscs, thin increments, up to tens of microns in thickness, of calcium carbonate-rich growth layers alternate with organic-rich layers. The time span represented by these increments varies between organisms and habitats, but lunar and solar days are commonly recorded in shallow water species. These increments can be seen with a microscope in appropriately prepared cross-sections of the shell (Appendices 1 and 2). No consistent nomenclature exists for the description of these growth features. They have been variously described as internal growth increments, microstructural or microscopic growth increments, or simply as microgrowth increments. The prefix *micro* is used to distinguish them from macroscopically visible growth "annulations" or bands seen on the external surfaces of many shells.[2]

Microscopic growth increments, observed in thin-sections of shell material, are determined by changes in the ratio of calcium carbonate to organic material. This is seen as a change in optical density of the shell. In acetate peel replicas of sectioned and acid-etched shells, this compositional periodicity results in differential etching of the shell and so the compositional change is observed in the peel as a topographic feature. Boundaries of increments can be gradational or abrupt. In the latter case, they may represent periods of non-decomposition or an erosional inconsistency produced through shell dissolution. These growth interruptions are sometimes called breaks, biochecks, or simply checks. They can be periodical, as in the case of shell resorption at each low tide, or aperiodical related to occasional predator attack or disturbance caused by storm turbulence. Physiological changes may also be reflected in the shell as a change in shell microstructure, for example, nacreous, prismatic, or crossed-lamellar structures, and/or a change in shell mineralogy and chemistry (Chapter 2).

Environmental changes may thus be recorded in the skeleton as a change in shell shape and form, microgrowth increments, shell microstructure, mineralogy, or chemistry. A specific environmental change may involve one or several of these variables. At the present time, most shell growth research is attempting to relate observed changes in these shell variables to specific environmental factors.

Ontogenetic growth studies involve correlating ecological stress factors such as temperature, salinity, dissolved oxygen, food concentration, substratum conditions, and water turbidity with the shell growth record. This may involve experimental manipulation of these variables in the laboratory or consist of correlating seasonally changing field conditions with growth of *in situ* populations. In some cases, transplantation of individuals from one habitat to another

[2]Macroscopic growth bands observed on the surfaces of many shells may be a surface expression of closely spaced internal growth increments. Not all species have surface expressions of their internal increments.

can provide interesting information about site-specific factors on ontogenetic growth.

The ontogenetic approach is not limited to the analysis of internal patterns of growth. Comparisons of allometric changes can be made in overall external shell dimensions as measured over relatively large intervals of shell growth (usually annual) (Chapter 1). Shell sections representing a complete record of ontogenetic growth are difficult to obtain in three-dimensionally coiled shells (e.g., spired gastropods). With spired shells, ontogenetic information must be obtained from external shell features.

Another ontogenetic approach concerns the earliest growth stages: larval and early juvenile shells. The size, ornamentation, and shape of molluscan protoconchs and prodissoconchs can be used to infer larval developmental types, time of metamorphosis, and dispersal potential (Chapter 4). In some cases, once the larval developmental type has been determined from the features of the top shell, it is possible to make further inferences about adaptive strategies, and hence, the response of an organism to past, present, or future ecological stresses.

Demographic Parameters

Demographic records of environmental change are based on the responses of populations to temporal and spatial gradients in environmental quality and ecological stress (Chapter 5). Such changes may be measured as changes in growth rate, recruitment, or survival as estimated from size or age-frequency distributions of shell parts.

Conclusions and Recommendations

A wide range of ecological problems can be addressed through shell research. The following paragraphs outline applications which can be made with current knowledge and techniques. In some examples, skeletal research has already proven fruitful. In other examples, the future potential value of skeletal research is indeterminate because, to date, some problem areas remain unexplored.

The responses of living organisms to changing environmental conditions is often explored by utilizing census sampling techniques; populations are sampled several times a year to define and follow recruitment patterns and population growth and mortality. Mark and recapture techniques are sometimes also employed to follow ontogenetic growth. These techniques are time-consuming and expensive because sampling must be carried out for at least one year. When completed, the results are applicable to only the year of study. This kind of approach is, of course, the only one available for organisms without skeletal parts. However, skeletonized organisms contain a great deal of ontogenetic and demographic information stored within their exoskeletons. Long-lived species may contain ontogenetic growth records which extend backward in time for several years.

After-the-Fact Pollution Studies

The effect of sublethal pollutants on ontogenetic growth and reproductive cycles can be deduced from analysis of ontogenetic shell growth records. Demographic analysis may also provide information about subsequent recruitment success and population growth. In the case of sublethal impacts, it is important to choose a species for study whose distribution extends beyond the limits of the polluted area so that ontogenetic and demographic data can be compared between affected and ambient populations.

If the pollution event is lethal to at least some members of a species population, the season of death and age at time of death can be reconstructed by noting the location of the shell edge relative to the seasonal pattern of internal growth patterns. Survival information provided by demographic analysis can identify those year classes that were killed relative to the total age-class structure of the affected population.

For this kind of work, species such as *Mercenaria mercenaria* or *Mytilus edulis* are ideal candidates for study because their long life spans allow analysis of skeletal records that encompass pre-disturbance growth conditions as well as post-disturbance recovery.

Identification of Adaptive Strategies

Shell growth parameters can be used by both the neontologist and paleontologist to recognize adaptive types. Opportunistic (pioneering) species have high rates of population increase, ontogenetic growth, and dispersal capability. Opportunists usually have short life spans and therefore reproduce at an early age. Mortality rates are also high. Equilibrium species have slower rates of population and ontogenetic growth. Birthrates are commonly balanced by death rates. All of these life history phenomena can be deduced from ontogenetic shell growth, larval top shells of molluscs, and population shell growth parameters. Once this is done, a sympatric association of species can be ordered into a relative spectrum of opportunism.

Fisheries Management

Fisheries management can also benefit from growth studies. Fish scales and otoliths have, for some time, been used to age fish, and this data has proven useful in the management of finfisheries. But the application of detailed shell growth analysis to shellfisheries has not yet received the attention it deserves. The shellfisheries' biologist is primarily interested in optimizing recruitment and maximizing the yield of soft-tissue biomass. Shell growth can reflect changes in soft-tissue biomass but only indirectly. During cold months, some molluscs experience negative growth of soft tissues, while the shell experiences slow positive growth. In other molluscs, both soft and calcified tissues may experience negative winter growth. Poor correlations between changes in shell growth and soft-tissue may decrease precipitously during spawning, while this reproductive event is recorded in the shell by only a few disturbance lines. During the period of summer growth, increases in soft-tissue biomass are usually positively correlated with maximum rates of shell deposition.

Shell growth is probably best used in shellfish management to construct ontogenetic and population growth curves. The ontogenetic curve can be used to determine the age at which growth becomes asymptotic to the time (age) axis. The time or age of maximum yield, in terms of population growth, can also be determined from a demographic analysis of growth. Finally, the age of first reproduction and the subsequent reproductive history can often be deduced from spawning lines in the shell. By relating these spawning lines to the seasonal clustering of internal growth patterns, the schedule of harvest can be planned so that the reproductive potential of the species is not compromised.

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