Observations on Habitat Structure, Population Regulation, and Habitat Use with Respect to Evolutionarily Significant Units: A Landscape Perspective for Lotic Systems

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Abstract.—In this paper we attempt to synthesize a variety of developments in the fields of landscape and population ecology and apply these ideas to the physical and biological characteristics of lotic systems. First, most attempts to manage evolutionarily significant units (ESUs) are based on the notion that the physical characteristics of lotic habitats are stable. Yet, data from three permanent 100-m reaches in the Coweeta drainage of North Carolina indicated that these reaches possessed substantial annual variability with respect to both substratum composition and flow rates. In addition, substratum data demonstrated that these reaches were patchy environments, and that a landscape-based approach might facilitate the management of species in this system. Second, a simple landscape-driven difference equation model of population dynamics based on biological characteristics common to many fishes indicated that the critical habitat for population maintenance may not always be the area in which the species is most abundant. Finally, two tests for habitat selection by stream fishes indicated that more biologically realistic models (e.g., a landscape-based model that included prey abundance) and a model that included explicit tests for the mechanism of selection itself (e.g., energy gain) may greatly increase our ability to identify and manage habitats that are crucial for survival of ESUs.

At present we are at a crossroads with respect to preservation of the earth’s genetic resources. Increasing population growth combined with questionable economic and management practices have driven us to a point at which the loss of biological diversity is occurring at an exponential rate, a rate previously unknown in modern times. Such losses dramatically increase our need for innovative management strategies for the conservation of evolutionarily significant units (ESUs). (We will use the term ESUs to refer to species, subspecies, or populations with extremely low abundances.) In this paper, we will attempt to synthesize a variety of developments in the fields of landscape and population ecology (Johnston and Naiman 1987; Pringle et al. 1988; Schlosser 1991) and apply these ideas to the physical environment of lotic systems, as well as to both population dynamics and habitat selection by lotic animals. We focus our observations on the speciose stream fish assemblages of the eastern and midwestern United States, rather than on the depauperate western fauna.

Within the last decade, ecologists have recognized that most habitats are embedded within a larger landscape that may influence many of the ecological processes occurring in discrete habitat patches (Forman and Godron 1986; Pringle et al. 1988). For example, research on energy transformations in eastern woodland streams has shown that these systems depend upon the surrounding deciduous forest for most of their organic energy inputs (Minshall 1967). Studies of anthropogenic disturbances such as logging also demonstrate that activities occurring in habitats far from the streambank can have substantial deleterious effects on both fish and invertebrate populations in lotic systems (Morgan 1975; Salo and Cundy 1987). Consequently, our understanding of rivers and streams from both a basic and applied perspective may be enhanced by the application of a landscape perspective to studies of these systems.

The field of landscape ecology is relatively recent; a text book on the subject was published in 1986 (Forman and Godron 1986) and the specialized journal Landscape Ecology began in 1987. Many of the conceptual underpinnings of this subdiscipline apparently have arisen from two disparate sources.
First, the general view that habitat types (i.e., woodlands, old fields) must be considered as part of a larger, interconnected landscape is an outgrowth of one of the canons of ecosystem ecology; one can not identify the true functional importance of subcomponents of ecological systems (i.e., patches of woodland, stream riffles) in isolation because everything is interconnected (Odum 1989). This approach highlights the problems inherent in the application of a strictly reductionistic approach to studies of ecological systems. The difference between landscape ecology and ecosystem ecology is that landscape ecology explicitly incorporates and focuses on the spatial components of ecological processes.

The second contribution to landscape ecology originates from studies of theoretical population genetics (Levins 1962, 1968). In these studies, populations or individuals were viewed as inhabiting a patchy landscape, each patch type having different fitness consequences for individuals. For example, individuals inhabiting patch A might have abundant food whereas those occupying patch B might encounter low food availability. All else being equal, the fitness of individuals in patch A would be substantially higher than those in patch B. The aggregate properties of the population are then obtained by summing the results for individuals in each patch type, and the fitness values for individuals are determined by the patches that they utilize. This perspective has been widely used in both theoretical population genetics and behavioral ecology to address the fitness consequences of life in a heterogeneous environment.

We will attempt to meld these two approaches in addressing three questions. First, can reaches in a North Carolina drainage be characterized as patchy environments with respect to their physical characteristics, and is this patchiness temporally stable? Second, can a fine-scale landscape approach increase our understanding of the population dynamics of ESUs and aid in the identification of habitats critical for the preservation of these units? Third, can mechanistic models of habitat selection aid us in identifying the critical factors affecting habitat use in lotic fishes?

Physical Environment of Lotic Systems

Traditionally, fisheries managers have viewed lotic environments as stable habitats comprising regularly ordered sequences of pools, runs, and riffles. However, since the work of Starrett (1951), it has become apparent that the physical environment of many streams is not particularly stable, especially with respect to flows (i.e., floods and droughts; Poff and Ward 1989, 1990). Temporal and spatial variability in flow may influence many other physical attributes of stream reaches including temperature, substratum composition, and import and export of substrata. Many streams experience both floods and droughts with a frequency that is sufficient to affect individual fitness and population size as well as assemblage composition (Grossman et al. 1982, 1990; Schlosser 1985; Poff and Ward 1989, 1990).

What are the consequences of environmental variability for ESUs? First, ESUs are typically rare or have restricted distributions. It is possible that the persistence of ESUs in lotic systems over both ecological and evolutionary time is facilitated by environmental variability. This hypothesis, the basics of which were suggested by Andrewartha and Birch (1954) and further developed as the intermediate disturbance hypothesis of Connell (1978), is that moderate levels of environmental variability prevent species that are superior competitors from ever gaining sufficient advantage over inferior competitors to cause their extirpation. If this coexistence mechanism is operating in systems where ESUs are present, their survival may depend upon the maintenance of both temporal and spatial environmental variability (Grossman et al. 1982, 1990). This would call for the use of different management strategies by fisheries managers, such as plans that include preservation of the variances of the physical characteristics of reaches as well as average values.

Regardless of whether or not survival of ESUs is linked to environmental variation, an ability to quantify the habitat requirements of ESUs is essential for their successful management. Traditionally, fisheries managers studying lotic habitats focused their efforts on stream reaches. By a reach, we mean a given physiognomic unit of a stream (i.e., a pool, a riffle, a run) or a larger sequence of these units (e.g., a 100-m section of stream containing several habitat units). These physiognomic units are assumed to be relatively homogenous or, to paraphrase Shakespeare, a riffle by any other name would still flow as swift. Nonetheless, it is unclear whether this assumption is warranted, for relatively few studies have examined variation of physical characteristics (i.e., depth, velocity, substratum) within reaches themselves. For example, if riffles are relatively homogeneous, then a small number of random physical measurements may be sufficient to describe the physical habitat occupied by an ESU. However, if riffles are patchy habitats, then a much more intensive sampling program will be required to quantify an ESU’s habitat. If units are patchy, the use of a landscape approach, with its focus on
patchiness, might improve our understanding of these reaches. From a management perspective, fine-scale environmental variation of this type may be particularly important to small benthic fishes such as darters (Percidae), sculpins (Cottidae), madtoms (Ictaluridae), and some minnows (Cyprinidae) that may depend upon small patches of substratum for both foraging and reproduction (Page 1983; Moyle and Cech 1988). To test the assumption that the physical characteristics of stream reaches are stable, we made repeated physical measurements on permanent quadrats in three reaches of a southern Appalachian trout stream.

The Coweeta Creek drainage comprises a series of first- to fifth-order streams located on the U.S. Forest Service's Coweeta Hydrologic Station, Otto, North Carolina. The streams in this drainage are typical of many lotic habitats in the southern Appalachian Mountains. Our research team selected three 100-m reaches along a longitudinal gradient ranging from second to fifth order. Specifically, the study sites were located in a second-order (Upper Ball Creek, henceforth UBC), a fourth-order (Lower Ball Creek, LBC), and a fifth-order stream (Coweeta Creek, CC). In autumn 1991, we started at the lower end of each site and placed permanent benchmarks at 5-m intervals along both banks of each site. We then stretched a tape measure between benchmarks at the same position on opposite banks and located a series of permanent quadrats along this transect at intervals ranging from 0.5 to 1 m. We recorded the wetted width of each transect and obtained the following data from each quadrat: water depth, average velocity (at 0.6 x depth from the surface; Bovee and Milhous 1978), and a visual estimate of the percent composition of bedrock, boulder, cobble, gravel, sand, silt, and organic debris in a 20-cm x 20-cm area directly under the quadrat mark. Substrata were classified on the basis of maximum diameter according to a modified Wentworth particle scale (Grossman and Freeman 1987). We have used similar techniques to quantify habitat availability in a variety of other studies (Grossman and Freeman 1987; Grossman et al. 1987; Grossman and Boule 1991; Grossman et al. 1995). We measured quadrats in autumn 1991, 1992, and 1993, and in spring 1993. Linear measurements were made with a straight edge or tape measure and velocity was measured with an electronic velocity meter.

Our first goal was to characterize the heterogeneity (patchiness) present within these reaches. For this analysis we have focused on the substratum due to its presumed importance to many species of benthic fishes. To assess whether a reach was spatially homogeneous or patchy, we first characterized a quadrat by its substratum. A quadrat was considered to be a member of a given substratum class if this class made up more than 50% of the total substratum. Substratum classes were: bedrock, boulder, cobble-gravel, sand-silt, and debris. An additional class, heterogeneous, was used for quadrats that were not dominated by the aforementioned classes. We then plotted these results on a graphical representation of the stream reach.

Besides determining whether or not these reaches were patchy, we also wanted to quantify the stability of these patches. Consequently, we compared the dominant substratum class of quadrats across all four sampling periods. We recorded the number of times the dominant substratum class of a quadrat changed between samples (maximum, three). In addition, if a quadrat went from submerged to exposed or vice versa, it was considered to have changed its dominant substratum class. We included these changes because if managers attempted to quantify the habitat requirements of an ESU in these reaches, their measurements would be affected by such shifts. In addition, we assessed variability in water flow by examining mean daily flow records from a gaging weir on an adjacent fourth-order stream (Swift and Cunningham 1986).

Our results demonstrate that stream reaches within the Coweeta drainage were, indeed, patchy environments (Figure 1). All five dominant substratum classes were present in the three reaches, often intermingled. The second-order reach (UBC) exhibited the greatest heterogeneity, whereas fourth- (LBC) and fifth- (CC) order reaches were considerably less heterogeneous and dominated by cobble-gravel riffles. Although we have presented data for only one season for each reach, similar substratum patchiness occurred in other seasons.

Each reach possessed areas that remained relatively constant over time as well as areas in which considerable transport of substrata occurred (Figure 2). As with substratum patchiness, the second-order reach exhibited the greatest amount of change in quadrats; the fifth-order site was the most stable. These changes also were reflected in the mean percentage composition of substrata within reaches (i.e., they changed from year to year: G. Grossman et al., University of Georgia, unpublished data). Flow data also exhibited substantial variability. Figure 3 shows that during the first 10 years of our study (1983-1992), annualized mean daily flows for the Coweeta drainage varied from some of the lowest to some of the highest in the 58-year period for which we have data.
FIGURE 1.—Schematic representation of study sites in Upper Ball Creek (UBC, second order), Lower Ball Creek (LBC, fourth order), and Coweeta Creek (CC, fifth order) showing substratum composition in 20-cm × 20-cm permanent quadrats: BB = bedrock-boulder; CG = cobble-gravel; SS = sand-silt; D = debris; HT = heterogeneous. Blank quadrats were not sampled every year.

What are the implications of these findings for the management of ESUs? First, we believe that characterization of the habitat requirements of ESUs as well as habitat management in general, can be enhanced through the use of a landscape perspective. This perspective directly addresses the patchiness present in many lotic systems and deals with reaches as dynamic habitats rather than as static entities. Such a view may be of particular importance to the scientific management of benthic fishes such as darters, sculpins, madtoms, and some minnows. These species may exhibit specialization for a given substratum (Winn 1958; Finger 1982; Page 1983) and small home ranges (Gerking 1959; Hill and Grossman 1987) that render the explicit identification of environmental patchiness essential to successful management.

Second, our results show that both mean daily flows and composition of the substratum were variable over the course of the study. Consequently, attempts to quantify the habitat requirements of ESUs should be made over several years to encompass the range of variation typically present in the habitat. This also suggests that studies of the habitat

FIGURE 2.—Schematic representation of the permanent study sites in Upper Ball Creek (UBC), Lower Ball Creek (LBC), and Coweeta Creek (CC) showing the number of times the dominant substratum class changed in a quadrat between samples (maximum, three).
needs of ESUs should be instituted before their populations decrease to critically low levels.

Landscape Approach to Population Dynamics

It seems worthwhile to explore the implications of patchy stream habitats for the population dynamics of ESUs. In a patchy environment, individuals may be distributed across a variety of patch types that differ in their effect on individual fitness (Levins 1962). Pulliam (1988) and Pulliam and Danielson (1991) explored the population-level consequences of this phenomena for birds and termed these models source–sink population models. Source–sink models lead to some counterintuitive results that may be of particular relevance to the management of ESUs in aquatic systems.

A common goal for the management of ESUs is identification of habitat patches that are favorable for the species. Fisheries managers commonly use habitat–abundance relationships to identify such areas (Fausch et al. 1988). Typically, researchers sample a variety of reaches occupied by the species, measuring both physical variables and abundance of the species of interest (Baltz 1990). The manager can then use correlation statistics to identify variables that are positively correlated with abundance, and they may infer that the physical attributes with the strongest correlation coefficients define the most favorable habitat for the ESU. However, it is not unusual for the predictive power of such models to range from moderate to low (i.e., $R^2$ values are below 0.50; Layher and Maugham 1985; Fausch et al. 1988; Jowett 1992). This might be due to several reasons such as insufficient sampling, but it might also be caused by a logical flaw in this approach. Use of the landscape population models developed by Pulliam (1988) illustrates this shortcoming.

First, let us envision a hypothetical ESU with a given set of demographic characteristics (Tables 1 and 2). These characteristics are common to many fish species (Moyle and Cech 1988). Now imagine that this ESU occupies two habitat patches, A and B, that have differing fitness consequences for individuals (Table 2). Patch A is a small area of bedrock–boulder substratum surrounded by cobble–gravel riffle. Few individuals can inhabit patch A (it has a low carrying capacity), but fish within it experience low mortality rates and high fertility rates (Table 2). Conversely, patch B has a high carrying capacity, but fish within it experience high mortality and zero fertility. We can now use a simple difference equation model to simulate changes in population size for the species (through summation of the output of this equation for both patches). This model is represented as

$$N_{t+1,X} = N_{0,X} + N_{0,X}(b_X - d_X) + (i_X - e_X);$$

where

- $N_{t,X}$ = number of the ESU in patch $X$ at time $t$,
- $N_{0,X}$ = number of the ESU in patch $X$ at time 0,
- $b_X$ = birth rate in patch $X$,
- $d_X$ = mortality rate in patch $X$,
- $i_X$ = immigration into patch $X$,
- $e_X$ = emigration from patch $X$.  

![Figure 3.—Mean annual daily flows for Watershed 8, a fourth-order stream in the Coweeta drainage (data courtesy of the U.S. Forest Service’s Coweeta Hydrologic Laboratory). The open histograms represent the first 10 years of our study.](#)
TABLE 1.—Characteristics of a hypothetical evolutionarily significant unit (ESU). These traits are typical for many fish species.

1. Intraspecific competition is substantial among individuals
2. Nonreproductive habitat requirements are general
3. Habitat patches are occupied in relation to quality; if a patch is full, individuals enter the patch with the next highest quality value
4. The ESU has specialized habitat requirements for reproduction; hence, reproductive success varies among patches
5. Fecundity is high relative to density

From Table 1, we can assume that patches are occupied in proportion to their effect on individual fitness. This means that individuals will occupy patch A until carrying capacity is reached, at which point new individuals will begin to occupy patch B. In addition, once patch B reaches carrying capacity, all emigrants die. If we insert the parameters presented in Table 2 in the model and round all fractional values up to the nearest individual, densities of animals in patches A and B remain at the respective carrying capacities and population size of the ESU is stable (Table 2).

Now if an ESU is behaving in the manner portrayed by this landscape-based model (Pulliam 1988), managers charged with the preservation of this population may find their job quite difficult. For example, if traditional habitat-abundance models are used to identify the most favorable habitat for the ESU, the managers will mistakenly conclude that patch B, with its higher density, is the habitat that is crucial for preservation (Pulliam 1988). This would soon lead to extinction for the ESU, however, because the reproduction necessary for population maintenance occurs in patch A. Although our example is somewhat contrived, in that successful reproduction occurs only in patch A, one can vary the parameters in a more reasonable manner and still obtain the same result (i.e., the majority of recruits for the population may not originate in the portion of the habitat in which densities are highest). By treating the habitat as a patchy landscape, however, and focusing on patch-specific demography, managers may increase the probability that their efforts will have a positive effect on an ESU.

Models of Habitat Selection

Fisheries managers typically use two techniques to quantify habitat selection by lotic fishes. The first method is the correlational approach to habitat-abundance relationships described in the previous section. The second technique involves locating undisturbed specimens in the stream and recording a series of physical measurements (e.g., depth, velocity, substratum composition) at the position of the fish (Baltz and Moyle 1984; Baltz 1990). These physical measurements are then compared with habitat availability data obtained from random measurements within the reach. If this comparison yields significant differences, it is assumed that the ESU is exhibiting habitat selection or at least nonrandom microhabitat use. We refer to this type of study as a microhabitat use study. Although these two designs are probably the most frequently used by fisheries scientists attempting to quantify the habitat requirements of fishes, they both possess two shortcomings that may affect a manager’s ability to identify and preserve critical habitat for an ESU.

First, the focus of both habitat-abundance and microhabitat use studies is on the physical habitat rather than on biological factors such as the abundances of prey, predators, or competitors—probably because physical variables are easier to quantify and manage than biological factors. Although there is no inherent reason why biological factors could not be included in habitat selection studies, such approaches appear to be uncommon (Orth 1987). It is also possible that exclusion of biological factors has contributed to the generally low predictive power of some habitat-abundance and microhabitat use studies.

An additional shortcoming of many habitat selection studies is that they neglect identification of the mechanism of selection itself. Thus, habitat selection typically is inferred from correlational analyses of physical data from reaches in which varying densities of fishes have been observed. Nonetheless, even when such approaches yield strong results (high $r$ values), they still can not directly establish a causal mechanism for the relationship. In addition, investigators typically do not directly examine the stimuli upon which individuals are basing their “choice” nor do they frequently identify the fitness consequences of choosing a given microhabitat. Once again, these foibles may limit a manager’s ability to correctly identify the habitat components
that are crucial for population maintenance or growth.

The two following approaches to the study of habitat selection by stream fishes should illustrate the advantages of including biological data with a landscape perspective and of the mechanistic approach to microhabitat use.

**Landscape Approach to Microhabitat Selection**

The mottled sculpin *Cottus bairdi* is the most abundant benthic fish in the Coweeta drainage (Freeman et al. 1988). We have studied microhabitat use by this species for the last 11 years (Grossman and Freeman 1987; Barrett 1989; G. Grossman et al., University of Georgia, unpublished data). Mottled sculpin have variable patterns of microhabitat use. Although these fish are always found on the bottom at low focal point velocities, they occur over wide ranges of average velocities and substrata (Grossman and Freeman 1987; Petty and Grossman, in press). Indeed, the use of physical microhabitat variables (average velocity, depth, composition of the substratum) by mottled sculpin typically does not differ significantly from values obtained by randomly sampling the environment (Grossman and Freeman 1987; Petty and Grossman, in press). In addition, physiological studies indicate that mottled sculpin are not metabolically restricted to low-velocity microhabitats (Facey and Grossman 1990, 1992). Finally, experimental and descriptive studies have shown that microhabitat use by mottled sculpin is not strongly influenced by predators (Grossman and Freeman 1987; Grossman et al. 1995) or the species' most common potential competitor (Barrett 1989).

These findings led us to reassess our approach to the study of microhabitat selection by this species. A dietary study of mottled sculpin in the Coweeta drainage (Stouder 1990) indicated they are generalized predators that feed primarily on benthic invertebrates. These results are supported by other dietary data for this species (Dineen 1951; Bailey 1952; Daiber 1956). Because the distribution of benthic macroinvertebrates in streams frequently is patchy (Resh and Rosenberg 1984; Downes et al. 1993), we hypothesized that mottled sculpin may be responding more to the patchy distribution of prey than to distinctive physical characteristics of the habitat. Specifically, we reasoned that if mottled sculpin are generalized predators without strong physiological constraints on microhabitat use, then a patch of sandy substratum with high prey abundance may be functionally equivalent to a patch of cobble substratum with high prey abundance. Consequently, we tested the null hypothesis that prey abundance at patches occupied by sculpins was not significantly higher than prey abundance at randomly selected locations.

We tested this hypothesis by making microhabitat measurements on mottled sculpin in two sites in the Coweeta drainage using the methods of Grossman and Freeman (1987). At the location of each sculpin we also collected a benthic sample using a Hess sampler with a 0.1-m² capacity. In addition, we also selected a paired, random location for each specimen and collected an identical set of data at this location (Petty and Grossman, in press). Our data consisted of six samples: four from a 150-m-long site in autumn 1991, late spring 1992, summer 1992, and autumn 1992, and two samples (late spring 1992 and summer 1992) from a similar 150-m site upstream from the first site.

We compared microhabitat use by mottled sculpins with data from random measurements to quantify microhabitat selection within a season (Petty and Grossman, in press). We also tested the aforementioned null hypothesis regarding prey abundance with a Wilcoxon signed ranks test on paired patches (with sculpin and random) within a seasonal sample. In addition, we analyzed two restricted data sets. The first contained only prey that represented at least 5% of the diet of mottled sculpin in the Coweeta drainage on either a numerical or volumetric basis (Stouder 1990). The second deleted prey that we deemed to be too large to be consumed by sculpin (Petty and Grossman, in press). For each data set, values for numerical abundance and biomass were tested separately.

As with previous microhabitat studies, mottled sculpin did not exhibit microhabitat selection for physical factors in four of six seasonal samples (Petty and Grossman, in press). However, they did occupy patches with significantly higher numerical abundances of invertebrates in five of six seasonal samples (Petty and Grossman, in press). Similar results were obtained with biomass data and both numerical and biomass data for the two other data sets (Petty and Grossman, in press). Consequently, prey abundance appeared to elicit a stronger microhabitat selection response from mottled sculpin than physical habitat characteristics.

These results demonstrate an important point with respect to the management of ESUs. First, as previously mentioned, successful management of ESUs depends upon identification of the aspects of habitat that are essential for population maintenance. For a variety of reasons (e.g., ease of mea-
measurement) fisheries biologists generally focus on the physical habitat when attempting to identify critical resources for fishes. Nonetheless, the use of physical microhabitat data alone provided few insights into the factors influencing microhabitat selection by mottled sculpin. It was only when we included biological data (prey abundance) that we were able to detect a pattern in microhabitat use by the species. In addition, these findings have important consequences for management of ESUs. For example, fisheries managers tend to emphasize manipulation of physical habitat when they conceptualize a management strategy for an ESU. However, if they wanted to manage a habitat with an endangered mottled sculpin, it might be more effective to employ techniques that would directly increase the forage base for this species (nutrient additions, supplemental feeding, etc.) rather than to rely on manipulation of the physical habitat, which might or might not produce increases in prey abundance.

**Energy-Based Model for Optimal Velocity Use**

The previous example demonstrates the advantages of including biological variables in the assessment of the habitat requirements of ESUs. Nonetheless, it still does not provide a complete picture of the causal factors influencing habitat selection for mottled sculpin. Our next example describes a mechanistic, energy-based approach to habitat selection by rainbow trout *Oncorhynchus mykiss* and rosyside dace *Clinostomus funduloides*. These species are the numerically dominant water-column fishes in Coweeta Creek (Freeman et al. 1988).

Our model is based on the assumption that an individual will increase, and perhaps maximize, its fitness if it behaves in a manner that will maximize its net energy gain (Fausch 1984; Hill and Grossman 1993). For lotic fishes that forage in the water column, there is a clear physiological cost for maintaining position at a given velocity, as well as a quantifiable benefit to be gained by foraging at a given velocity. By measuring these costs and benefits, one can construct a simple cost-benefit model (Figure 4) to yield a prediction regarding the velocity that should maximize net energy gain for individuals of a given species. We developed models for two size-classes of trout (small, 65.7 ± 1.5 mm; medium, 89.9 ± 8.1 mm) and dace (medium, 48.3 ± 0.7 mm; large, 60.9 ± 0.7 mm) for spring, summer, autumn, and winter. Eight models (two size-classes × four seasons) were examined per species. Details of these models were presented by Hill and Grossman (1993), who used the respirometry data of Facey and Grossman (1990) to estimate the energetic cost of maintaining position at a given velocity (i.e., to parameterize the cost curves). Hill and Grossman (1993) then derived benefit curves by measuring the amount of drift available (in calorific equivalents) at naturally occurring velocities in the stream, as well as by conducting foraging experiments to quantify the ability of rainbow trout and rosyside dace to capture prey at differing velocities. We then compared the cost and benefit curves to determine the velocity that yielded the maximum net energy gain for each size-class in each season (Figure 4). We tested the prediction of each model by comparing it with velocities occupied by the respective size-classes of trout and dace in Coweeta Creek during the four seasons (Hill and Grossman 1993).

To summarize our results, energy-based models of habitat selection yielded velocity predictions that were extremely close to those occupied by rainbow trout and rosyside dace in Coweeta Creek. The mean deviation between predicted and observed velocities was 2.5 cm/s for trout and 2.8 cm/s for dace. Velocities present in the stream during these seasons ranged from 0 to over 50 cm/s. The primary factor affecting the model was the relationship between velocity (independent variable) and the ability of the fish to capture prey (prey capture success). When an empirical model based on the third derivative of this curve (point of maximum rate of decline) was used as a predictor of optimal velocity, the mean absolute deviations between predicted and observed velocities decreased to 1.5 cm/s for trout and 1.9 cm/s for dace (Hill and Grossman 1993).

An energy-based mechanistic model of habitat selection for rainbow trout and rosyside dace proved to be an accurate predictor of the velocities occupied seasonally by these species in Coweeta Creek. These results have several implications for the management of ESUs. First, they provide an important datum for the scientific management of these species: changes in velocity may have strong impacts on trout and dace populations. If either species were an ESU, the optimal velocity data for Coweeta Creek would provide us with a starting point for the management of other streams inhabited by these fishes. For example, we could use such data to assess the potential impacts of water diversions, dams, or disturbances that may alter flow regimes. Or in a proactive sense, we could manipulate flows to increase the availability of optimal velocities, assuming that this would result in higher production of dace and rainbow trout.
Effective management of ESUs necessitates quantification of their habitat requirements. Nonetheless, most previous studies of the habitat requirements of lotic fishes have focused on the physical habitat. Our results for mottled sculpin, rainbow trout, and rosyside dace and those of Jowett (1992) for brown trout *Salmo trutta* demonstrate that habitat selection studies that include only physical factors may not provide sufficient information for the effective management of some lotic fishes. Consequently, the development of more biologically realistic approaches to the quantification of habitat requirements of lotic ESUs may increase our ability to prevent the extirpation of these fishes.

**Conclusions**

The preservation of biological diversity requires an innovative approach to the management of natural resources. In this paper, we have attempted to apply some of the techniques of landscape ecology to lotic systems (Johnston and Naiman 1987; Pringle et al. 1988; Johnston et al. 1990; Schlosser 1991) by incorporating biologically relevant information that is often lacking from fisheries studies: quantification of the physical habitat of stream reaches, quantification of spatial and temporal variability within reaches, inclusion of the potential effects of patchiness on population regulation, and use of biologically based models of habitat selection. Through this application we have tried to demonstrate that stream reaches can be viewed as patchy habitats from both a temporal and spatial perspective, and that this patchiness may have profound consequences for assessing habitat requirements of ESUs as well as their population dynamics. In addition, although we should not ignore studies of the physical habitat requirements of ESUs, it is likely that the development of more biologically realistic, mechanistic models of habitat selection will facilitate the preservation and management of these fishes. Finally, we suspect that the application of the landscape perspective to entire streams as well as their reaches will enhance our ability to effectively manage aquatic ESUs.

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