Environmental Physiology of Marine Animals

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Preface

Within recent years man has become increasingly aware of the disastrous environmental changes that he has introduced, and therefore society is now more concerned about understanding the adaptations organisms have evolved in order to survive and flourish in their environment. Because much of the information pertaining to this subject is scattered in various journals or special symposia proceedings, our purpose in writing this book is to bring together in a college- and graduate-student text the principal concepts of the environmental physiology of the animals that inhabit one of the major realms of the earth, the sea.

Our book is not meant to be a definitive treatise on the physiological adaptation of the animals that inhabit the marine environment. Instead, we have tried to highlight some of the physiological mechanisms through which these animals have been able to meet the challenges of their environment. We have not written this book for any one particular scientific discipline; rather, we hope that it will have an interdisciplinary appeal. It is meant to be both a reference text and a text for teaching senior undergraduate and graduate courses in marine biology, physiological ecology of marine animals, and environmental physiology of marine animals.

We are indebted to our students and colleagues present and past, who have helped formulate some of our ideas. We are grateful to the following people for critical reading of various parts of the manuscript: Mr. John Baptist and Drs. Anna Ruth Brummett, Richard Dame, Rezneat Darnell, Charlotte Mangum, Ernest Naylor, A. N. Sastry, Carl Schlieper, S. E. Woods, Ms. Barbara Caldwell, Ms. Cary Clark, and Ms. Susan Ivestor. We are especially indebted to Dr. P. J. DeCoursey for reading most of the manuscript and giving constant encouragement, Ms. Susan Counts for typing the manuscript, Ms. Vicky Macintyre for invaluable editorial assistance, and Mr. Gary Anderson for original art work. We also gratefully acknowledge assistance on the home front from Mr. Eric Vernberg and from the Misses Amy Vernberg, Melissa Holmes, and Bess Roberts.

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CHAPTER I

THE ORGANISM

Man has always had a vital and continuing interest in the sea. Coastal waters were an early source of food and means of travel, but the extent of the oceans was not recognized until the explorations of the 14th and 15th centuries. Another five centuries elapsed before man had the technology to truly begin underwater exploration.

Modern interest in the marine environment is based mainly on its scientific and economic value. Competition for the natural resources of the sea is already great in some parts of the world. Estuaries, for example, are multipurpose regions, serving as centers for living, industrial development, shipping, fishing, and recreation. Full utilization of the resources of the open ocean has not yet been realized, but the demand and competition for these resources are destined to increase rapidly within the next few years.

Until recently, the resources of the sea were assumed to be almost limitless. Now, of course, we know this assumption is false. In some areas of the world, estuaries already have been exploited to such an extent that they are biologically dead; hence, they are of limited use to man. Effective utilization of the great natural marine resources depends on proper management and manipulation based on scientific fact. The outcome of environmental manipulation is difficult to predict, mainly because little is known of the functional responses of marine animals to an altered environment. The principal goal of this book is to emphasize this one important aspect of the broad subject of marine science.

Rather than present a compendium of published papers on the physiology of marine animals, we propose to review the existing literature and present principles that may serve as a framework for present-day students. We hope that future generations of environmentalists will both alter and add to this framework. Certain physiological phases of marine organisms have been intensively studied, others scarcely touched. Many basic physiological processes common to all animals have been best studied using marine organisms, but these investigations have not been strongly oriented to answering environmental questions; hence, they are only of tangential interest to the theme of this book. Our theme is to emphasize the functional interrelationships of the component parts of an organism in meeting the stress of environmental fluctuation. To us the intact organism is the basic unit of biological organization, but at the same time we recognize that the various component physiological systems play a vital role in maintaining the integrity of the organism.

The organism is a discrete, easily recognized unit. It is a dynamic and energetic system, consisting of many functional subunits finely tuned to interact harmoniously and thus insure survival of the total system. To the organism in a harsh environmental complex, mere survival is the minimal level of performance; but for the perpetuation of the species, more highly integrated processes leading to reproduction must be operational. Irrespective of the levels of performance demanded of an organism, a constant interchange of energy takes place between the organism and its ambient environment. The sum total of the energetics of the organism is called *metabolism*. Various functional subunits of metabolism have been recognized, and these play an important role in the integrative functioning of the intact organism. The operation of the subunits requires a specific form of energy, each of which may in turn release energy in a different form. Specialization of cells into tissues and organ systems occurred as organisms evolved from unicellular to multicellular units. Although the degree of complexity in these organ systems is exceedingly diverse throughout the animal kingdom, certain principles are fundamental to all of these variant forms. In this chapter, physiological similarities will be stressed; later sections will describe modifications that relate organismic adaptation to a given set of environmental conditions characteristic of the organism's habitat.

To be functional, the organism must have an energy input followed by effective utilization of this energy. Over an extended period of time, energy input must equal energy utilization if an organism is to maintain itself. For brief periods of time, an organism can rely on stored energy reserves, which results in less energy input than energy utilization. This ability to operate at a negative level varies from species to species. Without food some animals will die quickly, but others can survive for years. When excess energy is available, the animal may either undergo a rapid period of growth and/or store the excess energy for future use.

Maintenance of a relatively balanced energy budget demands the integration of a number of processes. Energy input into a system requires that the organism be able to perceive the environment in terms of seeking and capturing food. Once food has been located, the animal must be able to go through the process of ingestion, digestion, and assimilation, circulation of the assimilated food to the body cells, and egestion of unusable portions. The energy that has been gained then must be released by the cells for utilization in active processes or stockpiled for later use. Most animals require oxygen for the release of this energy. During these metabolic processes, wastes are produced which must be removed, processed, and eliminated into the external environment. Other processes, including locomotion, mating activities, and production of gametes, also make demands on the available energy. In addition, energy is required for the chemical and nervous coordination of all of these activities necessary to sustain life.

A. METABOLIC SUBUNITS

1. Perception of the Environment

Although all cells are capable of performing basic functional processes consistent with their existence, mechanisms have evolved which permit all parts of multicellular organisms to function as an integrated unit. The degree of organismic integration varies from a more or less loose clump of cells to multicellular organisms consisting of tissues which have become specialized to perform certain functions. In general, both nervous and chemical controls are involved in the coordination of multicellular marine animals.

a. Nervous Coordination—Sensory Modalities

A highly coördinated organism has four main components: information-gathering modalities; methods of transmitting this information either to integrative centers or directly to effector organs; coordination centers; and effector structures.

Organisms must not only be sensitive to changes in their external environment in order to survive, but they must also have operative internal information-gathering mechanisms. Various forms of ***exteroceptive organs*** have evolved that permit the organism to perceive the external environment, and the relative role of each in the success of an organism is correlated in part with the organism's ecology. Laverack (1968) has extensively reviewed the sensory organs of marine animals. Internal receptors which perceive changes within an organism also show diversity in form, but relatively little is known about them in marine animals.

(1) Vision

In the marine environment, the most commonly used sensory modalities are those for light reception, phonoreception, chemoreception, and those largely undefined organs for the perception of gravity and pressure. Light receptors are common to almost all animals. These receptors may be dermal light receptors or well-defined organs, such as the vertebrate eye, the compound eyes of crustacea and insects, the simple eyes or ocelli of other arthropods and invertebrates. Only a small fraction of the total spectrum of radiation is perceived as light, and the visible spectrum of all light is limited to wavelengths between about 300 and 700 mμ. Photosensitivity is diffuse with dermal light receptors, whereas the more complex optic receptors can perceive qualitative, temporal, and spatial qualities of light. Sensitivity is several thousand times less in the dermal light receptors than in the more well-developed eyes, but it is thought that the photochemical systems responsible for all light reactions are similar.

Dermal light receptors are widespread throughout the animal kingdom, but they are most common in aquatic invertebrates having a simple epithelium or superficial nervous system. After reviewing the work on dermal light receptors, Steven (1963) concluded that the light response probably results from accumulation of small amounts of photosensitive substances in the cytoplasm.

There are three major types of responses in animals caused by the dermal light sense: orientation by bending the body; the shadow reflex or withdrawal of exposed parts of the body in response to a sudden change in illumination; and environment selection. In animals with well-developed visual organs, reception of light is used in environment selection, predator-prey relationships, and close-range communication.

(2) *Audition*

Animals are able to detect vibrations in the surrounding medium and the substrates by means of many different structures. The perception of vibrations may enable an organism to distinguish between frequencies, to measure relative intensity, and to determine the direction of sound. The term *phonoreception* has been suggested to designate reception of sound, irrespective of the type of receptor that is stimulated or the medium through which the sound reaches the body—be it solid, liquid, or air (Frings, 1964; Frings and Frings, 1967).

Sound receptor systems may be one of two types. One type, which is sensitive to molecular displacement, consists of a membrane or a hair suspended so that it responds to slight movements of the medium. Sound waves must have free access to it from all directions if it is a membrane. The other type of receptor is based on a pressure-sensitive system. In this type of system a heavy membrane is shielded on its inner surface from sound waves, and the inner chamber is kept at some stable reference pressure that is usually equal to the atmosphere. The stimulus is registered directly by displacement receptors; pressure receptors register only indirectly.

Many invertebrates will respond to substrate vibrations. A number of potential sound receptors in invertebrates have been described, including innervated projections from the body wall, sensillae in the body wall itself, proprioceptors located deep in the muscles or external organs, and specialized sensillae (Frings, 1964). Only some arthropods and vertebrates have an ability to detect airborne sound as well. In vertebrates, the ear functions as a pressure receptor and is the basic organ for sound perception. In aquatic mammals, the ear responds to pressure change in the surrounding medium. Fish that have a gas-filled swim bladder connected to the inner ear also respond in this manner. The lateral line organ of fish is a displacement receptor and enables the fish to perceive low-pitched vibrations. This organ is used as a "distant" touch receptor to detect and locate moving animals. Such a receptor can be very important for the orientation of fish in space, especially for those in murky waters. Animals respond to a very wide range of frequencies. Some fish perceive frequencies from below 100 Hz up to 3,000 Hz. In contrast the range of frequencies in man is from 20–20,000 Hz. Phonoreception functions in exploration of the environment, in finding food, in avoiding danger, in reproductive behavior, and in communication.

(3) Chemoreception

All living animals are able to perceive the chemical characteristics of the environment. There are three main types of chemoreceptors, classified according to relative sensitivity and the location of receptors on the body surface. The "general chemical sense," which may extend over large parts of the body, is the least sensitive of the receptors. Mediated by free nerve endings and by rarely identified, unspecialized receptors it is characteristic of both invertebrates and vertebrates. Usually the response to this sense is a simple avoidance reaction. The other types of chemoreception, taste and smell, are more varied responses. Taste requires contact between relatively large quantities of water-soluble substances and specialized taste receptors. *Olfaction,* or the sense of smell, responds to low chemical concentrations and is the most sensitive of the chemoreceptors. The chemical senses are used in selecting an environment, finding food, detecting enemies, and locating a mate.

(4) Perception of gravity

Gravity, one of the most constant mechanical forces in the environment, does not vary in either the direction of pull or the intensity in any given location. Gravity is used by animals as the basic plane of reference enabling them to maintain a definite attitude in space, and they may also have an orientation response to or from the gravitational force. The sensory equipment that allows perception of gravity basically consists of some free or attached structure that responds to gravity and, by a shearing force or pressure, acts upon sensory cells that provide information to the animals. Statocysts, which are present in animals from coelenterates to man, are one of the most common gravity detection devices. Usually these statocysts consist of a fluid-filled vessel lined with sensory hairs and containing a statolith or statoliths, which may be either grains of sand or secreted substances. Gravity is detected through the vestibular labyrinth of the inner ear in most vertebrates.

(5) Perception of pressure

The nature of the receptor organs in aquatic animals for perceiving pressure changes is not known, but many planktonic animals are sensitive to small changes in hydrostatic pressures—often to changes equivalent to less than a meter of water. Some organisms are restricted to a limited range of depth, while others can move relatively freely from one level to another. Pressure effects and responses in marine animals have been reviewed by Morgan and Knight-Jones (1966).

The conduction of nerve impulses to effector organs and/or to integrative centers involves nervous transmission, ranging in complexity from simple cell to cell (non-nervous) conduction to complex nervous systems. Although this extremely important aspect of coordination is influenced by the environment, the reader is referred to other references for detailed accounts (Bullock and Horridge, 1965). Coordination of the various kinds of information presented to an organism permits it to be more than a passive responder to every stimulus. Marine organisms with highly developed central nervous systems generally have behavior patterns which are complex, varied, and capable of being modified by past experiences.

Effector organs bring about responses to stimuli which reach them from coordination centers and/or a receptor organ. Thus, these organs respond to information from both the external and the internal environment. The various effector organs range in complexity from a ciliated cell to light-generating organs. The degree of complexity and the type of effector organs found in an organism appear to be an adaptation to a particular ecological requirement.

b. Chemical Coordination

Although all chemical substances must potentially exert some regulative effect on the organism, many species have evolved special glands (endocrine glands) which produce hormones effective in coordination of physiological processes. In addition, specialized cells (neurosecretory cells) of the central nervous system produce hormones which travel along the axons to specialized regions for storage until they are subsequently released. For a discussion of hormone action, consult a text in endocrinology.

2. Feeding

The bioenergetics of an animal is completely dependent on an input of energy and chemical necessities in the form of food. The "taking-in" of food involves separate processes: (1) perception and (2) capture and ingestion of food. Perception of food depends upon the ability of the organism to be stimulated by some external environmental cue. This cue may be a chemical entity, or it may have a physical basis, such as a visual or tactile stimulus. The relative dependence of feeding on specific physical and/or chemical mechanisms is associated with the ecology and mode of existence of the species. Animals living in clear and open areas (for example, mobile species in the intertidal zone) may use vision as the primary means for locating food. In poorly lighted habitats, audition, chemoreception, or thermal sense may be more useful. In many environments the animal is apt to rely on chemoreception if food must be located over long distances. In some animals the process of feeding requires more than an external cue. For example, food may be continuously present, but the animal feeds only intermittently; thus, in these animals feeding is dependent on internal factors, such as different thresholds of hunger.

Mechanisms for the capture and ingestion of food can be correlated with the niche an animal occupies. This relationship was clearly shown in the earlier classification of the feeding mechanism proposed by Yonge (1928), which was not based on phylogenetic relationships, but instead reflected the ecology of the organism.

Three main categories of feeding were proposed based on particle size and type of food: small particles; large particles or masses; and soft tissues or fluids. Detailed descriptions of these categories may be found in various textbooks and references (Jennings, 1970; Jørgensen, 1966; Yonge, 1928).

To be of energetic value to the organism and to provide the basic molecules needed for synthesis and growth, ingested food must be broken into smaller chemical units by digestive enzymes. Three general types of digestive enzymes are recognized: lipases, proteases, and carbohydrases, each acting on one of the three main types of food. The composition and relative activity of these types of enzymes can be correlated with the ecology and food requirements of animals. In general, herbivores have more powerful carbohydrases and weak proteases. The reverse is found in carnivores. In omnivores all three types of enzymes are secreted, and all are approximately of equal importance. The composition and activity of digestive enzymes are also influenced by external environmental factors, such as temperature and type of food. The size and shape of the digestive tract can also be correlated with an animal's environmental demands (Yonge, 1937).

3. Respiration

Energy taken into the body in food molecules must be released within the organism as free energy if it is to be functionally important to an organism for cellular activities. The release of free energy occurs through oxidation-reduction reactions. Classically, chemists thought oxygen was needed for oxidation, but since oxidation is defined as the transfer of an electron from one molecule to another, and reduction is the electron acceptance by a molecule, oxygen is not necessary for this process.

a. Metabolic pathways

Within a cell the total free energy available from a food molecule, such as glycogen, is not released all at once. Instead, the complete breakdown of food molecules is a step-like series of reactions; specific catabolic pathways have been described for various compounds. The relatively simple components that result may be used for various synthetic processes. Again, specific anabolic pathways exist for the synthesis of specific complex cellular constituents.

Detailed analyses of various metabolic pathways are presented in various biochemical textbooks and are beyond the scope of this book. However, exposure to certain general concepts is necessary for understanding pertinent biochemical studies involving marine organisms. Catabolic pathways begin with well-defined complex food substances which are altered into various intermediates, while anabolic pathways begin with these various intermediates

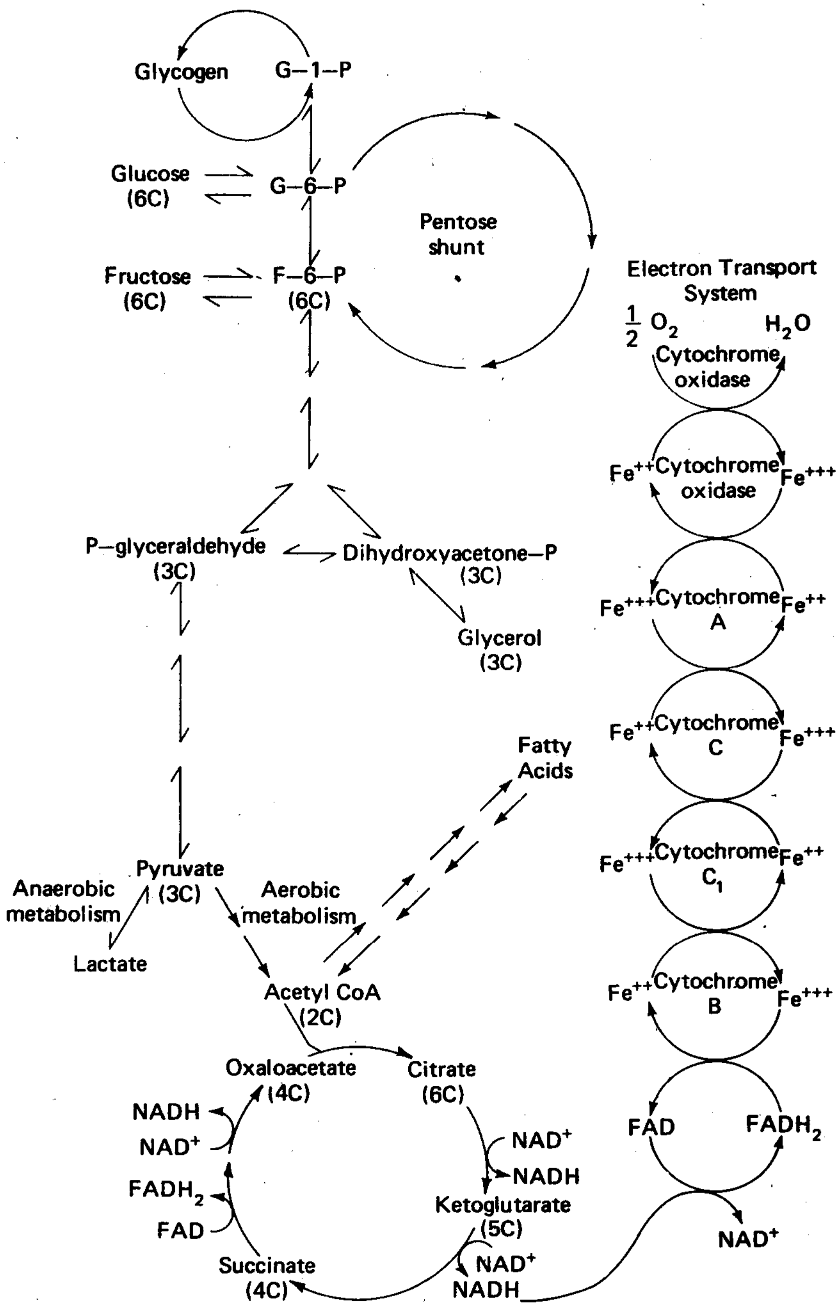

Fig. 1-1. Simplified scheme of one of the principal metabolic pathways involving carbohydrates.

which ultimately are synthesized into distinct end products. One of the principal pathways involving carbohydrates is presented in a simplified scheme in Fig. 1.1. At each step a small amount of energy is released that may be stored in high energy phosphate bond compounds, such as ATP. Whenever oxygen is present, it serves as the terminal hydrogen and electron acceptor.

b. Metabolic diversity

Oxygen utilization, CO_2 production, and utilization of foodstuffs are measurements of the energy metabolism of cells and the intact organism. Respiration is that phase of the metabolic process involved in exchanges of oxygen and carbon dioxide between an organism (or isolated cells) and its external environment. Primitive acellular organisms carry on gaseous exchange across body membranes. However, with increased size, oxygen needs are not adequately supplied by this process. It has been estimated that diffusion is an unsatisfactory mode of supplying oxygen to an active organism if the distance from body surface to a cell is greater than 0.5 mm. Basically the exchange of respiratory gases requires two conditions: a thin, moist membrane or body covering through which respiratory gases can diffuse; and a concentration gradient of gases whereby the ambient oxygen content is higher, and the CO_2 is lower, than that within the organism. Diversity in gaseous exchange mechanisms among marine organisms has proceeded along a number of major lines: (1) Specialized regions of the body modified for gaseous exchange. Crustacea and fish, for example, have external or internal gills, and many polychaetes have parapodia modified for gaseous exchange. In some animals, these regions are retractable or internal and thus are well protected. (2) Maintenance of an oxygen gradient across a diffusible membrane. This can be accomplished by the animal's swimming to new, relatively oxygen-rich regions, by moving the water at the surface of the respiratory membrane, by ciliary action, or by moving a respiratory structure, such as the waving of parapodia or tentacles. (3) Internal structural changes. Increased vascularization in regions of a respiratory membrane, or an improved circulatory system to remove oxygen dissolved in the body fluid from the body surface to the cells, including development of better circulation pathways and a pulsating organ, the heart. (4) Oxygen-carrying compounds. A number of chemical substances which have an affinity for oxygen have evolved. These substances, respiratory pigments, exhibit qualitative and quantitative differences that can be correlated with habitat preferences. (5) Behavior patterns, including swimming to areas of sufficient oxygen content, decreasing locomotor activity, or closing of a shell or protective plates during low oxygen stress. (6) Physiological adaptations, including shifts in metabolic pathways and changes in rate of heart beat or pumping rates.

c. Factors influencing respiration rate

The rate at which organisms consume oxygen is modified by many factors, some environmental, others intra-organismic, and not all animals are influenced in the same manner. Therefore, it is difficult to generalize, and the effects of these factors must be determined for each species. In this chapter, only general terms will be introduced; specific examples will be given later.

(*1*) *Extrinsic factors*

(*a*) *Oxygen tension:* On the basis of two generalized responses to external oxygen tension, organisms may be classified either as: conformers, which have oxygen consumption rates that are dependent on oxygen tension; or regulators, which have oxygen consumption rates that are constant over a wide range of oxygen tension (Fig. 1.2). Typically, at a critical oxygen tension (Pc),

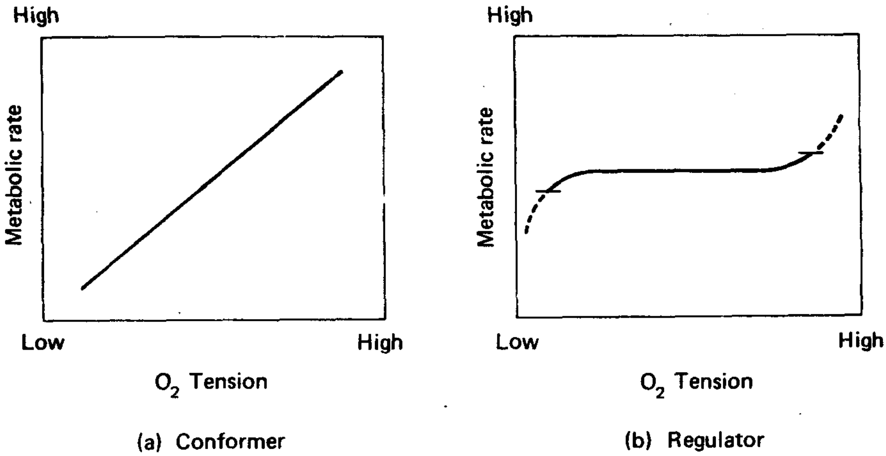

Fig. 1-2. Two generalized metabolic responses to variable external oxygen tension: (a) conformer, the metabolic rate varies directly with oxygen tension; (b) regulator, the metabolic rate is constant over a wide range of oxygen tension.

the oxygen independent rate shifts to become oxygen dependent. The Pc value may vary with both intra-organismic and environmental factors.

During periods of exposure to low oxygen tensions, the organism may be insured of adequate oxygen uptake by pumping more of the ambient medium over its respiratory surface. This is done by increasing the frequency of respiratory movements and/or increasing the volume of water (or air) pumped. Some of the overt expressions of respiratory movements include opercular movements in fish, pumping movements of worms which live in burrows, pleopod beating in many crustacea, and tentacular movements in certain worms. In some organisms increased CO_2 levels are more stimulatory in eliciting these responses than decreased O_2 content.

(*b*) *Temperature:* As in chemical reactions, an increase in temperature typically is accompanied by an increase in metabolic rate in poikilotherms. Two principal methods exist for expressing the influence of temperature on reactions as a coefficient. One method is termed Van't Hoff's equation, and the temperature coefficient is called the Q_{10}. Typically, for every 10°C increase in temperature the rate of a chemical reaction will increase by a factor of 2 to 3 ($Q_{10} = 2$ to 3). A Q_{10} value of less than 2, or more than 3, indicates some process other than a chemical one is involved, e.g., a change in permeability. A Q_{10} of 1 indicates temperature insensitivity. The other principal method of expressing the influence of temperature on reactions is the Arrenhius equation, and the temperature coefficient is designated as μ. The μ value of the Arrenhius equation reflects the amount of energy needed to activate a specific thermochemical reaction. A change in a μ value at a given temperature indicates the activation of a different biochemical reaction. A change in this value over a thermal range indicates a shift in the basic control mechanism(s).

(*c*) *Other factors:* Factors, such as salinity, light, food, CO_2 and cyclic changes in environmental parameters acting independently or in various combinations, also may influence the rate of oxygen utilization.

(*2*) *Intrinsic factors*

In general, small organisms consume more oxygen per unit time and weight than large ones (Hemmingsen, 1960). This trend has been reported both intra- and interspecifically (Vernberg, 1959). The relationship of size to metabolic rate is commonly expressed as a power function of body size. Results are written in two general ways. For total metabolism (amount of oxygen consumed per unit time) the equation is:

$O_2 = aW^b$ or $\log O_2 = \log a + b \log W$. For weight-specific metabolism (amount of oxygen consumed per unit time and unit weight), the formula is:

$$\frac{O_2}{W} = aW^{(b-1)} \text{ or } \log \frac{O_2}{W} = \log a + (b-1) \log W.$$

In these equations, O_2 is the oxygen consumed per unit time; W is the weight of animal, which may be expressed as wet weight, dry weight, nitrogen etc.; and a and b are coefficients, *a* representing the intercept of the y-axis and *b*, the slope of the function in the logarithmic plot. Respiratory rates are also influenced by other factors, such as locomotor activity, starvation, sex, stage of life cycle, reproductive stage, and molting stage.

Oxygen consumption values are determined under different experimental conditions, and specific terminology is associated with these conditions. ***Standard metabolism*** is the rate of oxygen uptake when an animal is maintained under a defined state of activity. During periods of controlled, heightened activity of an organism (such as swimming or flying), the oxygen consumption rate is termed ***activity metabolism***. ***Basal metabolism*** refers to the rate of oxygen utilization in an inactive organism and reflects the minimal metabolic rate consistent with life.

4. Circulation

a. Diversity in circulation

In unicellular and simple multicellular organisms, diffusion can supply to the cells the raw materials necessary for them to sustain metabolism and remove metabolic wastes. In more complex multicellular organisms, however, certain functional strategies have evolved which permit efficient circulation of body fluids to the inner cells. An inspection of existing animal groups reveals tremendous diversity in the types of body fluids and in the complexity of circulatory systems. Functionally, there are certain similarities in these groups that indicate the basic role of circulating fluids; dissimilarities may be correlated with unique habitat requirements and specialized functions.

The basic function of circulating fluids is twofold: the transport of substances throughout the body, including nutrients, oxygen, and various regulatory substances; and the removal from the cells of CO_2, metabolic wastes, and cell products. The circulating fluids can be very complex in composition; in addition to supplying cellular needs, these fluids may carry clotting substances, antigens, antibodies, and blood cells. In some species the total osmotic concentration and the specific ionic composition of circulating fluids are carefully controlled. The body fluid tends to give shape to some organisms and also aids in body movements, especially among the soft-bodied invertebrates.

Intracellular circulation of material is described in various cellular textbooks; in this book we will be concerned with the transport of substances to and from cells. Sea water is in close contact with various parts of the body in simpler marine metazoans—for example, sponges move sea water through a system of channels and chambers by flagellar action. Cnidarians offer another variation on this theme in that their cells are in close contact with sea water either through external body layers or through the lining of a convoluted gastrovascular cavity. There is no apparent vascular system that reaches all parts of the body, and diffusion seems to be the principal mechanism of intercellular transport. Generally, metabolic activity is low in animals that lack any type of vascular system.

There are two general types of circulatory systems, open and closed. The closed circulatory system consists of a network of interconnected blood vessels through which blood is pumped by a muscular structure or structures. Usually three types of vessels are recognized: arteries that carry blood away from the heart; veins that carry blood to the heart; and capillaries that are found between arteries and veins. Although the diameter of capillaries is small and their walls thin, it is here that exchange between the vascular fluid and the tissue fluid takes place. Generally, many capillaries are found together, forming a capillary bed. Since the capillary wall is semipermeable, the composition of blood and the tissue fluid differ. In contrast, the open circulatory system does not have a capillary connection between large blood vessels, and the vascular fluid comes into direct contact with tissue cells.