

# THE NICHE EXPLOITATION PATTERN OF THE BLUE-GRAY GNATCATCHER<sup>1</sup>

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## INTRODUCTION

The niche concept remains one of the most confusing, and yet important, topics in ecology. Traditionally the concept refers to the functional role, particularly in trophic interactions, of a species within a community. There has been little agreement, however, on what factors adequately define this functional role; in describing niches, various authors have chosen to stress different features of a species' diet, natural enemies, microhabitat, and periods of seasonal or diurnal activity. Much of the misunderstanding between ecologists concerning the competitive exclusion principle and the existence of "vacant" niches can be traced to this ambiguity (see reviews by Udvardy, 1957; Hardin, 1960; and DeBach, 1966).

In 1957, Hutchinson and Macfadyen, writing independently, defined the niche in a new and different way. Both authors cast the niche in terms of the range and combination of environmental conditions that permit a species to exist indefinitely. In other words, the niche is seen as an abstract "space" in the environment which some species must be able to exploit successfully for an extended period. While the Hutchinson-Macfadyen concept is no more helpful than the "role" concept in providing an operational definition for the niche, it serves to direct our attention to new types of investigation. For instance, the same species may occur in several different habitats

or cope with a changing set of conditions within a single habitat. Through a comparative investigation, one may hope to discover features common to these several environments. By this process, one may peel away all but the most critical features, leaving a core of limiting factors that defines the fundamental niche of a particular species. This approach has been attempted in the present study.

The niche may be thought of as composed of several dimensions (Hutchinson, 1957), each corresponding to some requisite for a species. Organisms are usually adapted to exploit only a portion of the requisites that are available in any environment. When the characteristics of these requisites are plotted on a continuous scale (e.g., prey size, position of the habitat in a vegetation continuum), the species exhibits a characteristic "exploitation curve" (Fig. 1). The exploitation curves for all requisites combine to form the species' "exploitation pattern". The shape of the exploitation curve will be determined by the interplay of several selective forces. The population will often respond to interspecific competition by becoming more efficient, through the evolution of specializations, in exploiting a more restricted range of requisites. Intraspecific competition will oppose this tendency toward greater specialization by causing the population to exploit the environment in a more generalized manner, thereby capturing a larger niche space (Svardson, 1949). Finally, the relative stability of the environment will influence the exploitation pattern (Klopfer, 1962). Species which occupy habitats that fluctuate widely in their suitability for existence must

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## Ecological Analysis of Species Introductions into Aquatic Systems<sup>1</sup>

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### Abstract

The introduction of new species into aquatic communities to increase fish production is a management technique that often has created more problems than it has solved. In large measure, this is due to the inability to correctly predict impact. Loop analysis is a tool of systems analysis and may be useful in predicting systems behavior of an aquatic community once an introduction is made, using the limited information usually available. Case histories of two lake systems examined by loop analysis suggest that nutrient-poor systems are most sensitive and become unstable after exotics become established. Rules developed by entomologists to guide selection of predators for biological control systems can be adapted for fisheries management. The "ideal" candidate for aquatic introduction is coadapted with some members of the new system, has a narrow niche breadth, is easily controlled if it escapes from the system, and is free of exotic diseases and parasites.

One of the more important tools of managers of inland fisheries long has been the introduction of fish and invertebrate species to supplement local faunas in order to improve fishing. In the past, most of these introductions have been of top-level carnivores, such as trout and centrarchid basses, but in recent years many of the introductions have been forage species for the favored carnivores. Such introductions essentially are attempts to change the structure of aquatic communities to enhance production of species favored by humans. Unfortunately, as Magnuson (1976) points out, these attempts have been largely "games of chance" and many of them have had unexpected negative consequences. For instance, trial-and-error experiments in restructuring fish communities in California form a repeated story of short-term successes and long-term disappointments (for example, von Geldern and Mitchell 1975; McCammon and von Geldern 1979; Wydoski and Bennett 1981, this issue).

The conventional approach to developing a reservoir species complex has been autecological as well as empirical. The first consideration before a species is introduced has been whether or not it will survive and grow in its new environment, and the second concern has been whether or not it will feed or be preyed upon by the other species of direct interest. After an introduction, measures of growth, standing crops, and yields to anglers are used as criteria of success or failure. Most of the models that have been used to examine the dynamics of economically important species are uncoupled, without linkages to the rest of the trophic network (for example, Larkin 1977, 1978).

As a result, management has been conducted without full appreciation of potential consequences of the long-term effects of an action. Species are introduced to fill an "empty," "vacant," or "free" niche within a system although the niche is a characteristic of a species rather than of an environment (Hutchinson 1958). The niche is described after the fact as a matter of practice, so description embraces only the realized portion of fundamental capacity. Therefore, an "empty niche" is difficult to predict because an exotic species may adopt a different realized niche as a response to new ecological conditions. Similarly, the dispersal

<sup>1</sup> Oregon State University Agricultural Experiment Station Technical Paper 5584.

<sup>2</sup> Cooperators are Oregon State University, Oregon Department of Fish and Wildlife, and United States Fish and Wildlife Service.



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- HD1694  
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HD1694  
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04 WATER QUANTITY MANAGEMENT AND CONTROL

C Effects on water of man's non-water activities

GB651  
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D Water demand

HD1694  
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E Water law and institutions

HD1694  
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G Ecologic impact of water development

HD1694  
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07 RESOURCES DATA

B Data acquisition

HD1694  
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Michigan State Univ., 334 Natural Resources Bldg., East Lansing,  
MI 48824, 1982.

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# Developments in Stream Ecosystem Theory<sup>1</sup>

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Minshall, G. W., K. W. Cummins, R. C. Petersen, C. E. Cushing, D. A. Bruns, J. R. Sedell, and R. L. Vannote. 1985. Developments in stream ecosystem theory. *Can. J. Fish. Aquat. Sci.* 42: 1045-1055.

Four significant areas of thought, (1) the holistic approach, (2) the linkage between streams and their terrestrial setting, (3) material cycling in open systems, and (4) biotic interactions and integration of community ecology principles, have provided a basis for the further development of stream ecosystem theory. The River Continuum Concept (RCC) represents a synthesis of these ideas. Suggestions are made for clarifying, expanding, and refining the RCC to encompass broader spatial and temporal scales. Factors important in this regard include climate and geology, tributaries, location-specific lithology and geomorphology, and long-term changes imposed by man. It appears that most riverine ecosystems can be accommodated within this expanded conceptual framework and that the RCC continues to represent a useful paradigm for understanding and comparing the ecology of streams and rivers.

Quatre importantes lignes de pensée fournissent une base pour l'élaboration d'une théorie détaillée sur les écosystèmes lotiques : (1) l'approche holistique; (2) le lien entre les cours d'eau et leur emplacement terrestre; (3) le cycle de matières dans les systèmes ouverts; et (4) les interactions biotiques et l'intégration des principes sur l'écologie des communautés lotiques. Le concept de continuum du milieu fluvial représente une synthèse de ces idées. On présente des suggestions pour l'éclaircissement, l'expansion et le perfectionnement de ce concept de façon à y inclure des échelles spatiale et temporelle plus larges. Sous ce rapport, les facteurs importants comprennent le climat, la géologie, les tributaires, la lithologie et la géomorphologie de chaque emplacement et les perturbations humaines à long terme. Il semble que la plupart des écosystèmes fluviaux peuvent être inclus dans cette structure conceptuelle élargie et que le concept de continuum représente toujours un paradigme utile pour comprendre et comparer l'écologie des ruisseaux et des rivières.

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**A**t the beginning of this century, limnologists studying streams focused in great detail on the morphology, life cycles, behavior, and trophic relations of stream organisms (e.g. Steinmann 1907; Wesenberg-Lund 1911; Thienemann 1912). The observed diversity of the stream biota

led several researchers to seek simplifying generalities in terms of the observed fauna (e.g. Steinmann 1915; Thienemann 1925; Carpenter 1928; Needham and Lloyd 1930). These early efforts stressed observation, and although a quantitative approach was soon adopted, the approach and the investigations conducted through the 1950's were largely descriptive and autecological in nature. Since that time, the direction of stream research has changed to incorporate a more synecological and holistic approach. In the following we briefly discuss four major areas in

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TABLE 1. Major areas in which developments in stream ecosystem theory have taken place in the past decade.

1. Progression from an individualistic to a holistic viewpoint
2. Realization of the critical linkage between a stream and its terrestrial setting
3. Development of ideas about material cycling in open systems
4. Recognition of the importance of biotic interactions to the stream community

which changes in perspective regarding stream ecosystems have occurred (Table 1) and which we believe form the foundation for further advances in stream ecology. With this foundation in mind, we then propose several adjustments to our earlier concept of riverine ecosystem dynamics (Vannote et al. 1980) which have grown out of our continued interest in this area (Cummins et al. 1983; Cushing et al. 1983b; Minshall et al. 1983, 1985; Petersen 1984; Sedell and Froggatt 1984; Vannote and Minshall 1982) and out of recent studies by others.

## Major Contributions in Stream Ecosystem Theory

### Progression from an Individualistic to a Holistic Viewpoint

A truly holistic view of streams as ecosystems did not begin until the late 1950's, being strongly influenced by Eugene and Howard Odum (e.g. Odum 1957; Teal 1957) and Ramon Margalef (e.g. Margalef 1960). The energy budget approach of Odum for stream segments led to a flood of stream ecosystem budgets (Warren et al. 1964; Mann et al. 1972; Hall 1972; Fisher and Likens 1973; Westlake et al. 1972) for both large and small streams which has continued to the present (Cummins et al. 1983).

The past 10 yr also have seen a shift in perspective from that of viewing streams, or different stretches within a stream, as individual entities to that of a synthetic (integrated) view which seeks generalizations about streams as ecosystems (e.g. Cummins 1974; Webster 1975; Wallace et al. 1977; Newbold et al. 1982a, 1982b; Minshall 1978; Minshall et al. 1983b). The prevalent synthetic view of stream ecosystems is that of the River Continuum Concept (RCC) (Vannote et al. 1980), its antecedents (see Ide 1935; Margalef 1960; Illies 1961; Hynes 1963; Ross 1963), and correlaries (Wallace et al. 1977; Newbold et al. 1981, 1982a, 1982b; Elwood et al. 1983; Ward and Stanford 1983) which emphasize the unifying aspects of flowing water (particularly geomorphology and fluid hydraulics) in structuring stream communities and providing a template for stream ecosystem function. Historically, a number of stream ecologists have recognized shifts in community structure along the course of a river. Most focused on macroinvertebrates and fish (see papers reviewed by Hawkes 1975) and many viewed the relationship as a series of distinct zones (Illies 1961) rather than a gradually integrating continuum (but see Maitland 1966). Few attempted to treat streams and rivers holistically, and particularly to view them as ecological systems (e.g. Rzoska 1978). Margalef (1960) and Mann (1979) are noteworthy exceptions.

The RCC (Vannote et al. 1980) conceptualizes the entire fluvial system as a continuously integrating series of physical gradients and associated biotic adjustments. Streams are seen as longitudinally linked systems in which ecosystem-level processes in downstream areas are linked to those in upstream areas. This approach has provided useful generalizations con-

cerning the magnitude and variation through time and space of the organic matter supply, the structure of the invertebrate community, and resource partitioning along the length of a river. These views are summarized by Cushing et al. (1983b) who stated, "... streams are best viewed as gradients, or continua, and that classification systems which separate discrete reaches are of little ecological value." The RCC is undergoing evolution, testing, and refinement — some aspects of which will be addressed below. However, even if nothing else were to come from it, this paradigm has served to focus attention on rivers as integrated systems and to stimulate the formulation and testing of systems-level hypotheses which have helped to move lotic ecology from a descriptive to a predictive mode.

### Realization of the Critical Linkage between the Stream and Its Terrestrial Setting

Illies (1961), Illies and Botosaneanu (1963), and Ross (1963) were among the first to note similarities among stream communities over broad geographic areas. Ross in particular was struck by the association between stream macroinvertebrates and terrestrial biomes or what he termed the landscape aspect. He postulated the importance to the stream of the combination of climatic conditions necessary for the existence of such vegetation zones plus the factors imposed by the physical nature of the vegetation itself. The importance of the land-stream interaction also is implicit in the watershed approach to the study of terrestrial ecosystems (e.g. Likens et al. 1977).

Also in the early 1960's, Hynes (1963) published the first of a series of studies which drew attention to the importance of terrestrially derived (allochthonous) detritus to stream dynamics. He summarized the importance of the stream-land linkage in his paper "The stream and its valley" (Hynes 1975). Among other things, he noted that the slope of the valley, the depth and permeability of the soil, and the patterns of precipitation greatly affect the pattern of flow and dissolved organic matter content of the stream. Hynes (1975) and others have stressed the importance of the type and density of the terrestrial vegetation and of its chemical and biological dynamics once it reaches the stream. The pioneering work in this area emphasized conditions in streams draining forests and consequently, allochthonously derived organic matter. But the broader implication of these studies is clear: the terrestrial setting for the stream — be it forest, desert, taiga, or grassland — is crucial to the operation of stream ecosystem processes. Additional support for this idea has come from investigations by Fisher and Likens (1973), Minshall (1978), Cushing et al. (1980), Fisher et al. (1982), Molles (1982), Cummins et al. (1984), Minshall et al. (1983b), Naiman (1983), Strayer (1983), and others. Early research on the importance of allochthonous detritus has in turn given rise to additional major developments in the processing of this material, particularly by microbes (see reviews by Anderson and Sedell 1979 and Bird and Kaushik 1981).

Prior to a surge of interest in the role of allochthonous detritus in streams, considerable attention had been given to the primary producers (e.g. Butcher 1932, 1933, 1940, 1946; Blum 1957; Douglas 1958; Gumtow 1955) and to their role in stream food chains (e.g. Percival and Whitehead 1929; Jones 1950). With the interest generated by almost continuous breakthroughs in the area of allochthonous detritus dynamics, the important supportive or primary role of autotrophy in stream ecosystems was virtually ignored. By the mid-1970's, however, stream researchers began to direct their attention outside of forested

headwater streams. It became clear in the broader river basin and interbiome contexts, as well as in moderately shaded headwaters everywhere, that autotrophs contribute significantly to ecosystem dynamics in both the mass and quality of material they provide (Minshall 1978). Now it is generally recognized that both terrestrial plant debris and aquatic primary production are important sources of simple carbon compounds and that they commonly complement one another, both seasonally and along a river, to provide a more reliable and varied food base for lotic consumers than either would do alone (Hornick et al. 1981; Cushing and Wolf 1982; Gregory 1983).

#### Development of Ideas on Material Cycling in Open Systems

Webster (1975) pointed out that nutrients in a stream do not cycle in place, but are displaced downstream as they complete a cycle. He described this coupling of transport and cycling as "spiraling" and suggested that the ability of a stream to utilize nutrients is associated with the tightness and magnitude of the spirals. Webster (1975) and Webster and Patten (1979) proposed nutrient spiraling as a mechanism to account for the apparent ability of stream ecosystems to withstand and recover from disturbance. Later, Wallace et al. (1977) applied the idea in describing the role of filter feeders in streams. They suggested that filter feeders, through their capture of seston, impede the downstream transport of organic matter and serve to reduce the distance between spirals. The present state of our knowledge in this area is largely a result of the mathematical models developed by Newbold and his colleagues at Oak Ridge National Laboratories (Newbold et al. 1981, 1982a, 1982b; Elwood et al. 1983). These collective studies are termed the nutrient spiraling concept.

In four stream systems studied in an interbiome test of the RCC (Minshall et al. 1983b), all first-through third-order stations had "tight" spirals associated with a high retention capacity; the larger stream locations (fifth- to seventh-order) all had long distances between spirals. Rate of recycling was considered "fast" for about half of both the small- and large-sized streams, indicating differences in degree of biological influence (Minshall et al. 1983b). But in all streams studied, spiraling distance was determined primarily by current velocity and the presence and effectiveness of physical retention devices; biological processes played a lesser quantitative role. Thus, in many cases, the retentive capacity of the stream exerts a significant influence on ecosystem dynamics. In another study, Wallace et al. (1982) have shown that experimental reduction of the lotic insect fauna reduces the breakdown, utilization, and subsequent downstream transport of organic matter, indicating that consumers are important in regulating energy flow and nutrient cycling in stream ecosystems (see also Brock 1967; Elwood et al. 1983). Thus, physical retention and macroinvertebrate processing are important mechanisms, along with the microbial action mentioned earlier, for closing or tightening the recycling process in streams and preventing the rapid throughput of materials.

Together, the RCC and nutrient spiraling concepts point to a shift from the view of streams as discrete segments to one of a continuous, interacting set of biological and physical processes along the stream gradient (Newbold et al. 1982b; Cushing et al. 1983b). This shift should lead to a reevaluation of the idea that streams are conduits that simply transport materials from the land to the sea, and hence to a greater appreciation of the metabolic and retention roles streams play.

#### Recognition of the Importance of Biotic Interactions within the Stream Community

One of the underlying biases of research in lotic ecology has been that streams are highly variable and hence unpredictable. Consequently, stream communities often are regarded to be dominated by physical factors and highly individualistic (e.g. Winterbourn et al. 1981; Grossman et al. 1982). However, we suggest that while stream communities are not strictly deterministic, neither are they a hodge podge of organisms resulting solely from stochastic events (see e.g. Barnes and Minshall 1983). The probability theory of fluvial geomorphologists (Leopold and Langbein 1962), and the thermal equilibrium theory (Vannote 1978; Sweeney and Vannote 1978; Vannote and Sweeney 1980), clearly suggest that there is a high degree of predictability (and hence opportunity for determinism) embedded in the apparent stochasticity of streams. Also, as pointed out by Turelli (1981) and Schoener (1982), relatively small amounts of environmental fluctuation have small biological effects so that the simpler deterministic approach often is adequate. In addition, not only does the opportunity for density-dependent (deterministic) phenomena exist in streams (Horwitz 1978; Shiozawa 1983; Minshall et al. 1985) but, in fact, biotic determinants are operable (e.g. Hildebrand 1974; Hildrew and Townsend 1976; Bohle 1978; Peckarsky 1979, 1980, 1981; Peckarsky and Dodson 1980a, 1980b; Hart 1981, 1983; Wiley and Kohler 1981; Allan 1982; Fisher et al. 1982; Bruns and Minshall 1983; McAuliffe 1983, 1984).

The RCC is primarily a deterministic model to some (Winterbourn et al. 1981; Winterbourn 1982; Grossman et al. 1982); others view it as largely stochastic (Barmuta and Lake 1982; Fisher 1983). Actually it lies somewhere in between (see e.g. Levins and Lewontin 1980). For example, the RCC focuses on physical features of the environment as providing much of the habitat template (sensu Southwood 1977) for stream communities, but it also is founded on trophic responses that are generally considered to be largely deterministic (Richardson 1980; Fisher 1983; Gorman and Karr 1978; Matthews 1982).

In addition to the relative spatial (longitudinal) and temporal predictability now believed to exist in stream environments, certain characteristics of the biota allow them to recover quickly from environmental fluctuations and thereby minimize the effects of what commonly are viewed as significant perturbations. In particular, the mobility, short life cycles, high reproductive rates, and ability to encyst or to burrow into the substratum allow stream organisms to avoid or adjust quickly to regular variations in the stream environment (e.g. flood resets) and to treat these variations essentially as *time constants* (see Hutchinson 1953) (e.g. Lehmkuhl and Anderson 1972; Minshall et al. 1985; Winget 1984). Studies of invertebrate colonization on introduced substrata (Minshall 1984) or following "catastrophic" flood and dewatering (Minshall et al. 1983a) also support the idea that rapid recovery from physical disturbance in streams is commonplace. Thus, these reset events are not really "stress," at the system level at least, and community structure is dependent on them in order to persist. Further, within the periods of physical variation (e.g. between spates) there commonly are sufficient time spans to permit the establishment and maintenance of equilibrium conditions. There seem to be certain periods during the year when equilibrium (hence deterministic or density dependent) conditions may prevail.

Most lotic consumers are trophic generalists or selective omnivores (Hutchinson 1981) that feed in proportion to the

broad kinds and amounts of foods available. Thus, the belief that competition for food is not a major factor in structuring stream communities is related to the widely held view that streams are highly variable and hence stochastic in nature. The RCC (and the data subsequently collected to test it: Hawkins and Sedell 1981; Minshall et al. 1982, 1983b; Cushing et al. 1983a) suggests that food relationships are important in structuring stream communities (see also Mackay and Wiggins 1978; Molles 1982). Lotic consumers also show morphological specialization with respect to food-gathering structures (Cummins and Klug 1979; Hale 1981; Merritt and Cummins 1978) resulting in considerable partitioning of food resources based on particle size, palatability, particle type, and constituents (Cummins 1973; Wallace et al. 1977; Anderson and Cummins 1979; Cummins and Klug 1979; Sheldon 1980; McAuliffe 1983). Ongoing competition for food has been demonstrated by Hart (1983) and McAuliffe (1983, 1984) whereas in other cases, resource partitioning (resulting in the "controlled" avoidance of competition) is evident (Minshall 1968; Mackay and Kalf 1969; Vannote 1978; Bruns and Minshall 1983).

Another important step in the development of stream ecosystem theory is the integration of certain principles of community ecology within the broader geomorphic/ecosystem context. The RCC, in conjunction with recent developments in population and community ecology (e.g. Cody and Diamond 1975; Southwood 1977; Anderson et al. 1979; Brown 1981; May 1981), suggests that the organization of lotic macroinvertebrate communities can be explained by the mean state of environmental variables and their degree of temporal variability and spatial heterogeneity. The gradient from headwaters to high-order reaches may be viewed as a spectrum of differentially variable habitats, and the patterns of species diversity for the total community and for specific functional groups appear to be interpretable within the context of habitat templates (see Southwood 1977). For example, we have found that components of community organization of lotic macroinvertebrates (e.g. species richness, niche breadth and overlap, and community complexity and stability) can be explained by the degree of temporal variability and spatial heterogeneity (D. A. Bruns, A. B. Hale, and G. W. Minshall, unpubl. data; Minshall et al. 1985). This structural approach complements previous RCC studies which emphasized ecosystem function. It also serves to introduce a conceptual basis for understanding lotic communities which in the past have been studied predominately from a descriptive aspect. And finally, it points the way for experimental investigations whereby mechanisms of community organization can be addressed directly.

### **Expansion of the River Continuum Concept to a Broader Geographic and Historical Model**

The RCC defines a standard for natural, unperturbed lotic systems against which existing streams can be compared. The utility of the RCC lies in its identification of a set of general conditions and relationships that can be used to study and compare stream systems. In this context, the RCC provides a framework for understanding the ecology of streams and rivers and is not intended as a description of biological components of all rivers in the individualistic context (i.e. it is an abstraction in the sense of Levins and Lewontin 1980). The RCC defines a general condition and in so doing explains the interrelationships between sets of unique conditions. Regional and local devia-

tions from the general pattern are a predictable result of specific variation in climate and geology, tributary influence, and location-specific lithology and geomorphology, as well as of long-term changes imposed by man. These factors are discussed more fully below.

#### **Climate and Geology**

Many geologists have accepted for sometime the idea that climate and geology are the ultimate determinants of river morphology through their effect on discharge and sediment load (e.g. Leopold and Wolman 1957; Gregory and Walling 1973; Lotspeich 1980). Together, climate and geology provide many factors influencing the characteristics of a river basin or watershed ecosystem. This has been accentuated by (1) the realization that river morphology and discharge can provide the template for stream ecosystem structure and function (Curry 1972, 1976; Horwitz 1978; Vannote et al. 1980), (2) examination of stream ecosystem dynamics over different North American biomes (Minshall et al. 1983b), (3) efforts to classify watersheds as ecosystems (Warren 1979; Lotspeich 1980), and (4) attempts to evaluate streams outside the north-temperate region in a broader context (Winterbourn et al. 1981). Climate, of course, affects the type and density of vegetation (Kuchler 1964; Bailey 1978; Garrison et al. 1977) and the effect of climate on the stream is in turn intimately bound up with the pattern of vegetation (Ross 1963; Gregory and Walling 1973; Hynes 1975). For example, precipitation and vegetation interact to affect runoff and erosion and hence sediment yield and organic matter loading. In other words, the action of flowing water, and hence such things as bed form and stability and organic matter storage and transport, varies with climate (e.g. Peltier 1950; Gregory and Walling 1973; Minshall et al. 1983b).

Geology affects the relative erosiveness of the parent material in a drainage basin and, consequently, watershed topography, chemical load, bed composition, and the like. Geology gives each physiographic region its distinctive appearance. Within each region, geologic structure, acted on by processes controlled by climate, gives shape to each land form (Lotspeich 1980). Recently, Strayer (1983) has shown that stream size and surface geology are the major factors controlling mussel distribution in the streams of southeastern Michigan. Others (e.g. Minshall and Minshall 1978; Magdych 1984) have demonstrated how differences in water quality mitigated or caused by the underlying geology can profoundly affect major segments of the benthic invertebrate community. In fact, as noted by Magdych (1984), these findings suggest the need to modify the RCC to allow for multiple gradients if it is to be useful in the generation of ecological models in regions where abnormal (nongradient) chemical inputs are important.

The riparian system (Swanson et al. 1982) can override the effects of climate and geology to some extent, especially in small (first to fourth) order streams below the tree line. The riparian vegetation is seen as a "ribbon of continuity" that makes many headwater streams look very similar worldwide (Cummins et al. 1984). Within rather broad climatic limits undisturbed headwater streams have temporally stable accumulations of large woody debris. Also, there seem to be biochemical equivalents along these streams in terms of riparian plant inputs that show fast, intermediate, and slow rates of decomposition (K. W. Cummins, pers. obs.). Thus, shading, geomorphic structuring by woody debris, and biochemically analogous inputs from the riparian system result in similar functional group assemblages in spite of differences in geology and climate.

Further, it is evident that even in larger stretches of a river (greater than fourth-order) the floodplain or riparian zone cannot be uncoupled from the stream channel itself. The RCC (Vannote et al. 1980) stressed that the influence of the terrestrial system on a stream diminishes as the stream becomes larger and that autochthonous carbon inputs to higher order streams (seventh- to tenth-order) should increase while allochthonous inputs of carbon decrease. However, Sedell and Froggatt (1984) have shown that many rivers in pre- and early settlement times also were heavily subsidized by their local flood plains. This subsidy took several forms including local litter fall from extensive riparian forests and carbon inputs from sloughs and side channels. In addition, Triska (1984), in his review of the Red River, reported that between 1828 and 1876, woody debris from the riparian zone of this eighth-order stream was enough to cause log jams along a 400- to 500-km stretch of the river. Besides being a direct carbon input to the river, the logs acted as a physical retention device that caused flooding of the riparian zone, drowning of trees, and a further addition of material to the river.

#### Tributary and Related Influences

Tributary additions to master streams have a significant influence on the continuum pattern. Where tributary inputs deviate from their usual summative influence on river water quality, expected (sensu Vannote et al. 1980) trophic and community patterns may be altered. The magnitude of change depends on tributary size (Fig. 1), regional drainage density, vegetation cover, land use, and lotic versus lentic source of inputs. A variety of effects may be envisioned. Concentrations of nutrients and/or food items in the tributaries may be higher than in the mainstream and serve to increase the mainstream levels. This could lead to increases in algal production or filter feeder densities if limiting concentrations were exceeded. Alternatively, a tributary may serve to dilute the mainstream concentrations or to provide a sustained input of coarse materials to a mid- or high-order master channel which could result in a biotic structure and function similar to upstream reaches. These postulates have been substantiated by the studies of Bruns et al. (1984) in the Middle Fork of the Salmon River. Not only were tributary influences demonstrated but the differing effects of small and large tributaries were contrasted.

A corollary to the RCC has recently been developed which emphasizes the impact of man-made dams on stream dynamics (Hauer and Stanford 1982; Ward and Stanford 1983). Ward and Stanford (1983) visualized the effect of relatively high dams as producing a shift in stream ecosystem structure and function in either an upstream or downstream direction depending on the size of the stream on which the dam is located and the position of outflow relative to the thermocline. The expected effects are similar to those postulated for tributaries. Extensive pools, whether generated by dams or associated with low gradient (Brown and Brown 1984), appear to have predictable impacts on stream conditions which represent local modifications to the trend expected for rivers in general (Vannote et al. 1980; Magdych 1984).

#### Local Lithology and Geomorphology

Here the focus is on location-specific variations in local geology and in the morphology of the river channel (perhaps most evident in flow patterns and substratum composition). The classic view of a river system is one of progressive change from

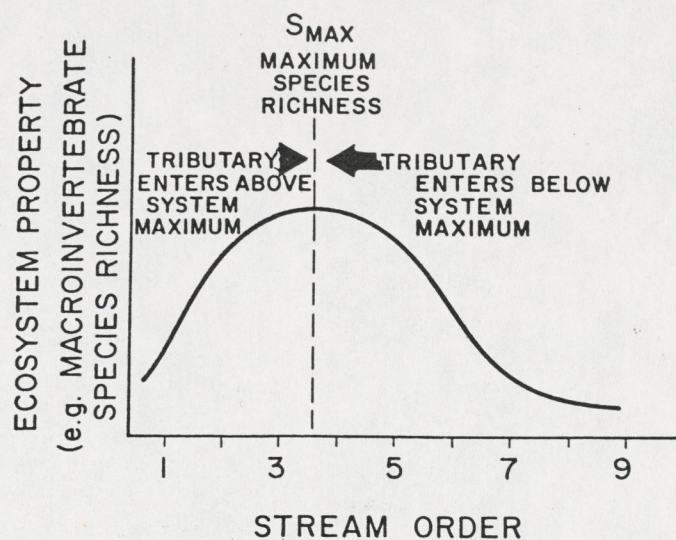


FIG. 1. The effect of a tributary on stream ecosystem parameters depends on where the tributary enters the larger stream. If a tributary enters above the point of system maximum it will drive the stream to that maximum. If it enters below it will move it back to reset that parameter. In this example, species richness reaches a maximum in third- to fourth-order streams. Tributaries entering above this cause the community to reach its maximum sooner. Tributaries entering below the peak increase richness by driving the system back.

high-gradient, turbulent, rocky headwaters to low-gradient, sluggish, mudbottomed rivers, and with a channel pattern progressing from straight, through braided, to meandering. Further reflection indicates that the ideal rarely is so clearly achieved. For example, in the Salmon River the steep-gradient headwaters descend immediately to a low-gradient glacial valley, and channel pattern varies from straight to meandering to braided and back to meandering, then straight, then braided. In addition to differences in hydraulic dynamics associated with these changes, one may expect major shifts in such factors as riparian inputs, channel storage of organic matter, and interchange with the flood plain (Fig. 2).

Studies on the distribution of *Gonidea angulata* and *Margaritifera falcata* in relation to substrate and periodic temporal variations in runoff amply demonstrate the influence of local lithologic and geomorphic processes on the relative abundance and population size structure of these organisms (Vannote and Minshall 1982). *Gonidea angulata* was predominant and possessed high population densities on stabilized sand and gravel bars; *M. falcata* was predominant in cobble and boulder areas. On cobble areas unprotected by block boulders, most *Margaritifera* populations were relatively young (20–40 yr) and had an approximately normal size distribution. On boulder controlled substrates, the size frequency was skewed towards the larger, old (100 yr) age-classes. Periodic floods, perhaps approaching a 50- to 100-yr return period, apparently cause high mussel mortality by bed scour in most canyon habitats. This periodic scour keeps populations relatively young with an approximately normal size distribution. In contrast, where mussel beds are protected by a field of large block-boulders, the dissipation of kinetic energy during floods is primarily through turbulence within the water column rather than bed shear. In these rare but highly stable habitats, *M. falcata* attains maximal density, old age, and a population structure that is skewed towards large individuals. Thus, local (site specific) conditions may alter both community and population structure and con-

GEOMORPHIC FEATURES			
	CANYON	BRAIDED	MEANDERING
PARAMETER			
Stream Surface Area : Discharge	LOW	HIGH	MEDIUM
Riparian Inputs	LOW	HIGH	MEDIUM
Detrital Storage	LOW	HIGH	MEDIUM-HIGH
Area Flooded	SMALL	LARGE	MEDIUM

FIG. 2. Shifts in important ecosystem parameters in response to changes in geomorphic features resulting from differences in hydraulic dynamics at different points in a stream reach.

found efforts to obtain an accurate holistic view unless they are taken into account.

#### Long-Term Effects of Man

Townsend (1980) contended that the spatial aspect of streams can be viewed without regard to the temporal. However, recent research (Molles 1982; Cummins et al. 1983, 1984) suggests that both a spatial and a temporal scale must be employed to obtain an understanding of stream dynamics. This is particularly important, since our concept of aboriginal conditions presently is so poor (at least 100 yr of nonendemic, man-made effects in South America and Africa, up to 400 yr in North America, and 1000 yr or more in Europe).

The impact of man on the structure of ecological communities is a common theme running through modern environmental science and pollution biology. However, man's greater responsibility for wholesale alteration of communities and extinction of species over the entire historical record has only recently been suggested (Goudie 1981; Lewin 1984) and may be a much larger effect than thought. In stream research the intimate connection between the stream and the adjacent terrestrial environment has focused attention on how man-caused disturbances such as fire (Minshall et al. 1981), silviculture (Molles 1982), riparian control (Cummins et al. 1984; Sedell and Froggatt 1984), and tree debris removal (Triska 1984) have potential for long-term changes in stream systems. This awareness has been accentuated by the need for resource managers to know the natural, presettlement conditions of areas under their supervision (Romme 1982; Romme and Knight 1982; Sedell and Luchessa 1982). Various postsettlement alterations likely to have had major impacts on the nature of stream ecosystems include the following: urbanization; deforestation; tillage; irrigation; dam construction; channel alteration for navigation, logging, mining, and flood control; virtual extermination of beaver, bison, and other large mammals including aboriginal man; grazing by

domestic animals; and fire suppression. These changes, many of them so subtle as to go unnoticed, have made it difficult for modern stream ecologists to place their findings in perspective with reference to natural, pristine conditions or to obtain meaningful measurements of certain aspects such as carbon budgets (Cummins et al. 1983). Nevertheless, incorporation of a broad temporal perspective has begun to aid substantially in the understanding of stream ecosystem structure and function both past and present (Molles 1982; Romme and Knight 1982; Sedell and Luchessa 1982; Sedell et al. 1982; Cummins et al. 1983; Fremling and Clafin 1984).

Side channels, braided channels, and off-channel backwaters (seasonal) may have an effect similar to that of tributaries. However, the massive snag removal that took place on essentially all North American rivers in the late 1800's and early 1900's, together with large-scale channelization efforts, has converted the majority of streams greater than fourth- to sixth-order from heavily braided or meandering systems to single, relatively straight channels (see e.g. Cummins et al. 1984; Fremling and Clafin 1984; Sedell and Froggatt 1984; Triska 1984). Thus, instead of a single fifth-order channel there might have been five third-order channels. Among other things, this would mean that the riparian effect was much different prior to such alterations. Wood, removed by man, probably produced a very different channel form in mid-sized rivers than that found today. Braids, off-channel backwaters, and side-channel streams probably caused many midorder rivers to behave more like headwaters. However, intensive beaver activity prior to the mid-1800's may have had a countereffect in that the extensive impoundments the beaver created would have made headwater streams wider, slower, and more midorder in character.

#### Implications to Stream Ecology

Deviations in regional and local conditions (associated with such things as climate and geology, tributaries and related



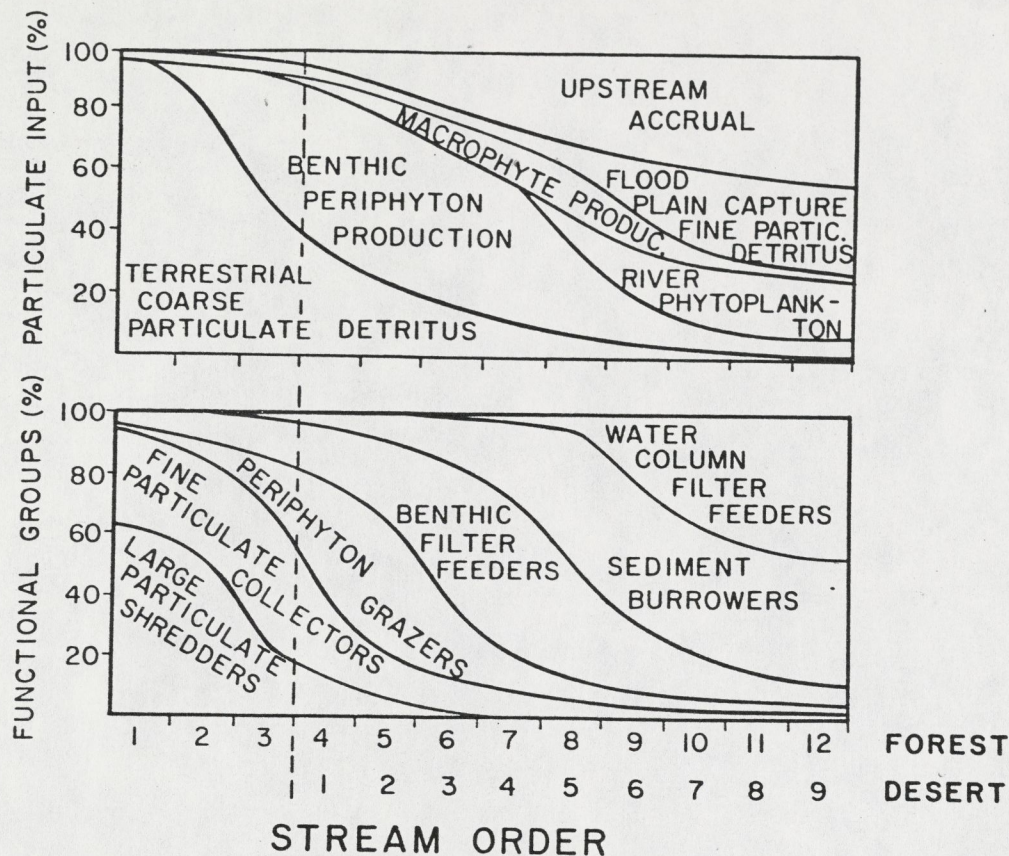


FIG. 3. Expected changes in particulate organic matter inputs and functional feeding group relationships along a river system (after Vannote et al. 1980). The abscissa is shown as a "sliding scale" to emphasize the fact that different streams enter the continuum at different points. In the two cases illustrated, forest streams begin with a strong terrestrial influence (reflected by a predominance of allochthonous organic matter and detrital processors) whereas desert streams, due to the lack of shading and reduced influx of allochthonous detritus, enter the sequence at a point displaced to the right and equivalent to a more downstream position of the forest stream.

influences, local lithology and geomorphology, and long-term effects of man) suggest that adjustments need to be made in the RCC if it is to be applied across biomes, especially when environmental extremes or unusual situations are involved. For example, in some wooded parts of Africa (e.g. Zimbabwe), large amounts of coarse particulate leaf detritus do not reach the stream. Most leaf material is processed by terrestrial detritivores during the dry season, and by the time the rains come, the coarse material has already been reduced to fine particles (R. C. Petersen, pers. obs.). Consequently, an important functional feeding group (shredders) is reduced or absent from such streams, and a sequence of adjustments in invertebrate trophic structure results (Fig. 3). The absence of large-particle shredders also appears to be typical of unstable, poorly retentive headwater streams in disturbed watersheds (Rounick and Winterbourn 1983a, 1983b). As another example, there are many areas of the world in which, for one reason or another, headwater streams (first-order woodland streams) simply do not occur. In areas dominated by porous calcareous geology such as in Florida (Odum 1957) or the western mountains of Jamaica (Petersen 1984; pers. obs.), the rivers begin as larger sized systems. In these rivers it still is expected that the basic sequential model will be followed but the river will skip the upper small-order categories and the effect that those small systems have on the downstream reaches will be removed. In Jamaican springs, which begin with a width of 30–40 m, the

streams below the springs are dominated by primary production (macrophytes and periphytic algae). The grazer functional group, consisting of snails, dominates the macrobenthos, and due to a lack of particulate organics, filter feeders are rare but collector-gatherers feeding on decomposing macrophytes are abundant. In short, the system structure is similar to a midorder woodland river but without the filter feeders that normally feed on the upstream losses of particles. The need to accommodate these sorts of changes are explicit in the original formulation of the RCC (Cummins 1975; Minshall 1978; Vannote et al. 1980) but the point has been missed by some investigators (e.g. Winterbourn et al. 1981; Rounick and Winterbourn 1983a).

Because streams are ecosystems with numerous linkages and feedback loops, care must be taken in developing and testing stream ecosystem theory that critical interrelations are not excluded or unconsciously left uncoupled. For example, some investigations have taken the absence of macroinvertebrate shredders from certain headwater streams as failing to support the RCC (e.g. Winterbourn et al. 1981). But the various facets of organic matter processing cannot be viewed in isolation. For one thing, it is unreasonable to expect macroinvertebrate shredders to be present if the coarse particulate organic matter supply is inadequate or unreliable. Also, various trade-offs may occur in which the macroinvertebrate shredders may be replaced or supplemented by other size-reducing mechanisms (microbes, beaver, physical fragmentation). The important point in terms

of the RCC is that when coarse particulate organic matter enters a stream it will be reduced to fine particulate organic matter and that this phenomenon generally is quantitatively most significant in the headwaters of a river system. It is only when these features are shown to be unimportant or absent that this aspect of the RCC can be shown not to hold. Furthermore, abnormal (often anthropogenic) factors may obscure or obliterate the expected response such as when the entrance of geothermal waters or other adverse environmental conditions selectively eliminates certain components of the community. Sometimes such influences may occur on a large scale (e.g. acid rain), further obscuring the relationship and giving the impression that the general presettlement pattern is being examined. This is especially true if the event is a temporally distant one where the cause is separated from its present-day effect by time as well as space. Examples include acid rain in Europe which began with the Industrial Revolution and deforestation of large tracts of land which in parts of England may date back 3000 yr to the Bronze Age (Dr. W. Pennington, Botany Department, University of Leicester, U.K., pers. comm.).

Since stream ecosystem dynamics also are coupled closely to the fluvial geomorphic conditions, these conditions must be taken into account when testing the RCC or devising alternative explanations. This suggests that, in examining conditions along a river system, samples should be taken so that the mean or most characteristic geomorphic conditions in each stretch are represented. For example, collections of organisms taken only from riffles along the course of a river may provide an erroneous view of general patterns of distribution, since the characterizing geomorphic properties of the stream reach may be being overridden by the sampling procedure and a depositional rather than an erosional biota may actually be the appropriate representative. Here, too, the long-term temporal perspective is an important one. Due to flow regulation, many stream channels, particularly in lowland areas, are over- (e.g. due to channelization) or under-fit (e.g. due to sedimentation) or otherwise managed in ways that alter the natural conditions (e.g. weed cutting). While these represent deviations, the extent of which can be measured against the RCC, they do not provide evidence of conditions that invalidate the concept.

## Conclusion

Stream ecosystem theory has seen a number of important advances, especially in the past decade. The RCC is consistent with these views and has served to synthesize most of them into a workable general hypothesis. Although the worldwide generality of the model remains to be further evaluated, it appears that most riverine ecosystems generally can be accommodated within the current conceptual framework. In this regard, it appears that even systems identified as "exceptions" (e.g. Winterbourn et al. 1981) represent no more than variations on a central theme (e.g. if coarse particulate organic matter is not there, neither will shredders or large-wood geomorphic control, etc.).

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# Conservation and Distribution of Genetic Variation in a Polytypic Species, the Cutthroat Trout

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**Abstract:** *The cutthroat trout (Salmo clarki) presents a series of unusual and difficult problems in conservation biology. As many as 16 subspecies have been recognized in the recent literature. The genetic distance between subspecies based upon 46 enzyme loci ranges from that usually seen between congeneric species to virtual genetic identity. Subspecies from the western portion of the range of the cutthroat trout are genetically more similar to rainbow trout (Salmo gairdneri) than they are to the other subspecies of cutthroat trout. In addition, much of the genetic variation within the westslope cutthroat trout (S. c. lewisi) results from alleles found in only one or two local populations, but they often occur at high frequencies in those populations. Thus, preserving the genetic variation in westslope cutthroat trout entails preserving as many local populations as possible.*

*Captive populations of cutthroat trout present a series of opportunities and genetic problems. A number of management agencies are using captive populations to supplement and reestablish natural populations. Basic genetic principles must be understood and followed in establishing and maintaining captive populations. We describe examples of unsuccessful and successful efforts by management agencies to develop captive populations.*

*The greatest danger to the conservation of the cutthroat trout is introgressive hybridization among subspecies and with rainbow trout. Several factors make salmonid fishes especially susceptible to problems associated with introgressive hybridization. We conclude that biochemical analysis provides a more reliable and informative means of detecting interbreeding than morphological characters. Interbreeding between westslope and Yellowstone cutthroat trout and non-*

**Resumen:** *La trucha (Salmo clarki) presenta una serie de problemas inusuales y difíciles en la biología para la conservación. Hasta 16 subspecies han sido reconocidas en la literatura reciente. La distancia genética entre subspecies, basada en 46 loci de enzimas, varía desde aquella generalmente vista entre especies congénicas hasta prácticamente identidad genética. Las subspecies de la porción occidental de la distribución de S. clarki son genéticamente más similares a la trucha arcoiris (Salmo gairdneri) de lo que lo son a otras subspecies de S. clarki. Adicionalmente, mucha de la variación genética de S. clarki de la vertiente occidental (S. c. lewisi) resulta de alelos que solamente se encuentran en una o dos poblaciones locales, pero frecuentemente éstos se presentan con alta frecuencia en esas poblaciones. Por tanto, para conservar la variación genética de S. clarki de la vertiente occidental se deben conservar tantas poblaciones locales como sea posible.*

*Poblaciones en cautiverio de S. clarki presentan una serie de oportunidades y problemas genéticos. Un buen número de agencias de manejo están empleando poblaciones en cautiverio para suplementar y reestablecer poblaciones naturales. Los principios genéticos básicos deben ser comprendidos y seguidos durante el establecimiento y mantenimiento de poblaciones en cautiverio. Describimos ejemplos de esfuerzos fracasados y exitosos de agencias de manejo para desarrollar poblaciones en cautiverio.*

*El mayor peligro para la conservación de S. clarki es la hibridación itrogresiva entre subspecies y con la trucha arcoiris. Varios factores hacen a los peces salmonidos especialmente susceptibles a problemas asociados con la hibridación itrogresiva. Concluimos que el análisis bioquímico*

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## Conservation Biology of Fishes

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"I love any discourse of rivers, and fish, and fishing."

Izaak Walton  
*The Compleat Angler*

The following three papers were presented at a symposium on the conservation biology of fishes at the Society for Conservation Biology meeting in June of last year. The first paper presents problems special to species living in rivers; the second paper discusses desert fishes; and the final paper considers one of the most popular sport fishes of North America, the cutthroat trout. A fourth paper on the genetics of exploitation in rockfishes was presented at the symposium by Keith Nelson but is not included in this issue.

Three or four papers are obviously not sufficient to provide a comprehensive overview of the conservation of a taxon with over 20,000 species that last shared a common evolutionary ancestor some 400 million years ago (Mayr 1969). Those interested in broader aspects of fish conservation may consult the following recent publications (FAO/UNEP 1981; Fetterolf 1981; Meffe 1987; Ono, Williams, & Wagner 1983; Ryman 1981). The three papers in this issue are concerned primarily with freshwater fishes native to North America. Nevertheless, all three papers stress general principles that are relevant to all fish species.

Some 70% of all the world's fishes listed as endangered or threatened are native to North America (Ono, Williams, & Wagner 1983, page 218). In addition, only one out of 83 species from throughout the world listed as threatened or endangered by the U.S. Fish and Wildlife Service (Federal Register 1987) is a marine species. It is unclear how much the predominance of freshwater fishes from North America on such lists is due to the fishes *per se* and how much is due to the geographical distribution of ichthyologists. Nevertheless, the topics of these three papers reflect current conservation efforts with fishes.

Fishes present some unusual challenges to conservation biologists because they are different from other vertebrates in a variety of ways. Their tremendous taxonomic diversity is the first challenge. Almost exactly one-half of all vertebrate species are fishes (Mayr 1969). Fish species occur in virtually every aquatic environment on the water-planet: lakes, streams, rivers, vernal pools, desert springs, estuaries, the open ocean, deep oceanic trenches, and underneath the polar icecaps.

Fish also show much more intraspecific phenotypic variation than most other taxa (Allendorf, Ryman, & Utter 1987). Individuals within a single species of fish sometimes show enormous differences in size. For example, females from ten populations of Arctic char (*Salvelinus alpinus*) range in mean weight at first sexual maturity from 23 g to nearly 1,000 g (Johnson 1980). However, the larger phenotypic variation within fish species is apparently not associated with greater genetic variability. Heritability is the proportion of the total phenotypic variation that is due to genetic differences between individuals. Heritabilities for such traits as body length and weight are generally much lower within fish populations than within populations of other vertebrates (Allendorf, Ryman, & Utter 1987).

These comparisons suggest that the genotypic-phenotypic relationship in fishes may be somewhat different from what it is in other vertebrates. The high phenotypic variation, coupled with lower heritabilities, indicates greater susceptibility to environmental factors. This difference is not surprising in view of the indeterminate growth capacity of most fishes and the greater metabolic sensitivity to temperature of fishes in comparison to birds and mammals.

The cichlid fishes of the New World and Africa probably best demonstrate the challenges to conservation biologists resulting from the great taxonomic diversity in fish species and their unusual genotypic-phenotypic

relationships. Some African rift lakes have "species flocks" consisting of over 300 described endemic species (references in Echelle & Kornfield 1984). However, two morphologically distinct sympatric 'species' of cichlids endemic to Cuatro Ciénegas, Mexico, have been shown to belong to a single reproductive population (Kornfield et al. 1982). In addition, laboratory experiments with cichlids have shown that changing their diet can result in large differences in morphology (Meyer 1987).

Fishes also show the greatest variety of reproductive systems among the vertebrates. Modes of reproduction in fishes include oviparity, viviparity, ovoviviparity, and ovi-ovoviviparity (Moyle & Cech 1982). Sexuality in fishes also runs the gamut of possibilities: simultaneous hermaphroditism, consecutive hermaphroditism, unisexuality, and bisexuality (Price 1986). Modes of sex determination in fish species includes male heterogamety, female heterogamety, multiple sex chromosomes, polygenic determination, single gene determination, and environmental determination (Price 1986).

The genetic systems of fishes show similar diversity. Most fish species show normal diploid Mendelian inheritance. However, alternative genetic systems in fish species include triploidy, tetraploidy, gynogenesis, and hybridogenesis (Turner 1984). Some of these alternative genetic systems also occur in amphibians and reptiles but they are more restricted in those taxa. For example, all of the described polyploid amphibian and reptilian species have closely related diploid counterparts, and no higher polyploid taxa have been found (Bogart 1980). Tetraploidy among fish taxa is much more widespread (Schultz 1980). Two of the more successful families of fishes apparently are descended from their own tetraploid ancestor: catostomids (suckers: 12 genera, 58 species; Nelson 1976) and salmonids (salmon, trout, char, whitefish, and grayling: 9 genera, 68 species; Nelson 1976).

This diversity in reproduction and genetics is of more than academic interest. The paper in this issue by Allendorf & Leary (1988) discusses several unusual problems associated with the conservation of cutthroat trout. Many of the conservation problems with this salmonid species apparently result from its polyploid ancestry (e.g., fertile hybrids between taxa with large amounts of genetic divergence).

Fishes are unique in that no other major food source of man is captured from wild populations. Nelson & Soulé (1987) have considered this attribute of fishes in a philosophical context. The commercial harvesting of fish also has a variety of important biological implications. Harvested fish populations are subjected to selection on a variety of characteristics that affect an individual's vulnerability to harvesting. Nelson and Soulé (1987) have reviewed the evidence that differential harvesting has caused genetic changes in fish stocks.

The paper presented at the meeting by Nelson examined this problem in detail in rockfish of the genus *Sebastes*. This genus contains at least 100 species of marine fish (Eschmeyer, Herald, & Hamman 1983); many of these species support important fisheries on the west coast of the United States. He concluded that our understanding of the effects of exploitation cannot be gained by ordinary genetic methods. He recommended detailed analysis of the empirical effects of exploitation on the age schedule of growth and on changes in the size schedule of fecundity.

The commercial and recreational value of fish populations has also led to widespread culture of fishes in hatcheries for release into the wild to supplement natural populations. There is no parallel among other taxa to the massive and continuous release of artificially cultured individuals over large areas such as became possible through the development of hatchery programs in the last century (Allendorf, Ryman, & Utter 1987). For example, a single hatchery on Yellowstone Lake collected and shipped over 818 million Yellowstone cutthroat trout (*Salmo clarki bouvieri*) eggs between 1899 and 1957 (Varley 1979)!

A discussion of the need to protect fishes on their spawning grounds from an article on "pisciculture" by G. Brown Goode of the U.S. National Museum in the 1898 edition of the Encyclopedia Britannica presents the view of early fish biologists:

How much must they be protected? Here the fish-culturist comes in with the proposition that "it is cheaper to make fish so plentiful by artificial means that every fisherman may take all he can catch than to enforce a code of protection laws."

The salmon rivers of the Pacific slope of the United States, the shad rivers of the east, and the whitefish fisheries of the lakes are now so thoroughly under control by the fish-culturist that it is doubtful if anyone will venture to contradict his assertion. The question is whether he can extend his domain to other species.

It is interesting to note that two whitefish species from the Great Lakes are extinct, and three additional species are threatened or endangered (Ono et al. 1983). The paper by Allendorf & Leary (1988) discusses problems in conservation related to artificial culture and release of salmonids throughout the western United States.

Fish are generally restricted to water. This obvious characteristic has some perhaps not so obvious effects on their conservation. For example, fishes are not as easy for humans to observe and appreciate as are birds and mammals. It has therefore been more difficult to attract public support for their conservation. Moreover, it also appears that fishes have been somewhat ignored by conservation biologists. For example, the most recent list of endangered and threatened species by the U.S. Department of the Interior (Federal Register 1987) includes over 300 species of mammals, over 200 species of birds, and only 83 species of fish, even though there



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## Chapter 12

# Management of Introduced Fishes

HIRAM W. LI AND PETER B. MOYLE

### 12.1 INTRODUCTION

The introduction of fish species into waters outside their native range has occurred since the common carp was first moved around by the Chinese over 3,000 years ago and by the Romans 2,000 years ago (Balon 1974). During the Middle Ages, common carp were spread throughout Europe by monastic orders, and Scandinavians were busy stocking "barren" alpine lakes with salmonids. In the following centuries, the great expansion of western civilization was accompanied by the worldwide distribution of species of Euro-American flora and fauna, including fish. This was a reflection of western attitudes that the natural environment was hostile and needed to be tamed, and that natural systems could be improved by introducing familiar, and therefore "superior" species (Crosby 1986). Throughout the world there are now important fisheries based on introduced species, e.g., trout and salmon in New Zealand, Mozambique tilapia in Sri Lanka, common carp in Europe, and brown trout in North America. Only recently have such widely known "success" stories been balanced by the realization that many introductions have done more harm than good.

The damage done by introduced plants and animals to natural systems has caused ecologists and resource managers much concern (Kornberg and Williamson 1986; Mooney and Drake 1986; Holcik 1991; Nesler and Bergersen 1991). The common complaint is that sustainable benefits have been sacrificed for short-term gains (Baltz 1991; Ogutu-Ohwayo and Hecky 1991; Philipp 1991; Spencer et al. 1991). The introduction of new species to improve fisheries is still a common management practice; therefore, it is important to understand the effects introduced species can have on native species and ecosystems. Without such understanding, well-intentioned management programs can create problems that actually subvert the original management intent.

This chapter (1) provides an overview of the reasons for introducing aquatic organisms with examples of successes and failures, (2) presents ecological concepts important for understanding the effects of introductions, (3) suggests some management alternatives to introducing new species, and (4) provides guidelines for evaluating proposed introductions.

## 12.2 REASONS FOR FISH INTRODUCTIONS

Fishes have been introduced for many and often multiple reasons: (1) to increase local food supplies, (2) to enhance sport and commercial fishing, (3) to manipulate aquatic systems, (4) by accident, and (5) for aesthetic reasons.

### 12.2.1 Food Supply

The earliest introduced species were semi-domesticated animals and plants that were moved about to create more reliable local food supplies. Domesticated plants and animals were keystones in the development of human culture and their spread was a natural outcome of human expansion across the globe. As human populations grew and moved, commensal species such as rats and weedy plants also spread and feral populations of domestic animals developed. Fish were relatively late additions to the ranks of domestic and commensal species; most species were added after about 1850. However, the worldwide spread of common carp and African tilapias began well before this time. Fishes such as common carp and tilapia are hardy so they can be easily transported, they establish populations quickly in a variety of new environments, and they grow rapidly, especially in ponds. These traits are characteristics of most animals used in aquaculture; they are also the characteristics of pest species.

In response to the increased human demand for fish and static or declining wild fish populations, aquaculture today is a rapidly growing industry. Fish farmers tend to use only familiar species which leads to two problems: (1) native fishes well adapted to local conditions are ignored for aquaculture, and (2) nonnative species escape into local waterways. The latter problem can result in the disruption of local wild fish populations, if not through direct interactions with the introduced fishes, then through exposure to new diseases and parasites.

### 12.2.2 Fisheries Enhancement

Izaak Walton was one of the first anglers to claim that an introduced fish was superior to native forms. In 1653, he pronounced the recently introduced common carp the "queen" of England's rivers because of its superior qualities as a sport fish. Local fish acclimatization societies formed in various countries, many of them predecessors of present fisheries management agencies. By the late 1800s, introducing species to solve management problems in North America had become a major activity of state and federal agencies. As a result, the dominant fishes in many lakes and rivers in North America are introduced sport fishes (see Courtenay and Kohler 1986; Moyle 1986).

This pattern has been repeated throughout the world, but particularly in the British Empire where sport fishing was a favorite upper-class affectation and local fishes were often considered to be unsuitable prey for the sophisticated angler. Favored sport fishes from Europe and North America were consequently brought to distant lands, often with great difficulty; today species such as largemouth bass, rainbow trout, and brown trout enjoy virtual global distribution. Such fishes are still the backbone of sport fisheries in many areas, but there is a growing realization that they are often poor substitutes for native fishes such as cutthroat trout of the interior basins of western North America. Similarly, the reduction in native cyprinodonts in Lake Titicaca (Peru-Bolivia), important in native subsis-

tence fisheries, resulted from the introduction of rainbow trout from North America and a predatory atherinid from elsewhere in South America.

Some of the most successful uses of introduced sport fishes illustrate the dictum of Giles (1978) that "importations are an admission of defeat in managing native populations to meet existing needs." The best example of this is found in Lake Michigan, which had its native fish communities severely disrupted by the inadvertent invasions of a predator (sea lamprey) and an efficient planktivore (alewife), coupled with the introduction of another planktivore (rainbow smelt) and severe overfishing of native fishes. The result was a nearly complete collapse of the native sport and commercial fisheries (see Chapter 22). Previous experience suggested that predatory Pacific salmonids could greatly reduce the numbers of alewives and rainbow smelt. This proved to be the case and a spectacular fishery for salmon soon developed. The reductions in rainbow smelt and alewives resulted in a marked increase in the numbers of some native planktivores, through reduced competition for zooplankton and, perhaps, reduced predation on planktonic larvae. In a way, the introduction of Pacific salmonids worked too well. Salmon and steelhead populations exploded as they "mined" the huge biomass of alewives, creating expectations in anglers that the fabulous fishing would continue indefinitely. However, alewife populations are apparently now being kept at low levels by salmonid predation which in turn limits the number of salmon and trout the system can support (Eck and Brown 1985).

Even though the effort in the Great Lakes to develop a new fish community based on introduced fishes was largely successful, most such efforts create as many problems as they solve. This is well illustrated by the introductions of warmwater sport fishes into reservoirs of the intermountain West, in order to mitigate the losses of riverine salmon and trout fisheries. Unfortunately, the introduced species often invade unimpounded reaches of river and prey upon or compete with native fishes. For example, native fishes of the Columbia and Snake rivers are now exposed to a greater intensity of piscivory than experienced during their evolutionary history because of the presence of introduced walleye, channel catfish, and smallmouth bass (Li et al. 1987; Tabor et al., in press). Juvenile salmonids constitute a significant part of the diet of these fishes and the establishment of these predators therefore counters the official policy of doubling salmonid escapement by the turn of the century.

There have been relatively few successful introductions of commercial fishes, although attempts have been numerous, especially in marine environments. Some of the more successful introductions have been those made to benefit both sport and commercial fisheries, such as the introduction of striped bass and American shad to California in the 1870s, and the spread of lake trout to coldwater lakes around the world. When angler demand for such fishes becomes high, the commercial fisheries are often banned. In North America, the main commercial fisheries on introduced fishes focus on species not favored by anglers, such as buffalofishes in Arizona reservoirs, Sacramento blackfish in a Nevada reservoir, and common carp in rivers and reservoirs of the Midwest.

Because commercial fisheries depend on large quantities of fish, a successful introduction for this purpose is bound to have a major impact on the receiving aquatic ecosystem. For example, in the former Soviet Union the introduction of European perch into Lake Kenon resulted in the extinction of five native species and reduction in the populations of three others (Karasev 1974). In Lake Victoria,

Africa, the introduction of the predatory Nile perch had catastrophic effects on the 200–300 species of endemic haplochromine cichlids that were once important to the native fishers, and many of those species now seem to be extinct (see 12.3.5).

Often the poor performance of a sport fishery is attributed to the absence of an adequate prey base for predatory sport fishes. A common management practice is to introduce a suitable prey organism on the assumption that a new prey base will enhance growth and survival of sport fishes (see Chapter 13). Thus, species such as threadfin shad, gizzard shad, and golden shiner have been widely introduced into warmwater lakes and reservoirs as forage, while rainbow smelt and opossum shrimp *Mysis relicta* have been widely introduced into coldwater lakes and reservoirs. Such introductions have had mixed success. Often growth rates of adult game fishes accelerate following the introduction and an initial period of outstanding fishing develops. However, it is common for the growth and survival rates of juveniles of the same game fishes to decrease because the forage species compete with them for food. Thus, the growth rates of juvenile white and black crappie in a California lake decreased considerably following the introduction of inland silverside, while the growth rates of adult crappie, which preyed on the silverside, increased. The net result was that the large crappie preferred by anglers were the same size at a given age as they were before the introduction (Li et al. 1976). Not surprisingly, some of the most successful forage fish introductions have occurred in reservoirs where the game fish, usually trout, are planted at a size large enough to prey immediately on the forage fishes. A better understanding of predator–prey relationships would allow more efficient use of forage introductions as a management tool.

### 12.2.3 Manipulation of Aquatic Systems

The use of fish as biological control agents for aquatic pests such as mosquitoes, disease-bearing snails, aquatic weeds, or stunted fishes is a very appealing concept. If effective, a successful introduction for biological control can obviate the need for pesticides, be inexpensive, and have a long-lasting effect. The increased use of fishes for biological control in recent years has been spurred by successes in the use of insects as control agents in agriculture, and the development of biological control theory by applied entomologists. The cost of pesticides is also rapidly increasing, as is public concern about the effects of pesticides on nontarget organisms and human health. As a result, species with good track records for biological control are being spread worldwide, most prominently mosquitofish and grass carp. The mosquitofish is perhaps the most widely distributed fish in the world today, found virtually everywhere in which the climate is suitable. It is successful at controlling mosquitoes because it can live in stagnant water, reproduces and grows rapidly, is a voracious insectivore, and is easy to raise in large numbers. The distribution of the grass carp may someday rival that of the mosquitofish, as it is being widely introduced as a fish that is not only effective at controlling aquatic weeds (often introduced species themselves), but one that converts these weeds to edible fish flesh. The grass carp is hardy, easy to culture, a voracious grazer, and relatively nonselective in its choice of plants to eat.

Even though there are many success stories in the use of mosquitofish, grass

carp, and other fishes for biological control, the use of such fish also entails considerable risk. This is because fish typically select a wide variety of prey species and will forage on pest species only when they are abundant and easily available. Fish are also longer lived than most of their prey, so have relatively slow population responses to increases or decreases in prey abundance. As a result, nontarget organisms can be adversely affected by control fishes. For example, if densities of mosquitofish are too low, their presence may actually increase mosquito populations because mosquitofish preferentially prey on larger insects that are natural predators of mosquito larvae; they switch to mosquitoes only after the large insects are depleted. Mosquitofish also can displace native fishes that may actually be better at mosquito control in some types of habitat.

Piscivores have been introduced to control prey, but aside from the Great Lakes experience, evidence of the success of this strategy in improving fisheries is largely equivocal (Noble 1981; Wydowski and Bennett 1981). The main reason for equivocal results is that predator-prey interactions are more complex than generally realized. For example, the tiger muskellunge, which is a sterile hybrid of the muskellunge and northern pike, has been proposed as a safe management tool to reduce populations of stunted sunfish in lakes and ponds. However, tiger muskellunge are only able to prey effectively on sunfish when prey densities are high, when vegetation is sparse, when no alternative prey are available, and when the tiger muskellunge are too large to be eaten by largemouth bass (Tomcko et al. 1984), a set of conditions not often met.

Limnologists have noted that water quality may be improved by manipulating the food chain (Shapiro and Wright 1984). One method is to introduce piscivores in order to reduce populations of small fishes that prey on zooplankton. Zooplankton populations then increase and this results in increased grazing by the zooplankton on phytoplankton, causing an increase in water clarity. Such shifts have been noted by Scavia et al. (1986) in Lake Michigan, but it is unusual for predation to be so effective. In addition, the goals of water quality management and fisheries management may not be compatible; high harvest rates of predatory fishes may result in increases of planktivores and decreased water clarity.

#### 12.2.4 Accidental and Unauthorized Introductions

The idea that an adequate forage base is necessary to produce large populations of game fish is so obvious that the introductions of minnows and other small fishes is a popular pastime of anglers. Often these introductions are simply the result of anglers collecting bait fish from one stream, fishing in a stream in a different drainage, and then releasing their unused bait. Such cryptic introductions are more common than generally realized and can explain many anomalies in fish distribution. Bait-bucket transfers are only one type of accidental introduction. Fishes and invertebrates have also become established in new waters after being transported through canals, carried as contaminants in truckloads of hatchery-reared game fish, or allowed to escape from fish farms. Increasingly, aquatic organisms are making their way into new waters through ships that carry cargo in only one direction and carry enormous quantities of water back as ballast (Carlton 1985). For example, the ruff (a small predatory perch), a predatory cladoceran, and the zebra mussel *Dreissena polymorpha* have recently been added to the fauna of the Great Lakes by this method and they have considerable potential for

altering the entire aquatic ecosystem (Scavia et al. 1988; Roberts 1990). In the Sacramento–San Joaquin estuary, recent ballast-water introductions include two species of gobies, two species of copepods, an amphipod, and a euryhaline clam. There is growing evidence that these species have altered food chains that lead to striped bass and other fishes (Nichols et al. 1990, Meng and Orsi 1991).

### 12.2.5 Aesthetic Considerations

A contributing factor to most deliberate introductions is aesthetics. People who make introductions have a cultural preference for the taste, appearance, or sporting style of the introduced species over native species. A few introductions have been made solely for aesthetic reasons, such as the planting of goldfish in urban waterways or of tropical fish in hot springs.

## 12.3 INTRODUCTIONS AND ECOLOGICAL THEORY

A species introduction is a type of ecological perturbation that, if successful, will alter the biotic community into which the species has become part. Therefore, the purpose of this section is to discuss the use of ecological theory to predict how a species proposed for introduction is likely to alter the receiving community, as well as the degree of community disturbance it is likely to cause. Relevant theory falls into two general headings: the niche concept and the concept of limiting similarity. These two ideas form the basis of the theory of island biogeography, which can be used as a general framework to explain how colonization and extinction processes shape communities of organisms. Following the presentation of these concepts, the mechanisms that enable introduced species to invade and alter biotic communities will be discussed: (1) competition, (2) parasite–host interactions, (3) predation, (4) habitat modification, (5) indirect interactions, and (6) hybridization. More detailed discussions of these and other concepts in relation to fish introductions can be found in Courtenay and Robins (1989).

### 12.3.1 Niche Concept

The most widely accepted description of the niche is that of Hutchinson (1958) who developed the idea as a multidimensional attribute of a species or population that contains many axes describing where and how the species lives. There are axes for such dimensions as prey size, prey type, depth of water, and velocity of water. The niche is therefore a characteristic of the organism, not the environment. Lack of understanding of this idea has led to the introduction of species to fill “vacant,” “unoccupied,” or “empty” niches. The vacant niche concept confuses available resources of the aquatic habitat with the ecological function of the organism (Herbold and Moyle 1986). Usually the vacant niche is identified as an abundant food resource located in a particular habitat. A species is introduced to use that resource based upon observations of its life history in other aquatic systems on the assumption that it will perform in the new system just as it did in the old. This assumption is often wrong because the niche expression of an organism in any particular ecological community is limited by local physicochemical and biological constraints.

The ecological niche as defined by Hutchinson (1958) has two aspects: the fundamental niche and the realized niche (Figure 12.1). The fundamental niche is

the total capacity of the organism to perform activities over a wide range of environmental conditions; it is circumscribed by genetically determined physiological limits. The realized niche is the fraction of the fundamental niche that is expressed as an adaptation to local conditions. For example, the presence of a competitor or predator of a species may prevent that species from using food or space it would use in their absence, resulting in a rather narrow realized niche (niche compression). If the constraints imposed by the other organisms are removed, the realized niche becomes larger (niche expansion). Therefore, at any given time and place a population of a species is using only a small part of its fundamental niche. A classic example of how the realized niche of an introduced organism can change is illustrated by the problems caused by the introductions of opossum shrimp into lakes throughout the intermountain West. It was presumed that this small shrimp would function elsewhere as it does in Kootenay Lake, British Columbia, Canada, where it subsists largely on phytoplankton and detritus. Instead, in new environments, the opossum shrimp has proven to preferentially feed on zooplankton. As a result, it has eliminated large zooplankton species that were often important foods for the very game fishes whose populations they were supposed to enhance (Lasenby et al. 1986; Nesler and Bergersen 1991).

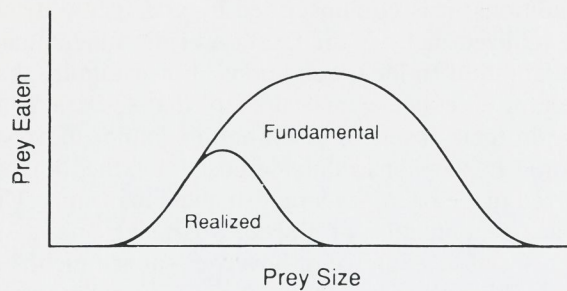
The niche of a species can change not only with its environment but also through ontogeny. Most fishes feed on quite different and smaller prey while young and switch to larger prey as they mature. These shifts in diets are often accompanied by shifts in habitat use. Most introductions are made without regard to the distinct niches of the early life history stages of the fishes in question, despite the fact that interspecific interactions for species change with life stage (Werner 1986). For example, introduced forage fishes can compete with juvenile piscivores for invertebrate prey or they can prey upon the young of their predators (Crowder 1980; Kohler and Ney 1980).

Niche expression may differ within a population because of individual differences. Specialization in feeding habits by individuals in populations of rainbow trout has been documented (Bryan and Larkin 1972). Nordeng (1983) found specialization in habitat use and degree of anadromy by individual Arctic char. If the number of genetically determined specialists within a population changes due to shifts in selection pressure, the fundamental niche of the population may change as well. Thus, intense selection pressure through periodic winter kills may select for cold-hardy strains of mosquitofish and swordtail, enabling these fishes to invade areas where they are not wanted. Similarly, rainbow trout in western Australia now live at higher temperatures than other stocks (Arthington and Mitchell 1986). In short, the niche of a species is flexible, its limits can be stretched genetically, and it can change rapidly through natural selection.

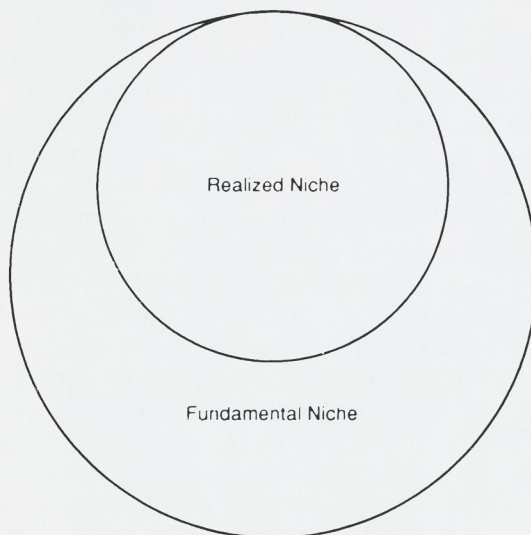
### 12.3.2 Limiting Similarity and Island Biogeography

As a new species invades an ecosystem, five types of outcomes are possible: (1) species addition with species extinction (species replacement), (2) species addition without niche compression of similar species, (3) species addition with niche compression, (4) multiple species extinctions because of alterations of food webs or the environment, and (5) failure of the invading species to become established. These are predictions based upon the theory of limiting similarity (MacArthur and Levins 1967) and the theory of island biogeography (MacArthur and Wilson 1967).

## A. Bivariate Niche Dimensions



## B. Multivariate Niche Dimensions



**Figure 12.1** The concepts of the fundamental and realized niches (Hutchinson 1958) displayed as a single-niche axis (A) and in multiple-niche dimensions (B). Note that the realized niche in (A) may be limited by several factors such as predator size distribution, size distribution of available prey, and available prey species.

The theory of limiting similarity undergirds the theory of island biogeography. It is also known as the species packing hypothesis: as the number of species in an assemblage increases, greater partitioning of resources occurs, resulting in niche compression. At some level resources cannot be partitioned further because there is a limit to the degree of niche similarity among species.

The theory of island biogeography applies not only to actual islands, but to isolated patches of habitats as well. Freshwater habitats are typically islands of water surrounded by a sea of land. The number of species supported by an "island" is a function of accessibility to colonists, as well as patch size and habitat diversity. These two factors affect immigration and extinction rates, thus limiting the number of species that an island can support. One prediction from this is that if repeated introductions are made into an aquatic system, extinction rates will be



high and the fish community will become unstable and difficult to manage (Magnuson 1976).

The logical extension of these two theories is that a species-rich fauna will be more resistant to invasion than one that is species poor (Diamond and Case 1986), but this generality is far from universal. For instance, some depauperate native fish communities in undisturbed California streams have repeatedly resisted invasions by introduced species (Baltz and Moyle 1993), whereas the extraordinarily rich fish fauna of Lake Victoria, Africa, has been devastated by a single introduction (see 12.3.5). The reasons that the two theories have limited reliability is that they presume steady state conditions and assume that competition among species is the most important factor structuring communities. These theories also do not take into account that moderately disturbed environments often have the highest diversity of species because random environmental fluctuations prevent the most efficient competitors from becoming dominant. Thus, mixed assemblages of native and introduced species are more likely to coexist where there are intermediate levels of disturbance. Highly disturbed environments are most likely to contain only a few tolerant species, typically human symbionts like common carp, goldfish, fathead minnow, and mosquitofish.

### 12.3.3 Competition

Competition occurs when two organisms require the same resource that is in limited supply. Competition is frequently cited as a major reason why introduced fishes replace native fishes, but most of the evidence is anecdotal or inferential and does not demonstrate conclusively that there is some limiting resource (Fausch 1988; Ross 1991). The most dramatic examples occur among territorial salmonids, where aggressive behavior leads to the dominance of one species over another (interference competition). For instance, Fausch and White (1986) found that introduced adult brown trout displaced native adult brook trout from the best habitats, making the brook trout more vulnerable to fishing and other forms of predation.

Exploitation competition has not been as well documented as interference competition because it is not conspicuous. However, it may be extremely common. It occurs when one species uses resources more quickly and more efficiently than the other. Thus, the redbreast shiner largely replaced juvenile rainbow trout in the littoral zone of a Canadian lake because they more efficiently exploited invertebrates associated with beds of aquatic macrophytes (Johannes and Larkin 1961). Declines in kokanee in lakes of western North America have been caused by the near elimination of large zooplankton species by introduced opossum shrimp (Lasenby et al. 1986), whereas declines and extinctions of whitefish in the Great Lakes have been at least partially caused by the removal of large zooplankton species by introduced alewife (Crowder and Binkowski 1983). Less characteristically, introduced creek chub forced brook trout in Quebec Lakes to switch from feeding on benthos to feeding on zooplankton, apparently causing reduced growth rates (Mangan and Fitzgerald 1984).

### 12.3.4 Parasite-Host Interactions

Introduced species can be sources of introduced diseases that severely deplete native populations. The transfer of these organisms worldwide during the 20th

Century has been without precedent (Ganzhorn et al. 1992). The European crayfish *Asticus* spp. was virtually eliminated from northern Europe by a disease brought in with signal crayfish *Pacifastacus leniusculus* from North America. Ironically, the demand this created for imported crayfish in Scandinavian countries caused the development of fisheries for crayfish in California. In the former Soviet Union, attempts to introduce a new species of sturgeon into the Caspian Sea failed, but did succeed in introducing a sturgeon parasite that devastated the populations of native sturgeons.

A more subtle effect of parasites is their "use" by an immune host as a weapon against a competitor by introducing an energy drain and a source of additional mortality. Coexistence between native and introduced species may depend on relative degrees of immunity from reciprocal parasites. Thus, whitefish are restricted to benthic prey in the presence of cisco, and they are further disadvantaged because of their increased susceptibility to parasites hosted by benthic invertebrates (Holmes 1979). One of the causes of the decline of the woundfin, an endangered species in Utah, is heavy infestations by an Asiatic tapeworm. This tapeworm accompanied the introduced red shiner, which seems to be replacing the woundfin in part because it is more resistant to the tapeworm. The red shiner, in turn, picked up the tapeworm in its own native range from introduced grass carp (Deacon 1988).

#### 12.3.5 Predator-Prey Interactions

Predation is a powerful evolutionary force and there are many studies that demonstrate that top carnivores can determine not only the kinds and numbers of potential prey species but also the kinds and numbers of species at lower trophic levels. However, the most dramatic effects are often on their prey species, and the introduction of a predator into a system containing prey species not evolved to counter its particular style of predation can lead to dramatic changes in the numbers and diversity of the prey assemblage (Zaret and Paine 1973; Li et al. 1987; Arthington 1991; Holcik 1991). There are many examples of how introduced predators have altered biotic communities of inland waters of North America, but in this section we will focus on the introduction of Nile perch into Lake Victoria in East Africa. We do this because it has been the most devastating introduction in modern times and because the introduction was based in part on the advice of western fisheries biologists.

The absence of large piscivorous fishes from most African rift lakes is at least partially responsible for their incredibly high species richness, mostly in small cichlids. These cichlids, with more than 300 species in Lake Victoria alone, are one of the world's marvels of natural history and evolution. In the 1950s, the introduction of the large, predatory Nile perch into Lake Victoria was proposed because (from a western perspective) the abundant, but small, cichlids did not provide an adequate fishery for the native peoples; they were eaten locally but were not considered suitable for export. Gee (1965) considered the introduction desirable because it would "control" the haplochromine cichlids and convert them to more useful, larger fish. While the debate on whether or not to introduce the Nile perch was occurring, it mysteriously appeared in the lake, justifying further introductions. Until about 1975, the Nile perch populations remained small. Suddenly, the populations exploded and in the process extirpated most of

the cichlids and 40 species of noncichlids (Hughes 1986). Today, three species dominate the fish fauna: Nile perch, an introduced cichlid, and a native zooplanktivore. The prey of the Nile perch has shifted from small cichlids to shrimp and its own young (Hughes 1986).

Initially, Nile perch did not find favor with the local peoples because they were too large to preserve by traditional methods of sun drying and difficult to catch by traditional methods. However, people soon adjusted their gear to catch the Nile perch and learned to process them for oil, which they used for cooking the fish. The fishery has greatly expanded and some of the Nile perch are now exported. However, one consequence of the new processing methods is an increased demand for charcoal, which is needed to render the fish oil. This is causing local woodlands to be cut, with unknown effects on the terrestrial biota. Because of the apparent success of the fishery, however, Nile perch may be planted in other rift lakes with similar devastating effects on local ecosystems.

The saga of the Nile perch is similar to what happened in the Laurentian Great Lakes following the invasion of the sea lamprey: drastic declines of fishes not adapted to lamprey predation. It is likely that the large native fishes would have disappeared from the Great Lakes altogether if a massive program of lamprey control had not been initiated and sustained at considerable cost. Predators need not be large in size, like Nile perch or sea lamprey, to have a major impact; predation on eggs and larvae of native fishes by introduced zooplanktivores can also cause major population declines (Crowder 1980; Kohler and Ney 1980).

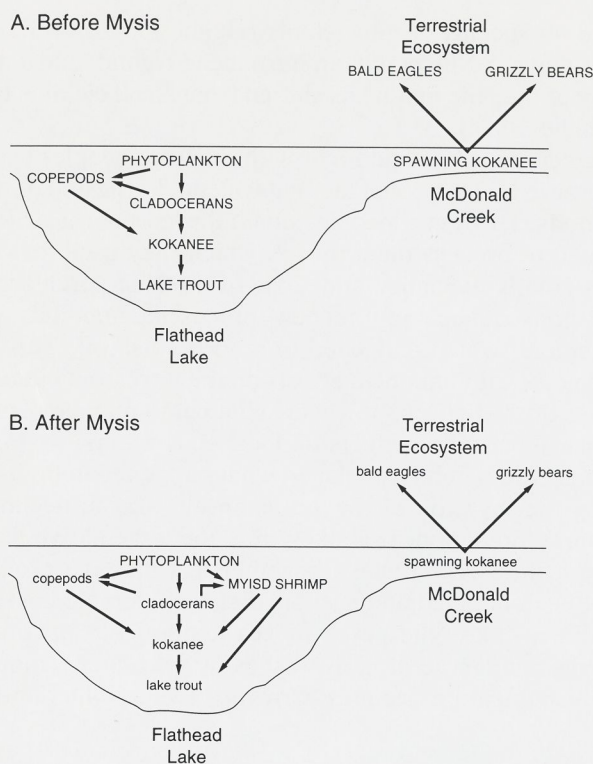
#### 12.3.6 Complex and Indirect Effects

More often than not, the effects of introductions are more complicated than previously described. The effects may be noticeable only as a gradual, indirect, restructuring of the recipient biotic community (Ross 1991). Two interrelated types of effects are most common: habitat modification and cascading trophic interactions.

The success of the common carp is at least partly the result of its ability to modify the shallow-water habitats it favors. It roots up the bottom and aquatic macrophytes, making ponds and shallow lakes more turbid. This decreases the abundance of visual feeding predators and competitors. Similarly, declines of sport fisheries have been associated with the invasion of the rusty crayfish *Orconectes rusticus* in lakes, where it eliminates aquatic plant beds used for cover by juvenile fishes and as a source of invertebrates for larger fishes (Lodge et al. 1985).

Some introductions are made because the species can alter habitats. The best example of this is the grass carp, which can eliminate large beds of troublesome aquatic macrophytes. A study by Rowe (1984) on a New Zealand lake revealed some of the possible indirect effects of macrophyte removal. After the introduction of grass carp, the following sequence of events occurred: (1) removal of macrophytes; (2) increase in phytoplankton production; (3) increase in zooplankton production causing an increase in growth rates of rainbow trout; (4) increase in predation on trout by cormorants because of lack of cover for the fish; and (5) shifts in feeding habits, relative density, and growth rates of other resident fishes.

When a top predator is introduced into a lake and severely reduces the populations of dominant planktivorous fishes, the effect cascades down the food



**Figure 12.2** Effects of mysid introductions to the Flathead Lake trophic network. Arrows denote the direction of prey consumption. The lowercase lettering in (B) denotes the diminution of affected populations. (Modified from Spencer et al. 1991.)

chain, resulting in alterations of zooplankton and phytoplankton abundances and species. This in turn affects the abundances of other fishes, including benthic species. Such effects have been called cascading trophic interactions (Carpenter et al. 1985). Thus, Scavia et al. (1986) suggest that the introduction of predators, coupled with some climatic changes, have drastically altered the trophic structure of Lake Michigan. The likelihood that an introduced species would produce such cascading effects seems to be related to ecosystem productivity (Li and Moyle 1981). All other things being equal, more eutrophic environments can support more species and be less susceptible to disruption by introductions. For example, large cladocerans (zooplankton) and introduced opossum shrimp coexist in mesotrophic lakes but not in oligotrophic lakes (Lasenby et al. 1986).

Occasionally, the effects of an introduction can cascade into terrestrial systems. For example, introduction of opossum shrimp into Flathead Lake, Montana, ultimately caused increases in mortality of bald eagles *Haliaeetus leucocephalus* (Spencer et al. 1991). The shrimp competed with kokanee for zooplankton resulting in fewer salmon carcasses available for eagles and grizzly bears *Ursus arctos* to scavenge upon in spawning streams (Figure 12.2). Eagles then shifted their foraging efforts to scavenging road-killed animals, with unfortunate consequences to both motorists and birds (J. A. Stanford, University of Montana, personal communication).

### 12.3.7 Hybridization

Introduced fishes commonly hybridize with closely related native species, usually to the detriment of the native species. For example, this has resulted in elimination of cutthroat trout by rainbow trout in much of the Great Basin. In recent years, an even bigger problem than hybridization between species has been hybridization between genetically distinct stocks of the same species. For example, indiscriminate introductions of Florida strain largemouth bass and northern strain largemouth bass may result in a loss of fitness of both strains in their native ranges (Philipp 1991). The same concern is shared by salmonid biologists on the Pacific Coast. Various genetic stocks may be highly adapted to local conditions so the interbreeding with other strains, especially hatchery strays, may reduce their ability to respond to fluctuations in environmental conditions (Utter 1981; Meffe 1992).

### 12.3.8 Evolutionary Overview

Ultimately, the degree to which alien organisms affect indigenous communities is dependent upon the evolutionary pedigree of the donor community in relation to that of the recipient community. The evolutionary trajectory of each community will determine the degree of preadaptation of the alien organism to its new surroundings and that of the recipient community to the newcomer. For instance, adaptability to hydrologic conditions can affect interactions among native and alien fishes and determine whether or not alien species will become established in a new environment. Coexistence of the Sonoran topminnow with introduced mosquitofish in the desert streams of Arizona is predicated upon periodic flash floods (Meffe 1984). The topminnow has evolved behaviors to cope with sudden increases in discharge, but the alien mosquitofish has not. In the absence of periodic flash flooding, predation by mosquitofish would extirpate the Sonoran topminnow within a few years. Similarly, the fish community of a small mountain stream seems to shift between two equilibria, one dominated by native fishes and one dominated by introduced brown trout, with the dominant species determined by the recent hydrological history of the stream (Strange et al. 1992). It would be mistaken to assume that interbasin transfers are safer introductions than exotic species from another country. Brown and Moyle (1991) suggested that the interbasin transfer of squawfish may result in the elimination of at least one native species in the Eel River of California. In short, evolutionary mismatches cause most of the disastrous losses of biodiversity cited throughout this chapter. Such disasters can be avoided in the future only if introductions are evaluated in both an ecological and evolutionary context.

## 12.4 ALTERNATIVES TO INTRODUCTIONS

To paraphrase Aldo Leopold (1938), introductions can serve as the perfect alibi for postponing the practice of fisheries management. Although most fishes are introduced with the best of intentions and may live up to the manager's expectations at the local level, at least for short periods of time, unexpected negative effects of introductions often outweigh the positive effects. This phenomenon was called the "Frankenstein effect" by Moyle et al. (1986) after the central figure of Mary Shelley's 1818 novel. Dr. Frankenstein thought he was

creating an improved version of man, but instead created a monster. There are many examples of the Frankenstein effect in North America, including many not mentioned previously: common carp have reduced the ability of waterfowl refuges to support ducks by eliminating aquatic macrophytes the ducks feed upon; introduced catfishes and cyprinids prey on the eggs of endangered fishes in the Colorado River, negating most efforts to restore the natives; introduced trout eliminate frogs from mountain regions.

Because the side effects of an introduction are difficult to predict, it is prudent to first consider alternative management strategies when an introduction is suggested as a solution to a management problem. Such strategies include (1) use of native fishes, (2) better water management, (3) habitat protection, and (4) use of sterile fishes.

#### **12.4.1 Use of Native Fishes**

Often a fish species is introduced simply because a fisheries manager is familiar with it. Native fishes may be underused because of ignorance. Often native species are superior to introduced species for aquatic pest control and for forage species because they are better adapted to local conditions. Ahmed et al. (1988) provided a system for rating the suitability of native fishes for aquatic pest control that could be modified for other purposes. Intensive investigation of native species should be conducted to see if they fit the management need before any introduction is made. For example, cisco and lake trout form a coadapted predator-prey complex in many of the Canadian boreal lakes. Therefore, cisco introductions to lakes with lake trout have long-lasting positive benefits, enhancing the production of lake trout (Matuszek et al. 1990).

For improving fisheries, there are many situations where increased fishing opportunities can be provided simply by educating the public about the value of underused species such as large cyprinids and suckers. Often these fishes already support small fisheries by people who know how to catch and prepare them. Expanding such fisheries can be accomplished by educating anglers on angling techniques and new ways of preparing the fish to eat. For example, suckers are highly acceptable to North American palates if smoked or pickled.

#### **12.4.2 Better Water Management**

Increasingly, North American waters are dammed, diverted, polluted, or otherwise made less suitable for fishes, especially high-value species like trout and salmon. Fisheries managers are given responsibility for managing the fish populations in such altered waters and are often blamed if the fishing is poor. Introductions of tolerant species or of hatchery-reared fish are then made as a way of providing better fishing because reversing environmental degradation is so difficult. Yet introductions into such altered waters are often undesirable because, while they may temporarily provide better fishing, they may also prevent the public from realizing the seriousness of the water quality and water management problems. For example, the unique fishes of the Colorado River survived the environmental changes of numerous impoundments, but introduction of predatory fishes may have guaranteed their extinction or at least made them forever

dependent on artificial propagation (Minckley 1991). If possible, attention should be focussed on the environmental causes of lost fisheries and the blame for poor fishing should be shifted onto the shoulders of water managers and polluters. They in turn should have the responsibility for providing the conditions necessary to support resident sport fishes. It is likely that such improvements would benefit not only fisheries, but also entire communities of aquatic organisms of which the "important" species are part.

A good example of the need for better water management is found in most reservoirs, which are often built using fisheries values as a partial justification. Reservoir water levels and outflows are rarely managed specifically for fish, even for short periods of time. For example, stabilizing water levels during the spawning period of centrarchids can greatly enhance their populations; releases from reservoirs to enhance streamflows can improve survival of migrating salmonids.

#### **12.4.3 Habitat Protection**

It is axiomatic that native fishes and most high-value sport fishes thrive in undisturbed habitats or in habitats that most closely resemble those in which they evolved. Habitat protection and, if necessary, restoration should therefore be cornerstones of fisheries management. These measures are often slow to produce results and are difficult to accomplish; however, they can result in more predictable and more manageable fisheries resources than are likely to occur through repeated introductions of new species.

Habitat is the template for community structure because control by geomorphic, climatic, energetic, and hydrologic factors set boundary conditions for community interactions (Steedman and Regier 1987). As such, its role should be carefully examined before introductions are made. The near extinction of lake whitefish after the introduction of walleye in Canadian lakes occurred because the role of habitat was not well understood. Mistakes such as this can be avoided in the future because the faunal composition can now be predicted from area, mean depth, water transparency, and nutrient availability; certain lakes are best suited for northern pike, others for lake trout (Marshall and Ryan 1987). The impact of rainbow smelt introductions was less severe in Lake Champlain than in other Laurentian Great Lakes because the lake's morphometry allowed for greater thermal, spatial, and temporal segregation of smelt from other fishes (Colby et al. 1987). A major reason that degraded habitat is more subject to invasions by exotics is that it is often less complex and diverse, and opportunities for ecological segregation are reduced (Evans et al. 1987).

#### **12.4.4 Use of Sterile Fishes**

There are many situations, mainly in highly disturbed or artificial habitats, where special management problems (mosquitos, weeds, heavy fishing pressure) make the introduction of fish the best management strategy. If at all possible, the fish planted in such situations should not be able to escape and populate habitats where they are not wanted. The best way to ensure this is to plant fish that cannot reproduce. The high demand for grass carp for weed control, coupled with the

widespread fear of the ecological damage they can cause, has led to the development of sterile, triploid stocks for planting in open waters. Another method that is being explored for grass carp, tilapia, and other fishes is to produce fish of only one sex (Shelton 1986). The biggest problem with planting fish incapable of reproduction is assuring that all fish are in fact sterile or of the same sex. This becomes increasingly difficult as sterile fish are mass-produced in hatcheries.

## 12.5 EVALUATING POTENTIAL INTRODUCTIONS

Despite the many problems created by introduced species, further introductions seem inevitable. For example, the newsletter of the Introduced Fish Section of the American Fisheries Society exists in part to inform its readers of new and proposed introductions in North America. Given the recent advances in ecological theory and our increased knowledge of the effects of introductions, no introduction today should be made without a detailed evaluation of its potential impact. Lasenby et al. (1986) pointed out that many of the problems created by opossum shrimp introductions would have been avoided if evaluation procedures such as those suggested by Li and Moyle (1981) had been followed. Kohler and Stanley (1984) provided a detailed protocol, including a review and decision model, for evaluating potential introductions.

The following guidelines need to be considered when an introduction is proposed.

1. No introductions should be made into the few aquatic systems left that show little evidence of human disturbance. Oligotrophic, nutrient-poor, or open marine systems should, in general, be considered to be poor sites for introductions.
2. Introductions should be considered mainly for systems that have been so altered by human activity that original fish communities have been disrupted or eliminated.
3. Introductions should be considered mainly for bodies of water that are sufficiently isolated so that uncontrolled spread of the introduced species is unlikely. Because most problem waters are not isolated, the best alternative is to evaluate potential effects of the introduction on all connected waters, no matter how distant. Nearby unconnected waters also have to be evaluated, as anglers are fond of moving fish around.
4. Any system being considered for an introduction should have its biota thoroughly inventoried and a list of species developed that might be sensitive to the introduction. Special consideration should be given to rare species or species ecologically most similar to the species proposed for introduction.
5. From the inventory, species should be categorized according to functional groups by habitat and trophic position. Food webs should be constructed using whatever information is available, and the potential effect of the introduction on trophic structure evaluated. This would essentially provide



an overview of the possible interactions among native and introduced species.

6. If major gaps of understanding emerge from the above exercise, then further research should be conducted on the system. Particularly recommended are experiments with the proposed introduction in isolated ponds or laboratory systems.
7. The potential of a proposed introduction for bringing new parasites or diseases into a recipient system should be thoroughly investigated. Ideally, a proposed species should be raised under quarantine conditions for several generations before being introduced.
8. The life history characteristics of the potential introduction should be thoroughly understood before the introduction is made. The ideal introduced species will be fairly specialized and have coevolved with many members of the assemblage to which it is being added. The broader the diet of the species, the more likely it will be to create unexpected problems. It should have low vagility in case it escapes from the original site of introduction so that its spread will be easier to control.
9. Each proposed introduction should be evaluated by an independent review panel of scientists familiar with ecological principles and aquatic systems. It is important not to be too hasty with an introduction, as most are irreversible.

## 12.6 CONCLUSIONS

The management of natural resources ultimately is based on value systems. Political, social, economic, and aesthetic values are powerful engines that drive management policies. Human values have permitted and even encouraged introductions as a management tool. This is likely to be the case for some time, but the indiscriminant methods of the past are no longer acceptable. The American Fisheries Society has adopted a position statement (Kohler and Courtenay 1986) that advises caution and restraint with respect to introduced species.

Ecological theory is well enough developed to say that introduced species will alter the communities into which they are introduced but not well enough developed to predict precisely what the changes will be in most cases. Therefore, extreme caution should be exercised in every proposed introduction to prevent irreversible damage to natural systems. The Frankenstein effect should always be kept in mind.

Fisheries managers also need to be cautious because values are changing, especially in the face of expanding human populations and declining natural habitats. Few fisheries managers in the 1950s or 1960s had any inkling of the present public concern for saving endangered species, for preserving natural diversity, for maintaining water quality, for protecting wild lakes and streams, or even for being able to angle for native fishes. Accordingly, we need to keep as many options open as possible for future fisheries managers; poorly considered introductions significantly reduce these options.

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## SOME ASPECTS OF AQUATIC PLANT ECOLOGY

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### Abstract

Nonplankton algae and aquatic angiosperms contain large amounts of macronutrient cations while phytoplankton samples are lower in these elements. Nitrogen and sulfur levels in phytoplankton usually exceed values for these nutrients in macrophytes. Substantial levels of micronutrients are found in most aquatic species.

Values for productivity rates and vegetative yields in pure stands of macrophytes often equal or exceed those for non-aquatic herbaceous vegetation. Quantities of minerals contained in standing crops of aquatic plants represent a large drain on available nutrient supplies in many lakes.

Ecological data indicate that distribution and growth of many macrophytic species are related to characteristics of the substratum. Rooted angiosperms have the necessary morphological and physiological adaptations for mineral absorption via the roots, but the role of hydrosol nutrients in sustaining plant growth needs critical experimental evaluation.

Apparent shortcomings in techniques of estimating aquatic fertility with bottom-soil and water chemical analyses are discussed.

### INTRODUCTION

MOST studies of primary production deal only with phytoplankton, and the role of nonplankton algae and aquatic angiosperms in production is largely ignored. In many reservoirs primary production by macrophytes is probably insignificant, but some reservoirs with large areas of shallow water contain macrophytes in abundance. The relation of macrophytes to overall productivity is either positive or negative (Hotchkiss, 1941; Wilson, 1939; Welch, 1952) depending upon primary use of the water, species of plants present, and relative abundance of macrophytic biomass. From the standpoint of fish production, most workers consider higher plants to be detrimental, but, with the exception of ponds, there is little reliable information on the correlation between macrophytes and fish production.

Recently much significance has been attached to the amount of carbon fixed by producer organisms (Odum, 1959). Although organic production is of great importance, the quantities of minerals, proteins, and other nutrients contained in plant biomass are equally basic to the nutriment of higher trophic levels. To a large extent these organic and inorganic nutrients determine the efficiency with which photosynthetically fixed carbon and energy will be utilized by other organisms. Therefore, a consideration of the chemical composition of the biomass should supplement primary productivity data. A knowledge of

the chemical content of plant material is also needed for a more complete understanding of freshwater biogeochemistry.

Rapid eutrophication of lakes and reservoirs because of increasing nutrient pollution is of concern. The exceedingly dense growths of aquatic plants (phytoplankton and/or macrophytes) often reach nuisance proportions, and control measures are sought. Such measures are frequently unsuccessful, and in the future management for desirable species will probably become a necessity. Before valid control or management procedures can be developed, a better understanding of the ecology of aquatic plants must be acquired.

This paper briefly summarizes the literature on the following aspects of aquatic plant autecology: 1) mineral composition of plants, 2) standing crop and productivity estimates for macrophytes, 3) relation of aquatic angiosperms to the substratum. The author hopes this discussion will stimulate plant ecological research in reservoirs and other aquatic ecosystems.

#### MINERAL COMPOSITION

Compared to economically important terrestrial plant species, relatively little is known about the mineral composition of water plants. Determinations of most essential inorganic plant nutrients have been made on several species of algae and angiosperm aquatics (Schuette and Hoffman, 1921; Schuette and Alder, 1927, 1929, 1929a; Misra, 1938; Nelson and Palmer, 1938; Allen and Pearsall, 1963; Anderson, *et al.*, 1965; Denton, 1966; Boyd and Lawrence, 1966).

In the research reviewed below, samples were obtained from essentially monospecific, natural populations. The material was oven dried (usually at 60 to 80°C), and chemical analyses were made by appropriate methods. Results were limited in that no information was obtained on either changes of composition with population age or influence of the environment on mineral content.

#### *Macronutrients*

Data for ash and macronutrients content for 20 aquatic plants were selected from the literature for illustrative purposes (Table 1). Analyses of other species are available. Mineral composition varies widely between species. Typical examples of intraspecific variation are illustrated in Table 2.

*Ash.* - Values for ash represent the inorganic content of plants. Considerable differences exist between the total mineral uptake of various groups of plants. Levels for chlorophycean and cyanophycean plankton are 4 to 8% (Birge and Juday, 1922; Phinney and Peek, 1961; Boyd and Lawrence, 1966). Diatoms are higher in ash; 7 genera ranged from 50 to 70% (Schuette, 1918; Nalewajko, 1966). Most non-plankton algae are 12 to 20% ash, but higher values are found for algae, such as *Chara* and *Pithophora* which precipitate marl on external surfaces (Table 1). Mayer and Gorham (1951) and Gorham (1953) reported ash results on a large number of angiosperms. Sub-

TABLE 1. Mean ash and macronutrient content (% dry weight) of some common aquatic plants

Species	n	Ash	N	P	S	Ca	Mg	K	Na
<i>Microcystis aeruginosa</i> <sup>1</sup>	4	6.20	8.08	0.68	0.27	0.53	0.17	0.79	0.04
<i>Aphanizomenon flos-aquae</i> <sup>1</sup>	3	7.21	8.57	1.17	1.18	0.73	0.21	0.68	0.19
<i>Spirogyra</i> spp. <sup>1</sup>	30	13.33	2.70	0.21	0.25	0.70	0.38	0.95	1.42
<i>Rhizoclonium</i> sp. <sup>1</sup>	14	17.16	3.16	0.34	0.27	0.60	0.19	2.37	0.08
<i>Chara</i> spp. <sup>1</sup>	59	43.41	2.46	0.25	0.55	9.03	0.92	2.35	0.13
<i>Nitella</i> sp. <sup>?</sup>	3	19.11	2.70	0.23	0.34	1.89	0.95	3.73	0.28
<i>Hydrodictyon reticulatum</i> <sup>1</sup>	5	17.94	3.87	0.23	1.41	0.69	0.17	4.21	0.38
<i>Pithophora</i> sp. <sup>1</sup>	38	27.77	2.57	0.30	1.42	3.82	0.20	3.06	0.07
<i>Mougeotia</i> sp. <sup>1</sup>	2	14.54	1.77	0.25	0.36	1.68	0.57	1.20	0.49
<i>Elodea canadensis</i> <sup>2</sup>	3	21.87	4.29	0.57	0.27	2.80	0.65	3.65	0.90
<i>Myriophyllum spicatum</i> <sup>2</sup>	3	13.83	4.14	0.42	0.43	2.77	0.74	1.87	0.75
<i>Vallisneria spiralis</i> <sup>2</sup>	3	15.64	2.42	0.21	0.38	1.55	0.76	6.77	2.39
<i>Potamogeton illinoensis</i> <sup>3</sup>	2	26.49	3.43	0.12	—	2.76	0.84	2.66	0.19
<i>Eichhornia crassipes</i> <sup>3</sup>	8	15.93	2.61	0.17	—	1.99	0.40	4.16	0.10
<i>Alternanthera philoxeroides</i> <sup>3</sup>	14	18.39	3.04	0.17	—	1.43	0.31	4.56	0.37
<i>Typha latifolia</i> <sup>3</sup>	2	9.70	1.59	0.18	—	1.48	0.12	2.24	0.55
<i>Lemna minor</i> <sup>3</sup>	1	18.71	2.55	0.63	—	0.70	0.51	5.20	0.30
<i>Paspalum fluitans</i> <sup>3</sup>	3	12.71	1.91	0.10	—	0.26	0.22	2.54	0.22
<i>Najas flexilis</i> <sup>4</sup>	1	19.16	1.86	0.30	0.48	6.11	0.97	1.82	0.78
<i>Phragmites communis</i> <sup>5</sup>	11	5.90	1.83	0.10	—	0.43	0.27	0.52	0.26

<sup>1</sup>Boyd and Lawrence (1966)<sup>2</sup>Nelson and Palmer (1938)<sup>3</sup>Denton (1966)<sup>4</sup>Schuette and Alder (1929)<sup>5</sup>Allen and Pearsall (1963)TABLE 2. Sample variation (n=32) for macronutrients in *Pithophora* as determined by Boyd (1966)

Analysis	% dry weight		
	Min.	Mean (+C.I.) <sup>1</sup>	Max.
Ash	14.04	27.77 ± 3.06	54.17
N	0.49	2.57 ± 0.31	5.19
P	0.14	0.30 ± 0.05	0.64
S	0.69	1.42 ± 0.13	2.34
Ca	0.67	3.82 ± 1.20	12.00
Mg	0.06	0.20 ± 0.02	0.45
K	0.98	3.06 ± 0.53	6.24
Na	0.03	0.07 ± 0.02	0.32

<sup>1</sup> ± 95% confidence interval.

merged species ranged from 15 to 30% with most values being around 20%. Submerged species with floating leaves usually contained less than 18% ash, whereas the emergent and marginal vegetation took up less mineral matter (2 to 10% ash).



*Nitrogen and phosphorus.*- Phytoplankton samples generally contain 5 to 10% nitrogen and 0.4 to 1.2% phosphorus (Birge and Juday, 1922; Gerloff and Skoog, 1954, 1957). Mean nitrogen values for nonplankton chlorophyceans range from 2 to 4%, but the cyanophycean, *Lyngbya*, contained 5% (Boyd and Lawrence, 1966). Phosphorus levels for these algae were between 0.1 and 0.6%. Many nitrogen and phosphorus analyses were made on vascular aquatics (Harper and Daniel, 1934; Gortner, 1934; Misra, 1938; Gorham, 1953; Gerloff and Krombholz, 1966); also see Table 1. In general, submerged plants contained 3 to 4% nitrogen, whereas emergent and marginal vegetation contained less than 2.5% nitrogen. Phosphorus levels for angiosperms ranged from 0.1 to 0.6%, but there was insufficient evidence to indicate quantitative distribution of this element in the various groups of plants.

*Sulfur.*- Little information is available for sulfur levels in angiosperms (Table 1). Sulfur determinations made by the author are given in Table 3. Compared to algae, most of these plants are relatively low in sulfur.

*Sodium and potassium.*- Although sodium is required by green plants in microquantities, it occurs as a macro component of many plants. The values in Table 1 are representative of sodium composition. Most species contain less than 0.5%, but some plants accumulate large amounts. Levels of potassium are usually below 1% in phytoplankton (Table 1). In macrophytes values range from 1 to 6%. The values for samples of a particular species are extremely variable (Denton, 1966; Boyd and Lawrence, 1966); however, potassium is frequently the most abundant cation.

*Calcium and magnesium.*- Phytoplankters are usually composed of less than 1% calcium and 0.3% magnesium (Boyd and Lawrence, 1966). Macrophytes normally range from 1 to 3% calcium and contain less than 0.7% magnesium (Table 1). However, the marl en-

TABLE 3. Sulfur content (% dry weight) of some aquatic angiosperms<sup>1</sup>

Species	n	Sulfur
<i>Alternanthera philoxeroides</i>	14	0.14
<i>Myriophyllum brasiliense</i>	9	0.14
<i>Potamogeton illinoensis</i>	5	0.20
<i>Myriophyllum spicatum</i>	3	0.19
<i>Justica americana</i>	3	0.13
<i>Paspalum fluitans</i>	3	0.35
<i>Eleocharis acicularis</i>	3	0.18
<i>Elodea canadensis</i>	2	0.14
<i>Ceratophyllum demersum</i>	2	0.18
<i>Cabomba caroliniana</i>	2	0.10
<i>Lumna minor</i>	1	0.30

<sup>1</sup>Analyses according to Bardsley and Lancaster (1960).

crustations frequently found on macrophytes increase the quantities of these elements. Nelson and Palmer (1938) reported samples of marl-encrusted *Potamogeton*, *Myriophyllum*, *Najas*, *Heteranthera*, and *Ceratophyllum* to be 4 to 14% calcium and around 1% magnesium. Wetzel (1960) made determinations of marl encrustations on a number of plants. The biomass of several submerged species was often more than 50% marl. The underwater portions of some emergent species precipitated marl to a lesser extent.

TABLE 4. Mean iron and manganese levels (ppm dry weight) in aquatic vegetation

Species	n	Fe	Mn
<i>Microcystis aeruginosa</i> <sup>1</sup>	12	382	68
<i>M. aeruginosa</i> <sup>2</sup>	4	2751	322
<i>Aphanizomenon flos-aquae</i> <sup>2</sup>	3	833	167
<i>Nitella</i> sp. <sup>2</sup>	3	2180	2388
<i>Chara</i> spp. <sup>2</sup>	59	2520	2926
<i>Spirogyra</i> spp. <sup>2</sup>	30	1552	1649
<i>Pithophora</i> sp. <sup>2</sup>	31	2836	929
<i>Hydrodictyon reticulatum</i> <sup>2</sup>	5	1313	1963
<i>Mougeotia</i> sp. <sup>2</sup>	2	1080	2300
<i>Elodea canadensis</i> <sup>3</sup>	1	1320	2440
<i>Potamogeton perfoliatus</i> <sup>3</sup>	1	550	480
<i>P. alpinus</i> <sup>3</sup>	1	3030	2880
<i>Myriophyllum spicatum</i> <sup>4</sup>	3	660	5130
<i>Vallisneria spiralis</i> <sup>4</sup>	3	450	390
<i>Eichhornia crassipes</i> <sup>5</sup>	8	250	3940
<i>Alternanthera philoxeroides</i> <sup>5</sup>	14	720	440
<i>Typha latifolia</i> <sup>5</sup>	2	170	2370
<i>Lemna minor</i> <sup>5</sup>	1	1690	750

<sup>1</sup>Gerloff and Skoog (1957a)

<sup>2</sup>Boyd and Lawrence (1966)

<sup>3</sup>Mayer and Gorham (1951)

<sup>4</sup>Nelson and Palmer (1938)

<sup>5</sup>Denton (1966)

#### Micronutrients

*Iron and manganese.*- Results for a number of plants are listed in Table 4. As illustrated by these values, both iron and manganese content is subject to considerable interspecific variation. Intraspecific differences among samples is also of considerable magnitude; the means for 31 *Pithophora* sp. samples were  $929 \pm 542$  ppm manganese and  $1552 \pm 421$  ppm iron. Even wider 95% confidence intervals were calculated for other species of macrophytes (Denton, 1966; Boyd and Lawrence, 1966). The ratio of iron to manganese in various plants was erratic (Table 4). Mayer and Gorham (1951) reported that emergent and marginal vegetation was lower in iron and manganese than submerged species, and that hydrophytes contain much higher levels of these two elements than the typical terrestrial flora.

*Zinc and copper.*-Analyses of algae (Boyd and Lawrence, 1966)

and angiosperms (Denton, 1966) revealed that zinc exceeded copper in quantity. Zinc levels were generally in the range from 80 to 200 ppm and copper seldom exceeded 75 ppm; however, sample to sample variation within a species was so great that averages were of little meaning. Algae did appear to accumulate more copper than vascular aquatics.

*Boron.*- *Lyngbya* and *Pithophora* concentrated large amounts of this nutrient (means of 112 and 65 ppm, respectively). Samples of other algae rarely contained more than 10 ppm boron (Boyd and Lawrence, 1966). The author made boron analyses on a few aquatic angiosperms (Table 5). The results indicated that these plants were relatively high in boron, particularly *Paspalum fluitans*.

*Other elements.*- A number of the studies reviewed above included analyses for one or more of the following minerals: chlorine, cobalt, molybdenum, silicon, aluminum, strontium, and barium. The data are too incomplete for generalization, but some species appear to accumulate substantial levels of these elements. Several other elements were qualitatively identified by emission spectrograph analyses of algae (Boyd, 1966). Some of the elements mentioned here were not essential to plant growth, but the uptake of nonessential ions by plants was common.

TABLE 5. Boron content (ppm dry weight) of some aquatic angiosperms<sup>1</sup>

Species	n	Boron
<i>Myriophyllum brasiliense</i>	6	23.5
<i>Alternanthera philoxeroides</i>	4	29.4
<i>Justicia americana</i>	3	12.1
<i>Paspalum fluitans</i>	3	69.0
<i>Myriophyllum spicatum</i>	1	30.0
<i>Potamogeton illinoensis</i>	1	21.2

<sup>1</sup>Analyses by the curcumin method (Jackson, 1958).

### Discussion

Where a sufficient number of analyses were made on a plant species, a fairly wide range of sample values was obtained for most elements. The levels of macroelements were generally more constant than microelement concentrations. Variations for a particular mineral were because of such factors as age of population, concentration of the mineral in the environment, interactions of other minerals with the uptake of the one in question, light intensity, debris attached to plant material, and errors in analytical procedures. In addition, certain species will selectively accumulate large quantities of one or more nutrients - for example, sulfur and boron by *Pithophora* and sodium by *Spirogyra*.

Phytoplankton species are very high in nitrogen and phosphorus, and with the exception of diatoms, low in ash when compared with macrophytes. Nonplankton algae and submerged and emergent angio-

sperms compare very favorably with terrestrial forage species (Morrison, 1949) in nitrogen (crude protein) and phosphorus, and are much higher in ash. Macrophytes are particularly good sources of trace elements. Submerged angiosperms are also much lower in fiber than land plants (Gortner, 1934; Nelson and Palmer, 1938). In view of this evidence and the large standing crops, the possibility exists for using submerged aquatics in preparation of animal feeds. Experimental evidence indicates that these plants are nutritionally suitable as a component of animal feeds (Mrsic, 1936; Nelson and Palmer, 1938; Bailey, 1965), but economically feasible harvesting and processing methods remain to be developed. The high moisture content (90 to 95%) is undesirable.

#### PRODUCTIVITY AND STANDING CROP ESTIMATES FOR MACROPHYTES

A large body of literature is available on primary production by phytoplankton, yet relatively few studies have dealt with macrophytes. A brief summary of most of the published works is presented here. All estimates are given as dry weights of plant biomass;  $\text{g. m}^{-2}$  for standing crop data and  $\text{g. m}^{-2} \cdot \text{day}^{-1}$  for rate of net productivity. Multiply by 8.7 for a close approximation of standing crop in pounds per acre. Some authors prefer to report productivity data as loss on ignition (organic matter) or as carbon values. Producer organisms not only fix carbon but accumulate minerals and synthesize protein and other compounds essential to higher trophic level nutrition; therefore it appears more reasonable to work with dry weight of biomass. In the following works, the standing crop was obtained by collecting all plants within random quadrants of known area. Productivity data were generally obtained by dividing the weight of biomass by the days required for its production.

Rickett (1922, 1924) made comprehensive quantitative vegetation surveys of Lake Mendota and Green Lake, Wisconsin. Average standing crops of macrophytes were  $202 \text{ g. m}^{-2}$  and  $178 \text{ g. m}^{-2}$ , respectively. Much smaller yields were reported for three northern Wisconsin lakes (Wilson, 1935, 1937). The Wisconsin results have been discussed at length by Welch (1952). If the samples are considered to be 10% dry matter, maximum standing crops of macrophytes during a 4-year period ranged from 30 to  $200 \text{ g. m}^{-2}$  in a Minnesota bog lake (Lindeman, 1941). The mean yield of vascular aquatics (data include only the five most abundant species) in 19 Illinois River Valley lakes (Low and Bellrose, 1944) was  $127 \text{ g. m}^{-2}$ . Natelson (see Penfound, 1956) gave standing crop estimates of 422, 434, and  $539 \text{ g. m}^{-2}$  in 3 spring-river systems in Florida. An average of  $621 \text{ g. m}^{-2}$  of rooted aquatics was obtained from Silver Springs, Florida (Odum, 1957). Primary production of macrophytes in four Michigan ponds was determined by Knight, *et al.* (1962) during the 1960 growing season as follows:

Pond	Standing crop (g. m <sup>-2</sup> )	Production rate (g.m <sup>-2</sup> . day <sup>-1</sup> )
A	118	1.45
B	265	3.27
C	229	2.83
D	486	6.00

Plant communities of different species composition at single selected sites of four English streams contained maximum standing crops of 320 to 385 g. m<sup>-2</sup> of macrophytes. Production ranged from 5.0 to 8.8 g. m<sup>-2</sup> . day<sup>-1</sup> (Owens and Edwards, 1962). Four additional sites along one of the streams yielded maximum values of 107 to 519 g. m<sup>-2</sup> and had production rates of 1.1 to 4.0 g. m<sup>-2</sup> . day<sup>-1</sup> (Edwards and Owens, 1960; Owens and Edwards, 1961).

Quantitative data on pure stands of several species are available (Table 6). As expected, yield estimates and production rates are greater in pure stands than in the vegetation of a lake taken as a whole. Very high standing crops for water hyacinth (*Eichhornia crassipes*) and cattail (*Typha*) communities have been reported. A medium sized 8-year-old mat of water hyacinth contained approximately 2500 g. m<sup>-2</sup> of plants, 1800 g. m<sup>-2</sup> of which were living (Penfound and Earle, 1948). Yields for *Typha* communities sampled during September

TABLE 6. Standing crop data (g . m<sup>-2</sup>) and production rates (g . m<sup>-2</sup> . day<sup>-1</sup>) for several species of macrophytes from pure stands

Species	Location	Standing Production		Source
		crop	rate	
<i>Nitella mucronata</i> <sup>1</sup>	Sweden	310	2.5	Forsburg (1959)
<i>Chara fragillist</i> <sub>1</sub>	-do-	1130	8.6	Forsburg (1960)
<i>Chara</i> sp. <sup>1</sup>	California	764	—	Wetzel (1964)
<i>Ceratophyllum demersum</i> <sup>1</sup>	Sweden	680	5.7	Forsburg (1960)
-do-	Illinois	325	—	Low and Bellrose (1944)
-do-	Florida	—	24.6	Odum (1957)
<i>Najas guadalupensis</i>	Illinois	108	—	Low and Bellrose (1944)
-do-	Florida	1950	17.9	Odum (1957)
<i>Eichhornia crassipes</i> <sup>1</sup>	Louisiana	1276	14.6	Penfound (1956)
-do-	Florida	—	10.3	Odum (1957)
<i>Pista</i> sp.	-do-	463	15.3	-do-
<i>Sagittaria lorata</i>	-do-	—	13.4	-do-
<i>Scirpus</i> sp.	-do-	1970	—	-do-
<i>Pontederia</i> sp.	-do-	980	—	-do-
<i>Myriophyllum verticillatum</i> <sup>1</sup>	Sweden	240	2.8	Forsburg (1959)
<i>Potamogeton pectinatus</i>	Illinois	222	—	Low and Bellrose (1944)
<i>P. americanus</i>	-do-	144	—	-do-
<i>Typha lotifolia</i> <sup>1</sup>	Oklahoma	1527	23.5	Penfound (1956)

<sup>1</sup>Maximum level for several estimates made at different dates. All other values represent individual or average determinations.

1963 (McNaughton, 1966) were as follows: Pembina, N. D., 1316; Watertown, S. D., 1250; Columbus, Neb., 972; Oklahoma City, Okla., 1534; Austin, Tex., 3982 g. m<sup>-2</sup>. McNaughton also extensively investigated the effect of several environmental factors on *Typha* production. A high primary production in *Typha* communities has also been reported by Pearsall and Gorham (1965), Bray, *et al.* (1959), and Bray (1960, 1962).

Vegetative yields in pure stands and the standing crop of macrophytes in aquatic ecosystems were somewhat higher in warm climates. Production in streams, springs, and lakes appeared to be roughly comparable. According to Penfound (1956), insufficient data are available to determine whether a lake, a tall grass prairie, or a deciduous forest is the most productive. Many of the yield estimates presented here fall within, or exceed the range 400 to 1400 g. m<sup>-2</sup> given by Pearsall and Gorham (1956) for crops of non-aquatic herbaceous vegetation types in Britain. In considering production rates, it should be emphasized that most of the values reported here are for the optimum growing season. When taken over the entire year, the values are considerably lower, for example 0.89 to 3.14 g. m<sup>-2</sup> . day<sup>-1</sup> for low and high altitude populations of *Typha* (McNaughton, 1966). Production is lowest in the winter, increases to a maximum in the spring, then tapers off during the summer and fall; however, maximum standing crops are often reached in the summer months.

Standing crop and production studies on some of the reservoirs in the southeastern United States are badly needed. Such investigations would undoubtedly reveal very high yield values. Production rates for nonplankton algae such as *Spirogyra*, *Hydrodictyon*, and *Rhizoclonium* would be of value for comparative purposes.

When the quantity of minerals contained in certain aquatic vegetation is estimated (Table 7), the tremendous drain on available nutrient supplies by macrophytes is obvious. For example, assuming an average depth of 5 ft., the *Chara* biomass has removed 18.22 ppm nitrogen and 1.85 ppm phosphorus from the water, and *Ceratophyllum* assimilated 11.07 and 0.89 ppm of nitrogen and phosphorus, respectively. Compared with typical water analysis values for these elements in reservoirs, the uptake represents a very large quantity of available nutrients. Removal of certain trace elements is probably of a comparatively greater magnitude. Competition of macrophytes with phytoplankton for minerals has been recognized (Lawrence, 1958; Moore, 1950, 1952).

#### RELATION OF ROOTED ANGIOSPERMS TO THE SUBSTRATUM

*Physiological considerations.*- Foliar absorption and subsequent translocation of mineral nutrients has been demonstrated in vascular aquatics (Lowenhaupt, 1956). Roots of the floating aquatic *Lemna minor* are probably of little importance in mineral uptake (Hillman,

TABLE 7. Amounts of mineral nutrients contained in the standing crop of three macrophytes (Forsburg, 1960). Mineral composition values for the plants (% dry weights) taken from various sources are in parentheses

Plant	lb. acre <sup>-1</sup> (dry wt.)	Mineral content of standing crop (lb. acre <sup>-1</sup> dry wt.)						
		Ash	N	P	S	Ca	Mg	K
<i>Chara</i> <sup>1</sup>	10,000	4341.0 (43.41)	246.0 (2.46)	25.0 (0.25)	55.p (0.55)	803.0 (8.03)	92.0 (0.92)	235.0 (2.35)
<i>Myriophyllum</i> <sup>1</sup>	2,000	276.0 (13.83)	82.8 (4.14)	8.4 (0.42)	8.6 (0.43)	45.4 (2.77)	14.8 (0.74)	37.4 (1.87)
<i>Ceratophyllum</i>	6,000	1335.6 (22.26) <sup>2</sup>	149.4 (2.49) <sup>2</sup>	12.0 (0.2) <sup>3</sup>	10.8 (0.18) <sup>4</sup>	156.0 (2.6) <sup>3</sup>	66.0 (1.1) <sup>3</sup>	—

<sup>1</sup>Chemical composition of *Chara* from Boyd and Lawrence (1966) and *Myriophyllum* from Nelson and Palmer (1938).

<sup>2</sup>Values from Gortner (1934).

<sup>3</sup>Data from Forsburg (1960).

<sup>4</sup>Refer to Table 2 for sulfur content.

1961), but information on other floating plants is not available. The function of roots of anchored angiosperms is not clear; for example, Brown (1913) considers the root system of these plants to be of no significance in ion uptake, but Muenscher (1959) indicates the roots to be of functional importance in mineral absorption.

Pond (1905), Snell (1908), and Riede (1921) found that the roots of several species of aquatics absorb nutrients from the substratum, but quantitative measurements of uptake were not made. The movement of minerals from roots to shoots depends upon the upward movement of water (Kramer, 1949). Vascular conduction of water in submerged and emergent hydrophytes has been verified (Hochreutiner, 1896; Thoday and Sykes, 1909; Wilson, 1947), and Thut (1932) measured the rate of conduction in several species. The literature on vascular conduction in submerged plants was discussed by Stocking (1956).

Mineral uptake is usually against a concentration gradient and dependent upon aerobic respiration (Hoagland, 1944; Lundegardth, 1955). Aquatic muds are generally very deficient in oxygen (Conway, 1940), but the evolution of a gas transport system has ensured adequate root aeration. A network of cavities and storage organs, aerenchyma tissue, communicates between roots, stems, and leaves, allowing oxygen to diffuse from leaves to roots and carbon dioxide to move upward from the roots. Photosynthetic oxygen is conserved in the aerenchyma, permitting submerged plants to maintain suitable internal oxygen levels in anaerobic water. Emergent species can exchange gases with the atmosphere. The gas transport system has been considered in detail (Conway, 1937, 1940; Liang, 1940, 1940a; Barber, 1961; Williams and Barber, 1961; Teal and Kamwisher, 1966).

*Ecological observations.*- Rooted angiosperms grow at a slower

rate when deprived of a substratum (Pond, 1905; Snell, 1908), but Brown (1913) claimed that growth differences in rooted and non-rooted *Elodea* were related to the former having a more adequate carbon dioxide supply and not a response to soil nutrients. Yields of *Najas flexilis*, *Potamogeton perfoliatus*, and *P. foliosus* rooted in soil were greater than yields of nonrooted individuals that were supplied with large amounts of carbon dioxide (Bourn, 1932).

The distribution and yield of several species of aquatic angiosperms have been related to such edaphic factors as soil particle size, organic matter content, and mineral levels (Pearsall, 1918, 1920, 1921, 1929; Misra, 1938; Moyle, 1945; Pearsall and Gorham, 1956; Gorham and Pearsall, 1956; Allen and Pearsall, 1963). A classification of aquatic soils based on relationships between soils and plants was proposed (Veatch, 1932) for Michigan lakes.

A correlation between mineral nutrient levels in bottom soils and the quantity of certain minerals contained in the aquatic vegetation was reported (Misra, 1938; Gorham, 1953). Pearsall and Pearsall (1923) and Pearsall and Hanby (1925) observed different growth characteristics for *Potamogeton perfoliatus* and *P. praelongus* growing on soils of different mineral composition.

*Discussion.*- Hydrophytes have the necessary physiological and morphological adaptations for mineral uptake through the roots, and experimental evidence indicates that the roots absorb nutrients. Edaphic factors influence growth and distribution of many species. The extent of dependency upon the substratum for mineral nutriment is unknown, and studies to determine the proportion of the total mineral uptake that occurs via the roots are needed. In view of existing information, it appears likely that the roots of aquatic plants play an important role in mineral uptake; however, this role probably varies greatly in magnitude between species and environmental conditions.

Except for the possibility of contact exchange of cations (Jenny, 1951) between roots and soil colloids, nutrients absorbed by plant roots are thought to be in aqueous solution (Meyer, *et al.*, 1960), but by root absorption the aquatic plant could obtain an ion from the aqueous phase of the mud without necessity of the ion diffusing or moving by turbulence to the overlying water for foliar absorption. In the littoral zone where rooted plants occur, the interfacial mud and overlying water are usually aerobic. The release of most solutes and particularly iron, manganese, and phosphorus is greatly facilitated by reducing conditions at the soil-water interface (Mortimer, 1941, 1942). Therefore, penetration of roots into anaerobic layers probably allows for the uptake of quantities of nutrients in excess of the amounts that would otherwise reach the water for foliar absorption. Upon death and decomposition of plant biomass, minerals are released into the water, which represent a contribution from the bottom soil.

Rank growths of rooted angiosperms are usually associated with



reservoirs having large areas of shallow water that receive good light penetration. These reservoirs generally have a relatively shallow mean depth and small volume of water, therefore containing proportionally less solutes than deeper lakes of similar chemical characteristics. The physical and chemical release of minerals is probably of comparatively greater magnitude in reservoirs with a small volume to soil ratio, but the importance of the soil nutrients supply in sustaining large plant biomasses should not be disregarded. Even if the root system of angiosperms is not functional in absorbing nutrients, the question of whether by assimilating minerals aquatic plants displace the equilibrium of nutrients between soil and water, thereby cropping the muds of minerals, needs answering. The data in Table 7 for the standing crop and minerals contained in the biomass of plants in a fairly static lake indicate that some reserve supply of nutrients is present in aquatic ecosystems that supplements the quantity of solutes dissolved at a particular time.

Water analyses are commonly used in assessing the fertility of reservoirs. In large deep oligotrophic reservoirs or in reservoirs with short retention periods, such analyses are probably indicative of the nutrient supply. In shallow eutrophic reservoirs, the store of soil minerals is probably of greater significance, and in addition a large quantity of nutrients are bound in biomass. Water analyses, therefore, are of limited value in estimating anything other than the supply of solutes at the instant of sampling. Soil samples are usually analyzed for the total amount of a particular nutrient, or extracted for analysis with solvents used in agricultural soil testing. Agricultural procedures ideally extract a fraction of nutrients which is correlated with plant response (Jackson, 1958). Nutrients extracted from muds by these procedures have no particular relation to aquatic plant growth. Just as in terrestrial species, aquatic plant growth is related to available nutrients and not to the total supply. Only when the proportion of aquatic soil nutrients available to plant growth is ascertained, and extraction procedures are calibrated against nutrient availability and plant response, can valid interpretations of bottom soil chemical analyses be made. At present, data from bottom soil samples should be evaluated with caution; however, the agricultural procedures are useful for comparisons within or between reservoirs provided a standardized technique is adhered to.

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[Species]  
No Date

23

An Aid for Recording Animal and Plant Species Relations to the  
NATIONAL WETLANDS INVENTORY AQUATIC HABITAT CLASSIFICATION SYSTEM

This aid was developed for recording species relations/associations to wetlands for inclusion in the USFWS Endangered Species Information System. Portions of the following material were taken from the USFWS National Wetlands Inventory "Information and Legend for Large Scale Draft Topical Wetland Overlays."

Use of Wetland Legend: Species are related to wetlands by a series of letters and numbers (alphanumerics) which indicate the wetland type. The first letter represents the wetland system (riverine, estuarine, etc.); the subsequent alphanumerics sequentially represent subordinate levels of detail down to the wetland subclass (vegetation type, bottom type, etc.).

Example: The wetland code "E2EM5" would be broken down in the following manner:

P

<u>E</u> -----	System:	Estuarine
<u>2</u> -----	Subsystem:	Intertidal
<u>EM</u> -----	Class:	Emergent
<u>5</u> ----	Subclass:	Narrow-leaved persistent

Therefore, in checking the code "E2EM5," you are indicating that the species is associated with intertidal estuaries with emergent, narrow-leaved, persistent vegetation.

Instructions: Though the wetland types are presented at different levels, please attempt to record all known (through literature or expert opinion) wetland associations at the subclass level. Note that this system is hierarchical and thus, only certain combinations of system-subsystem-class-subclass are valid (only valid combinations are presented in the workbook checklist). This hierarchy is presented on the last page of this aid.

If a species' association to a particular group of wetlands is known, but not to the subclass level of detail, you may step back up the hierarchy and check the "higher order" code. At these levels, the codes will have periods in them to indicate that the species is associated with that type of wetland, but the details of the association are unknown. For example, if the literature indicates that a species relates to estuarine, intertidal wetlands with emergent vegetation, but no reference can be found which describes the specific type of vegetation occurring in this habitat (persistent, nonpersistent, etc.), then the relationship to that level is considered "unknown" and the applicable code to check would be "E2EM." while the more detailed lower level codes would remain unchecked. Other examples of checking at higher levels (when the more detailed levels are unknown) would be "E2..." and "E....".

It is very important to distinguish between "unknown" and "all." If, in the above example, you believe the species to be associated with that wetland type regardless of whether the vegetation is persistent or nonpersistent, then you would check all the "E2EM" wetland types ("E2EM1"- "E2EM6") rather than the higher level. If at all possible, avoid checking the relations at higher levels, as this lessens the usefulness of the data field.

Wetland Legend: The following page contains a legend which can be used to translate the codes presented in the checklist. For definitions of the wetland types, consult "Classification of Wetlands and Deepwater Habitats of the United States," by L.M. Cowardin et al.

WETLAND LEGEND

     System  
     Subsystem

M Marine  
  1 Subtidal  
  2 Intertidal

P Palustrine  
  0 No Subsystem

R Riverine  
  1 Tidal  
  2 Lower Perennial  
  3 Upper Perennial  
  4 Intermittent

E Estuarine  
  1 Subtidal  
  2 Intertidal

L Lacustrine  
  1 Limnetic  
  2 Littoral

     Class  
     Subclass

AB Aquatic Bed  
  1 Submergent Algal  
  2 Submergent Vascular  
  3 Submergent Moss  
  4 Floating-Leaved (rooted)  
  5 Floating (not rooted)

OW Open Water  
  0 No Subclass

RB Rock Bottom  
  1 Bedrock  
  2 Boulder

BB Beach/Bar  
  1 Cobble/Gravel  
  2 Sand

RF Reef  
  1 Coral  
  2 Mollusc  
  3 Worm

EM Emergent  
  1 Persistent  
  2 Nonpersistent  
  3 Narrow-Leaved Nonpersistent  
  4 Broad-Leaved Nonpersistent  
  5 Narrow-Leaved Persistent  
  6 Broad-Leaved Persistent

RS Rocky Shore  
  1 Bedrock  
  2 Boulder  
  3 Vegetated Nonpioneer

FL Flat  
  1 Cobble/Gravel  
  2 Sand  
  3 Mud  
  4 Organic  
  5 Vegetated Pioneer  
  6 Vegetated Nonpioneer

SB Streambed  
  1 Cobble/Gravel  
  2 Sand  
  3 Mud  
  4 Organic

FO Forested  
  1 Broad-Leaved Deciduous  
  2 Needle-Leaved Deciduous  
  3 Broad-Leaved Evergreen  
  4 Needle-Leaved Evergreen  
  5 Dead  
  6 Deciduous  
  7 Evergreen

SS Scrub/Shrub  
  1 Broad-Leaved Deciduous  
  2 Needle-Leaved Deciduous  
  3 Broad-Leaved Evergreen  
  4 Needle-Leaved Evergreen  
  5 Dead  
  6 Deciduous  
  7 Evergreen

ML Moss/Lichen  
  1 Moss  
  2 Lichen

UB Unconsolidated Bottom  
  1 Cobble/Gravel  
  2 Sand  
  3 Mud  
  4 Organic



NATIONAL WETLANDS INVENTORY CODING HIERARCHY

(for coding species relations to wetland types.)

