Metapopulations and salmonids: a synthesis of life history patterns and empirical observations

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Abstract – Metapopulation theory has attracted considerable interest with reference to the salmonids. There has been little empirical evidence, however, to guide the evaluation or application of metapopulation concepts. From knowledge of salmonid life histories and our own work with bull trout (*Salvelinus confluentus*), Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) and westslope cutthroat trout (*Oncorhynchus clarki lewisi*), we suggest that simple generalizations of salmonid metapopulations are inappropriate. Although spatial structuring and dispersal mechanisms are evident, the relevance of extinction and colonization processes are likely to vary with life history, species, scale, and landscape. Understanding dispersal, the role of suitable but unoccupied habitats, and the potential for extinction debts in non-equilibrium metapopulations are key issues. With regard to conservation of salmonids, we suggest that efforts to understand and conserve key processes likely to influence the persistence of populations or metapopulations will be more successful than efforts to design minimal habitat reserves based on metapopulation theory.

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

Metapopulation theory has attracted considerable interest in conservation biology and management (Doak & Mills 1994; Hanski & Simberloff 1996). The proposal that regional populations of a species may persist in variable environments as collections of local populations interacting through dispersal (Hanski & Simberloff 1996) is intuitively appealing and has been largely embraced by biologists and managers (McCullough 1996). Metapopulation theory seems to hold a particular relevance for threatened or sensitive populations of salmonids in the Pacific northwest of the United States. It has been repeatedly invoked in recent discussions regarding conservation and land management relevant to these fishes (Rieman & McIntyre 1993; Bisson 1995; Li et al. 1995; Reeves et al. 1995; Schlosser & Angermeier 1995; Independent Scientific Group 1996; National Research Council 1996; Lee et al. 1997; Policansky & Magnuson 1998), although to date there has been little apparent direct application in land-use management.

A metapopulation view implies that the spatial geometry (size, number, distribution) of suitable habitats matters to the dynamics and long-term persistence of these species' populations. Such issues may be particularly relevant for land managers that must decide about the priority of habitat or watershed conservation and restoration efforts (Doak 1995). How much habitat or how many watersheds are necessary; which ones; and how should they be distributed? Ostensibly, metapopulation theory should offer guidance for managers who face these issues (Rieman & McIntyre 1993; Li et al. 1995; Schlosser & Angermeier 1995). Conceivably, we might learn to identify a network of critical habitat reserves that would allow popu-

lations to persist in the face of ongoing development and disruptive land use.

Despite the interest there has been little empirical work to evaluate or guide the application of metapopulation theory to salmonids. Some authors caution that there are important risks of over-generalization and misapplication of intuitively appealing, but poorly supported theory (Simberloff 1988; Doak & Mills 1994; Hanski & Simberloff 1996). Unquestionably, large-scale processes have been important in the distribution and phylogeny of salmonid fishes in the Pacific Northwest. Current knowledge of local adaptation (E. B. Taylor 1991; Adkison 1995; National Research Council 1996), zoogeography (McPhail & Lindsey 1986; McPhail 1997) and colonization of new habitats following introduction (Quinn 1993) or glacial retreat (Milner & Bailey 1989) clearly demonstrate the importance of spatial processes, environmental heterogeneity, and extinction-recolonization dynamics for these fishes. The question is not whether space is important; rather, how important is it (Karieva 1990)?

In an applied setting, this question is constrained by the spatial and temporal scales of management decisions likely to influence these species. In our view, the metapopulation question becomes most relevant at the scale of large watersheds or moderately sized river basins (10^2 to 10^3 km^2) where biological and socio-political processes overlap in a unique way. It is at this scale in the United States that land management is often controlled by a single or a few entities (e.g., U.S. Forest Service; Bureau of Land Management) charged with managing much, if not most, of an entire basin in a coordinated fashion. With the exception of the anadromous forms, it is at this scale that many of the salmonids fully express their life history potential (Northcote 1997; Thurow et al. 1997). Even forms that move more widely than the stream network encompassed at this scale are likely to use individual tributary systems within such an area as localized spawning and rearing areas. It is also at this scale that dams or habitat loss have created insular networks of habitats that now function as discrete units regardless of historical connections (Sheldon 1988; Lee et al. 1997).

This article briefly reviews metapopulation theory. We then consider both the general knowledge of life history patterns, and recent empirical results for several salmonids as evidence of metapopulation dynamics. We conclude with a brief synthesis as guidance for further research and to identify the generalities and uncertainties relevant to the application of metapopulation concepts for salmonids.

Metapopulation theory

The concept of spatially structured populations is not new, but the formalization of metapopulation theory has advanced dramatically in the last decade (Hanski & Simberloff 1996). In the classic view, metapopulations were considered collections of roughly equivalent demes or local populations with similar, but independent risks of extinction through environmental variability. In the simplest models and subsequent extensions, local extinctions are balanced by migration and recolonization from the extant populations (Hanski & Simberloff 1996; Harrison & Taylor 1996; Hanski 1997).

Metapopulation models have been extended to consider a variety of more complex systems. These may include substantial variation in the characteristics and dynamics of local populations and the patterns and rates of dispersal among them (Hanski & Simberloff 1996; Harrison & Taylor 1996). In the current view three conditions define metapopulations: 1) habitat consists of discrete patches or collections of habitats capable of supporting local breeding populations; 2) the dynamics of occupied patches are not perfectly synchronous; 3) dispersal among the component populations influences the dynamics and/or the persistence of the metapopulation or at least some of the local populations. Structuring and at least partial independence of local populations are the fundamental concepts that distinguish a metapopulation from a simple panmictic group in a patchy environment.

In reality, conformity to these conditions will vary across temporal and spatial scales, species and landscapes. Harrison & Taylor (1996) conceptualized this variation as a continuum along two axes (Fig. 1). One axis represents relative dispersal among patches. The second represents variation or heterogeneity in patch quality, which
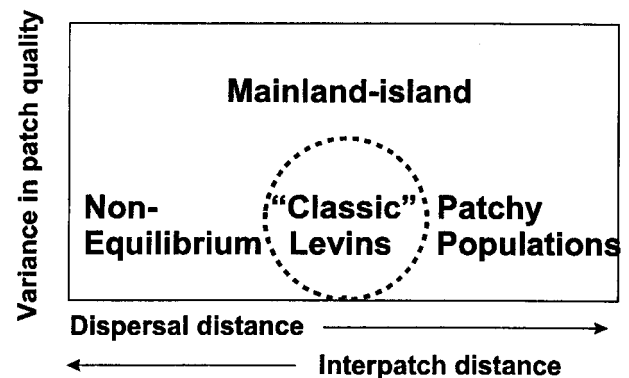

Fig. 1. Metapopulation structure in relation to variance in patch quality, dispersal distance and interpatch distance (modified from Harrison & Taylor 1996).

includes patch size or other characteristics likely to influence the size and dynamics of local populations.

At one extreme, relatively high rates of dispersal lead to high levels of recolonization and patch occupancy, yielding a "patchy" population structure. If rates of dispersal and/or recolonization are very low, a non-equilibrium metapopulation structure may result. Non-equilibrium refers to a progressive pattern of local extinctions that occurs when rates of extinction exceed recolonization, such that patch occupancy ultimately declines to zero.

If variation in patch quality is high, some local populations may be relatively resistant to extinction, whereas others may be extinction-prone. This type of structure is often referred to as "mainland-island," where the largest local populations (defined in terms of population size or patch area) or "mainlands" are key to persistence of the metapopulation. Smaller "island" patches have relatively high rates of turnover, due to higher rates of local extinction and recolonization from mainland patches.

Harrison & Taylor (1996) noted that variability in habitat quality, rather than patch or population size, may produce a similar structure. In this context quality may be defined as the capacity of a patch to support populations with positive rates of growth. Patches with negative growth rates often are referred to as "sinks" (Pulliam & Danielson 1991; Dias 1996). Persistence of local populations in sink habitats depends on immigration of individuals from "source" habitats. In practice, mainland-island and source-sink structures may be difficult to distinguish (Dias 1996).

When variability in patch quality is low, and dispersal and/or recolonization probabilities are "just right," patch occupancy will approximate the dynamics of a classic or "Levins-type" metapopulation, where even the largest patches have a substantial risk of extinction, but no patches are too isolated to be recolonized (Hanski 1996; Hanski & Simberloff 1996). Though important for some species, this type of metapopulation structure may be rare in nature (Hanski 1996; Harrison & Taylor 1996).

There have been a variety of methods used to study metapopulations, each with unavoidable limitations. The application of multiple and complementary sources of information, however, can provide a more rigorous descriptive and quantitative understanding (Utter et al. 1993; Dunham et al. 1999a). Common approaches have included the analyses of distributions, population dynamics and genetic structuring.

Patterns in species distributions have proven particularly useful. A general approach has been to describe the geometry of suitable habitat patches and then inventory those patches to describe patterns of occupation. Incidence functions (B. L. Taylor 1991; Hanski 1997) have been used to model the probability of species presence or persistence in relation to patch characteristics. This approach, often focused on patch area effects (B. L. Taylor 1991), has been used to estimate extinction and colonization rates as well. The latter application requires an assumption of an extinction-colonization equilibrium (Hanski 1997), or a time series of observations of extinction and colonization events (Ouborg 1993; Sjögren-Gulve & Ray 1996). Even when data are limited to a simple snapshot in time and an assumption of equilibrium is not justified, incidence functions can provide valuable insight regarding the patch characteristics associated with a species' occurrence and persistence. Incidence functions have been widely applied (see Hanski 1997), but applications with fishes are limited and presently we are familiar only with our own attempts with salmonids (Rieman & McIntyre 1995; Dunham et al. 1997; Dunham & Rieman 1999).

Analyses of population dynamics and demographics have played a central role in the development of metapopulation concepts. Spatially detailed demographic models have been widely used in theoretical exploration of metapopulation dynamics (e.g. Fahrig 1992, 1997). There has been a more limited application to specific metapopulation questions, presumably because parameterization of such models can be extremely difficult (Doak & Mills 1994; Taylor 1995; Ims & Yoccoz 1996; Mills et al. 1996; Ruckelshaus et al. 1997). That does not mean demographic models are not useful. Patch-specific models can provide important tests of the common assumptions in metapopulation models (Ims & Yoccoz 1996); for example, to determine whether local populations are internally self-sustaining or likely dependent on outside demographic support (e.g. Stacey & Taper 1992). Recent work with salmonids has focused generally on the dynamics of individual populations (e.g. Lee & Hyman 1992; Emlen 1995; Ratner et al. 1997; Shepard et al. 1997; Botsford & Brittnacher 1998).

Patterns of molecular genetic variation may reflect underlying processes of gene flow and dispersal and have been employed to characterize potential metapopulations (Driscoll 1998; Saccheri et al. 1998). Molecular genetic markers have been widely applied in the analysis of salmonid distributions (Allendorf & Waples 1995) but direct inferences regarding metapopulation dynamics have been relatively recent (e.g. Tallmon 1996; Fontaine et al. 1997; Spruell et al. 1999).

Metapopulations and salmonids

Salmonids would seem prime candidates for meta-populations. The spatial discreteness of spawning and rearing habitats, combined with the possibility of among-habitat dispersal, effects of local environmental variability, and disturbance regimes may create a patch dynamic that can be described by metapopulation models (e.g. Rieman & McIntyre 1993, 1995; Li et al. 1995; Reeves et al. 1995; Schlosser & Angermeier 1995; Dunham & Rieman 1999). Well-known patterns of natal homing (Quinn 1993; National Research Council 1996) and local adaptation (E. B. Taylor 1991; Utter et al. 1993; Allendorf & Waples 1995) may reinforce structuring of local populations. Periodic straying among natal streams also is well known (Larkin 1981; Labelle 1992; Quinn 1993; Tallman & Healey 1994), however, providing a mechanism for dispersal. Coupled with the knowledge that salmonid numbers may vary and that local extinctions have occurred or are more likely with increasing habitat loss and fragmentation (e.g. Rieman & McIntyre 1993; Dunham et al. 1997), this basic understanding has prompted repeated reference to metapopulation theory. The evidence seems compelling and salmonid metapopulations are sometimes taken for granted (Policansky & Magnuson 1998).

While it is clear that a metapopulation view of salmonids may be appropriate, the details of metapopulation structure and dynamics may depend critically on the large-scale structure of habitats, and how habitat and life history variability interact (Dunham & Rieman 1999). If metapopulation theory is to be meaningfully applied to salmonids, such issues must be considered in some detail. General knowledge of salmonid life history patterns and recent empirical work provide a foundation from which to start.

Life history

Metapopulation structure is a function of quality, spatial distribution, and isolation of habitat patches (Fig. 1). Quality and distribution of potential patches can be defined as a function of physical factors including habitat size and condition, and biotic factors including habitat requirements and the modifying effects of other species. Isolation is a function of distance between patches, the nature of the intervening environment, and rates of dispersal (Wiens 1996). The term "straying" is often used in place of dispersal (Quinn 1993). We use both terms in this article. Straying implies that an individual is lost, although it still may reproduce outside its natal habitat. Dispersal implies movement with the potential for colonization or demo-graphic support of other patches. While straying may limit individual reproductive success (e.g. Tall-man & Healey 1994), it is necessary for dispersal in salmonids and we wish to avoid the implication that it is maladaptive (see Cury 1994; LePage & Cury 1997).

Definition of patches, their distribution, and isolation, can depend strongly on the life history of the species in question. Migratory behavior may be particularly important in this regard. There is little question that migratory individuals can move the distances required to disperse among tributaries. Straying among tributaries obviously occurs, but straying and dispersal rates are poorly known (Quinn 1993). There is evidence that dispersal varies among species and with the particular circumstances of the species and systems in question (Quinn 1993; Quinn & Unwin 1993; Tallman & Healey 1994).

The salmonid literature is rich with examples of life history variability (see for example E. B. Taylor 1991; Groot & Margolis 1991; Northcote 1997; Willson 1997). Available evidence suggests three general patterns of migration for salmonids: migratory, resident, and mixed (resident + migratory individuals in the same populations). These categories may be further divided into "obligate" and "facultative", depending on the relative influences of genetic and environmental factors, respectively, on migratory behavior.

From a metapopulation perspective, the distinction between obligate and facultative migratory behavior may be important. Examples of obligate migratory behavior are provided by several species of Pacific salmon (e.g. *O. gorbuscha*, *O. keta*, *O. tshawytscha*, *O. kisutch*). These species are almost exclusively anadromous; adults that mature in freshwater (if present at all) are primarily precocial males (Groot & Margolis 1991; Stearley 1992). Individuals of these species require several spatially discrete habitats for different portions of their life cycle (e.g. upstream spawning and rearing habitat, downstream migration corridors, estuary and marine feeding habitats). Habitats used by salmonids with obligate migratory behavior are non-substitutable in the sense that different stages of the life cycle must occur in specific habitats (see Dunning et al. 1992; Schlosser 1994). Loss of any specific habitat required for a critical life stage will therefore result in extinction of associated local breeding populations. An unfortunate example of non-substitutability is recent extirpation of Pacific salmon in many habitats where migration barriers have been placed between upstream spawning and rearing habitats and downstream migration corridors and critical feeding habitats (Lee et al. 1997).

Many salmonids exhibit flexibility in their use

and substitution of habitats (Northcote 1997). An excellent example is provided by sockeye salmon (*O. nerka*), where local populations of resident, fluvial, or lacustrine individuals may co-occur with anadromous individuals (Burgner 1991; Wood 1995). Individuals with different migratory life histories may occasionally interbreed (e.g. Taylor et al. 1996; Wood & Foote 1996), but each life history type can function independently. In the case of sockeye salmon, many anadromous populations have been decimated by degradation of migration corridors and lack of passage over dams (Lee et al. 1997), but resident populations of kokanee salmon have persisted. Resident forms may even produce anadromous offspring (Rieman et al. 1994).

For some species and populations of salmonids, movements of individuals are largely restricted to headwater stream habitats, where distributions of adults, juveniles, and spawning habitats overlap considerably. Such resident ("non-migratory") populations have been observed for bull trout (*Salvelinus confluentus*), where unsuitable thermal habitat may isolate headwater populations (Rieman & McIntyre 1995). Occurrence of downstream populations of predators or competitors (especially nonnative salmonids) has also been hypothesized to be an isolating mechanism that may promote residency (Fraser et al. 1995; Dunham & Rieman 1999). Resident populations may occur upstream of more obvious barriers, including impassable waterfalls (Northcote 1992) and dams (Näslund 1993). In this latter example, opportunities for development of metapopulations are limited, as recolonization of above-barrier habitats is not possible.

Migratory behavior of salmonids can have important implications for the degree to which the dynamics of local populations covary within a metapopulation. In the case where most adults undergo extensive migrations, habitats used for spawning and early rearing may be distributed as discrete patches throughout a drainage basin but migratory juveniles and adults may coalesce downstream. Use of these common habitats may act to link the dynamics of local breeding populations. For example, decadal cycles in marine productivity can produce correlated dynamics of salmonid populations that spend their adult lives in common oceanic domains (Pearcy 1997).

On the other hand, environmental variability and disturbance in upstream spawning and rearing habitats may decrease the degree to which local populations covary (Reeves et al. 1995; Rieman & McIntyre 1996). Even when most individuals in a system may be migratory, variability of time spent in feeding habitats, timing and distance of migrations, and spatial and temporal overlap of spawning and rearing (E. B. Taylor 1991) may affect the degree of synchrony among local breeding populations.

For species and systems where migratory behaviors are more flexible (i.e. "facultative"), additional complexity is added by interactions between resident and migratory individuals (as with sockeye salmon and kokanee). Species with primarily resident populations may have a much restricted or even nonexistent interaction dynamic among local populations.

Our overview of salmonid life histories implies a potential for complex interactions between life history diversity and the structure and dynamics of metapopulations. While the evidence for salmonid metapopulations seems compelling in some cases, specific empirical studies are sorely lacking for salmonids and freshwater fishes in general (Schlosser & Angermeier 1995). In the following section, we review examples of recent empirical work, focusing on three inland salmonids that have been the subject of our own research. With regard to our discussion of life history complexity in the previous section, these examples are limited in that complexities posed by contrasting life histories are not fully addressed. Even so, we find evidence of very different patterns among these species.

Empirical evidence

Bull trout

Bull trout (*Salvelinus confluentus*) can be found virtually anywhere in the network of streams in river basins of at least sixth order. Some individuals can move hundreds of km (Bjornn & Mallet 1964; Swanberg 1997) while others remain within a local stream network throughout life. Bull trout have an indeterminant life cycle with first maturity occurring roughly between ages 3 to 6 with the possibility of subsequent repeat spawning (Fraley & Shepard 1989).

The distribution of resident and juvenile migratory bull trout is strongly associated with gradients in stream size and elevation or local climate (Rieman & McIntyre 1995; Rich 1996; Dunham & Rieman 1999). Natal habitats are restricted to headwater streams as discrete patches in a matrix of the larger stream network representing an entire river basin (Fig. 2). Topography and hydrologic development interact with climate to create a mosaic of patches that can vary in size and isolation by stream distance among those patches (Dunham & Rieman 1999). Because spawning is not known in lakes, populations associated with tributaries of lake systems may be structured similarly even when gradients in stream size and local climates are not large. These patterns indicate that spatially
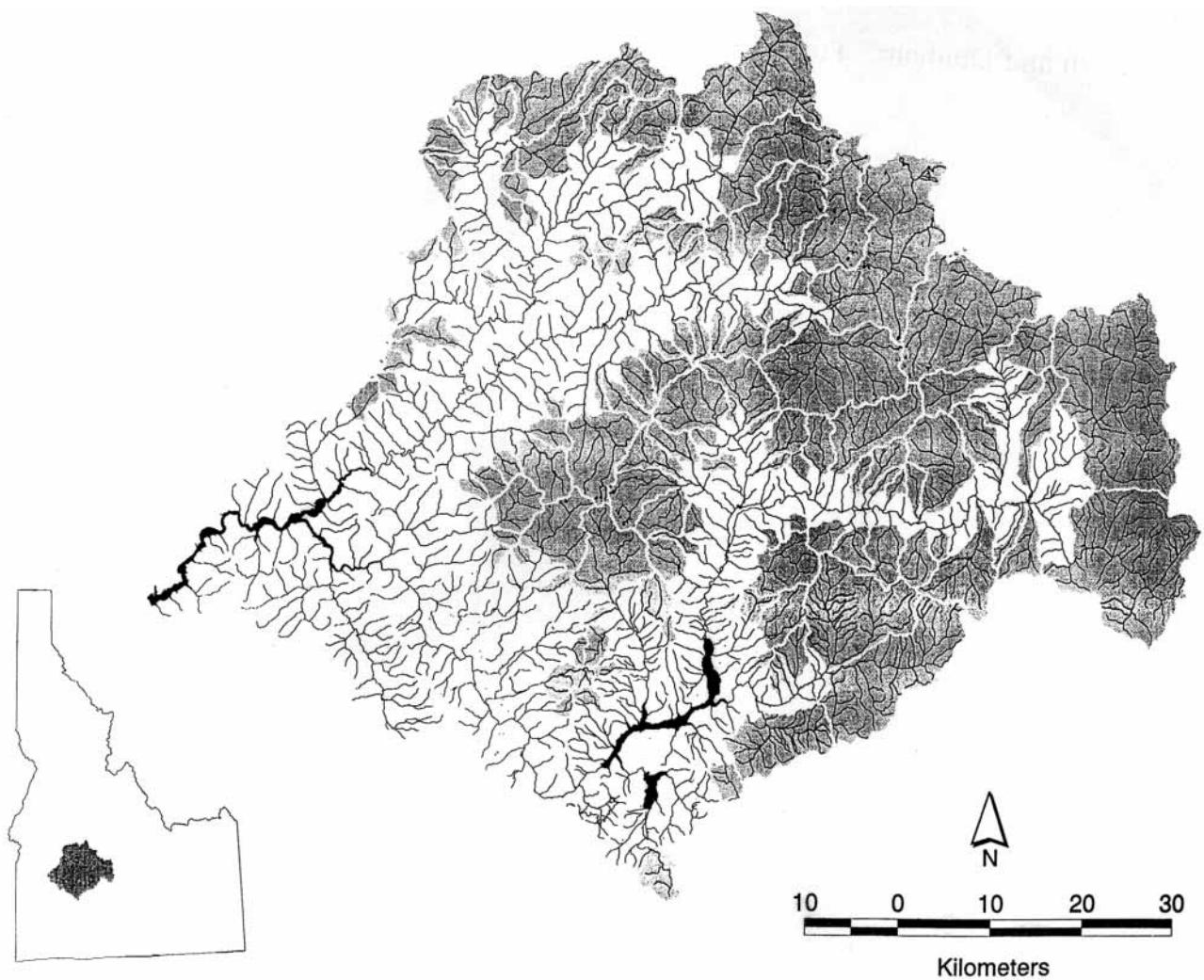
Fig. 2. Patches of suitable habitat (shaded catchments) for local populations of bull trout in the Boise River basin, Idaho. Patches were defined from patterns in juvenile bull trout distributions and are assumed to represent the distribution of potential spawning and initial rearing habitats (see Rieman & McIntyre (1995) and Dunham & Rieman (1999)).

discrete local populations of bull trout are likely to exist in river basins as small as 100 km². Genetic analyses provide supporting evidence of homing and population structuring at this scale (Kanda et al. 1997; Spruell et al. 1999).

Rieman & McIntyre (1995) found the occurrence of bull trout in the Boise River basin, Idaho to be strongly associated with the size (catchment area) of the habitat patches described in Fig. 1. Dunham & Rieman (1999) analyzed an expanded data set and found both patch size and isolation (stream distance to nearest occupied patch) were strongly associated with the occurrence of bull trout. Variability in the size and distribution of patches within the basin suggested metapopulation structure was a complex mosaic of several elements found in conceptual models (Fig. 1). Potentially confounding effects such as spatial autocorrelation linked to undescribed environmental variability did not appear to be important. Human disturbance (as indicated by road density), however, was negatively correlated with occurrence.

Some of the best demographic information available for bull trout comes from annual redd counts (a measure of adult population size) for a number of tributaries associated with the large lakes of northern Idaho and Montana. Rieman & McIntyre (1993) used the analytic models proposed for time series by Dennis et al. (1991) to estimate the extinction parameters for these populations. They estimated that few could be expected to persist for an extended period (i.e. 100 years), if it was also assumed that each population existed in complete isolation. Other analyses of related data showed that interannual variation in adult number was not strongly correlated among tributaries, but

there did appear to be a general pattern of decline across many of these populations (Rieman & McIntyre 1996; Rieman & Myers 1997). If these populations have always been at risk of extinction then dispersal among populations is necessary to explain their existence. Because a few very large and stable populations are found in these systems (Rieman & McIntyre 1993), source-sink or mainland-island metapopulation structures are logical alternatives.

Genetic analyses provide a different perspective. Phylogenetic work suggests an historical pattern of periodic contraction and local extinction followed by expansion and colonization from local refugia has been important across the species' range (Leary et al. 1993; Williams et al. 1997). Analyses of fine scale (i.e., within a river basin) genetic variation and divergence, however, suggest patterns that are not consistent with either the frequent extinction-colonization dynamic of a classic metapopulation structure or the source-sink possibilities suggested by the demographic data (Tallmon 1996; Spruell et al. 1999).

Lahontan cutthroat trout

In contrast to bull trout in the Boise basin, distribution of suitable habitat for Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) has been dramatically reduced by habitat degradation, especially that related to increased water temperatures and migration barriers, and nonnative salmonids (Coffin & Cowan 1995; Dunham et al. 1997). It is estimated that Lahontan cutthroat trout has been extirpated from almost 90% of over 5700 km of formerly occupied stream habitats in the Lahontan basin of northeast California, southeast Oregon, and northern Nevada (Coffin & Cowan 1995). Most populations of Lahontan cutthroat trout exist as isolated enclaves in headwater stream habitats within the Humboldt and Quinn River basins of Nevada and Oregon. Historically, most of these habitats were interconnected via larger downstream river habitats that are no longer occupied (Coffin & Cowan 1995).

Analysis of factors associated with contemporary distribution limits of Lahontan cutthroat trout (Dunham et al. 1999b) has produced a predictive model that can be used to estimate patch size and isolation. Over 70% of the variation in the elevation of downstream distribution limits for Lahontan cutthroat trout in streams was explained by latitude and longitude alone. This pattern was related to regional thermal gradients, and Dunham et al. (1999b) hypothesized that patch structure may be a function of suitable thermal habitat in streams, a factor that appears to explain bull trout

distributions as well (see above). Relationships between water temperature and the distribution of Lahontan cutthroat trout within streams (JBD, unpublished data) further supports this hypothesis.

Persistence of Lahontan cutthroat trout in streams appears to be strongly tied to fragmentation of habitat. Dunham et al. (1997) analyzed occurrence of Lahontan cutthroat trout in 119 stream habitats in the Humboldt and Quinn River basins of northern Nevada. They found a strong negative association between occurrence of Lahontan cutthroat trout and fragmentation of habitat. Due to uncertainties in defining the distribution of suitable habitat within streams, they could not clearly distinguish the effects of habitat size and isolation. An improved definition of patch structure based on recent distribution models (Dunham et al. 1999b, and unpublished data) will be used to revisit this analysis to quantify the individual effects of patch size and isolation.

Observations on apparent local extinctions of Lahontan cutthroat trout in small tributary streams following catastrophic drought conditions in the early 1990s (Dunham 1996) offer additional insights into the relevance of isolation and life history diversity to population persistence. Following the drought, recolonization in isolated streams was never observed. Tributaries with close proximity to a larger river, however, often were quickly (within 1 year) repopulated. In the latter case, it was not clear whether fish distributions were restored through surviving members of the population that had migrated out of the tributary during the drought or through dispersal from another population. Similar patterns of recolonization in tributaries or stream sections have been observed with other salmonids following catastrophic disturbances (Rieman et al. 1997).

Westslope cutthroat trout

Work with westslope cutthroat trout (*Oncorhynchus clarki lewisi*) is preliminary but offers an interesting contrast to that emerging for the other two species. The distribution of westslope cutthroat trout also has been strongly associated with stream size (Platts 1979). Although westslope cutthroat trout may move throughout whole river basins, at least temporarily occupying habitats from second-order through sixth- or seventh-order streams (Bjornn & Mallet 1964), spawning and initial rearing has been linked primarily to the smaller tributaries (Johnson 1963; Fraley & Shepard 1989). Dunnigan (1997) found that age 0 cutthroat trout in the Coeur d'Alene River basin of Idaho were generally restricted to first- to third-order streams. The distribution may be a response

to availability of suitable habitats, predation, or the influence of spring stream flows and patterns of scour (Johnson 1963; Lukens 1978; Dunnigan 1997). In any case, the pattern indicates spatial structuring of westslope cutthroat trout populations is also likely within river basins of a few hundred km^2.

The numbers of subadult and adult cutthroat trout observed in the mainstem rivers of the Coeur d'Alene basin declined to very low levels in the last 30 to 40 years (Lewinsky 1986). Because fish in the larger rivers are believed to be the migratory representatives of local populations associated with individual tributaries, the decline might represent an important loss of the potential for dispersal among those populations.

Working with collaborators, we hypothesized that if cutthroat trout in the Coeur d'Alene basin functioned as a metapopulation, extinctions among tributary populations would be more pronounced with increased isolation. Dunnigan (1997) found that the network of streams representing tributary patches often supported very low densities of cutthroat trout. Extrapolations based on available habitat indicate that many local populations must number fewer than 200 total individuals (BER, unpublished data). Despite the small size of these populations, 3 years of inventory including more than 90 tributary systems produced no evidence of a local extinction (i.e. all surveyed streams were occupied in all years). In 1996 following a large winter flood (approximately 100-year return interval, Beckwith et al. 1996), we resurveyed more than 50 tributaries and again found no evidence of local extinctions.

The persistence of tributary populations of cutthroat trout in this system may be explained in two ways. First, extinction and recolonization occurs very quickly (i.e., patchy population). Alternatively, even very small populations of westslope cutthroat trout are not prone to extinction through environmental variation on the scale we have considered. Analysis of genetic structuring among these tributary populations may provide a test of these alternatives. The absence of fish in the mainstem, however, and the persistence of westslope cutthroat trout in numerous small streams isolated by natural and human caused barriers (BER, unpublished data) support the latter alternative.

Discussion

The empirical evidence does not support a generalizable model of metapopulation dynamics for inland salmonids. The basic elements of spatial structuring and dispersal almost certainly are present in many systems, but the dynamics of these populations do not appear to be simple or consistent. Although much of the emerging information is consistent with metapopulation processes, those results can be interpreted in a variety of ways.

For example, the current demographic and distribution patterns may be recent (in ecological time) results in changing systems. Both Lahontan cutthroat trout and bull trout were more likely to be found in large or interconnected habitat patches. From that we suggest that local extinctions are more likely in small or isolated patches. That pattern is consistent with an extinction-colonization equilibrium, but we cannot exclude a second alternative: a regional decline or non-equilibrium system (Harrison & Taylor 1996), where the large or closely interconnected patches are simply the last to go extinct. Both Lahontan cutthroat trout and bull trout have declined throughout a large portion of their historical ranges. The condition of local habitats has been degraded and fragmentation has been aggravated by human-related disturbance (Rieman & McIntyre 1993; Coffin & Cowan 1995). We simply cannot be certain whether we are observing evidence of a metapopulation dynamic characterized by a balance between extinction and recolonization, or a deterministic slide toward growing local and regional extinctions (Doak & Mills 1994; Hanski & Simberloff 1996).

Our understanding of salmonids and metapopulations is constrained by the spatial and temporal scales over which they can be, or have been studied. Evidence that some local populations are prone to extinction without demographic support from neighboring populations does not mean that dispersal has been important in stabilizing the system. Genetic information for some bull trout populations, for example, suggests dispersal has been limited (Spruell et al. 1999). Alternatively, evidence of limited extinction and colonization in the past also does not mean these processes will not be important in the future. Conceivably, the loss and fragmentation of habitats can accentuate metapopulation processes where they were less important before. If dispersal is strong enough, a metapopulation dynamic may emerge in mosaics of remnant habitats.

It is important to consider that dispersal and straying rates probably are not stable through time but occur as punctuated events or vary with population densities, the degree of local adaptation, and the disruption or condition of local habitats or migratory corridors (Quinn 1993; Quinn & Unwin 1993; Walters 1997). Over longer time scales, variability in rates of dispersal may result as distributions of some species track long-term trends in habitat availability and suitability. For example, the geometry of bull trout habitats is apparently

influenced by climate. The current distribution of bull trout may reflect relatively recent climatic variation occurring on decadal scales (e.g. Pulwarty & Redmond 1997) or longer term expansion and contraction of habitat associated with the cooling and warming trends of the last several centuries (Stine 1996).

Given enough time and a source of colonists, expansion of populations into suitable habitats across whole river basins would seem almost certain for most salmonids. Whether dispersal can occur quickly enough or in the numbers necessary to influence local rates of extinction or even local dynamics on the time scales we observe is another question. Metapopulation dynamics are likely important within stream basins at the spatial scales we have considered here, but they may play out over centuries rather than years or decades.

The temporal scale we have defined may be more consistent with finer spatial scales than we have considered. Recent work with the response of fishes following catastrophic defaunation at relatively small spatial scales (10^1 to 10^3 m) shows that numbers of some species may recover very quickly (Detenbeck et al. 1992). For a variety of species, dispersal within streams can be an important element in the local dynamics of recovery (Armstrong et al. 1994; Dunham 1996; Gowan & Fausch 1996; Rieman et al. 1997). It is not clear, however, whether these observations represent dispersal among local populations or the local dynamics of a panmictic group in a patchy environment. Conceivably, local populations and the extinction-colonization dynamic of a metapopulation play out within streams at a smaller scale than we have considered in our work. It will be necessary to resolve the nature of population structuring at even finer scales than we have attempted to understand such results in the context of metapopulation theory.

Finally it is possible, and we think likely, that all of the above are true. Populations within river basins may be hierarchically structured (e.g. Kotliar & Wiens 1990; Wu & Loucks 1995) and temporally and spatially variable. For example, we have recognized dispersal and colonization on both very large (i.e. zoogeographic patterns) and small (river reaches following catastrophic events) spatial and temporal scales. This, combined with the heterogeneity of species and environmental characteristics, suggests a continuum of processes resembling metapopulation dynamics. At some locations, at some scales, with some species, and at some times, extinction and dispersal processes will undoubtedly influence the dynamics and distribution of salmonid populations.

Clearly, far more work is needed to understand the relevant scales of metapopulation processes for salmonids. Emerging patterns indicate the answers will not be simple. Important advances in our understanding of salmonids and metapopulations will require a host of empirical approaches, not only to define patterns, but to identify and quantify important processes and mechanisms as well. Our brief review suggests details necessary for understanding individual species and the complexity of metapopulation processes are generally lacking. What then, are the important issues that must be addressed?

For salmonids, we have shown that patches of suitable habitat and other landscape features can be delineated to consider the spatial structuring of local populations. Our examples of inland salmonids point to the importance of patch size and/or isolation to persistence of some populations (Rieman & McIntyre 1995; Dunham et al. 1997; Dunham & Rieman 1999). These patterns potentially reflect metapopulation structuring, but our understanding of processes that actually link local populations (i.e., metapopulation dynamics) remains limited.

Empirical studies of metapopulation dynamics in other animals have relied on time series of extinction and colonization events that occur over relatively short (less than a decade) time periods (e.g. Sjögren-Gulve & Ray 1996). For some inland salmonids at the spatial scale we have considered here it seems likely, however, that extinction and colonization may occur more slowly. Alternative approaches to understanding the spatial dynamics of inland salmonid populations and new work with anadromous forms are needed.

One possible alternative to direct study of extinction-recolonization dynamics is to indirectly estimate dispersal parameters from patterns of molecular genetic variation (e.g. Neigel 1997). High-resolution genetic markers such as DNA microsatellites offer the potential to define fine-scale relationships among local populations (Fontaine et al. 1997; Spruell et al. 1999). Direct tracking of individual movements by tagging studies also may contribute important information, but such studies likely underestimate actual levels of dispersal in metapopulations (e.g. Peacock & Smith 1997). Modeling of dispersal processes to identify patterns consistent with observed data (e.g. Karieva et al. 1997; Turchin 1998) also may prove useful, though we are unaware of specific applications to salmonid metapopulations. We caution, however, that with any of these methods precise estimates of migration parameters can be difficult to obtain (Ims & Yoccoz 1996), and that errors in estimation may produce misleading metapopulation and landscape models (e.g. Ruckelshaus et al. 1997).

Another alternative is to focus on dispersal processes and mechanisms, rather than estimation of specific patterns within metapopulations. For salmonids, dispersal appears to be intrinsically constrained by the tendency of fish to imprint on and home to natal habitats to reproduce (Quinn 1993; Cury 1994). Straying does, however, occur, and the ability of fish to disperse to and recognize suitable habitats can have important effects on population dynamics (LePage & Cury 1997). External constraints on among-habitat movement imposed by changes in landscape structure (e.g. Weins 1996; Yahner & Mahan 1997) and the ability of individuals (both adults and juveniles) to detect key habitats (Pulliam & Danielson 1991; Dunning et al. 1992; Schlosser 1994), such as refuge habitats (Northcote 1997), also may have strong effects. Contributions to a better understanding of proximate causes and ecological and evolutionary consequences of habitat selection and dispersal by salmonids (e.g. Jonsson & Jonsson 1993; Smith & Skulason 1996; Willson 1997) are needed.

Given the present limited understanding of salmonid metapopulations, we caution that application of unrealistic models may do more harm than good (see also Doak & Mills 1994; Hanski & Simberloff 1996). We see at least two issues.

First, our own experiences with land management issues and inland salmonids point to a critical problem for conservation: that of resolving the importance of contemporary metapopulation dynamics versus short or long-term changes in suitable habitat (see also Hanski & Simberloff 1996; Harrison & Taylor 1996). In essence, this is a question of how these fishes can track changes in availability of suitable habitat.

If new habitats are made available through protection or active restoration, colonization of that new habitat may lag behind due to the nature of, or constraints on, dispersal. Metapopulation structure implies, to varying degrees, that suitable habitats may not always be occupied. This creates problems for definitions of suitable habitat based on occurrence or standing crop of salmonids (Dunham & Rieman 1999). In a metapopulation context unoccupied, but suitable habitat is important. Habitat conservation and restoration are currently focused on occupied habitat with little knowledge of the importance of succession and patch dynamics (Reeves et al. 1995).

If habitat has been fragmented or lost and the potential for dispersal and recolonization is limited, lagged extinctions in presently occupied habitat also may be anticipated. When rates of local extinction lag behind rates of habitat loss, a "debt of extinction" is incurred (Hanski 1996), so even if further habitat loss is prevented, local extinctions will continue to occur until a new equilibrium between extinction and recolonization is established. To borrow a phrase, many extant local populations may indeed be the "living dead" if extinction debts are a reality. The implication is that conservation of existing habitats alone may not be adequate for the long-term conservation of some species.

Second, a metapopulation-based reserve system for one well-studied species likely will not be adequate for many others. It seems highly likely that there are important differences in the life history/dispersal, patch structure, and relevant scales among species. Throughout the Pacific northwest of the United States, multiple salmonids co-occur in the subbasins of interest to managers. Even if one could clearly define the metapopulation requirements of each species it seems likely that the resulting management scheme would be extremely complex if not impossible to implement.

We suggest that the primary value of metapopulation theory to conservation of salmonids is not in finding simplifying generalizations or providing minimum reserve designs, but in understanding the relevance of diversity and complexity of these species. The fact that salmonids exhibit complex life histories is a reflection of the diversity of habitats they live in. The interaction between spatial and temporal habitat heterogeneity and life history diversity is central to the concept of "risk spreading" (den Boer 1968; Dunning et al. 1992; Kozakiewicz 1995) in population biology: the idea that naturally diverse populations may have more stable dynamics in the face of environmental changes. Within suitable habitats, increased habitat heterogeneity and risk-spreading may explain why some salmonids are more likely to occur in larger or less isolated patches (Rieman & McIntyre 1995; Dunham et al. 1997; Dunham & Rieman 1999). At a larger scale, habitat heterogeneity and the structure of landscapes may also be a central component of metapopulation structure, dynamics, and persistence (Wiens 1996; Dunham & Rieman 1999). In particular, the interaction between dispersal of individuals and landscape characteristics may be critical (Pulliam & Danielson 1991; Schlosser 1991, 1995; Tyler & Rose 1994; Yahner & Mahan 1997).

Considerable work is needed to understand the implications and applications of metapopulation theory for salmonids. We suggest that the most important application, however, will be conceptual. Managers and biologists will likely be more successful in trying to understand and conserve key processes (for example dispersal and linkages between landscapes, life history, phenotypic diversity, and patch size requirements) that likely contribute

to persistence whether metapopulations exist or not than in designing minimal networks based on perceived, underlying metapopulation dynamics.

Resumen

1. La teoría de las metapoblaciones en su aplicación a las poblaciones de salmónidos ha despertado gran interés. Sin embargo, la evidencia empírica que permita evaluar o aplicar los conceptos metapoblacionales es escasa. A partir de los datos publicados sobre los ciclos biológicos de diversos salmónidos y de nuestro propio trabajo en *Salvelinus confluentus*, *Oncorhynchus clarki henshawi* y *Oncorhynchus clarki lewisi*, sugerimos que las generalizaciones simplistas en el caso de las metapoblaciones de salmónidos son inapropiadas.

2. La presencia de estructura espacial en las poblaciones y de mecanismos de dispersión es evidente, pero la importancia de los procesos de extinción y colonización probablemente varía con el ciclo biológico, la especie, la escala espacial o temporal, y las características geográficas. Por esta razón, es clave una mejor comprensión de las posibilidades de débito de extinción en metapoblaciones en desequilibrio, la dispersión y el papel de los hábitats adecuados aunque no ocupados.

3. En el caso de la conservación de salmónidos sugerimos que serán de mayor utilidad los esfuerzos destinados a entender y conservar procesos clave que probablemente influyen en la viabilidad de sus poblaciones o metapoblaciones que aquellos enfocados al diseño de reservas mínimas de hábitat basadas en la teoría de las metapoblaciones.

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