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The Ecological Niche in Aquatic Ecosystems

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Introduction

Niche, in everyday English usage, means a place or situation that is especially well suited to an individual or inanimate object. No doubt the word was used in this general way by ecologists before they began adapting its meaning to a more specific purpose, through the concept of ecological niche. niche, defined ecologically, can be pronounced as a rhyme either with 'rich' or 'quiche'.

J. Grinnell (1877–1939) was first to convert the niche in its generic sense to the niche as defined ecologically. Grinnell's ecological niche grew out of his observation, shared with other ecologists that species are associated with specific ranges of environmental conditions that correspond to their spatial distribution in nature. Thus, Grinnell's niche was drawn from the idea that the persistence or success of a species in a given place is determined by a suite of environmental variables associated with that place.

Grinnell also explained that the distribution of a species within the range of environmental variables favorable to it is affected by the presence of other species. He drew the analogy of soap bubbles: a single bubble takes a symmetrical shape, but multiple bubbles are distorted as they press one upon the other. Thus, Grinnell foresaw the relevance of the ecological niche concept to the study of interspecific competition.

In his classic book, *Principles of Animal Ecology* (1927), Charles Elton (1900–1991) defined the ecological niche somewhat differently than Grinnell had. He stated that the niche of an organism consists of what it is doing rather than what it looks like. This was probably Elton's way of setting ecology apart from the dominant fields of taxonomy and natural history, which had emerged much earlier than ecology. Ecologists, according to Elton, want to understand the functions of organisms in relation to their environment and each other.

Ecological niche could have been a minor concept had it not been for the importance of interspecific competition in the development of ecology. In his studies of interspecific competition, G.F. Gause (1910–1986), following the mathematically based predictions of V. Volterra (1860–1940), conducted experiments that demonstrated what became known as the 'competitive exclusion principle'. An example from Gause's work consists of an experiment in which two species of protozoan were held in a laboratory medium with a suspended food source (bacteria).

Often one species declined to extinction, and thus was excluded from the habitat provided by the laboratory vessel. In some cases, two species coexisted because they avoided competition through differing adaptations. For example, one experimental contest ended in coexistence because one species was adapted to feed on bacteria that had settled to the bottom of the vessel, whereas the other fed only on suspended bacteria. The general conclusion was that competition across the entire niche excludes one competitor in the end, whereas coexistence is based on the expression of differing requirements of species, i.e., differing niches.

Decades later, G. Hardin (1915–2003) attacked the concept of competitive exclusion as a tautology, i.e., a self-evident truth. If so, the principle, while correct, would have little application to nature. It became increasingly clear as the study of competition progressed that different species, even if similar, do not occupy the same niche because they have different suites of adaptations; that environmental conditions change constantly, thus reversing competitive advantages from one species to another; and that environments in nature are heterogeneous spatially in a way that allows species appearing to be very similar to coexist indefinitely.

Ecologists now think in terms of niche overlap; the underlying scientific problem is to determine the degree of overlap that can produce strong competition. By wondering whether there may be empty niches in nature, J. Grinnell forecast modern thinking on the packing of apparently similar species together in a common environment such as the pelagic zone of a lake. Studies of population dynamics, viewed in large part through biological succession, also influenced the ecological concept of niche. In a famous paper entitled *Homage to Santa Rosalia*, G.E. Hutchinson (1903–1991) pointed out that the pelagic zone of a lake or ocean is filled with dozens of species that have similar functions (e.g., all phytoplankton species in a given lake, or all herbivorous zooplankton species in a given lake). While the open water of a lake may seem similar to Gause's laboratory vessel, it is not. As Hutchinson pointed out, environmental conditions including temperature, nutrient availability, turbulence, and solar irradiance vary from week to week, allowing first one group of species to have an advantage, and then another. Competition in such a community does not go to completion because conditions are not stable.

Quantification of the Ecological Niche

The concept of ecological niche was modernized in 1957 by G.E. Hutchinson. One of Hutchinson's many gifts to the ecological sciences was his consistent use of quantitative tools in the formulation of ecological concepts. Such an approach opened new potential for old ideas, many of which had stalled in argumentation based on field observations and experiments. In essence, Hutchinson added a touch of something like physics to the rich mixture of taxonomy, natural history, population sampling, and field experiments that made up the bedrock of ecology in the first half of the twentieth century.

Hutchinson's idea of niche was that ecological space is defined by all environmental variables that have any influence on the welfare of a given kind of organism. Because more than three influential variables usually can be named for any kind of organism, the ecological niche space cannot be shown as a diagram or physical model; it has numerous ('*n*') dimensions, where *n* might not be known exactly but would be greater than 2 or 3. Hutchinson called the ecological niche defined in this way as an '*n*-dimensional hypervolume.' The idea of dimensions exceeding 3 was unusual but not bothersome in 1957, by which time physicists had already conveyed at least to the science community that not only the three dimensions of space, but also time, a fourth dimension, define physical realities of the universe. Thus, conceptually, we may think of the ecological niche of a species as a hypervolume that has any number of dimensions, and all important factors affecting a particular species of organism are accounted for by it. With the *n*-dimensional hypervolume, Hutchinson generalized the idea of the ecological niche so that it would fit all species, regardless of the numbers or types of dimensions that might describe its requirements for persistence.

Elaborating on the *n*-dimensional niche concept, Hutchinson pointed out that there are actually two kinds of niches. The 'fundamental niche,' according to Hutchinson, is the *n*-dimensional hypervolume that will be occupied by a species in the absence of competition from other similar organisms ([Figure 1](#)). The 'realized niche', in contrast, is the portion of the fundamental niche that can be occupied in the presence of one or more other kinds of competing organism.

It follows from Hutchinson's thinking that the realized niche is never greater than the fundamental niche and typically is smaller. Furthermore, the realized niche is site-specific. The realized niche of a weak competitor at a location with little or no competition could be quite large. On the other hand, the realized niche of the same species in a place with fierce competition could be small, even leading to the extirpation of the species population at that site.

It is clear from these examples that Hutchinson's redefinition of the niche offers many more possibilities than the earlier, simpler definitions. Like J. Grinnell's original concept, it invites a biogeographic interpretation and is based jointly on environmental variables and competition.

Current Controversies Surrounding the Ecological Niche Concept

Analysis of competition and niche has moved in new directions over the last few decades. Some ecologists have concluded that the niche has been overestimated as a determinant of community composition. S. Hubbell, for example, has proposed a 'neutral theory of biodiversity and biogeography,' one component of which is denial of the significance of niche for understanding the relative importance of a species at a given location. Hubbell's reasoning is that even species with very similar ecological requirements are sufficiently different to have offsetting advantages and disadvantages during competition. Thus, according to Hubbell, the distribution of species in relation to each other is much more a matter of chance than it is a reflection of the outcome of competition.

Modern analysis of the ecological niche has returned to some concepts that originated with C.S. Elton in the early twentieth century. As explained by M. Leibold (1995), the Hutchinsonian niche has as its basis the amount of environmental space that can be occupied by a species either with or without competition. In contrast, the earlier and simpler Eltonian concept is based conceptually on the per capita effect (impact) that a given species has on the environment. The two concepts are related, but Leibold argues that a niche concept based on per capita effect leads to mechanistic (quantitative) analysis that is more realistic and therefore more productive.

Some ecologists also believe that the niche is a valuable determinant of species composition in communities of a given place, but they fault the original notions of niche for being overly vague about the means by which competition occurs. In a recent synthesis, J. Chase and M. Leibold (2003) argue, as Hutchinson had speculated in 1957, that the possibility of *n* dimensions for a niche is eclipsed by the likelihood that the distribution of a species is
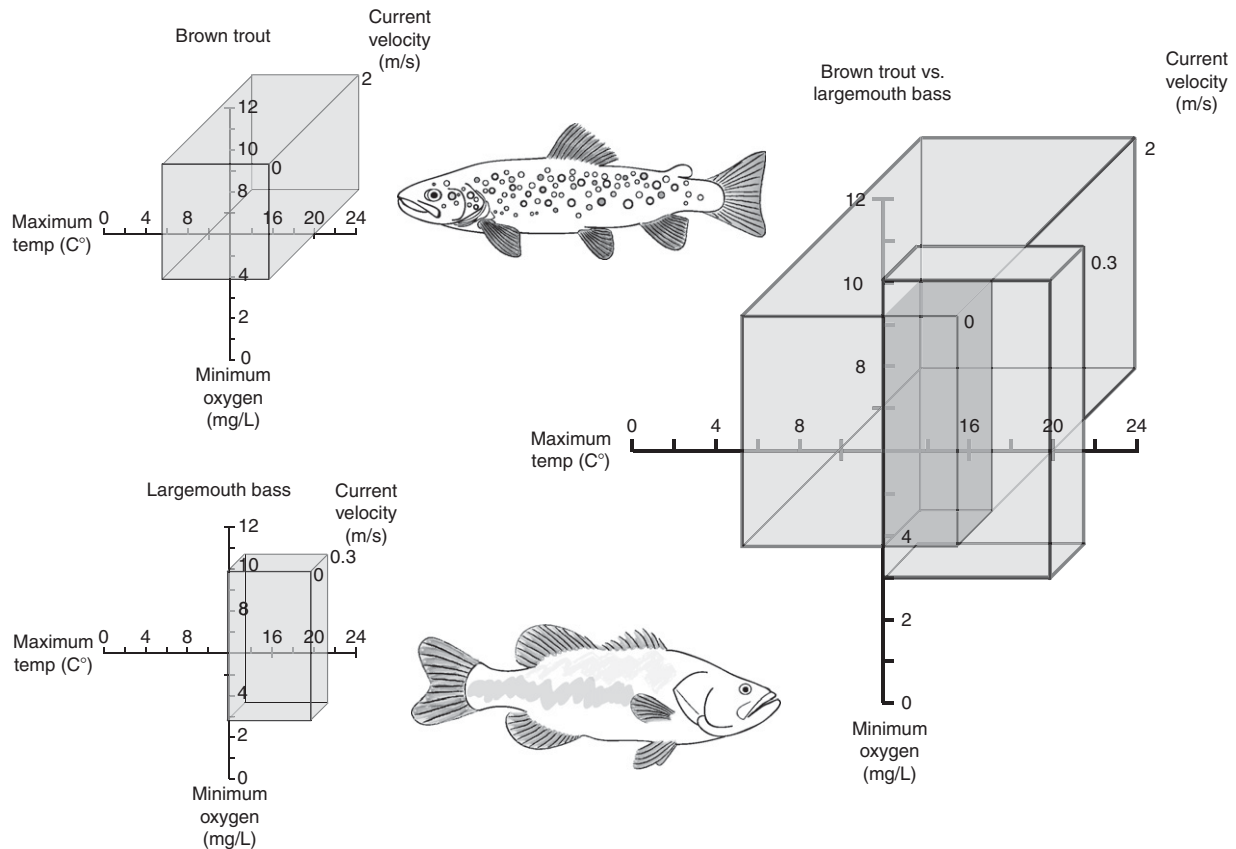
Figure 1 A simplified depiction of niche space defined by three important environmental variables for a coldwater predator (brown trout, *Salmo trutta*) and a warmwater predator (largemouth bass, *Micropterus salmoides*). The fundamental niches are shown on the left, and their overlap is shown as the darkly shaded area on the right. More exact information on niche boundaries would most likely show the niche spaces as rounded and somewhat irregular rather than rectangular. The overlap shown on the right could lead to reduction of space (corresponding to the realized niche) for one or both species as a result of competition in a given ecosystem where the two species could occur together.

most likely defined by only two or three of the *n* dimensions. This re-examination of the Hutchinsonian model opens new possibilities for analysis because it presents the outcome of competition as a byproduct of a relatively small number of interaction types.

One further change in treatment of the ecological niche has been an increase in connectivity of the niche concept with other ecological concepts. Disturbance is one example; temporal changes at the ecosystem and community level explain why many species that might not coexist in a stable environment persist in an environment that is subject to constant change. Yet another example is the relationship between stability of an ecosystem or community and its number of species (species richness). The multiplicity of species occupying overlapping niches is viewed as a collective shock absorber that stabilizes ecosystems against externally induced change. Connection of the niche concept to a mechanistic understanding of ecosystems

and communities insures that niche will continue to be a useful concept.

Aquatic Ecological Niches

Ecological niches are found in all types of ecosystems. At the level of concept or definition, there is no distinction between aquatic niches and terrestrial niches. Even so, aquatic environments are distinctive in that some (but not all) of the niche axes most likely to be important differ from those of terrestrial environments. Important dimensions of the ecological niche for aquatic organisms include temperature, dissolved oxygen, habitat structure, predation, and plant nutrients.

The range of temperature for aquatic ecosystems is much narrower than the range for terrestrial ecosystems because liquid water has a minimum temperature of $0\,°C$. Thermal thresholds are weak for

phytoplankton and zooplankton, as shown by the distribution of species across wide ranges of latitude and elevation. Thermal thresholds are more important for large invertebrates and especially for fishes. For example, the family Salmonidae (salmon and trout) contains many species that are intolerant of waters exceeding 15–20 °C. Similarly, perennially cool waters, such as montane or subarctic lakes, cannot sustain populations of many kinds of warmwater fishes, such as most species of the sunfish family (Centrarchidae).

Water holds only approximately 10 mg/L of oxygen at low temperatures and 6–7 mg/L at high temperatures. Thus, respiration can make water anoxic if it is not offset by photosynthetically produced oxygen or by contact of water with the atmosphere. High rates of respiration in water that is in contact with sediment, for example, can remove all oxygen from water in a matter of a few days.

Some aquatic environments are much more subject to oxygen depletion than others. Mountain streams of high gradient with low amounts of respiration are on one end of the spectrum, in that they have very little potential for oxygen depletion, whereas fertile lakes or wetlands, where there is much respiration and less efficient gas exchange with the atmosphere, show a much higher probability of oxygen depletion.

The distribution of organisms reflects in part their ability to tolerate oxygen depletion. Fishes, for example, show a wide range of tolerance to oxygen depletion. On one extreme are fishes that can obtain oxygen from the atmosphere (e.g., the tropical labyrinth fishes such as the beta and gouramis) and fishes that have a small, upturned mouth capable of drawing oxygen from the top 1–2 mm of water in contact with the atmosphere (cyprinodont fishes, including the mosquito fish). Intermediate in tolerance are fishes that have no special means of obtaining oxygen, but have high physiological resistance to oxygen depletion (some catfishes, such as the bullhead, an ictalurid, and the common carp, a cyprinid). In contrast, other fishes are moderately or highly sensitive to oxygen depletion: trout and salmon, as well as largemouth bass, bluegill and other sunfishes, and many others. Thus, the fish fauna of a particular waterbody reflects the likelihood of oxygen depletion. Invertebrates follow similar patterns. Aquatic larvae of midge species, for example, vary in oxygen tolerance, which explains their contrasting distributions in aquatic environments.

Habitat structure (cover) is a consistent component of most terrestrial environments; it is provided to a large extent by vegetation, which appears on all but the driest surfaces or on ice sheets. In contrast, the pelagic (open-water) environment of lakes provides no structure. Thus, organisms living in pelagic zones are specialized for living in an environment that lacks spatial stability and offers no refuge from predation. Variation in cover, ranging from the open waters of lakes and sandbed streams to richly vegetated littoral zones, vegetated wetlands, and rocky streams, offer a very wide range of possibilities on the niche axes that relate to habitat.

Limnologists and aquatic ecologists have shown repeatedly that predation has strong effects on the species composition of inland waters. Top predators are especially important in that they often remove or greatly suppress the abundance of their prey. Visual predators of lakes in particular may be much more efficient in eliminating their prey than would be the case in most other environments. In fact, some large invertebrates are unable to inhabit aquatic ecosystems that contain fishes. Small fishless lakes, for example, contain a rich abundance of large invertebrates that are not found in similar lakes that are stocked with fish. Thus, the niche dimension related to predation is critical to the distribution of many invertebrates.

Aquatic environments show an exceptional range of potential for producing autotroph biomass. Waters that have very low concentrations of nitrogen and phosphorus have production potential that falls well below that of any soil-based environment where moisture is present. In contrast, aquatic ecosystems with high concentrations of phosphorus and nitrogen have production potential for autotrophs that may be 1000 times higher than the least productive waters. Competition for nutrients is paramount in unproductive waters, which contain species having very high affinity for phosphorus and nitrogen. The most productive aquatic environments also support specialized taxa, but with different kinds of adaptations. Balance of nutrients may also be an important determinant of niche. For example, the nitrogen-fixing blue-green algae (heterocystous cyanobacteria) are, unlike other algae, capable of converting gaseous N_2 to ammonia that can be used in making amino acids. When inorganic nitrogen is short of supply, these organisms are capable of continuing growth when other autotrophs cannot.

Conclusion

The ecological niche concept applies to all environments and should be seen as means of understanding the distribution and functional roles of species. Thus, ecological niche is a root concept for analysis of biodiversity, species distribution, ecosystem stability, and all other concepts that relate to the composition of communities. Critical niche dimensions of aquatic

ecosystems provide some contrasts with terrestrial environments, and set the stage for comparison of aquatic ecosystems with other ecosystem types.

Glossary

Competitive exclusion – Elimination of one species population by another species population at a given location caused by competition between the two species.

Fundamental niche – An ecological niche for a given species in the absence of any competing species.

Niche – All combinations of environmental attributes that are favorable to the persistence of a given species.

Niche overlap – Components of an ecological niche for one species that are shared with those of another species.

Realized niche – An ecological niche for a given species in the presence of competing species with overlapping requirements.

See also: Competition Among Aquatic Organisms; Lakes as Ecosystems; Streams and Rivers as Ecosystems.

Further Reading

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