Environmental adaptation to lagoon systems

ABSTRACT

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Organisms residing in lagoon systems on a permanent or transient basis have evolved numerous adaptive ploys to meet the evolutionary challenge of a dynamic environment, including functional, behavioral and morphological mechanisms. The lagoon environment not only consists of « normal » biotic and abiotic factors, but the number and types of « man-induced » factors are increasing rapidly. Hence pollutants and perturbations are now a permanent part of this habitat type. The dynamics of organismic-environmental interaction involves lethal and sublethal responses of all life cycle stages. Various physiological systems not only are independently adapted to environmental changes but intersystem integration has occurred. The principal purposes of this paper are to review briefly existing literature, to highlight some current research trends, and to attempt a synthesis of integrative mechanisms. The principal emphasis is on individual species, as community metabolism, will be discussed elsewhere, but symbiotic relationship and population characteristics will be discussed.


RÉSUMÉ

Adaptation environnementale aux systèmes lagunaires


INTRODUCTION

Animals and plants residing in the coastal lagoon habitat, either as permanent residents or as transients during various seasons of the year, face a complex of environmental factors each of which may vary widely. Traditionally this habitat has been described as being hostile, demanding, or physically stressed when compared to more stable environments, such as the deep sea. Hence, organisms in lagoons would be expected to demonstrate a wide array of adaptations to the numerous physical, chemical, and biological factors which comprise this ecologically interesting segment of the Earth's

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biosphere. Although biologists frequently study the influence of one or a few environmental factors at a time, we must not forget that many factors may vary independently or in concert to affect an organism. Recognition of the dynamic interaction between an organism and its entire environmental complex is referred to as the principle of the holocoenetic environment (see review, Billings, 1952).

As background for developing the theme of this general review paper, functional adaptation to the lagoon habitat, the dynamic interaction between the internal functioning of an organism and its external milieu must be recognized. For discussion the environment commonly is subdivided into two major components: 1) abiotic factors, and 2) biotic factors. The abiotic component consists of various physical, geological, and chemical factors, such as oxygen, temperature, sediment, geomagnetism, pressure, and pH, while the biotic component includes all interorganismic relationships, such as competition, predator-prey relationships, and symbiosis. Some factors are not easily classified as either biotic or abiotic; for example, a metabolite (chemical factor) produced by one organism may act as a prey attractant when released to the external environment (biotic interaction).

Internally, the various physiological processes of an organism are influenced to varying degrees by changes in external factors. This paper will present a few selected examples of how organisms living in lagoons respond to their external environment.

For each species a certain sector of the potential range of expression of an environmental factor is compatible with life. At either end of this range or gradient there is a point beyond which an organism is unable to survive. The broad middle sector of a gradient has been given various names: the zone of compatibility, the zone of tolerance, the biokinetic zone, or the zone of capacity adaptation. The region at either end of the zone of compatibility is called the lethal zone or the zone of resistance. The point of transition between these two zones is referred to as the upper or lower incipient lethal point. The upper and lower incipient lethal points are defined as that exposure level which kills a stated fraction of the population (usually 50%) within an indefinitely prolonged exposure. This point of transition between the zones of resistance and compatibility is difficult to characterize, since factors such as sex, season, starvation, or interaction of various environmental factors may cause it to vary.

At the onset of this paper, it is necessary to delimit the use of the term environmental adaptation because it is a term which has been used in so many ways that it has limited descriptive value. Evolutionary adaptation connotes a genetic basis for adjustment among the parts of an organism and between the organism and its environment (Allee et al., 1949). Within the existing gene pool of an organism, adaptive morphological, behavioral, and/or physiological responses to environmental stress may occur and need not rely on mutations. Some biologists refer to these responses as nongenetic or environmentally induced adaptation. Physiological adaptation, as viewed by Prosser (1975), is the property of an organism which favors survival in a specific environment, particularly a stressful one. He includes in this definition both environmentally and genetically determined responses. Two terms used in discussing differences in responses of organisms are environmentally induced (phenotypic) variation and genotypic variation. The responses of an individual organism to a certain environmental complex may be liable. In order to determine whether an observed response of an animal is nongenetic or genetic, certain experimental approaches have been used: 1) the breeding and rearing of organisms under different environmental conditions that are controlled; and 2) acclimation studies in which responses of organisms exposed to a new environmental condition are observed. In the present discussion, physiological adaptation will be equated with environmental adaptation.

This paper has the following major objectives: 1) to present an overview of earlier studies and to review recent research on environmental adaptation to coastal lagoons; and 2) to suggest some future research needs. Because of limitations on the length of the present paper and the voluminous literature on this subject, many exciting papers cannot be cited. I hope my colleagues who are not included will be understanding and forgiving.

OVERVIEW OF PAST STUDIES

Early naturalists recognized the uniqueness of organisms being restricted to specific modes of existence. Semper (1881) and Davenport (1897 and 1899) reviewed the pre-20th century literature on functional, behavioral, and morphological adaptations to various habitats, while Allee et al. (1949) summarized the literature for the first half of this century. These works are not restricted to coastal lagoons, but deal with many habitats. A classic contribution to coastal lagoon sciences is the book of Remane and Sliefer (1971, Second edition) «Biologie of brackish water» with the first edition appearing in 1958. In 1964 an international conference on estuaries was held and the proceedings edited by Lauff were published in 1967. A comprehensive review of estuarine research was presented, including the subject of adaptation. Other recent symposia proceedings and books have relevance to the theme of this paper: Vernberg and Vernberg, 1972; Vernberg, 1975; Wiley, 1976; Kinne, 1977; McLusky and Berry, 1978; Staneyk, 1979; Vernberg and Vernberg, 1981. In general, the principal lines of research described in these references have emphasized the lethal limits of organisms and sublethal (zone of compatibility) responses, including respiration, ionic and osmoregulation, and other functional responses.

CURRENT RESEARCH

Since World War II an ever-increasing research effort in all aspects of coastal lagoon science has taken place. Examples of a few dominant research directions in the field of environmental adaptations follow.

Lethal zone

The lethal effects of temperature, salinity, oxygen, H₂S, and desiccation are abiotic factors which have received considerable attention.

Temperature

Animals living in cold-water lagoons generally survive lower temperatures than animals inhabiting warm-water habitats while the reciprocal response is noted at elevated thermal levels. Also animals, which are typically exposed to marked seasonal thermal changes, are better able to survive a wider range of temperatures than those organisms residing in a region of relative thermal stability. Furthermore, the upper and lower thermal lethal points of organisms from widely fluctuating thermal regimes can be shifted more widely with thermal acclimatization than organisms from more temperature-stable environments (Vernberg, 1981). Within one lagoon, organisms may evade high or low thermal stress by behavioral ploys. For example, if the temperature is too high, intertidal snails cluster and the body temperature of organisms in the center may be 5 to 6°C cooler than ambient levels (Rohde, Sandland, 1975). Boddeke (1975) reported that shrimps (Crangon crangon) leave coastal embayments in the Netherlands during the autumn for the offshore waters of the North Sea. This migration allows animals to inhabit the warmer winter waters offshore and avoid frozen inshore lagoons. This response is correlated with the relative inability of this species to osmoregulate at the low winter temperatures within the lagoons (Spaangra, 1971). In addition, Boddeke (1975) found other factors to be important: fluctuations of water temperatures in the
Autumn initiated the off-shore migration, especially of sexually mature animals.

Thermal resistance of adults may be similar to that of developmental stages (Andronov, 1975) or they may differ. For example, larvae of certain tropical fiddler crabs survive lower temperatures than adults, whereas, adult fiddler crabs from the temperate zone have wider thermal limits than their larvae (Vernberg, Vernberg, 1975). Gable and Croker (1978) reported that over-wintering, immature amphipods showed the best tolerance to low temperature and salinities, while juveniles from freshwater were closer to their upper level thermal limits. Earlier Patel and Crisp (1960) demonstrated a relationship between upper lethal thermal limits and the temperature range during the breeding season; species from colder waters bred at lower temperatures and had lower upper thermal limits than did species inhabiting warmer-water environments.

**Salinity**

Numerous reviews have summarized the data on salinity tolerance and the ecology of lagoon animals (Kline, 1971; Remane, Schlieper, 1971; Vernberg, Silverthorn, 1979). Earlier, Remane (1933) suggested that a critical salinity boundary (5.5‰) separates freshwater from marine environments and Kliebovich (1969) later expanded this concept by incorporating much more data. Pronounced physiological changes occur within this critical salinity boundary region, including distortion of cellular electrochemical properties, tissue albumin fraction alterations, and changes in growth, locomotion, and osmoregulation.

Typical of the evolution of research on a given environmental problem is the finding that a simple relationship between a given factor and its influence on an organism does not exist; other variables also are important. In the past five years, numerous additional examples have not only documented the importance of salinity as a limiting factor, but they have stressed the interaction of multiple factors. For example, although Norse and Estevez (1977) found a correlation between the salinity tolerance of 10 species of portunid crabs and their distribution along a salinity gradient, ranging from full-strength oceanic sea water to the upper reaches of an estuary, other factors, such as competition, predation, and food availability were important. Earlier Croghan (1961) emphasized the interplay between interspecific competition and mechanisms of osmoregulation: a species which expends less energy in osmoregulation may have a competitive advantage over a second species which is less efficient in that more energy is available for other functions, such as defending a habitat, finding a mate, or capturing food.

Another line of research is to report on the unexpected distribution of organisms into coastal lagoons. This approach is illustrated in a report by Hendrix et al. (1981). They found that the bay squid (Loligo plebeia) living in Galveston Bay, Texas could survive 16.5‰ salinity for 48 hours whereas most cephalopods are marine stenohaline organisms. Although this species can survive exposure to reduced salinities, it cannot osmoregulate over the range of 17.5 to 36‰ salinity, a response similar to other euryhaline, osmoconforming echinoderms and bivalve mollusks (Vernberg, Vernberg, 1972).

**Oxygen**

Consistent with the correlation of the responses to temperature and salinity and distribution in a coastal lagoon are the results on oxygen lethal limits. The correlation of resistance to anoxic or hypoxic conditions and habitat is well documented by Theede et al. (1969), Vernberg (1972), and Van Winkle and Mangum (1975). Theede et al. (1969) also showed a similar correlation with tolerance to H₂S. Differences in anoxic resistance of different life history stages indicate variations in physiological mechanisms and also influence the distribution of the different stages in a lagoon.

In the case of the common mud-flat snail (Nassarius obsoletus), the adult, inhabiting mud-flats which may be anoxic periodically, is more resistant to oxygen depletion than is the more aquatic larvae (Vernberg, Vernberg, 1975).

**Desiccation**

In general organisms inhabiting the higher regions of the intertidal zone survive increasing desiccation better than those organisms living lower in the intertidal zone or subtidally (see review, Vernberg, 1981). A few examples are cited here. Young (1974) reported that the most terrestrial of three species of estuarine hermit crabs lost body water more slowly when subjected to low moisture conditions than two subtidal species; similar findings for subtidal and intertidal decapod crustaceans have been reported (Ahsanullah, Newell, 1977). Recently Price (1980) examined the water relations of a salt marsh snail (Melampus bidentatus) which represents a transitional stage in the movement of molluscs from the marine environment to land and freshwater habitats. When exposed to dry conditions in the field, this species had 15% less body water compared with specimens from moist sites. In the laboratory, it could withstand 0% relative humidity extremely well. For example, after exposure for 36 hours, the LD₅₀ was 80% body water loss. Rehydration occurs rapidly: within 0.75 hours "normal" body water content of 90% was reached from a level of 50% water loss. Based on latitudinal distribution, Hijibish (1981) reported that populations of Melampus from the more northerly locations of Massachusetts and Delaware were more resistant to freezing than were animals from South Carolina. This geographical difference did not disappear when laboratory acclimation experiments nor did transfer of animals from South Carolina to field conditions in the two northern sites alter this pattern of response. This suggested the existence of at least two physiological races. A generality to be drawn from this and related studies is that functional responses of a species living within one lagoon may be different from those of a population of the same species living in another lagoon having a different range of environmental conditions.

**Multiple factor interactions**

Although data on the influence of a single factor on an organism are important, most organisms live in an environmental complex consisting of numerous factors each of which may vary independently of the others. Therefore to be able to clearly delineate between the zone of compatibility and the lethal zone, in order to have more meaningful ecological interpretation of laboratory results, greater emphasis is being placed on multiple factor experiment (see reviews, Alderdice, 1972; W.B. Vernberg, 1975; F.J. Vernberg, 1979). A few recent examples will illustrate this important line of research. Two populations of the harpacticoid copepod Zaus spinatus from Robin Hood's Bay, England and Oresund, Denmark were subjected to 30 combinations of temperature and salinity at different seasons of the year (Hicks, 1980). Seasonal shifts in survival occurred and statistically significant geographical differences were reported. Man-induced environmental perturbations may influence the ability of a species to survive. For example, low sublethal concentrations of cadmium, a heavy metal, dramatically altered the ability of fiddler crab zoae to withstand various combinations of temperature and salinity; in the presence of cadmium, mortality was increased, salinity sensitivity was increased, but slightly increased tolerance to low temperature was noted (Vernberg et al., 1974).

In 1976, Simpson and Kliebovich (1976) published a detailed paper on factors controlling vertical migration of six species of molluscs living in different zonal positions along a transect from the high tide mark to the sublittoral region. Generally, the habitat and zonal position are related to tolerance to temperature, desiccation, and salinity, however, in some
cases the laboratory-determined lethal limit was much greater than the degree of exposure the species would experience in the field. This was clearly demonstrated in the case of limpets. But elevated temperatures, salinity extremes, or desiccation effects were debilitating, resulting in a higher rate of predation on the enfeebled animals. This is a good example of biotic and abiotic factor interaction to limit the distribution of a species. Simpson concluded that the investigator should be wary of placing too much emphasis on results from studies of a single factor and that synergistic effects of factors are limiting and that the effective combinations and factors may differ for each species or geographical population.

Most of the previously cited papers have dealt with relatively short-term exposure to lethal combinations of environmental factors, times ranging from minutes to a few days. However, chronic exposure to a lethal level of mercury may have serious consequences to a population over a few generations. The term sublethal is used to describe exposure to a given concentration of a factor which does not result in 50% mortality or more within a defined period of time. To illustrate these long-term populational effects, the work of Vernberg et al. (1978) on fiddler crabs and mercury exposure is cited. Based on field data on population dynamics, and laboratory experimentation, Vernberg et al. (1978) developed a model which predicted the decrease in population size after a four-year exposure to various levels of mercury. This work not only illustrates a new trend to model ecological-physiological systems, but, also, it emphasizes the need to understand the long-term implications of environmental perturbations when establishing pollution criteria or making decisions on environmental manipulation.

Zone of compatibility

Between the high and low lethal environmental extremes, an organism survives, but its success will depend upon a number of factors. Of interest to the theme of this paper is what mechanisms have developed in lagoonal species to allow them to successfully survive. In order to maintain life, energy is required. This is true for whatever level of biological organization we are examining, either organisms, populations, or ecosystems. That this concept has received increasingly wide acceptance is seen by the heightened research activity on bioenergetics in recent years. Not only is the amount of energy taken into an organism accounted for, but the partitioning of this energy within the individual is determined. This method of accounting for energy input and energy usage is referred to as developing an energy budget. The commonly accepted equation for estimating the energy budget is as follows:

\[ C = P + R + F + U \]

where \( P = P_1 + P_2 \) and \( P = \Delta B + E \).

Each component may be measured in kilocalories per annum. \( C \) is the energy content of the food consumed by the population; \( P \), the total energy produced as flesh or gametes; \( P_2 \), the energy content of the tissue due to growth and reproduction; \( B \), the net increase in energy content of standing stock; \( F \), elimination, or energy content lost to the population through mortality; \( P \), the energy content of the gametes liberated during spawning; \( R \), the energy lost due to metabolism (respiration); \( F \), the energy lost as feces; and \( U \), the energy lost as urine or other exudates.

Obviously, the development of an energy budget is a complex process involving determination of various functional processes. Although it is beyond the scope of the present paper to present a detailed review of bioenergetics, some examples of recent studies will indicate current problems.

Because energy intake is basic to organismic survival, it is not unexpected that various mechanisms have evolved in lagoonal organisms. Dissolved organic substances may be removed by organisms from the surrounding sea water (see review, Jorgensen, 1976) and/or by ingesting larger particles (see review, Pandian, 1975; and Jones and Wolff, 1981). One of the basic problems in developing an energy budget is to determine energy input to an organism. Under laboratory conditions, input has been estimated for a number of species but the question can be raised: Is this what the organism eats in the field? In many cases the natural diet of lagoon animals is unknown let alone data on quantitative aspects of ingestion. Two recent papers illustrate attempts to fill this data void. A prominent inhabitant of salt marsh systems is the killifish Fundulus heteroclitus, and its role in carbon cycling within this ecological system is thought to be significant. To determine the source of carbon for Fundulus throughout the year, Kneib and Stiven (1980) measured the stable carbon isotope ratios of their muscle tissue and gut contents seasonally. This ratio, expressed as δ¹³C values, gives an indication of food source in that marsh flora which is at the base of the food chain has a wide and distinguishable range of ratios. Their data indicate that assimilated carbon probably originated from a mixture of benthic algae and Sparrina ingested by prey species utilized by Fundulus.

The ratios for these prey species in July varied from −15.6 to −17.3. The ratio for small fish differed from that of large fish during the warmer months, suggesting different dietary requirements. The reason for the seasonal change in muscle tissue is not known; the authors suggested either a change in diet or a change associated with reproduction. Because many of the routine methods of determining food intake (direct observation in the field, gut analyses, or tracer studies) are not applicable to all components of a trophic food web, Feller et al. (1979) adapted immunologic methods when studying a soft-bottom benthic community. They were able to detect phyletic and trophic relationships among 20 taxa and identified trophic links which would otherwise have gone undetected.

Another important component of bioenergetics is respiration. Numerous variables have been shown to influence oxygen uptake (Vernberg, Vernberg, 1972). Recently Professor Dame and I demonstrated that the yearly respiration of an adult population of mudcrab, Panopeus herbstii, varied depending on whether the animals were maintained at constant, but seasonally representative temperature, or at cyclic temperature (Dame, Vernberg, in press). Wu and Levings (1978) also determined the rate of respiration and its contribution to the annual energy budget for barnacles (Balanus glandula) during their first year after settlement. Approximately 67% of the energy was lost in respiration with egg production being the second major component at 12.3%.

The energy balance of a species may be different depending on where it lives. For example, Griffiths (1981) reported that the energy budget of a mussel population (Choromytilus meridionalis) living intertidally was distinct from that of a subtidal population. Upper-shore mussels had a reduced growth rate and reduced metabolism during aerial exposure computed for the first years of growth when compared with subtidal forms. Although she calculated that the energy requirements of the intertidal population was half that of totally submerged animals, the amount of energy allotted to reproduction in both population was not markedly different. Not only may energy utilization patterns vary among populations of the same species found in one geographical area, but this response has been reported for latitudinally separated populations (see review, Vernberg, 1962). This was shown by Vernberg and Morcira (1974) who reported on the differences in the metabolic rates of Euperna acutifrons from Brazil and South Carolina, USA.

Another functional response which has adaptive significance in determining the success of a species in inhabiting a specific lagoonal habitat is its ability to remove oxygen from the external milieu.

In response to oxygen concentration levels, some species are oxyconformers while others are oxyregulators with Pe values (the critical level of oxygen tension below which the
organism becomes an oxyconformer) varying with different factors, such as body size, food, molting, locomotor activity, and acclimation to various oxygen tensions influence metabolism (see review of Vernberg, 1972).

To provide a quantitative description of the relationship between aerobic metabolism and decreasing environmental oxygen levels, Mangum and Van Winkle (1973), using data from 31 species of aquatic invertebrates, described a quadratic binominal equation which fit the data best. Based on this equation, they reported a phylogenetic trend of increasing regulation of aerobic metabolism in response to declining environmental levels. This trend could be correlated with the acquisition of structures by organisms that would effectively insulate their respiring tissue from the surrounding habitat. In many of these species the removal of oxygen would cease long before the available supply of oxygen was exhausted, with those species without substantial oxygen storage capabilities switching to anaerobic pathways.

Fiddler crabs, Uca pugilator and U. pugnax, living in burrows in sandy-muddy substrates, may experience low oxygen tensions when the tide is in, since they apparently do not pump water through their burrows. These species are not only relatively resistant to anoxia, but also the critical oxygen tension is low: 1.3 % of an atmosphere for inactive and 3.6 % for active crabs. These crabs continue to consume oxygen down to a level of 0.4 % of an atmosphere; in contrast, the non-burrowing wharf crab stops respiring at a somewhat higher value (Teal, Carey, 1967).

Although direct correlation between oxygen uptake and heat production, as measured by calorimetric techniques, has been reported for many animals, Pammat (1978) found the two processes to be more or less independent of each other in this fiddler crab, Uca pugnax. Hence in this species and presumably in other species experiencing either hypoxia or hypercapnia, ecological considerations should be determined by measuring heat production since «aerobic shutdown» and a switch to anaerobic metabolism may occur when relatively high levels of oxygen are present. Two xanthid crabs, Panopeus herbstii and Menippe mercenaria, decrease their rate of oxygen consumption in proportion to ambient oxygen levels (Lefler, 1973), however, the rate of decrease is less than that of the blue crab (Callinectes sapidus), a response apparently correlated with habitat differences in that the xanthid crabs often live in mud while the blue crab does so less frequently. Callianassa californiensis and Upogebia pugettensis, two species of burrowing crabs, regulate their metabolic rates over a wide range of oxygen concentrations. However, Thompson and Pritchard (1969) found species differences that correlated with habitat differences; Callianassa lives under more hypoxic conditions than Upogebia and has the lower metabolic rate, the lower Pc value, and is more resistant to anoxia. Recently, Torres et al. (1977) found that C. californiensis, when placed in simulated burrow conditions, regulates oxygen levels in its immediate microhabitat by using its pleopods. Body movement plays a large role in water exchange between the surface and the burrow. After oxygen deprivation, the presence of feeding activity at the surface of the burrow. A related species, C. jamaicensis, which lives in estuarine mud flats in the northern Gulf of Mexico where hypoxic conditions are common, was reported by Felder (1979) to be very tolerant of anoxia. It exhibited metabolic regulation to a low Pc, had a low metabolic rate, and showed toxic responses to altered oxygen tension: all adaptations to an hypoxic habitat.

When experiencing external environmental changes, animals may switch from aerobic to anaerobic metabolism (Theede, 1973; Breteker, 1977; Spaargaren, 1977), as demonstrated by Carcinus maenas. Down to oxygen pressure of about 20 mm Hg, this species regulates oxygen uptake when measured at both 17°C and 20°C (Spaargaren, 1977). The gill ventilation rate is unchanged, and the heart rate is more or less constant until the oxygen tension reaches 60-80 mm Hg (Taylor, 1976) and then decreases (Uglow, 1973). Although there is a reduction in energy production during anoxia, sufficient energy for ionic regulation results from anaerobic pathways to insure internal constancy. Under anoxic conditions the loss of locomotor ability makes this species vulnerable to predation, but it can withstand changing salinities. These results demonstrate that biotic interaction is potentially more limiting under anoxic conditions than are abiotic factors.

Associated with lagoon systems are organisms who have invaded the adjacent high lands for varying periods of time. They show a range of responses. Variations in the respiratory adaptations of terrestrial crustaceans were reported by Mc Mahon and Burggren (1979), Birgus, Geecarcinus, and Cardisoma are less influenced by hypoxia than hypercapnia, a response to be expected of animals living in a habitat rich in oxygen. However, the land hermit crab, Coenobita clypeatus, was more sensitive to hypoxia than hypercapnia. Apparently this difference in response can be correlated with the continued association of C. clypeatus with a fluid-filled molluscan shell which permitted the crab to retain some aquatic tendencies.

In general the respiratory pigments of animals living in regions of low oxygen concentrations are more oxygen sensitive than that of those living in relatively oxygen-rich habitats. Recently Wells et al. (1980) reported the following adaptive features for an intertidal polychaete (Terebella insculpta). Its hemocyanin had a high affinity for oxygen (P50 value of 7 mm Hg at 20°C) and the amount of hemoglobin in the blood vessels was high. The shape and the position of the oxygen-binding curve were sensitive to changes in temperature, pH, and pCO2, suggesting that these changes facilitated oxygen delivery during exposure at low tide. The ultrastructural architecture of the gills and blood vessels enhanced the rate of oxygen diffusion from the external environment by permitting short diffusion distances and large surface areas.

Lagoonal organisms faced with fluctuating salinity regimes must adapt or perish. Within the zone of compatibility, organisms have demonstrated various response patterns, ranging from osmoregulating to osmoconforming. Although the response pattern is genetically determined, the environment may greatly influence the expression of the pattern. Temperature, season, and food are a few known variables. Gilles (1979) edited a book which comprehensively dealt with the ionic and osmoregulatory mechanisms of aquatic organisms in response to environmental changes. Recently, the effect of salinity on the ionic and osmoregulatory responses of five species of penaeid shrimp was reported by Castille and Lawrence (1981). All five species responded similarly: the hemolymph is hypotonic to sea water at salinities below the isosmotic concentrations and hyposmotic to higher salinities. However, species differences were noted in that Penaeus aztecus and P. duorarum were weaker ionic and osmoregulators at low salinities than the other three species. This response may be correlated with the distribution of these shrimps: P. aztecus and P. duorarum are least abundant in lower salinities. Although shrimp regularly inhabit coastal lagoons, most coastal coastal waters over the continental shelf. One exception is the bay squid Lolliguncula brevis which may invade coastal bays and lagoons, however, it is not well adapted to an estuarine existence in that it is an osmoconformer over the range of 17.5 to 36% and shows signs of severe osmotic stress in salinities below 17% (Hendrix et al., 1981).

The response of Carcinus when subjected to sudden changes in salinity was determined by Taylor (1977); the earlier work was done on animals acclimated to low salinities. In nature, this crab is frequently subjected to marked fluctuation in salinity since it lives in estuaries and in rock pools. After exposure to reduced salinity the oxygen consumption rates were highest during the ensuing 2-3 hours, after which they declined. However, the rate was always higher than that reported during the periods before exposure to low
Temperature influences the ionic and osmoregulatory functions of the rainbow eel (Leffler, 1975). When exposed in the intertidal region during periods of low tide, these animals acclimate rapidly to reduced salinity, even after 3 to 5 days. This increased oxygen consumption rate lasted even after 3 to 5 days in water of reduced salinity, a response indicating that the respiratory rate of Carcinos maenas does not acclimate rapidly to reduced salinity.

In estuaries, the salinity can fluctuate rapidly with the changing tides. Findley et al. (1978) examined the effects of a simulated tidal cycle on the respiration of two common estuarine species, the blue crab (Callinectes sapidus) and the oyster drill (Thais haemastoma). Respiratory rates of animals acclimated to 10, 20, and 30% salinity were measured at ambient temperature (20°C) after exposure to various semidiurnal salinity regimes (10-5-10%, 20-10-20%, 30-10-30%, and 10-30-10%). Blue crab respiration more rapidly at 10 and 20% S than at 30% S. With fluctuating salinity, their metabolic rate varied inversely, although relatively minor changes occurred. Typically, the respiration rate dropped during the initial phase of declining salinity at a rate directly proportional to the rate of salinity decrease. This transitory response could represent a metabolic adjustment period since this species is capable of regulating extracellular fluid osmotic and ionic composition. In contrast, the oyster drill exhibits incomplete volume regulation and its metabolic rate was more directly influenced by salinity change.

The metabolic response to salinity may be an indicator of the distribution of species along a salinity gradient as illustrated in a study of two brackish water isopods by Frier (1974; Frieria hookeri and Carganus serratus). The rate of respiration is higher in S. hookeri and increases more rapidly in low salinities than that of S. ruigcicauda. However, Frier reported no direct correlation between the degree of osmoregulation and the rate of respiration as S. ruigcicauda maintained blood more concentrated at low salinities than did S. hookeri. Temperature influences the ionic and osmoregulatory ability of many lagoonal species (see review of Vernberg, Silverthorn, 1979). A few examples demonstrate this point. As reported in adult blue crabs by Lynch et al. (1975), juvenile blue crabs have higher haemolymph salt concentrations in cold water than in warmer water of the same salinity (Leffler, 1975). Part of this increase is due to increased haemolymph Na⁺ concentration. The permeability to salts of the crab, Carcinos maenas, changes with salinity. Although changes proceed more slowly at 5°C to 20°C, temperature does not greatly influence the final permeability (Spaargaren, 1975). The ability of an isopod (Sphaeroma serratum) to regulate the sodium concentration in the haemolymph varies seasonally. Ionic regulation increases with low temperature and is important during the winter (Charmantier, 1975).

To be successful in the lagoonal habitat, an organism must be able to perceive changes in its external environment. At times when the waters may be murky and visual cues would be of limited value, the ability to communicate by means of sound has adaptive value. One example of an animal using acoustical communication is the male toadfish, Opsanus tau. He produces a characteristic boat whistle call which acts not only as a stimulus to attract females but it probably causes other toadfish to leave the area where the male has established a nest (Gray, Winn, 1961). Visual cues are important in the life of the fiddler crabs (i.e., Uca pugilator). These crabs are active and completely exposed in the intertidal region during periods of low tide and many of their activities have directional components that are adaptive. For example, to escape the approach of a predator when the crabs are some distance from their burrow, they may run landward and enter burrows or vegetation, or they may run offshore. In either event, the crabs are able to orient and return to the beach, guided primarily by visual mechanisms (Herrnkind, 1968). The primary cues for guidance are sun position and plane of polarized light, but the crabs can also use landmarks to supplement celestial cues. Fiddler crabs use both visual and acoustical signals during courtship. The displays of the males, which involve the waving of large major cheliped, are especially conspicuous. Recent investigations have revealed that sound production is also an important component of courtship behavior that is distinctive for each species (Salmon, Atsaiides, 1969). In U. pugilator, when females are absent, the crabs wave during the day and produce sound at night. If a female is nearby during the day, the male waves more rapidly, and if she approaches closer to the male’s burrow, the waving is followed by sound production. At night a male produces sounds at low rates, but will increase sound rate when touched by a female. Females have been observed in the field to orient and move toward males at night in response to sound from distances as great as 25 cm. Animals also rely on other sensory modalities in their perception of the environment. Some are able to utilize tidal salinity changes to their advantage in seeking a suitable environment using rheotactic and chemoreceptive modalities. While reduced salinities can prevent animals from carrying out normal vertical migrations, changing salinities associated with the ebb and flow of the tide can be utilized to advantage by others, such as the European eel Anguilla vulgaris (Cruzelberg, 1961).

Salinity also influences the migration of some species of shrimp in and out of estuaries. In laboratory studies on the pink shrimp Penaeus duorarum, Hughes (1969) indicated that inshore movement of post-larval shrimp and subsequent offshore movements of juveniles were aided by flood and ebb tides, respectively.

Man-induced changes influence the functional responses of animals living in lagoons and estuaries. For example, De Coursey and Vernberg (1975) reported on the effects of dredging on zooplankton. They were exposed to water samples taken from the immediate area of dredging, a site 200 yards downstream, and from the disposal region where the water drained back into the estuary through a weir. The swimming activity of zooplankton was reduced, their metabolism also decreased, and mortality rates were increased most dramatically in the “weir” water while the water from the dredge site was least toxic.

Reproductive phenomena, including gonad development, spawning and larval development, are greatly influenced by reduced and/or fluctuating salinities. Detailed reviews of this subject are in the continuing series “Reproduction of Marine Invertebrates” edited by Giese and Pearse (1974; 1975; 1977; 1979) and a volume on reproductive ecology edited by Stancyk (1979). One example cited to show the effects of various factors on reproduction is the work of Scedel et al. (in press). The mysid, Mysisopsis bahia, is important in the ecology of semitropical bays and recently it has been widely used for laboratory studies of full life cycle pollution toxicity. The geographical origin of Artemia, the principal laboratory food used in rearing experiments, fed to the species influences its survival, growth, and reproductive potential. For example, Artemia from five geographical locations (Utah, Brazil, Australia and California and Utah, USA) were used. Survival was significantly lower in animals fed Artemia from California; growth highest in mysids fed Artemia from Utah and Brazil and lowest when fed Artemia from California. The reproductive potential was greatest in Mysisopsis fed Utah Artemia. This work illustrates the complex interaction between food, growth, reproduction and bioassay studies.

FUTURE RESEARCH

That lagoonal ecosystems are important to human society has been well documented. However, the level of our scientific understanding of how organisms function in this ever-fluctuating environment is far from adequate to provide the necessary basis for predicting the effects of natural and “man-related” perturbations. Some major areas of
research which need attention are discussed below, but these are only a few examples.

**Synthesis studies**

A critical evaluation and synthesis of published studies are needed to assess the current state of our knowledge and to serve as a source to direct future research efforts. Although there is an inherent thread of continuity in all environmental studies encompassing all levels of biological organization, ranging from molecules to ecosystems, the coherent integration and synthesis of the results of studies at different levels is lacking. The biosphere functions as an integrated whole, and, if we want to understand how it functions, we must begin to analyze it as an integrated whole and not restrict our investigation to a series of isolated but detailed studies.

**Interlagoon comparative studies**

As a better understanding emerges of various lagoon systems, one wonders if the results are site specific or are they applicable to all systems. What are the general characteristics of all lagoons and what are the variability ranges of site specific characteristics. Are the adaptive mechanisms enabling one lagoon to survive perturbation the same as those of another lagoon? Are the pathways of secondary production the same in tropical, temperate, and polar lagoons? The answers to these questions are important.

**REFERENCES**

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