

**Abstract.**—Because of their tendency to return to natal streams, salmonid populations have often been viewed in ecological isolation, although the notion of an evolutionarily significant unit (ESU) recognizes dispersal on evolutionary time scales. We investigated the consequences of dispersal (straying) on an ecological time scale where straying creates a metapopulation structure for salmonid streams within an ESU. We developed a simple model for salmonid metapopulations, focusing on source and sink populations, and used the model to highlight the dangers of ignoring this structure in conservation efforts. We show that exactly the wrong conservation efforts may occur if metapopulation structure exists but is ignored.

## The dangers of ignoring metapopulation structure for the conservation of salmonids

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The U.S. National Marine Fisheries Service (NMFS) Status Review of Coho Salmon (*Oncorhynchus kisutch*) from Washington, Oregon, and California (Weitkamp et al., 1995) formalized the agency's approach to defining both the boundaries and conservation status of distinct segments of salmonid populations for potential listing under the Endangered Species Act. With this approach, originally developed by Waples (1991), a population or group of populations is considered distinct if they are "... substantially reproductively isolated from conspecific populations," and if they are considered "... an important component of the evolutionary legacy of the species" (Weitkamp et al., 1995, p. 3). A distinct population or group of populations is referred to as an evolutionarily significant unit (ESU) of the species.

For a group of populations to be classified as an ESU, the populations must be reproductively isolated from other populations but not from each other. An ESU also implies successful dispersal and reproduction between populations on an evolutionary time scale. A metapopulation is a group of populations (demes) linked by dispersal of indi-

viduals on a shorter ecological time scale such that dispersal affects both the genetics of the individual demes and their abundance and dynamics (Levins, 1969; Ruxton, 1996; Ruxton and Doebeli, 1996). To maintain consistency with the ecological literature, we have used the term "metapopulation" to refer to the group of populations or demes, and the term "population" or "deme" (often used interchangeably, see Policansky and Magnuson, 1998) to refer to one of the individual populations that make up the metapopulation. ESUs and metapopulations overlap on the continuum of population structures. Although a metapopulation will always compose part of, or the entire, ESU, an ESU does not have to contain any metapopulation structure. Dispersal between demes within a metapopulation must be great enough to affect the dynamics of the demes and the recolonization of habitats of extinct demes. Within an ESU, dispersal must only be great enough to contribute to the genetic make-up of component populations; it does not have to lead to recolonization events or affect the population dynamics.

Salmon typically return to their natal streams to spawn. However,

some individuals stray to streams other than their natal one, and those streams may be inhabited or uninhabited by other conspecific populations (Ricker, 1972; Quinn, 1993). Indeed, straying constitutes the process by which salmonids colonize new habitats (Milner and Bailey, 1989; Wood, 1995). Individuals that stray during the spawning migration may thus serve as the mechanism for dispersal between salmonid populations on both an evolutionary and ecological time scale.

Reliable estimates of the magnitude of straying are rare and span a wide range of values across and within species (Quinn, 1993; Pascual and Quinn, 1994). Quinn and Fresh (1984) documented a straying rate of 1.4% in their study of wild chinook salmon (*Oncorhynchus tshawytscha*) from the Cowlitz River Hatchery, Washington. Quinn et al. (1991) estimated hatchery straying rates ranging from 9.9 to 27.5% for five populations of autumn chinook on the Columbia River. Heard (1991) estimated that, in general, nearly 10% of wild pink salmon (*Oncorhynchus gorbuscha*) stray from their natal streams. Labelle (1992) estimated that approximately 4.7% of individual coho salmon strayed between nine separate streams along the coast of Vancouver Island, British Columbia, but that straying could be greater than 40% for some streams in some years. Genetic studies such as that of Gall et al. (1992) suggest that the average number of migrants exchanging genes per generation ( $Nm$ ) in west coast Chinook salmon populations is on the order of 5–15 individuals.

Because the incidence of straying is common and the magnitude of straying is so variable, it is quite likely that metapopulation structure could exist for at least some salmonid populations. In fact, the National Research Council's report on Pacific Northwest salmonids recognizes that "... maintaining a metapopulation structure with good geographic distribution should be a top management priority to sustain salmon populations over the long term" (NRC, 1996, p. 8). Given the geographic scale of the straying documented in the previous studies, compared with the range of an ESU (note that the entire West Coast comprised only six ESUs), it is possible that a single ESU may even contain multiple metapopulations, as would be expected because ESUs are explicitly evolutionary constructs, whereas metapopulations are explicitly ecological constructs.

In this paper, we investigate the implications of metapopulation structure for conservation efforts given a variety of spatial scales. In particular, we identify the problems such structure could cause for managers if it left undetected. If one is concerned strictly with the risk of extinction for a species, metapopulation structure may be quite beneficial

(Levins, 1970; Hanski and Gilpin, 1991; Hanski, 1994; Ruxton, 1996; Ruxton and Doebeli, 1996). Because the metapopulation occurs in patches (each of which contains a deme with its own probability of extinction) and because these demes are connected through dispersal, if any single deme becomes extinct, then there is a nonzero probability that the patch will be recolonized by individuals from another deme. Over time, an individual patch may therefore experience multiple extinctions and recolonization events. These events result in the metapopulation as a whole persisting far longer than any one of its individual demes. Potential problems arise when one is concerned not just with the risk of extinction but with the management (and therefore monitoring) of these populations.

In the most simple metapopulation model, one assumes that all demes, and the patches they inhabit, are identical (Levins, 1970). This, however, need not be the case, and in the real world, is likely not to be the case. One metapopulation model that takes such variation into account is the source-sink metapopulation model (Pulliam, 1988). In this model, sink habitats are patches where local mortality exceeds local reproduction (so that  $R_0 < 1$  or  $r < 0$ ). In other words, without individuals immigrating to the patch, a sink population cannot sustain itself. Source patches, on the other hand, are patches where local reproduction exceeds the sum of local mortality and emigration (so that  $R_0 > 1$  or  $r > 0$ ). Populations in source habitats can persist without the populations in the sink habitats, but the opposite is not true. There are no assumptions regarding the relative abundance of individuals between these source and sink patches. In fact, it is quite possible for the sink patches to have larger populations than source populations (Pulliam, 1988). For example, if competitively dominant individuals hold territories of fixed size (as is the case with some bird species), a source habitat would be highly productive, yet would have a constant population size because all subdominant individuals would be forced to disperse. If this dispersal rate into the sink habitats were greater than the natural rate of decline (the difference between births and deaths) in the sinks, then sink habitats could contain more individuals than the source habitats. In such a case, undetected metapopulation structure could lead managers astray.

When metapopulation structure (especially source-sink dynamics) exists, the abundance of a species in an area can be disconnected from the specific survivorship and fecundity rates of that area owing to the effects of immigration. If ignored, this disconnection poses two problems for managers, both of which are made worse if the jurisdiction of the manager does

not cover the complete metapopulation. First, if managers are looking strictly at the abundance of individuals, they could be lulled into a false sense of security. The size of the demes in the source and sink habitats could be relatively constant despite the fact that, without the demes in the source, the demes in the sink would become extinct. Brawn and Robinson (1996) uncovered this very scenario with Neotropical migrant birds in Illinois.

The second problem is even more insidious. If deme abundance is no longer a good indicator of habitat quality, managers could be led into conserving the wrong type of habitat (van Horne, 1983; Pulliam, 1988). Gowan and Fausch (1996) demonstrated how this could occur regarding the effects of habitat changes on the demography of a variety of trout species in Colorado, although they did not discuss their results in terms of metapopulations. Over an eight-year period (four generations of trout), Gowan and Fausch (1996) discovered that the addition of woody debris in treatment areas significantly increased the number of individuals and the total trout biomass in treatment areas in relation to the control areas. However, with the aid of fin marks (clipped fins) and individual tags, they discovered that survival, individual growth, and recruitment rates in the treatment areas were not significantly different from those in the control areas. Immigration from outside the study area to the treatment sites was solely responsible for the increase in abundance and total biomass. If Gowan and Fausch (1996) had not been able to account for immigration to the site, they would likely not have been able to discern the true effects of the addition of woody debris and would have likely mistaken increased density for increased habitat productivity (cf. Hunter, 1991). Although source-sink metapopulation structure was not the cause of these results, such an example demonstrates how reliance on abundance or density estimates can lead managers astray when immigration or emigration is not taken into consideration.

Those faced with the responsibility of managing salmonid populations may encounter these very problems and issues. In the remainder of this paper, we develop a model to help focus ideas about the potential dangers of undetected metapopulation structure for salmonid conservation.

## Materials and methods

### The model

The model is simple, and the form of the model was chosen for ease of comprehension. We found that even

such a simple model was adequate to illustrate the possible consequences of ignoring metapopulation structure.

We considered a group of generic salmonid demes that reside in streams that are distributed evenly along some waterway but that are close enough so that straying between any of the two groups is possible (though not necessarily with equal probability). The scale was completely generic. The streams could be tributaries to a single river, rivers within a watershed, or even separate watersheds. Next, we numbered these streams consecutively along this waterway. Each deme was then indexed by the number associated with the stream in which it resides (e.g. deme 4 resides between deme 3 and deme 5 along this waterway). For computational purposes, we considered 10 streams, which is equivalent to a metapopulation consisting of 10 demes spread over 10 patches. Assuming that density-dependent effects could be ignored (which, except for Allee effects, would be the case for any recovering population), the fundamental variables are

- $N(i, t)$  = the deme abundance in stream  $i$  in year  $t$ ;
- $r(i, t)$  = the per-capita reproduction in stream  $i$  in year  $t$ ;
- $s(j, i, t)$  = the number of fish that stray from their natal stream  $j$  to stream  $i$  in year  $t$ ; and
- $f$  = the fraction of fish that stray from their natal stream (assumed equal for all demes).

For simplicity's sake, we assumed that strays have the same reproductive potential as nonstrays in a given stream. This assumption decreases the parameter space but does not affect overall dynamics of the model. It does, however, limit the direct applicability of our specific examples to streams that are relatively close in proximity, yet, as will be explained, does not diminish the danger for management at the watershed, basin, or even ESU level. By incorporating an additional parameter to account for the differential reproductive potential, some of the dynamics would simply have been dampened, making them more difficult to perceive. Therefore, the population dynamics for a deme are

$$N(i, t+1) = r(i, t) \left\{ N(i, t) (1 - f) + \sum_{j \neq i} s(j, i, t) \right\}. \quad (1)$$

As with differential reproduction, the assumption that there are more complicated population dynamics (e.g. Ricker stock-recruitment relationships) would not change the basic message of our paper but would make it harder to perceive. In a more compli-

cated model, or one designed for a nongeneric salmonid, the model would be indexed by generation time instead of year, but the potential problems described in this paper would still apply.

We assumed  $s(j, i, t)$  is an exponential function of the distance between stream  $i$  and  $j$  (see Hanski, 1994). We assumed that the streams are evenly spaced along the waterway and numbered consecutively, so that the distance between stream  $i$  and stream  $j$  is proportional to  $|i-j|$ . Therefore, the number of individuals straying from stream  $j$  to stream  $i$  is

$$s(j, i, t) = \frac{N(j, t) f e^{-m|i-j|}}{\sum_{k \neq j} e^{-m|k-j|}} \quad (2)$$

where  $m$  defines the rate at which straying decreases with distance, and the denominator is a normalization so that all strays end up in a stream (i.e. none are lost to the system).

We assumed that per-capita reproduction rate of each deme is a function of some baseline rate of per-capita reproduction that is equal for all streams (e.g. ocean conditions and harvest) plus a function of a component of the habitat that contributes positively towards per-capita reproduction (e.g. width of the riparian zone) and a function of a component of the habitat that contributes negatively to per-capita reproduction (e.g. road density). If  $z_0$  is the baseline per-capita rate of reproduction and  $z_1(i, t)$  and  $z_2(i, t)$  are the amounts of the beneficial and detrimental habitat components for stream  $i$  in year  $t$ , then the per-capita rate of reproduction for stream  $i$  in year  $t$  is modeled as

$$r(i, t) = z_0 + g \left\{ 1 - e^{-z_1(i, t)} \right\} - b \left\{ 1 - e^{-z_2(i, t)} \right\} \quad (3)$$

where  $g$  = the maximum increase in the per-capita reproduction due to the beneficial habitat component; and

$b$  = the maximum decrease in the per-capita reproduction due to the detrimental habitat component.

As  $z_1(i, t)$  increases,  $e^{-z_1(i, t)} \rightarrow 0$ , so that the effect of the beneficial habitat component approaches an asymptote at  $g$ . Similarly, the detrimental habitat component approaches an asymptote at  $b$ . Therefore,  $r(i, t)$  is constrained to lie between  $z_0 - b$  and  $z_0 + g$ . When  $r(i, t)(1-f) \geq 1$ , the deme is a source population (rate of change due to per-capita reproduction counteracts the rate of change due to emigration); when  $r(i, t)(1-f) < 1$ , the deme is a sink population (it

can not sustain itself without immigration from other streams).

To include the effects of temporally varying environments, we added

$$q \sin\left(\frac{2\pi t}{w}\right)$$

to the per-capita reproduction. This causes per-capita reproduction to change sinusoidally with a maximum change of  $2q$  with a  $w$ -year period. Such oscillations could be due to events such as El Niño (Pearcy, 1992) and essentially represent changes in the baseline conditions ( $z_0$ ) over time.

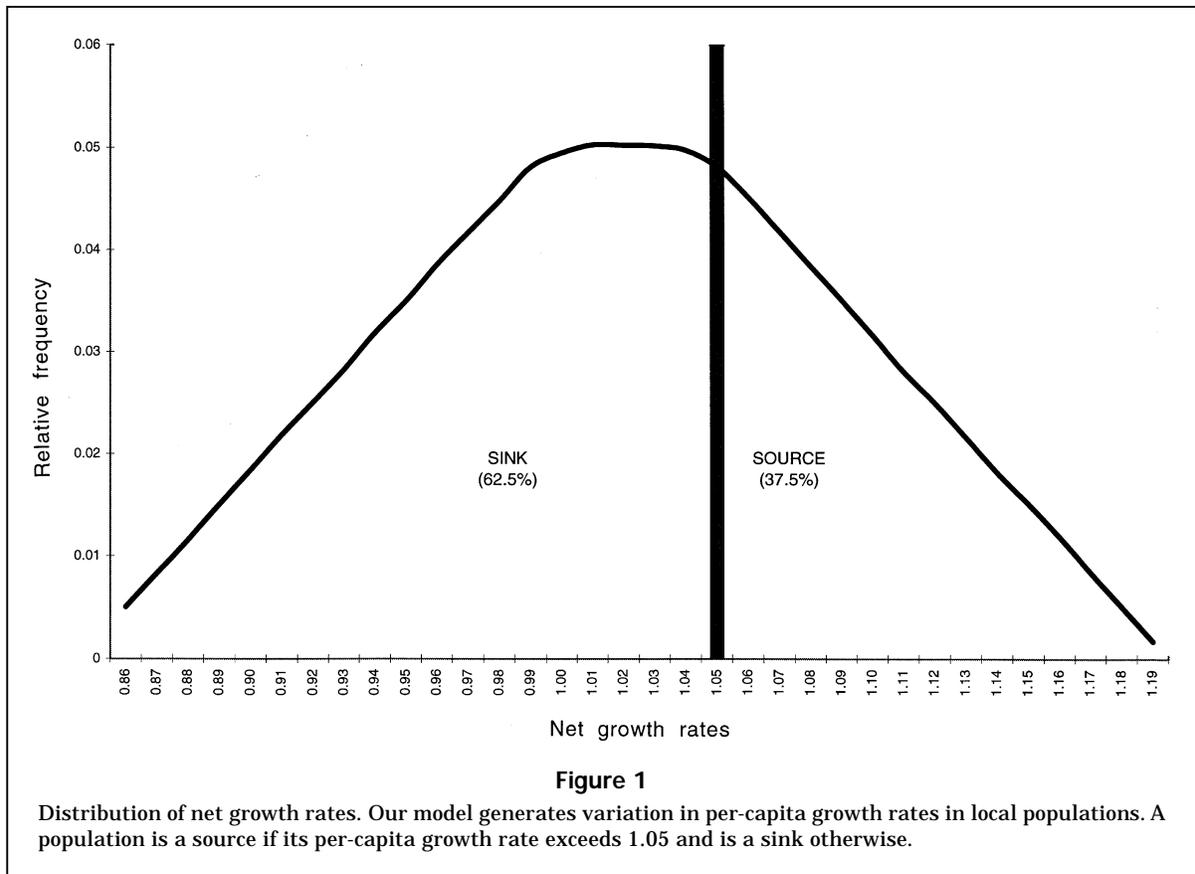
### Simulations

We set the baseline per-capita rate of reproduction with  $z_0=1$ ,  $g=0.2$ , and  $b=0.15$ . Thus per-capita reproduction was constrained to  $0.85 \leq r(i, t) \leq 1.2$ . We drew the  $z_1(i, 0)$  and  $z_2(i, 0)$  from a gamma distribution with parameters 1 and 1 (Hilborn and Mangel, 1997).

We set  $f = 0.05$  for all populations. This value lies within the ranges found by most of the previously mentioned research on salmonid straying rates. Streams were labeled as sources and sinks on the basis of their initial per-capita rate of reproduction given this straying rate. Therefore, a source population was one with an initial per-capita rate of reproduction greater than or equal to 1.05, and a sink population was one whose rate was less than 1.05. With these parameters, about 40% of the streams were sources and 60% were sinks, as would be the case for a heavily impacted region (Fig. 1). We set  $m = 0.1$ .

The initial deme abundance for each stream was assumed to be proportional to the initial per-capita reproduction rate for that stream, even though such relationships may not hold over time (van Horne, 1983). As such, the initial deme abundance,  $N(i, 0)$ , was set equal to  $100r(i, 0)$ . We simulated each metapopulation over a 100-year period, using four scenarios with at least 150 replications for each scenario:

- 1 All parameters were constant over the 100-year period;
- 2 Starting in year 5, for all initial source populations ( $r(i, 0) \geq 1.05$ ), the good habitat component ( $z_1$ ) decreased by 5% of its value from the year before, and the bad habitat component ( $z_2$ ) increased by 5% of its value from the year before.
- 3 Same as scenario 2, except that all habitats with  $r(i, 0) > 1$  were degraded.
- 4 Temporally varying environment was incorporated into scenario 2. In this case, the baseline per-capita rate of reproduction ( $z_0$ ) oscillated between 0.95 and 1.05 over a 20-year period.



## Results

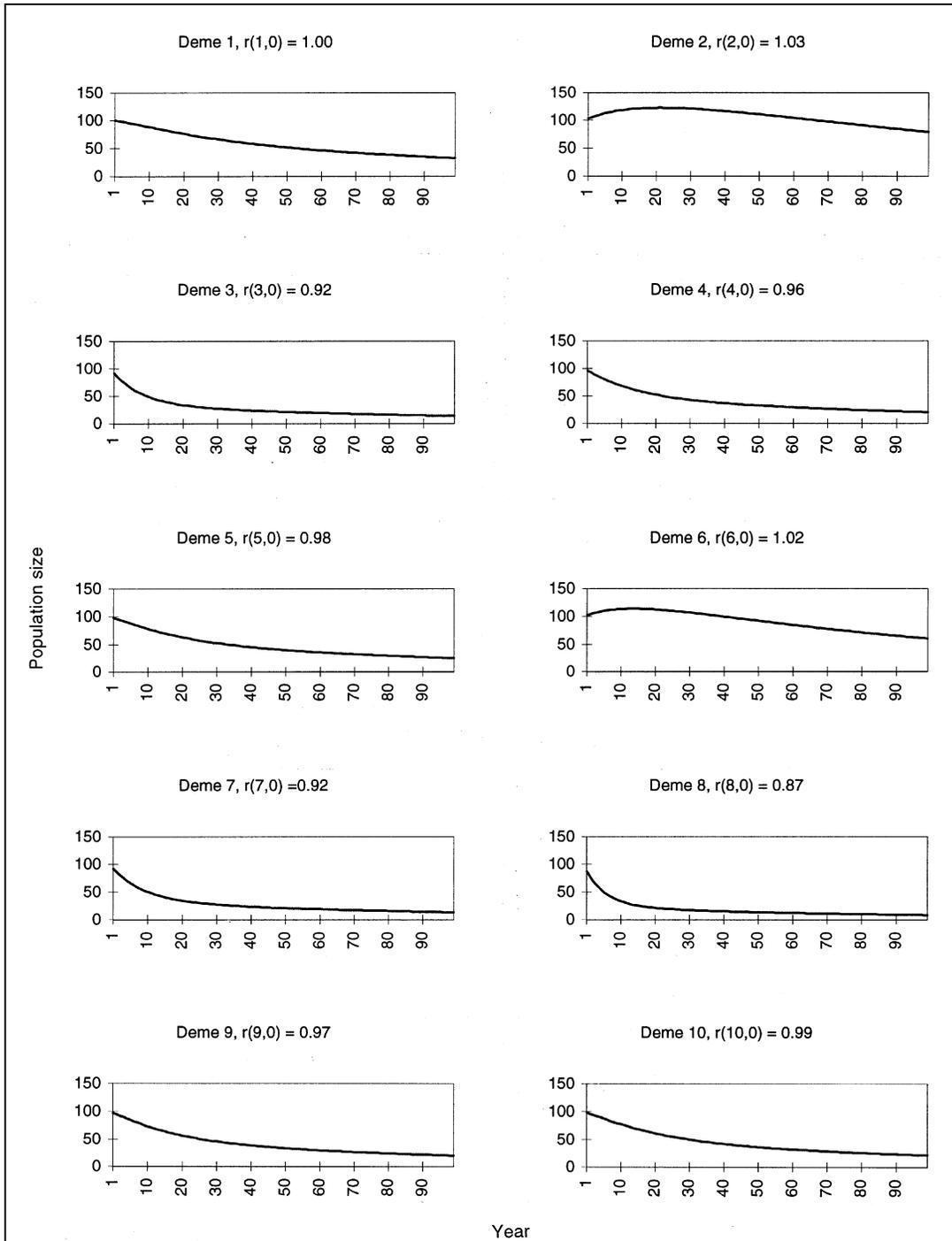
When habitats are constant over the simulation period, exponential growth occurs 98% of the time. Because no density dependence was incorporated in the model, demes in the source habitats increased exponentially, as did the number of strays from these sources. Such a situation could occur if, for instance, harvesting pressure was decreased on a deme that had been severely overharvested in the past (leading to low abundance) but whose habitat was relatively pristine (maintaining high productivity). This results in all dynamics in the sink populations being obscured by the massive number of immigrants.

It is possible that all the streams constitute sinks (all  $r(i,0) < 1.05$ ); this occurred in 1.3% of the simulations. In this case, there is still the possibility that the metapopulation as a whole could persist for decades before all populations began to decrease (Fig. 2). The reason for this persistence is that individuals that stray are lost only to their natal stream, not to the metapopulation as a whole. The case shown in Figure 2 results when the losses due to some habitats (where  $r(i,t) < 1$ ) are nearly offset by production in other habitats (where  $r(i,t) > 1$ ). Forty percent of

the all-sink metapopulations produced populations that did not decrease over the course of the 100-year simulation. If we had incorporated a parameter to represent decreased reproductive success of strays, the incidence of nondecreasing, all-sink metapopulations would have been lower.

In scenario 2 (Fig. 3), the source populations (demes 3, 4, and 5) initially increased exponentially but eventually began to decrease as the habitat degradation increased. Habitat degradation leads to peaks in local deme abundance (Fig. 4A). The mode of this distribution was around year 20 despite the fact that habitat degradation began in year 5. Furthermore, in over 3% of the sources, deme sizes increased throughout the 100-year simulation.

The population trajectories for the sink habitats were less intuitive (Fig. 3). None of their habitat components changed, yet some demes increased (deme 1) or stayed constant (deme 9) over a number of decades, whereas others decreased. The result depends on the proximity to sources (noting that deme number translates to the location of the deme along the waterway), the per-capita rate of reproduction in those sources, and the sink's own per-capita rate of reproduction. Over 9% of the sink habitats never attained

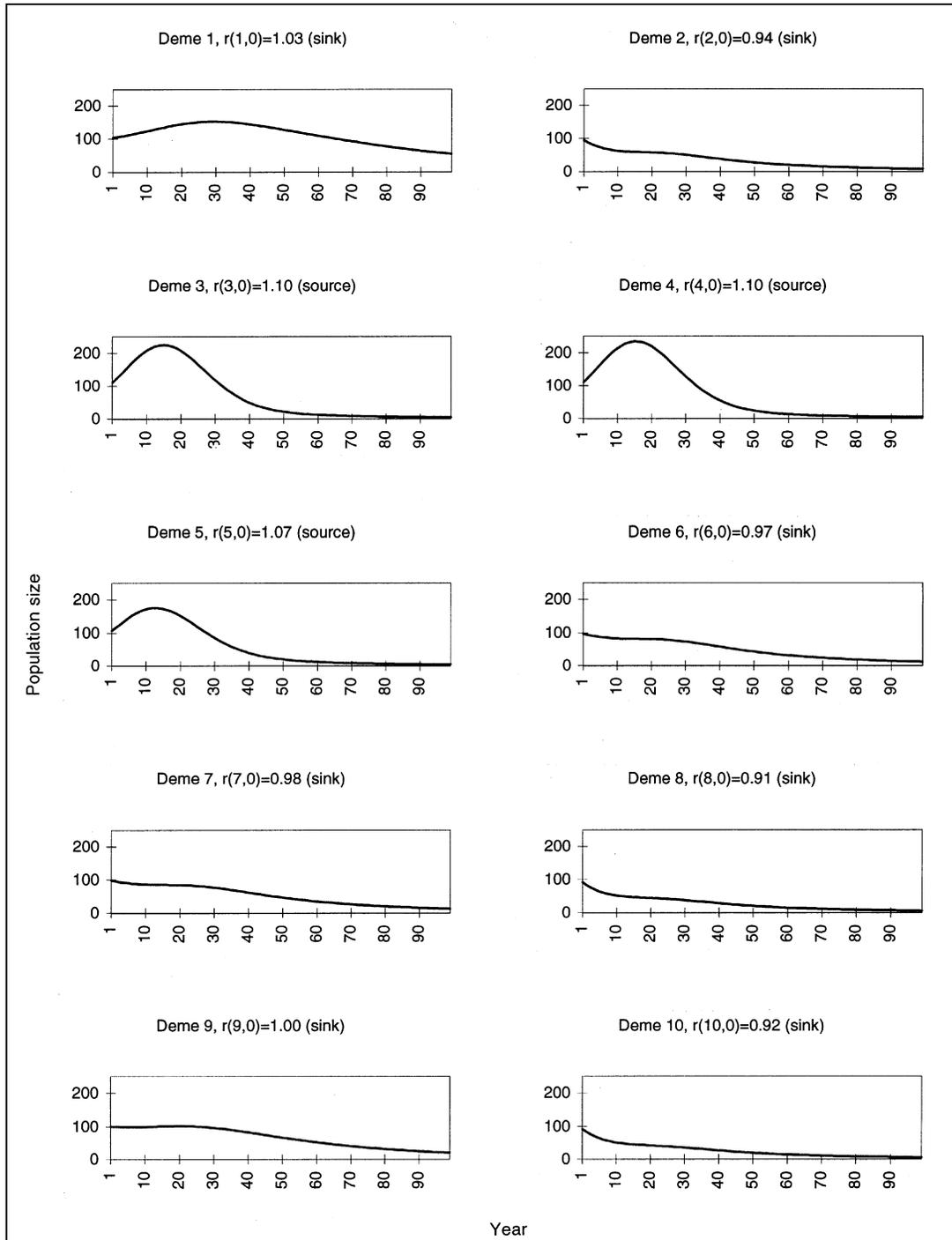


**Figure 2**

The dynamics of the metapopulation when all local populations are sinks. With scenario 1 or 2 (see "Simulations" section), metapopulation structure and dispersal actually lead to an increase in some population sizes over the short term, before they decline.

deme sizes larger than their initial deme size, but nearly 7% of the demes in sink habitats continued to increase over the entire simulation (Fig. 4B). The fact that deme sizes in some sink habitats do not decrease

over the simulation period is a result of the time of the simulation in relation to the rate of habitat degradation in the sources. If the simulations had been longer, all habitats would eventually have reached

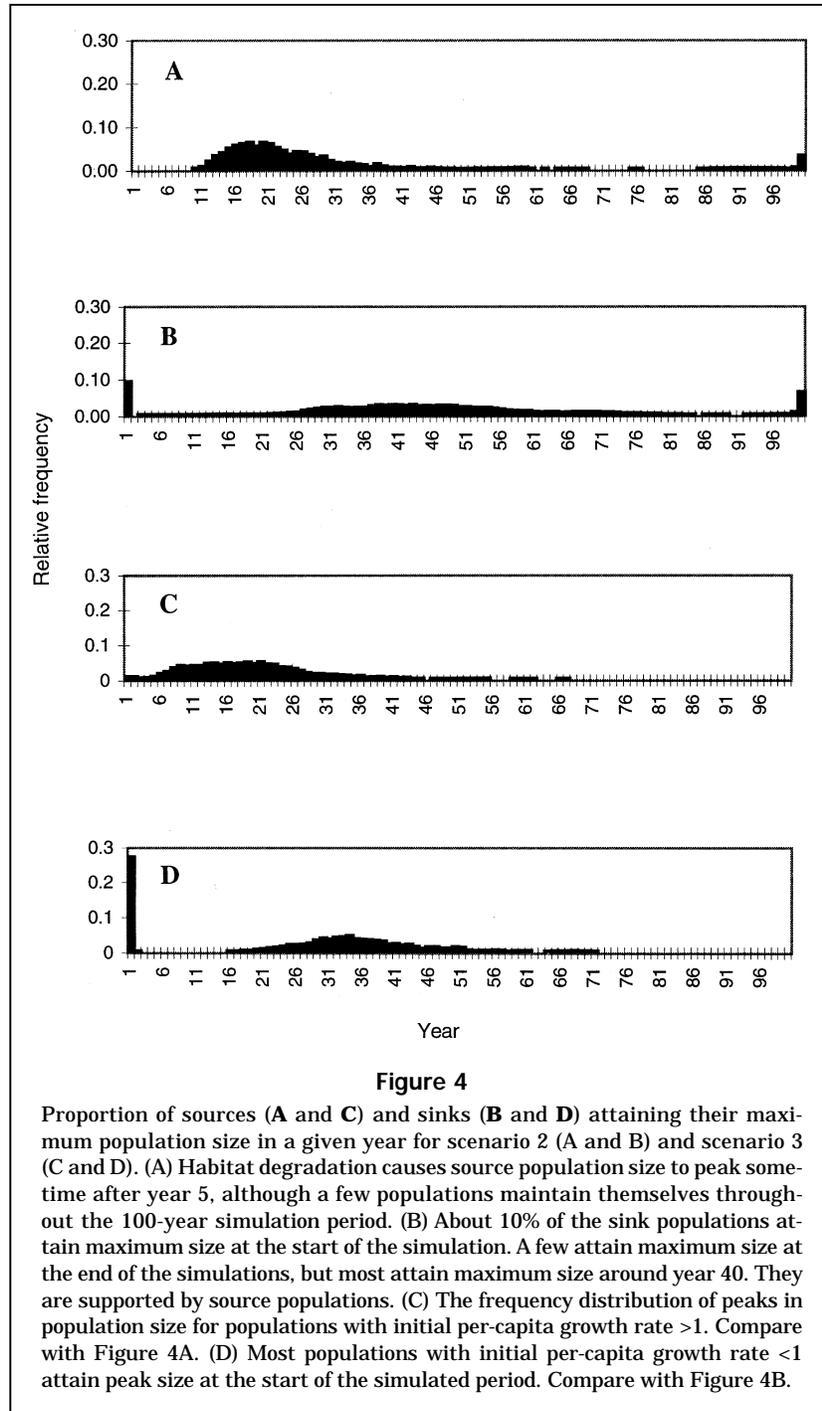


**Figure 3**

The dynamics of the local populations when some are sources and some are sinks. With scenario 2 (see "Simulations" section), as habitat degradation proceeds (starting in year 5), habitats for source populations slowly become degraded and end up as sinks.

the state of being sink habitats, which would then have resulted in only a few instances of sustained or increasing metapopulations (as described above). Because the number of migrants from one deme to

another decreases with distance, the year in which the maximum deme size is attained by the sink decreases as the distance from a source increases; thus the sinks rely on source populations for their viabil-

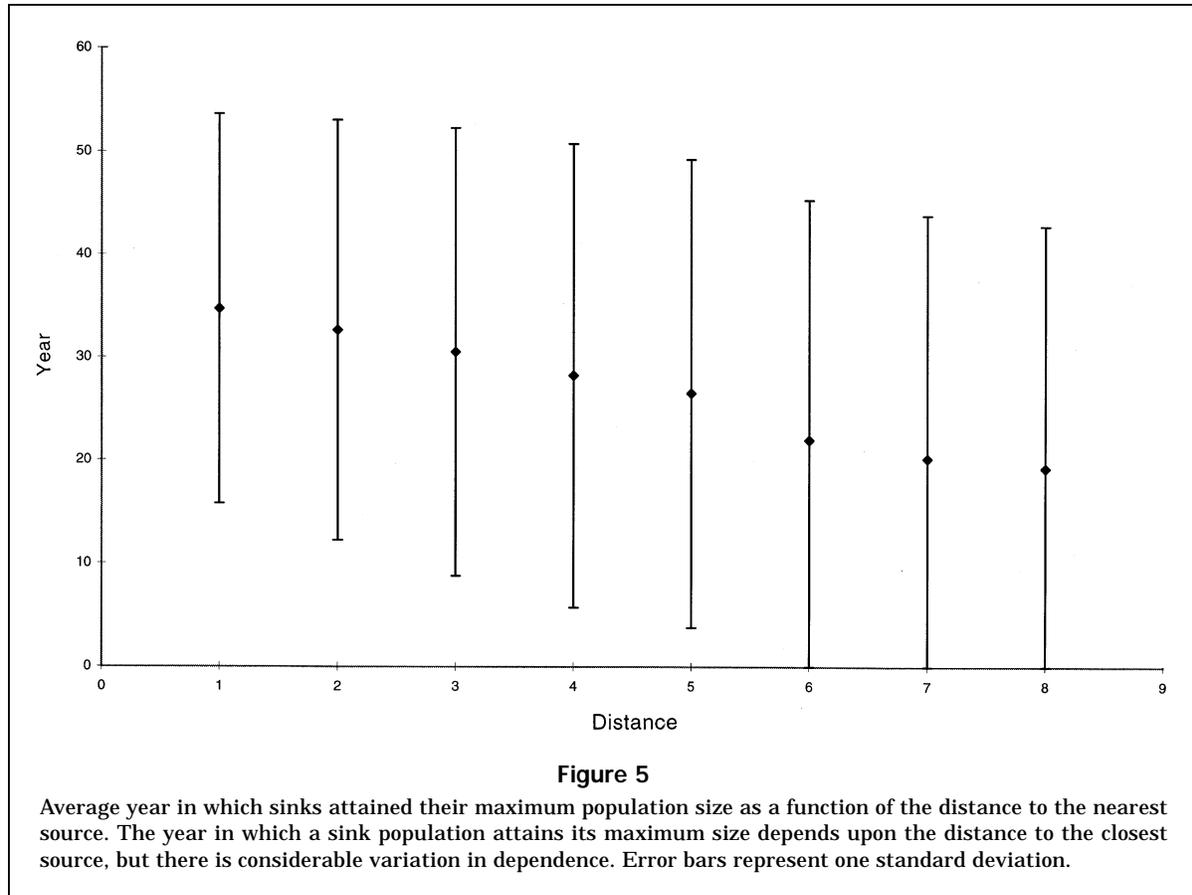


ity (Fig. 5). The variance about these points is due not only to the per-capita reproductive rate of the sink and its nearest source but also to a failure to account for the location of any other sources that may be of equal or greater distance from the nearest source and thus contribute to the sink's dynamics.

When all demes with initial per-capita growth rates greater than one are affected by habitat degradation,

declines in deme size occur more frequently, more rapidly, and sooner than in the previous case (Figs. 4 and 6). In this scenario, 100% of the demes were driven towards extinction.

When an oscillating environment is incorporated, the general trends in abundance are similar to those in scenario 2, but now each deme also tracks the environment (Fig. 7). All sources (demes 3, 5, and 7)



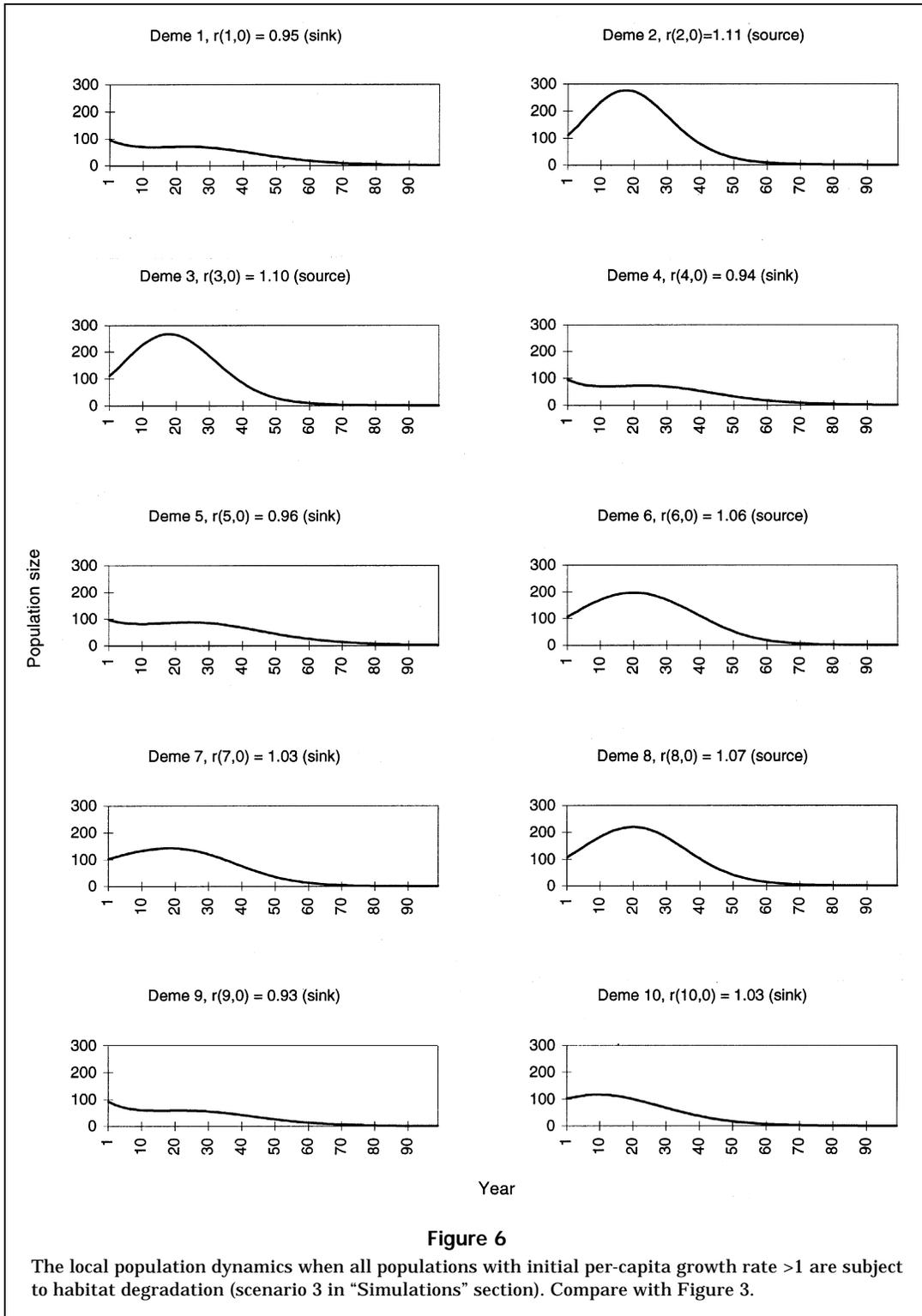
initially increase but then decrease as habitat degradation progresses. Some demes in sink habitats, such as demes 1 and 4, were relatively stable if not increasing over a fair portion of the simulation period before declining towards extinction.

## Discussion

Undetected metapopulation structure in salmonid populations may obscure the signals that managers use to determine the need for conservation action. Abundance trends, either absolute numbers or simple indices of abundance, constitute the primary input into analyses used for fisheries management and decision-making (Hilborn and Walters, 1992). The majority of these techniques assume that the population in question is a closed system, that any immigration or emigration can be considered negligible.

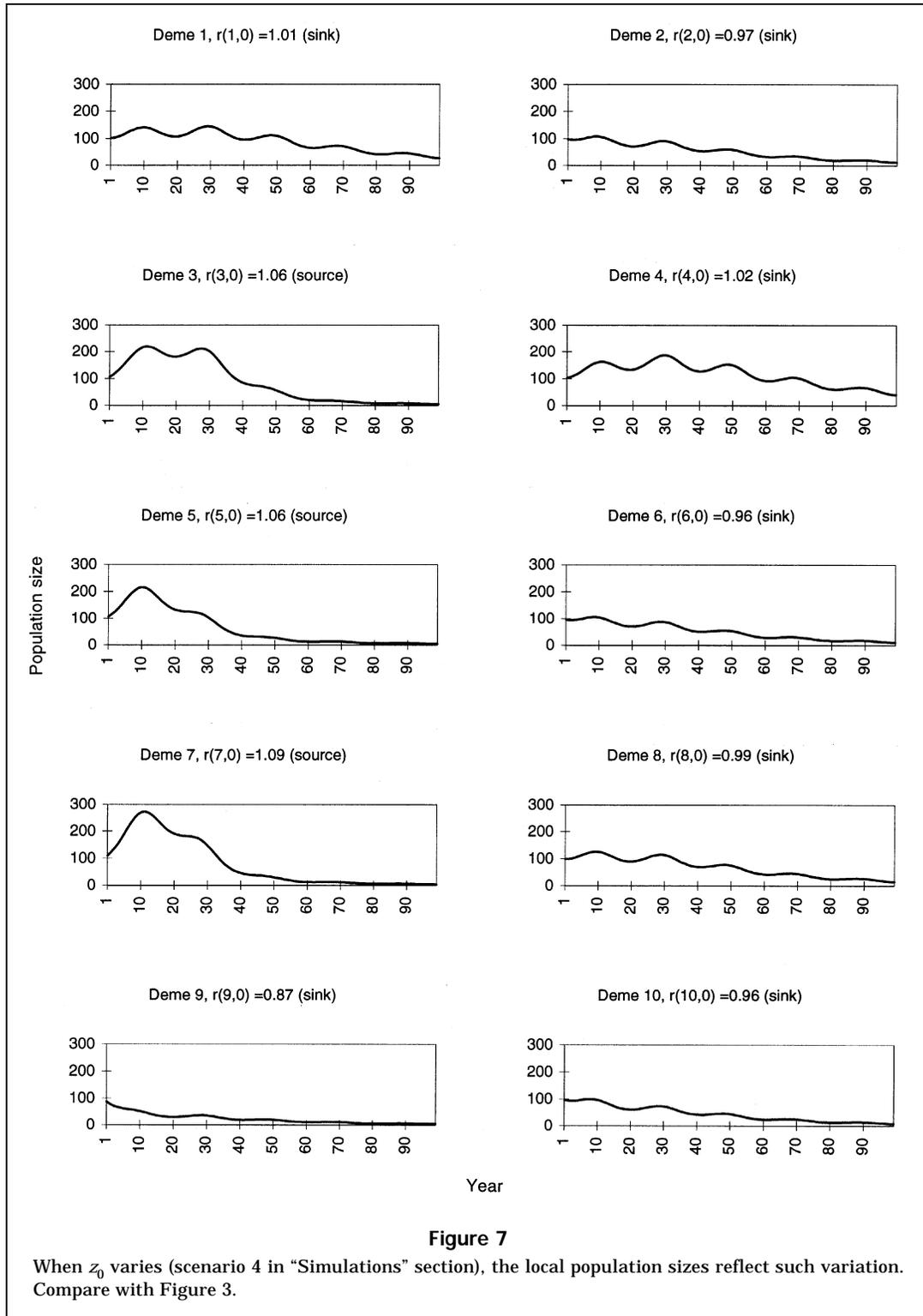
In California, Oregon, and Washington, estimates of population or run size for most salmonid species are commonly based on number of spawning fish or redd counts taken from index reaches or streams (WDFW, 1994; ODFW, 1995; Weitkamp et al., 1995).

The absolute numbers of spawning fish or redds counted in these index streams, which incorporate only a minute portion of the available spawning habitat within the watershed, are then used to extrapolate watershed- or basin-level abundance estimates, the very estimates upon which managers base their decisions. In fact, in their discussion on the data available for assessing the population size and risk of extinction for coho salmon along the west coast of the United States, Weitkamp et al. (1995, p. 106) stated “. . . where [stream] surveys were conducted, they are the best local indication we have of population abundance trends.” Index reaches and streams such as these are precisely the situation modeled in the specific examples discussed in this paper; straying between these reaches is likely and differential reproductive success between strays and natal fish may not occur. The NMFS’s analysis of coho salmon populations considered short- and long-term trends in abundance to be the main indicators for the risk of extinction but avoided using estimates based on index streams (Weitkamp et al., 1995). Using the trends in abundance for an entire ESU, Weitkamp et al. (1995) attempted to avoid the problems associated with the



assumption of a closed-system. However, depending on the time scale of the data available and the decrease in reproductive success for strays, undetected metapopulation structure could still cause problems. The second

problem arises because metapopulation structure can disconnect the abundance-habitat quality relationship. This could lead managers to make erroneous inferences regarding the habitat requirements for a species. The



sample metapopulations from the simulations provide demonstrations of how this may occur.

Figure 3 demonstrates one example where metapopulation structure could obscure management sig-

nals. Keep in mind, there is neither density dependence, observation error, nor stochasticity in the population dynamics, and a deme could represent an index reach (conforming to our uniform reproductive

success assumption) or an entire stream (where the uniform success assumption may be less accurate). If a manager had the entire time series data for all of the demes, the problem (though not the solution) would be evident; all demes would have declined significantly. Suppose, however, the manager is currently in year 30, and has only 25 years of data (years 5–30). Over that time period, all demes in sink habitats would be relatively stable or decline only slowly, even though none could sustain themselves without immigrants. In fact, deme 1 had been increasing until year 30. The demes in the source habitats, however, showed the effects of habitat degradation. Seeing these trends, the manager could perhaps stabilize these demes and thus inadvertently save the entire metapopulation. Still, the true risk for the sink populations would be unknown to the manager. The sink populations would appear stable not because they were in good condition but rather because of their interconnectedness with one another and the source populations.

Rieman and McIntyre (1995) suggested that a similar process is occurring with bull trout (*Salvelinus confluentus*) populations in Idaho. Although bull trout were found to use small streams, they do so only at a very low frequency. Rieman and McIntyre (1995) concluded that the presence of trout in these streams may be influenced by habitat preference but that these populations depend on dispersal of individuals from larger streams for their sustainability.

The addition of a varying environment clouds the picture even more (Fig. 7). The manager must now distinguish between decreases due to environmental factors and decreases due to factors that can be controlled. Imagine a manager starting in year 1. How can one recognize that the metapopulation is collapsing due to anthropogenic effects and not simply to environmentally induced effects? When would the alarms sound? Probably not until sometime after year 30, when even the most historically productive demes do not begin to increase. Seven out of ten of the demes could not maintain themselves without immigration, there is neither observation error nor stochasticity, and it would still take over 25 years of habitat degradation before the problem was noticed and the alarms sounded.

These problems become even more serious when management boundaries do not coincide with metapopulation boundaries or when only a portion of the metapopulation is used as index streams, as is likely the case. In such a situation, a manager will be concerned with, have jurisdiction over, and maybe have data on some subset of the metapopulation. Returning to Figure 3 (where managers do not have to deal with fluctuating environments), imagine if a manager had responsibility, and therefore data, for

only demes 6, 7, 8, 9, and 10, which are nevertheless a significant portion of the metapopulation. Between years 5 and 30, all demes were relatively stable, despite the fact that without immigration, even the most productive deme (deme 9) would decrease at a rate of 5% per year. After year 30, all these demes begin to decline. The manager would, of course, begin looking at these demes to try and see what was causing this decline; a good manager would try to find what had changed. In fact, nothing has changed with these demes; they have exactly the same rates of per-capita reproduction and straying over the entire simulation. Only the number of immigrants has changed. Without looking beyond their own jurisdiction or at streams other than the index streams, managers would not find the true cause for the change in dynamics. As the number of demes that are used as index streams or that lie within a manager's jurisdiction decreases, the likelihood of such a problem increases. Considering that over 90% of the sink populations increased in size during some portion of the simulation time horizon (i.e. their maximum size was reached sometime after year 1, Fig. 4B), the fate of sink populations has as much, if not more, to do with the health of the demes in other habitats as with the quality of their own habitat.

Another problem associated with undetected metapopulation structure arises directly from this last example. A manager may see a change in the dynamics in the populations and look for the cause. However, the cause of this change is outside the manager's jurisdiction or data set; it is not local. If the manager looks only for local causes for this change, she or he is likely to find some variable that is correlated with this cause and possibly infer local causality. Having attributed causality to a local variable, the manager would likely start funding projects to fix the perceived problem in the correlated variable. If one is lucky, very lucky, this variable might have some relationship to the per-capita reproductive rate and thus improve the situation a bit. This might, then, slow the rate of decline, but because it is not the true cause of the decline, the situation would likely continue to deteriorate. How much of a manager's limited resources might be spent on such activities before the true causal relationship was discovered? The study by Gowan and Fausch (1996) suggests that this problem may be occurring with habitat enhancement projects for trout in Colorado; managers promote the addition of woody debris in streams because it increases trout density, even though it does not seem to improve the demographic parameters of the population.

Including density dependence (as in Ricker stock-recruitment relationships) and observation or pro-

cess uncertainty (Hilborn and Mangel, 1997) in the model will not change any of the main conclusions. These factors will make recognizing the problem even more difficult, as is the case in the real world. To uncover metapopulation dynamics, one must explore two aspects of each population's life history in reference to its habitat: dispersal (in the form of immigration and emigration) and the per-capita reproductive rate (defined by survival and reproduction). Watershed-scale estimates of these rates, however, are not appropriate. Given their reliance on index stream counts, managers must know the rates of immigration, emigration, and reproduction specific to that stream to be able to understand the true dynamics of that stream. The dispersal of individuals is important to determine the extent of the metapopulation structure. The focus should be both on absolute numbers as well as on the effective migration rates that account for differences in survival and productivity between the residents and the migrants. Survival and reproduction estimates (the components of the per-capita reproductive rate) will allow the manager to assess the potential importance of the metapopulation structure (i.e. to define sources and sinks). As long as the risk exists for abundance and density estimates to be disconnected from habitat quality and per-capita reproduction, all the above information is required to make an accurate assessment of the conservation status of the individual demes and to choose the appropriate management actions.

A great deal of time, money, and effort is currently directed toward the conservation and improvement of salmonid populations and their habitats. The NMFS report alludes to the fact that metapopulation structure may exist between some salmonid populations, and the NRC (1996) report lists the maintenance of metapopulation structure as one of its most important recommendations. Without investigating the possibility of metapopulation structure, researchers, managers, and policy makers are setting themselves up to fall into the traps described above: that of either not seeing a problem that may exist or, if they do see it, not knowing the true causes of such a problem.

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## Literature cited

- Brawn, J. D., and S. K. Robinson.**  
**1996.** Source-sink population dynamics may complicate the interpretation of long-term census data. *Ecology* 77: 3–12.
- Gall, G. A. E., D. Bartley, B. Bentley, J. Brodziak, R. Gomulkiewicz, and M. Mangel.**  
**1992.** Geographic variation in population genetic structure of chinook salmon from California and Oregon. *Fish. Bull.* 90:77–100
- Gowan, C., and K. D. Fausch.**  
**1996.** Long-term demographic responses of trout populations to habitat manipulation in six Colorado streams. *Ecol. Appl.* 6:931–946.
- Hanski, I.**  
**1994.** A practical model of metapopulation dynamics. *J. Anim. Ecol.* 63:151–162.
- Hanski, I., and M. Gilpin.**  
**1991.** Metapopulation dynamics: brief history and conceptual domain. *Biol. J. Linnean Soc.* 42:3–16.
- Heard, W. R.**  
**1991.** Life history of pink salmon (*Oncorhynchus gorbuscha*). In C. Groot and L. Margolis (eds.), *Pacific salmon life histories*, p. 121–230. Univ. British Columbia Press, Vancouver, B.C.
- Hilborn, R., and M. Mangel.**  
**1997.** The ecological detective: confronting models with data. Princeton Univ. Press, Princeton, NJ, 315 p.
- Hilborn, R., and C. J. Walters.**  
**1992.** Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Chapman and Hall, New York, NY, 570 p.
- Hunter, C. J.**  
**1991.** Better trout habitat: a guide to stream restoration and management. Island Press, Washington D.C., 320 p.
- Labelle, M.**  
**1992.** Straying patterns of coho salmon (*Oncorhynchus kisutch*) stocks from southeast Vancouver Island, British Columbia. *Can. J. Fish. Aquat. Sci.* 49:1843–1855.
- Levins, R.**  
**1969.** Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Ent. Soc. Am.* 15:237–240.
- 1970.** Extinction. In M. Gerstenhaber (ed.), *Some mathematical questions in biology*, p. 77–107. Am. Mathematical Society, Providence, RI.
- Milner, A. M., and R. G. Bailey.**  
**1989.** Salmonid colonization of new streams in Glacier Bay National Park, Alaska. *Aquacult. Fish. Manage.* 20(2): 179–192.
- NRC (National Research Council).**  
**1996.** Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington, D.C., 452 p.
- ODFW (Oregon Department of Fish and Wildlife).**  
**1995.** Oregon coho salmon biological status assessment and staff conclusions for listing under the Oregon Endangered Species Act (Commission decision draft). Oregon Dep. Fish Wildlife, Portland, OR, 59 p.
- Pascual, M. A., and T. P. Quinn.**  
**1994.** Geographical patterns of straying of fall chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), from Columbia River (USA) hatcheries. *Aquacult. Fish. Manage.* 25(suppl. 2):17–30.

- Pearcy, W. G.**  
**1992.** Ocean ecology of North Pacific salmonids. Univ. Washington Press, Seattle, WA, 179 p.
- Policansky, D., and J. J. Magnuson.**  
**1998.** Genetics, metapopulations, and ecosystem management of fisheries. *Ecol. Appl.* 8(suppl. 1): S119–S123.
- Pulliam, H. R.**  
**1988.** Sources, sinks and population regulation. *Am. Nat.* 132:652–661.
- Quinn, T. P.**  
**1993.** A review of homing and straying of wild and hatchery-produced salmon. *Fish. Res.* 18:29–44.
- Quinn, T. P., and K. Fresh.**  
**1991.** Homing and straying in chinook salmon (*Oncorhynchus tshawytscha*) from Cowlitz River hatchery, Washington. *Can. J. Fish. Aquat. Sci.* 41:1078–1082.
- Quinn, T. P., R. S. Nemeth, and D. O. McIlsaac.**  
**1991.** Homing and straying patterns of fall chinook salmon in the lower Columbia River. *Trans. Am. Fish. Soc.* 120:150–156.
- Ricker, W. E.**  
**1972.** Hereditary and environmental factors affecting certain salmonid populations. In R. C. Simon and P. A. Larkin (eds.), *The stock concept in Pacific salmon*. p. 27–160. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver, B.C.
- Rieman, B. E., and J. D. McIntyre.**  
**1995.** Occurrence of bull trout in naturally fragmented habitat patches of various size. *Trans. Am. Fish. Soc.* 124: 285–296.
- Ruxton, G.**  
**1996.** Synchronization between individuals and the dynamics of linked populations. *J. Theor. Biol.* 183:47–54
- Ruxton, G., and M. Doebeli.**  
**1996.** Spatial self-organization and persistence of transients in a metapopulation model. *Proceedings of the Royal Society of London (series B)* 263:1153–1158
- van Horne, B.**  
**1983.** Density as a misleading indicator of habitat quality. *J. Wildl. Manage.* 47:893–901.
- Waples, R. S.**  
**1991.** Definition of “Species” under the Endangered Species Act: application to Pacific salmon. U.S. Dep. Commer., NOAA Tech. Memo., NMFS F/NWC-194, 29 p.
- WDFW (Washington Department of Fish and Wildlife and the Western Washington Treaty Indian Tribes).**  
**1994.** Washington State Salmon and Steelhead Stock Inventory (S.A.S.S.I.). Northwest Indian Fisheries Commission, State of Washington, Dep. of Fisheries, Dep. of Wildlife, Olympia, WA, 212 p.
- Weitkamp, L. A., T. C. Wainwright, G. J. Bryant, G. B. Milner, D. J. Teel, R. G. Kope, and R. S. Waples.**  
**1995.** Status review of coho salmon from Washington, Oregon, and California. U.S. Dep. Commer., NOAA Tech. Memo., NWFSC-24, 258 p.
- Wood, C. C.**  
**1995.** Life history variation and population structure in sockeye salmon. In J. L. Nielsen (ed.), *Evolution and the aquatic ecosystem: defining unique units in population conservation*, p. 195–216. American Fisheries Society Symposium, no. 17: symposium on evolution and the aquatic ecosystem: defining unique units in population conservation, Monterey, CA, 23–25 May, 1994.