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A Series of Monographs, Texts, and Treatises

FUNCTIONAL ADAPTATIONS OF MARINE ORGANISMS

Edited by
F. John Vernberg
Winona B. Vernberg

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Preface

To function is to live. To the scientist concerned with understanding how organisms function in their environment, the sea offers diverse marine biota which are subject to very different sets of environmental factors, thereby providing an unequalled source of experimental material. The marine biota offer an opportunity to study organismic responses to "natural" sets of environmental factors as well as man-made sets of perturbations, whether they be the introduction of foreign substances, dredging, off-shore drilling, or overfishing.

This book is written to provide an insight into some of the functional adaptations of marine organisms to both natural and man-made sets of factors. It is organized into chapters representing an ecological orientation. The physiology of plants is presented in terms of both primary producers and decomposers, while functional adaptations of animals are discussed in relation to the major ecological divisions of the sea: zooplankton, meiofauna, benthic macroinvertebrates, and pelagic and deep-sea organisms. We have also written for both marine and nonmarine scientists who have broad interests in acquiring knowledge about the adaptations of organisms in changing environments. We hope that students, our hope for future progress, will be particularly stimulated, learn what has been accomplished, and then, with enthusiasm, seek answers both to persistent and to new problems.

F. John Vernberg
Winona B. Vernberg

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Introduction 1

F. J. Vernberg and W. B. Vernberg

I. Introduction

In recent years society has shown an unprecedented interest in the dynamic impact of environment on plants and animals. Not only has this ecological awareness stirred the thoughts and emotions of the layman, but also scientists from diverse scientific disciplines have become professionally involved. As would be expected, this diversity of scientific input inevitably has led to a greater understanding of the interrelationships between organisms and their environment. At the same time, the boundary lines of older scientific disciplines have become blurred, and new ones have emerged. Physiological ecology is an excellent example of a newly forged discipline which has come to the forefront in recent years by drawing on the expertise of scientists who often come from traditional scientific backgrounds. This field is concerned with understanding the basic mechanisms of organismic response to the surrounding environmental complex. Physiological ecologists attempt to interpret physiological responses in terms of their adaptive environmental significance, viewing each organism as a highly integrated system of multiple functional components that may be differentially influenced by environmental factors. The functioning of these component parts must be integrated to ensure that the intact organism can survive and perpetuate the species.

Although the principal unit of study is the individual organism, it is obvious that the organism is both part of a population and of the ecosystem containing this population. Thus, physiological ecologists are concerned with the physiological attributes of populations and communities based on responses of individuals. This continuum of interest over a range of responses from the molecular to the community level of biological organization is necessary to gain insight into the adaptive significance of these responses. The breadth of interest in ecology is restricted only by the vision of the individual investigator and not by artificially

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imposed discipline boundaries. Thus, while physiological ecologists may vary in their background and training, they are unified by their interest in understanding a very fundamental question; how and why do organisms live where they do?

Each organism is exposed to an external environment that consists of a complex combination of interesting factors. Internally the functional machinery must respond to these factors in such a way that the organism can survive. For our convenience in analyzing this environmental-organismic interaction, the external environment can be divided into abiotic and biotic factors. Abiotic factors are numerous and include temperature, salinity, geomagnetic forces, multiple chemical substances, gases, hydrostatic pressure, light, and currents. In the biotic category are such factors as predator-prey interaction, commensalism, and competition. Both biotic and abiotic factors can interact significantly to influence an organism. For example, low oxygen concentrations may adversely affect the ability of a prey species to escape from its predator. Of interest to the theme of this book is the observation that the dynamic equilibrium between the organism and its environment is constantly changing with time and fluctuation in the several components acting individually or in concert. A combination of factors that results in the death of an organism is termed the zone of lethality. When studying a single factor, there is typically a lethal point at a high and low expression of this factor. Between these "high" and "low" lethal points, there is a broad range of sublethal environmental combinations that influence the organism, known as the zone of compatibility. Within the zone of compatibility an organism may survive, but its ability to function efficiently may be markedly reduced. For example, a sublethal temperature may allow the organism to move about and feed, but curtail the reproductive potential to such an extent that the species cannot survive.

The oceanic biota represents a particular challenge to the physiological ecologist—what are the functional ploys that the diverse species from markedly different habitats utilize to survive and reproduce? Briefly, let us now consider some of the multiplicity of habitats within the marine environment.

II. Oceanic Habitats

The sea, with a volume of approximately 315 million cubic miles, covers over 71% of the earth's surface. Although tremendously vast, the unity of the sea environment is demonstrated in that the entire seawater mass is continuous, so that a drop of water could potentially make its way to any part of the total sea. In recent years, the topographical density of the ocean floor has been established by mapping. We now know that there are sea mountains with peaks that break the ocean surface to form small islands, tremendously deep trenches that cleave the ocean floor (such as the 35,800 foot Mindanao Trench), and a submerged mountain range (mid-Atlantic ridge) that extends for 10,000 miles in the North Atlantic Ocean. The ocean floor is now considered to be a dynamic system owing to the concepts of continental drift, seafloor spreading, and plate tectonics. On a geological time scale, a habitat at one specific geographical location changes constantly, and the populations of organisms that live there must adapt to new environmental stresses in an evolutionary sense. An understanding of the physiological ecology of these organisms is a great challenge.

Numerous classifications of marine environments have been proposed, but the one that has been most widely excepted is graphically represented in Fig. 1. This classification was proposed by the Committee on Marine Ecology and Paleoecology. The two major divisions of this classification are benthic and pelagic, and these may be further subdivided. Each assemblage contains a characteristic fauna and flora. Benthic environments extend from high ground to the ocean depths and have been divided into six different zones; (1) supralittoral, (2) littoral or intertidal, (3) sublittoral, (4) bathyal, (5) abyssal, and (6) hadal. The regions of the deep sea are the least well defined, although this area is the largest benthic habitat type, occupying nearly 90% of the ocean floor. The pelagic region can be divided into two main areas; the neretic zone, which comprises the water mass over the Continental Shelf, and the oceanic zone, which includes the main mass of seawater. The oceanic region may further be divided into four sub-regions; (1) the epipelagic, (2) mesopelagic, (3) bathypelagic, and (4) the abyssopelagic.

Marine environments may also be described ecologically. A good illustration are those terms that refer to the amount of light since light steadily decreases in intensity with increasing depth. The terms aphotic and euphotic generally denote regions of darkness or light. Other bases have been proposed to describe marine environments by referring to a general region of the sea, such as divisions of shore and shallow water seas, or to taxonomic groups, such as the level bottom molluscan community or the laminarian intertidal zone. Marine organisms may also be classified on the basis of the habitat type in which they live. For example, benthic organisms are associated with the bottom substrata; those species associated with the surface of the bottom are the epifauna while those that dig or are buried in the substratum are the infauna. Benthic organisms may be further divided into groups based on size; macrobenthos are organisms too large to pass through a 1 mm mesh sieve, meiobenthos are organisms smaller than the macrobenthos, but which are retained by 0.1 mm mesh sieve, and the microbenthos are organisms that are so small that they pass freely through a 0.1 mm mesh sieve. Free-moving organisms that inhabit the water column are called pelagic species, those that can control direction and speed of locomotion are called the nekton, and those primarily dependent on water movement for location or locomotion are called plankton. In turn, plankton are generally recognized as being either phytoplankton (the plant species) or zooplankton (the animal species). Nannoplankton are small plankton ranging in length from 5 to 60 μm,

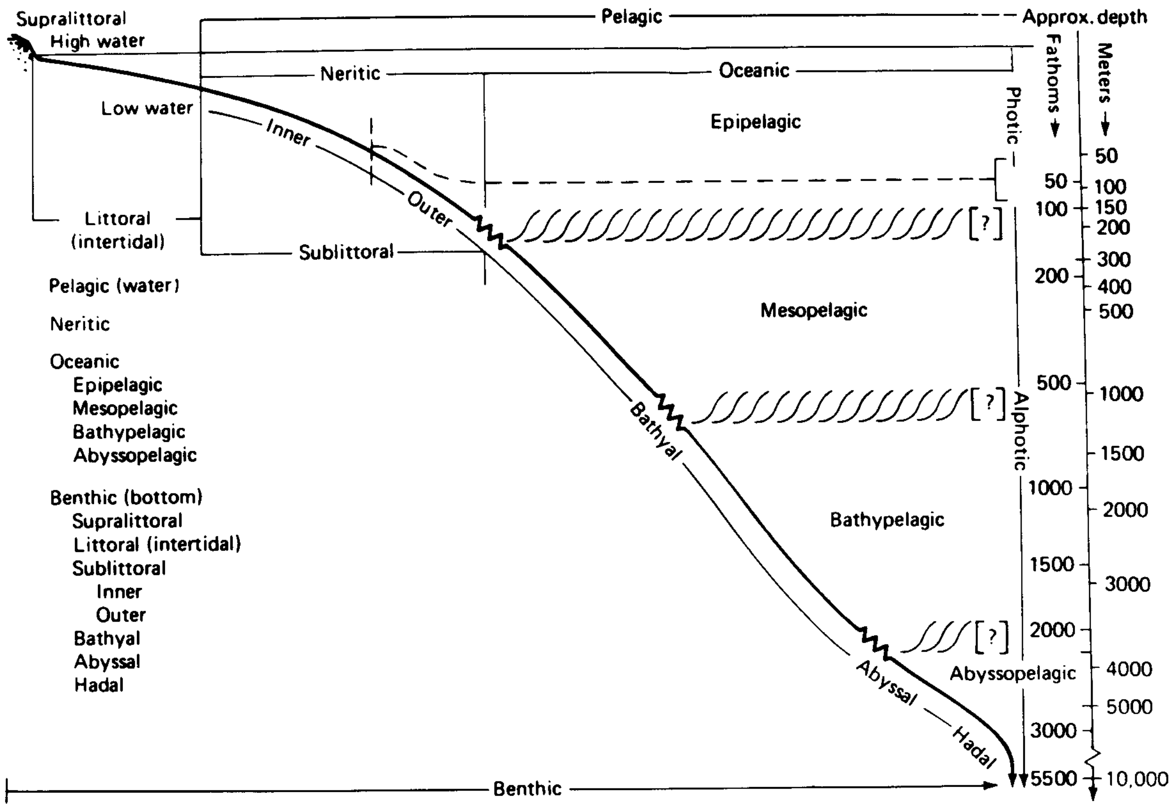

Fig. 1. Classification of marine environments. From J. W. Hedgpeth, 1957. *In* "Treatise on Marine Ecology and Paleoecology" (J. W. Hedgpeth, ed.), Vol. 1, Geol. Soc. Am. Mem. No. 67, New York, pp. 17–28.

and the ultraplankton are smaller than 5 μm. The complex terminology resulting from various classifications of plankton also include some terms that are relevant to physiological ecology. For example, holoplankton species are those in which all of the developmental stages are part of the plankton, while in other species certain life history stages are associated with the benthic environment. If nektonic species regularly occur in the benthic regions they are described as demersal; if plankton are found in the benthic regions they are said to meroplanktonic.

III. The Intertidal Zone

The intertidal zone is a narrow fringe between the ocean and land, and organisms living there are alternately exposed to air and covered by water. This zone is not homogeneous in structure or in physical, chemical, or biotic characteristics. There are, however, three major types of habitats: rocky shores, sandy beaches, and mud-flats. These habitats may be found on the edge of the open ocean and bordering protected regions such as harbors and estuaries.

Characteristically animals living in the intertidal zone are subjected to widely fluctuating environmental conditions, particularly in regions of noticeable tidal change. In such regions, animals may be exposed to wide ranges of seasonal and temporal temperature fluctuations, to salinity changes, and to desiccation. Thus it is not surprising that animals of the intertidal zone tend to be more eurythermal, euryhaline, and resistant to desiccation than other organisms in other marine environments. Many also experience periods of oxygen stress and often must function anaerobically for varying periods of time.

Mechanisms through which intertidal zone animals are able to feed, select their environment, or find a mate may be correlated with their way of life. A burrowing animal, such as a polychaete, will obviously utilize different physiological responses than will a semiterrestrial intertidal-zone crab.

A common characteristic of intertidal zone animals is their tendency to have pelagic larval stages so that their reproductive cycles must be geared to ensure release of gametes into a favorable watery environment.

Thus it can be seen that the intertidal zone offers a nonhomogenous and fluctuating environment with a multiplicity of habitats and microenvironments.

IV. Estuaries

The estuary is a dynamic environment where freshwater mixes with the sea. One of the chief characteristics of this environment is fluctuation in salinity. Tidal changes affect salinity by increasing salinity on a flood tide and decreasing it on an ebb tide, and typically the water is fresher at the surface than at the bottom. Changes in salinity can be sudden and dramatic; e.g., a change in estuarine salinity from 30 to 10‰ within a one-hour period is not atypical. It is also common for the salinity of estuarine waters to vary seasonally, so that the water may be nearly fresh during winter and spring rains, but strongly saline in summer. Although not as great as in the intertidal zone, temperature changes in an estuarine system often are greater than those of either offshore waters or the open ocean, since inflowing river waters tend to be colder than seawater in winter and warmer in summer. Thus, organisms living an an estuarine environment must be able to tolerate a wide range of salinity and, to a lesser degree, change in temperature.

Estuaries are almost always turbid because of the amount of silt in the water. Light cannot penetrate to as great a depth as it does in coastal and open waters, and the animals living in an estuary must depend on sensory cues other than vision to carry out such functions as locating food or avoiding predators. Siltation in the water column is often a major factor affecting primary production, and it also covers the substratum so that mud is the most common type of bottom. These bottom muds are rich in organic detritus (derived primarily from the vegetation along upper tidal levels) and therefore provide a ready source of food for many estuarine organisms. However, this often means that conditions are anoxic a few centimeters beneath the surface of the substrate.

Thus, estuaries offer a murky environment in which salinities and temperature fluctuate markedly, but where food supplies are abundant. While estuarine species are few in number, those that have become adapted to this environment are present in large numbers.

V. Coastal and Open Ocean Waters

Coastal and open ocean waters offer more stable environmental conditions than do either the intertidal zone or an estuarine system. Salinity and temperature are much less variable, although coastal waters will vary in chemical composition more than open ocean water and the range of variation in physical factors also typically is greater in coastal water. These differences are due in large part to some run-off from land masses and the shallowness of coastal areas (less than 200 m). Wave action stirs up bottom sediments and allows mixing and recycling of nutrients and other organic matter.

In contrast to the murk of the estuaries, where light often penetrates only a short distance, the clarity in the upper layers of coastal and open ocean waters permits light penetration to considerable depth. Not surprisingly, light is one of the most important environmental factors in these waters. The depth of the photic zone depends on latitude, season, and amount of particulate matter. The quality of light is variable in the photic zone because of differential penetration of the wavelengths. As a general rule, the yellow-green wavelengths penetrate inshore waters, and the blue-green wavelengths reach deep oceanic water. Vertical migrations of many oceanic species appear to be related to light intensity, and others use the sun as an orienting or navigational device.

Unlike the estuarine environment, the pelagic zone of coastal and open ocean waters have been characterized as a nutritionally dilute environment, for although food supply is essentially limitless, it may be so thinly dispersed that the problem of getting enough to eat is formidable. Consequently, animals living here have per force evolved diverse and efficient methods to feed. Plankton tend to dominate this environment; phytoplankton are the primary producers and zooplankton are the primary herbivores.

Thus, coastal and open ocean waters offer a more stable salinity and thermal environment than do estuarine systems, and light is a major factor in the upper layers of oceanic waters.

VI. The Deep Sea

For the most part, the deep-sea environment (depths below 2000 m) is relatively stable; the salinity is approximately 34.8%, the temperature may vary from 3.6° to 0.6° C, the oxygen concentration is typically high and constant, and no light is present (except for bioluminescence). Food supplies are generally low and organisms exhibit feeding mechanisms characteristic of this type of environment. One unique feature of the deep sea is increased hydrostatic pressure. Since the hydrostatic pressure is increased one atmosphere with every increase of 10 m, it is one variable experienced by deep sea organisms. An organism at 2000 m is subjected to 200 atm while an individual living at 6000 meters experiences a pressure of 600 atm.

With this brief overview as background, we can now proceed to examine some of the physiological adaptations that permit marine organisms to live in such diverse environments.

The following chapters are organized both on an ecological basis of trophic function and habitat. Chapters 2 and 3 deal with primary producers and decomposers, respectively, while the remaining chapters discuss zooplankton, meiofauna, benthic macrofauna, pelagic macrofauna, and deep-sea organisms.