Implications of temporal and spatial scale for Atlantic salmon (*Salmo salar*) research

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Abstract: The Atlantic salmon (*Salmo salar*) is a model species for studying scale issues (i.e., the extent, duration, and resolution of a study or natural process) in ecology. Major shifts in behavior and habitat use over ontogeny, along with a relatively long life span and large dispersal and migration distances, make scale issues critical for effective conservation, management, and restoration of this species. The scale over which a process occurs must be linked to the research design and we illustrate this with a discussion of resource tracking by Atlantic salmon. Identifying scale inconsistencies (e.g., when a process is evident at one scale but not another) is shown to be an effective means by which some scale-dependent processes are understood. We review the literature to assess the temporal and spatial scales used in Atlantic salmon research and find most current studies appear to sacrifice spatial and temporal extent for increased resolution. Finally, we discuss research strategies for expanding the temporal and spatial scales in salmon research, such as conducting multiple scales studies to elucidate scale inconsistencies, identifying mechanisms, and using techniques and approaches to generalize across studies and over time and space.

Résumé : Le saumon de l'atlantique (*Salmo salar*) est une espèce modèle pour l'étude des problèmes d'échelle (c'est-à-dire l'étendue, la durée et la résolution d'une étude ou d'un processus naturel) en écologie. Les changements majeurs dans le comportement et l'utilisation de l'habitat durant la vie du saumon atlantique, ainsi que la longévité relativement grande et l'importance de la dispersion et de la migration de ce poisson, rendent critiques les problèmes d'échelle pour la conservation, la gestion et le rétablissement de cette espèce. L'échelle sur laquelle se déroule un processus doit liée au protocole de recherche, et nous examinons cette question en rapport avec la recherche de ressources par le saumon atlantique. On montre que le repérage du manque de cohérence entre les échelles (p.ex., quand un processus est évident à une échelle donnée mais pas à une autre) est un moyen pour comprendre les processus dépendants de l'échelle. Nous avons examiné la documentation scientifique pour évaluer les échelles temporelles et spatiales utilisées dans la recherche sur le saumon atlantique et avons trouvé que la plupart des études actuelles semblent étendues spatiales et temporelles pour obtenir une plus grande résolution. Enfin, nous traitons des stratégies de recherche permettant d'étendre les échelles temporelles et spatiales dans la recherche sur le saumon; on propose notamment d'effectuer des études à échelles multiples pour élucider les incohérences d'échelle, de repérer les mécanismes, et d'utiliser des techniques et des permettant de faire des généralisations à partir des diverses études et dans le temps et l'espace.

[Traduit par la Rédaction]

Introduction

Ecologists increasingly recognize the importance of scale (i.e., the extent, duration, and resolution of studies and natural processes) to many issues, including salmonid ecology, conservation, and restoration. Because different biotic and abiotic processes act at different spatial and temporal scales, the conclusions of research studies often are influenced by the scale of investigation (Allen and Hoekstra 1992; Levin 1992; Fahrig 1992; Ray and Hastings 1996). Interest in the effect of scale on diverse topics can be seen from the number of recent reviews addressing scale in aquatic habitats. These reviews have considered the importance of scale to questions such as the design and interpretation of research (Frost et al. 1988), fish habitat conservation and restoration programs (Lewis et al. 1996), and the effect of environmental constraints on species distributions and abundances (Poff 1997)

The Atlantic salmon (*Salmo salar)* is a good model species for evaluating the importance of scale because processes affecting its growth, reproduction, survival, and evolution span a wide range of temporal and spatial scales. Atlantic salmon undergo major ontogenetic shifts in behavior and habitat use (Mills 1991), are relatively long-lived (2–10 years), occupy a broad geographical range (circum North-Atlantic from southern New England to the Iberian peninsula) and disperse and migrate over extremely long distances (up to 1000s of kilometres).

As a result of these processes, a number of important questions about Atlantic salmon cannot be adequately addressed without taking temporal or spatial scale into consideration. For example, effects of logging on salmonid habitat clearly vary over different spatial and temporal scales (e.g., are scale dependent). Consider the temporal and spatial scales of impact resulting from clear-cutting the forest along a 500 m stream reach. Effects of increased light penetration on instream temperature and primary productivity due to

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canopy opening are likely to be evident at relatively limited temporal (in the year following logging) and spatial (~500 m) scales (Hicks et al. 1991). In contrast, effects of the clear-cut on stream sediment load, channel morphology, and large woody debris loading are likely to extend beyond the stream reach where logging has occurred (larger spatial scale) and not be fully manifest until years following the logging event (larger temporal scale). Moreover, effects at the large scale can also feed back over longer time periods to influence small-scale food web processes through their influences on life cycles and interactions among species (Power et al. 1996; Wootton et al. 1996). Despite its recognized importance, few studies of Atlantic salmon have specifically included more than one scale in their design.

To understand fundamental processes underlying Atlantic salmon ecology requires linking physical and biological processes at appropriate temporal and spatial scales. In this review, we address scale-dependent processes that can affect the dynamics of salmon and other fish species. This paper is an overview, using a few key examples to illustrate how scale can affect the interpretation of pattern and process. We review the literature to assess the scales of investigation most frequently used in Atlantic salmon research and discuss how scale can affect research conclusions. Finally, we emphasize the benefits of combining observations with experimental and manipulative approaches for elucidating mechanisms and identifying appropriate scales in the study of Atlantic salmon.

What is scale?

"Scale" is the spatial and temporal dimension of a process or an entity (Lewis et al. 1996). For example, habitat selection by salmon is a *process* whereby individuals make certain "decisions" based on information they have integrated over particular distances and times. The size of a study area and the duration of a study are attributes of an *entity* (the research study) whose characteristics are in part defined by these dimensions (e.g., diversity may increase with plot size up to a certain point; more behaviors are observed as observation period increases).

Allen and Hoekstra (1992) define three dimensions of scale: (1) spatial extent (the size of a process or entity), (2) temporal extent (the duration of a process or entity), and (3) grain (the finest level of spatial and temporal resolution, often determined by the frequency and density of samples or observations, or by levels of data aggregation). For example, Elliott's (1994) long-term study of brown trout population dynamics at Black Brow's Beck is of small spatial extent (conducted in a single stream reach of approximately 60 m^2), large temporal extent (stretching more than 20 years, encompassing multiple generations), and fine-grained (the population was sampled multiple times each year).

Extent and grain tend to be related in study design. Fine-grained (high-resolution) studies generally are performed over limited spatial and temporal scales. The terms "small-scale" tend to refer to processes or entities that are small in extent and (or) relatively fine-grained, and "large-scale" for processes or entities that are large in extent and (or) relatively coarse-grained. Given finite research resources, increased resolution (fine grain) is generally achieved by reducing the spatial or temporal extent of the study, or vice versa.

We illustrate these aspects of scale with three hypothetical studies of salmon summer growth rates and show that the questions that can be adequately addressed differ among the designs due to differences in extent and grain. First, in a single stream, growth is measured only once at the end of the season, for 10 consecutive years (small spatial extent, large temporal extent, coarse-grained). This study could be used to examine the influence of between-year variation in climate and discharge on growth of a single population. Second, also in a single stream, growth is measured at 10 intervals over a single growing season (small spatial extent, small temporal extent, fine-grained). This study could be used to examine the importance of short-term critical growth periods, but only for one population (among basin comparisons could not be made). Third, in 10 different streams, growth is measured once at the end of a single growing season (large spatial extent, small temporal extent, coarse-grained). This study could be used to address effects of stream-scale differences in geomorphology and water chemistry on annual first-year growth, but not within season patterns of growth within a site or the importance of yearly variation. Extending the extent or grain can reveal potentially important processes that operate at different scales.

Review of the Atlantic salmon literature reveals cases where information gathered at a particular scale is broadly applied without considering implications of the scale of the original sampling design (i.e., when inferences drawn from a single site are assumed to apply over broader spatial or temporal extent). To avoid this problem, careful attention must be given to the scale over which a process occurs and is measured and over which it influences a specific aspect of salmon biology. Fahrig (1992) states this succinctly. "To understand the relationship of an organism to its environment, one must understand the interactions between the intrinsic scales of heterogeneity within the environment and the scales at which the organism can respond to this heterogeneity." In Table 1, we list three environmental factors (current speed, temperature, and prey abundance) that are known to have a strong influence on spring/summer juvenile salmonid growth and survival and are highly variable in streams (Bjornn and Reiser 1991). These processes are driven by different factors at different spatial scales (Table 1). For example, stream flow at small spatial scales (within in pool or riffle) is strongly affected by local substratum characteristics. Over the entire basin, stream flow (i.e., discharge) is influenced by the geology, slope, regional land use, and precipitation.

Similarly, the effects of temperature and prey abundance on salmon growth patterns can vary at different scales. Temperature, for example, may vary only slightly at a small spatial scale and hence produce no variation in growth rate among fish within a pool, riffle, or stream reach. Nevertheless, temperature variation across basins may be great and drive large among-basin variation in salmon growth, physiology, and production (Elliott 1985; Holtby 1988; Nicieza et al. 1994; Filbert and Hawkins 1995). In seeking to understand growth patterns small-scale studies might obscure the overriding influence of temperature, even if temperature across a region was the single most important explanatory

Table 1. Environmental determinants of three factors (current speed, temperature, and prey abundance) influencing spring/summer parr production at different spatial scales (from review by Bjornn and Reiser 1991).

Scale	Current speed	Temperature	Prey abundance
cm–m	Local substratum characteristics and small-scale channel geometry (width/depth)	Little influence at this scale	Availability of appropriate habitat patches (i.e., where are the patches of high invertebrate abundance?) Local current speeds (i.e., influences prey delivery rates and foraging success)
m – 100 m	Channel slope, sinuosity, macrohabitat transitions (riffle to pool)	Ground water sources	Larger scale habitat units (riffles runs) Shading effects on primary production
100 m – km	Land use, impoundment	Overhead cover, shading, impoundment	Downstream dispersal Temperature effects on invertebrate production Allochtonous inputs
km – 100 km	Basin size, parent geology	Basin-wide influences on runoff and temperature	Basin chemistry and geology
>100 km	Regional precipitation and runoff	Regional climate	Regional species pool

variable. Prey abundance also may vary less over small spatial scales than large scales. As for temperature, it could be difficult to isolate the influence of food abundance on salmon production even from numerous small-scale or high-resolution studies.

Important processes also have influence at different temporal scales (Table 2). For example, size related shifts in habitat and diet of Atlantic salmon may be explained in part by seasonal shifts in prey phenology and stream discharge that occur over periods of weeks to months (Cada et al. 1987; Keeley and Grant 1997). Over the short term, we may expect the most productive reaches to be those with the most food and the best discharge conditions. Yet, over the long term, overall patterns of fish or prey abundance may be driven by infrequent extreme events (e.g., massive discharges or dry periods) that are regulated by climate trends operating over years to decades and beyond. These long-term processes may result in low population numbers persisting in reaches that in any given year (or in a short-term study) appear to provide highly suitable habitat.

In the next section, we illustrate the importance of scale by examining the relationship between stream dwelling salmon and their food resources. We then discuss inferences that can be made by looking at this question over different spatial and temporal scales and with different resolution.

Resource tracking and the importance of scale

It is common in fisheries science to predict fish production from the quantity of resources (e.g., food, physical habitat type) in an area. The term "resource tracking" has been used to describe situations where there is a significant positive correlation between the abundance or performance of consumers and the abundance or productivity of their resources (Hart and Fonseca 1995). If resource tracking occurs, the resource levels can be used for goals such as identifying habitats likely to yield high fish production, evaluating the efficacy of habitat remediation, and understanding how fish production will respond to variation in resource abundance.

Much effort has been directed towards testing whether salmon abundance (density, standing stock biomass, production) and performance (growth, survival, reproduction) track the abundance of resources such as prey (Mason 1976; Cada et al. 1987; Hinch 1991; Richardson 1993; Filbert and Hawkins 1995) or habitat (Fausch et al. 1988; Hicks et al. 1991; Fausch et al. 1994). These studies have been conducted over a range of spatial and temporal scales and illustrate how scale affects the examination of an important ecological process. We use studies from various systems relevant to and including Atlantic salmon to show that (1) different types of resource tracking require different measurements, (2) resource tracking may be measurable over one spatial scale but not another (we term this "scale inconsistency"), and (3) understanding the mechanism underlying the resource tracking relationship or scale inconsistency helps identify the appropriate measurement scale.

Types of resource tracking

Fish production tracks resources in two, non-mutually exclusive ways. Understanding their differences is necessary to interpret patterns and to predict the extent and resolution necessary to detect resource tracking in nature. We term the first type, "numerical resource tracking" (NRT), which occurs when more individuals are found at the highest resource productivity. NRT arises from an increase in recruitment or by immigration into high resource areas. We term the second

Table 2. Temporal scale of important environmental processes and implications for Atlantic salmon (from review by Bjornn and Reiser 1991; Hicks et al. 1991).

Scale	Environmental patterns and processes	Effects on salmon
Hour–weeks	Diel cycles in oxygen temperature	Hypoxia for alevins and incubating eggs
	Diel cycles in prey availability (i.e., drift periodicity	Diel feeding and activity cycles of fry and parr
	Small-scale (aseasonal) stream discharge and temperature changes	
Weeks–year	Prey phenology	Size-related habitat and diet shifts affects feeding and growth for fry and parr
	Seasonality in temperature and discharge at high latitudes	Seasonal habitat and behavioral shifts and summer/winter habitat shifts for parr Migration cues/physiological changes for parr-smolts Redd de-watering and scouring (eggs/alevins)
Years–decades	Between-year climatic variability (ENSO, oceanic processes)	Oceanic prey availability and temperatures affecting growth and survival of adults Variation in precipitation and streamflow associated with ENSO, ocean circulation events (all freshwater life stages)
>Decades	Climate change, adaptation and changes in migration patterns, fishing pressure, land use change	Changes in the timing, magnitude and variability of extreme events Changes in stream habitat morphology (LWD availability and dynamics) sediment/substratum characteristics, channel characteristics

type, "performance resource tracking" (PRT), which occurs when individual performance (but not necessarily density) increases with resource productivity. When both NRT and PRT occur more individuals with greater individual performance are observed under high resources.

If populations are dense, so that resources have become limiting, numerical resource tracking can preclude performance tracking (PRT) and vice versa. For example, under the "ideal-free distribution" model (IFD, sensu Fretwell and Lucas 1970), individuals fill habitats sequentially, filling the best habitats first, and occupying the second best habitat when crowding lowers the quality of the first habitat to that of the second. The outcome of this ideal free distribution is that abundance tracks habitat quality, but individual performance is similar across habitats. Algivorous catfishes in tropical streams provide an example of the IFD model in situ (Oksanen et al. 1995). Non-territorial catfish in a Panamanian river showed evidence of NRT because there were more catfish in stream pools with higher algal productivity. However, there was no evidence for PRT, in that fish from high and low productivity pools exhibited similar individual growth and survival rates (Power 1984).

Distinguishing between NRT and PRT has management implications. First, different measurements over different spatial and temporal scales are required to detect each process. For example, testing for a correlation between abundance and habitat characteristics, probably the most basic and often used metric in salmon habitat studies (Bovee 1986; Fausch et al. 1988), will not yield evidence of resource tracking if only PRT occurs. Similarly, measures of individual performance do not correlate with resource abundance under an IFD/NRT-only situation. In either case, it could be erroneously assumed that a particular resource was not limiting. Second, the management of a particular system may depend on whether the performance (bigger or more fecund fish) or the abundance (more individuals) is the outcome to be maximized. Understanding the mechanistic link between resources and their specific effects on growth or abundance could be effective for improving assessment and management.

Surprisingly, there is not a clear answer in the literature as to what happens to salmon production when food resources are increased. Do you get more small fish (NRT), few big fish (PRT), more big fish (NRT and PRT), or no change at all? There are plausible models to explain any of these outcomes, but few direct tests. The relationship between food resources and NRT or PRT for Atlantic salmon can be difficult to detect and therefore easy to ignore for several reasons. First, food resource abundance and productivity can be extremely hard to quantify (Resh and Rosenberg 1979). Second, salmon may respond to an increase in resources in ways that result in either NRT or PRT. For example, territory size of individual salmon may decrease with an increase in prey flux. NRT could then arise by packing in more territories at high resources. If, as in the IFD model, territory size declines in direct proportion to an increase in food density, consumption rates remain equal across territories, and there is no PRT. In contrast, salmon territory size may not decrease with food resource density, if, for example, it has a fixed relationship with body size. Then more territories will not "pack in" at high resource levels, and NRT should not be observed. If consumption rates still increase with increasing food resources, there will be PRT without NRT.

The literature includes studies that partially support and reject NRT and PRT for salmonid systems. Elliott (1994) measured an increase in individual growth rates with an increase in food resources, providing strong evidence for PRT by brown trout in Black Brow's Beck. His study also provided evidence against an IFD/NRT situation, because territory size did not decline with an increase in resources. In contrast, both Dill et al. (juvenile coho, 1981) and Keeley and Grant (Atlantic salmon, 1995) found mild support for territory size compression at higher food, and thus indirect support for NRT and aspects of the IFD model. However, the effect of food on territory size was very small, explaining ~2% of the variance in territory size for Atlantic salmon parr (2.90–14.50 cm fork length; Keeley and Grant 1995). Instead, body size was a much stronger determinant of territory size. Direct tests of both NRT and PRT are needed to assess their relative importance as mechanisms linking food and production. Increasing consistency in the methods for assessing food and territory size will expand our general understanding of this issue.

Scale inconsistencies

Consideration of the extent and resolution of each study is critically important for interpreting the relationship between salmonids and their resources. If either salmon abundance or performance tracks resources at one scale but not another, studies at different scales will arrive at different answers (i.e., there will be scale inconsistencies). Scale inconsistencies present another layer of complexity in testing for resource tracking. Mason (1976) provides a good example where identifying scale inconsistencies can reveal important processes. In a stream fertilization experiment run over a period of several months (small temporal extent), juvenile coho salmon survival and growth strongly increased with increased prey productivity (NRT and PRT). Yet, when followed for several years (greater temporal extent), all evidence of NRT or PRT was absent, because they were apparently offset by heavy winter mortality. The evidence for NRT and PRT depended on the temporal scale or extent of the study, and examination of both temporal scales was necessary to fully assess the relative importance of food, performance, and a third key variable, winter survival.

Additional examples from both riverine and marine environments also show that fish track resources at some scales, but not others. Rose and Leggett (1990) found that the correlation between the abundance of Atlantic cod and its major prey, capelin, in the North Atlantic (NRT) differed strongly over different spatial scales. At the largest spatial scale measured (4–10 km), predator abundance was strongly positively correlated with prey abundance, and both species were concentrated in large-scale oceanic fronts. However, at smaller spatial scales (2–3.5 km) prey and predator abundance were either negatively correlated or uncorrelated. They interpreted this scale inconsistency as evidence for either small-scale predator avoidance by capelin or small-scale prey depletion by cod. The importance of scale inconsistencies, in this and other examples, is often that they provide the strongest tool for assessing the scale over which different processes operate.

In riverine habitats, Fausch et al. (1994) also found scale inconsistencies in the relationship between abundance of two species of char (genus *Salvelinus*) with physical and biotic factors on Hokkaido Island, Japan. Char abundance correlated positively with certain physical characteristics at large and intermediate spatial scales (e.g., watersheds and tributaries within watersheds), but was uncorrelated with these features at smaller spatial scales (e.g., within tributaries or stream reaches). In contrast, the presence of the congeneric species did not influence species' presence or abundance at larger spatial scales, but correlated with abundance at small spatial scales. By comparing processes at several spatial scales, the scale inconsistencies could be identified, and the mechanisms underlying them could be elucidated.

Elucidating mechanisms to resolve scale inconsistencies

We and others (Hart and Fonseca 1995; Lewis et al. 1996; Power et al. 1998) recommend a two-part approach to identify and then resolve scale inconsistencies. This approach combines taking explicit measurements or observations at several scales and using experiments or models to test mechanisms underlying the patterns and to probe inconsistencies that are revealed. Moreover, as Power et al. (1998) argue, if the spatial scale addressed increases (e.g., from microhabitats to watersheds), carefully designed field measurements and direct observations become even more important because large-scale manipulations are difficult to carry out and virtually impossible to replicate. They suggest that nesting experiments or models within observational field studies is most effective for clarifying mechanisms and extrapolating across systems or scales.

We illustrate the strength of this combined approach for studying resource tracking with Power's study of algivorous catfish in large tropical rivers (Power 1984; Oksanen et al. 1995; see also Power et al. 1998 for additional examples). Resource tracking was explicitly compared at two spatial scales. Power found NRT at the relatively large spatial scale (between river pools), but no evidence for NRT at the smaller scale (within pools). Catfish were more abundant in deep microhabitats farther from the riverbank, while algal standing crops were higher in shallow, nearshore sites. The mechanism underlying the inconsistency was elucidated in predator exclusion experiments. Catfish were found to avoid nearshore habitats to reduce predation risk from wading birds, who could not forage effectively in the deeper, offshore water (Power et al. 1989). In contrast, catfish resource tracking was not constrained by predation at the between-pool scale because they spent relatively little time in shallow intervening riffles when moving between pools.

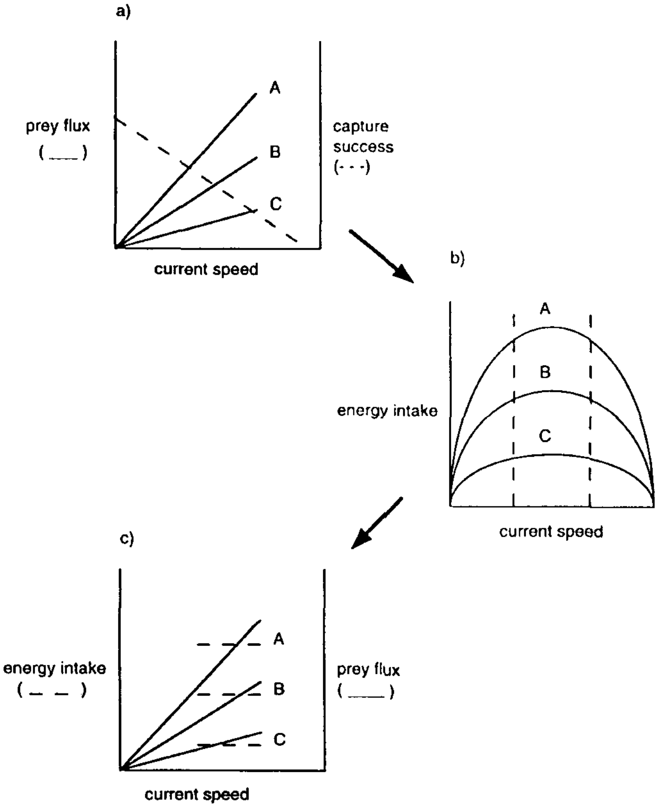
Our second example involves resource tracking by age-0 Atlantic salmon. In a study of prey availability and foraging by Atlantic salmon parr in several New England streams, Nislow et al. (1998) assessed PRT at two spatial scales. They compared salmon foraging rates (by watching fish via snorkeling) as a function of potential food availability (1) among salmon occupying different feeding locations within a reach (small scale) and (2) among salmon living in different streams. Within each stream, territory-specific drift rates were predicted as the mean free stream velocity in each territory times the mean drift concentration within the reach. Between streams, mean foraging rates tracked food resources (PRT). Foraging rates were significantly reduced by experimental reduction of the mean density of drifting prey to the reach and were higher in the high-food stream. In contrast, at the small scale (comparing among fish within a reach), there was no PRT (i.e., there were not higher foraging rates in high-current-speed, high-food locations (territories) within each stream). These results indicate a scale inconsistency in resource tracking by age-0 salmon.

One explanation for this scale inconsistency derives from understanding the mechanisms relating current speed, food flux, capture success, and microhabitat selection by stream salmonids. Among microhabitats within a stream reach, invertebrate drift rates tend to be strongly positively correlated with microhabitat current speed (Waters 1972; Bjornn and Chapman 1968; Hill and Grossman 1993; Nislow et al. 1998). However, high current speeds also decrease the ability of fish to detect and capture drifting prey. Because of this tradeoff, consumption rates are predicted to be maximized at intermediate current speeds (and thus at intermediate prey flux rates), and juvenile salmonids are predicted to preferentially occupy those microhabitats where consumption is predicted to be maximized (Hughes and Dill 1990; Hill and Grossman 1993).

Some stream salmonids, including Atlantic salmon, appear to select habitats in accordance with tradeoffs predicted by this model (Hughes and Dill 1990; Hill and Grossman 1993; Nislow et al. 1999). Under these model conditions, it is unlikely that performance (as foraging rate) tracks food resource abundance at the within-reach scale (Fig. 1), for two reasons. First, optimal current velocities (i.e., the velocities predicted to produce within ±10% of the highest feeding rates based on tradeoffs between capture success and prey flux with current speed) can span a fairly wide range (i.e., roughly the same feeding rates are predicted to result over a range of current velocities). Second, because capture success declines with current speed and prey drift rate increases with current speed, high prey drift rate is not the same as high resource availability. Therefore, food abundance alone is not a proper currency for assessing food availability, and feeding will not necessarily track food abundance. Like the catfishes studied by Power (1984), salmon do not track their food on some scales, due to the positive correlation between resource abundance and factors that impede resource use (predation risk in the case of the catfishes; reduced capture success at high current speed in the case of salmonids).

In contrast, differences in resource abundance between salmon rearing streams are correlated with differences in performance (Nislow et al. 1998). In fact, any constraint at the within-reach scale that reduces within-reach variation in foraging may make it easier to detect differences between high and low resource reaches, and reinforce PRT at the larger spatial scale. This example therefore illustrates both how understanding mechanisms can help resolve "scale inconsistencies," and how processes that occur on small scales can influence processes at larger scales of observation. Lewis et al. (1996) provide other examples where multiscale investigations were effective for determining the appropriate scale for restoration and management practices such as liming to increase pH (Lacroix 1996; Keller and Gunn 1995 in Lewis et al. 1996) or habitat management (Crowder et al. 1996).

Fig. 1. Diagrammatic representation of resource tracking at the between-microhabitat vs. between-reach scales for juvenile Atlantic salmon. Figure 1*a* describes the relationship between current speed, prey flux (prey/time), and capture success (% of prey successfully captured) in three hypothetical stream reaches of different mean prey densities (prey density = slope of the current speed prey flux relationship; reaches labeled A-C in descending order of mean/prey density). Figure 1*b* shows the corresponding relationship between energy intake (prey flux · % capture success) vs. current speed in the three reaches. Dashed vertical lines define the range of current speeds (predicted to yield within 10% of maximum energy intake rates) predicted to be occupied by salmon. Figure 1*c* shows that consumption is predicted to track differences in prey between reaches (A > B > C), but not to track differences in prey flux as a function of local current speed within reaches (no significant linear relationships (indicated with dashed lines in the diagram) between current speed and energy intake within each reach).



Over which scales are most studies conducted?

The need to consider temporal and spatial scale to address important issues for Atlantic salmon ecology is becoming widely appreciated. This volume includes a number of papers that deal explicitly with scale issues at the physiological, population and community level, and in freshwater and oceanic phases. Major shifts in behavior and habitat use over ontogeny, along with a relatively long life span and large dispersal and migration distances, make scale issues critical for effective conservation, management, and restoration of

Atlantic salmon. Nevertheless, relatively few studies have been conducted at more than one spatial or temporal scale, resolution varies across studies, and experimental field studies to tease apart mechanisms are still uncommon.

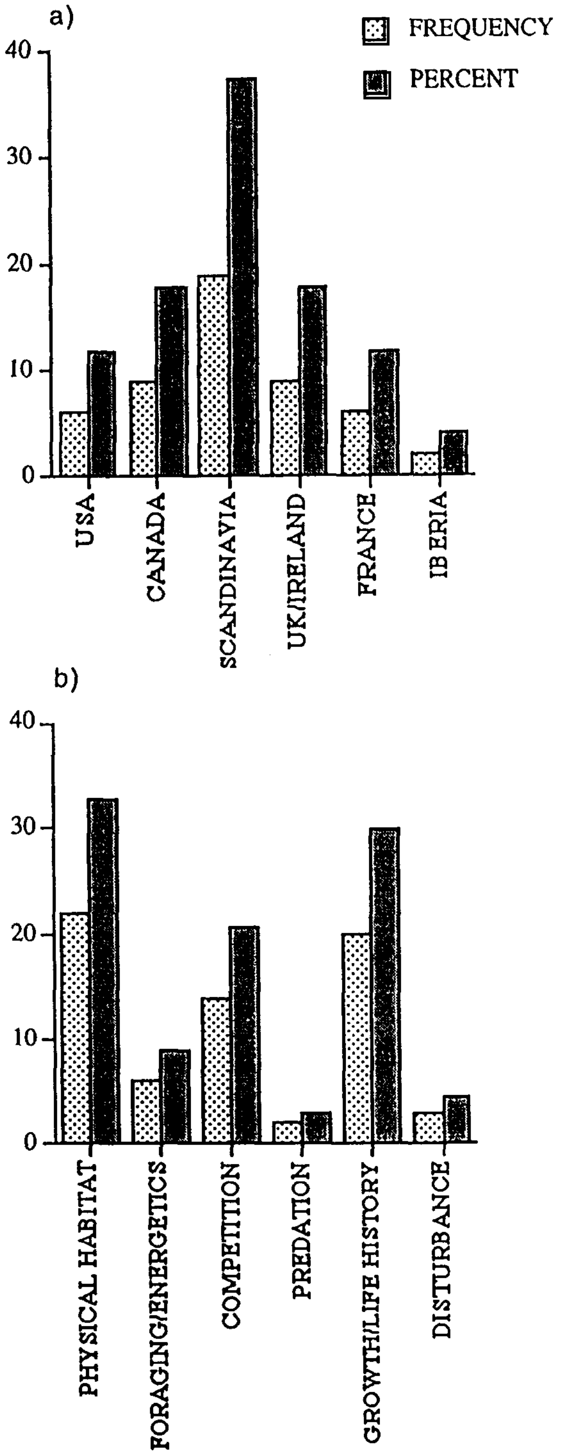
To determine the spatial and temporal scales over which most Atlantic salmon studies have been conducted, we ran an on-line computer search. We considered two components of scale: (1) extent — the number of years or streams in a study and (2) grain — the number of samples/year or sites/stream in a study. We used the on-line search engine (Ovid: Gateway) to search the major life sciences database (BIOSIS for the Life Sciences) for all citation abstracts containing the key words "Atlantic salmon" and "ecology" from 1990 through February 1997. Of these citations, we included only papers which assessed, using field manipulation, correlations or comparisons, factors affecting habitat selection, life-history strategies, growth, and survival of freshwater-phase anadromous Atlantic salmon. Laboratory and aquaculture studies were excluded.

Studies were classified by both spatial and temporal extent and resolution. We distinguished four levels of temporal extent, equivalent to study duration: ≤1 year, 2–5 years, 6–10 years, and >10 years. We distinguished two levels of temporal grain or resolution, equivalent to the within-year sampling frequency: one sampling period a year (coarse grain) or multiple sampling periods a year (fine grain). For spatial extent, we distinguished four categories: studies which took place within 1 stream or river, 2–5 rivers, 6–10 rivers, and greater than 10 rivers. For spatial grain, we classified studies on the basis of whether they sampled one site/river (coarse grain) or multiple sites/river (fine grain).

It was more difficult to classify the spatial scale of each study than the temporal scale. Depending on the design and objective of the study, studies conducted in multiple tributaries of the same river system can be considered as multiple rivers in our classification system or as multiple sites within a single drainage system. For example, if multiple tributaries of a single river were sampled, we classified this study as being conducted in more than one tributary or stream (i.e., increased spatial extent) if the aim of the study was to compare some factor among streams (grain depends on whether there were replicate sites sampled). However, if the study was conducted in multiple tributaries of a single river, and the object was to use the average of these sites to obtain a average for that single drainage system, then we classified the study as characterizing a single river system, but with finer grain (e.g., more replicates).

To illustrate our classification scheme, consider McMenemy's (1995) study of the effect of stocking density on juvenile Atlantic salmon survival in the West River, Vermont, U.S.A., over 7 years. Sampling sites were distributed among different tributaries of the West River, and were censused once each year. The study tested the effects of variation in stocking density across years averaged across tributaries and did not address between-tributary differences. Therefore, we considered the spatial extent of this study to be a one river system (the West River), and the spatial grain to be multiple sites/river (fine grain). The temporal extent is 6–10 years, and the temporal grain is one sample/year (coarse grain).

Fig. 2. Distribution of Atlantic salmon studies (1990–1997) uncovered by literature search over geographic locations (Fig. 2*a*) and general research topics (Fig. 2*b*). Additional details on literature search given in text. N = 51 studies, some studies were placed in more than one research topic category.



We identified 51 field studies that fulfilled our selection criteria. Of these we were able to determine spatial extent of 50 studies, temporal extent of 41 studies, temporal grain of 32 studies, and spatial grain of 33 studies. These studies

Fig. 3. Frequency and percentage of Atlantic salmon studies conducted at 5 categories of temporal (Fig. 3*a*) and spatial (Fig. 3*b*) extent. Details of the literature search and classification criteria given in text.

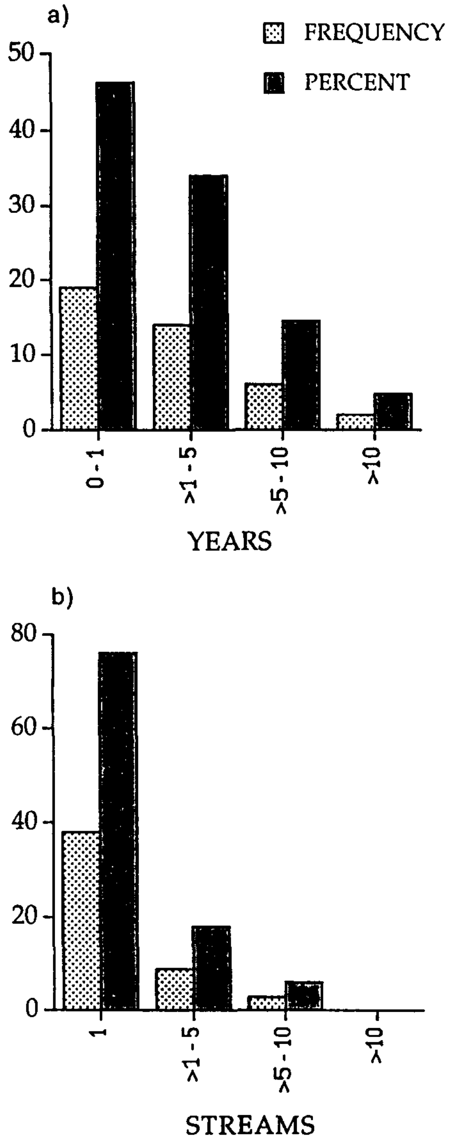
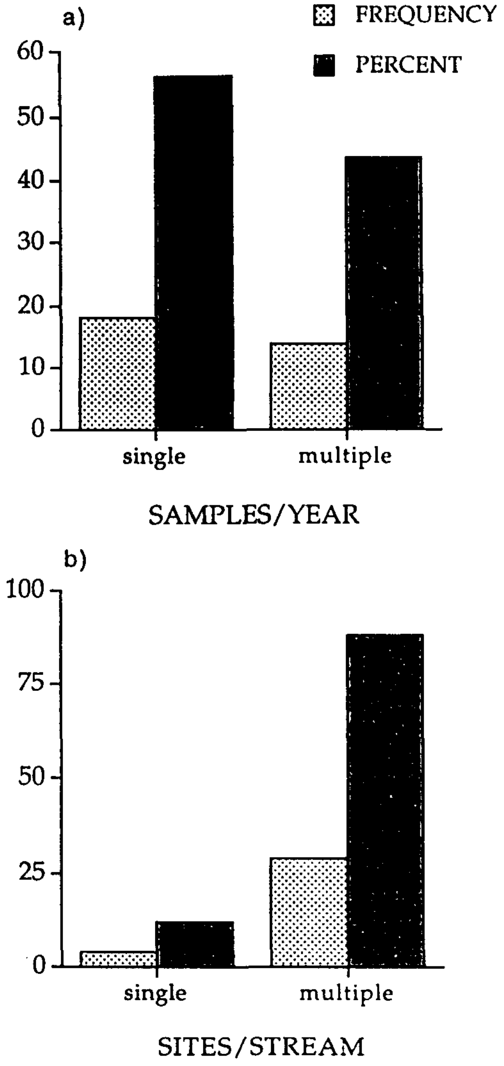


Fig. 4. Frequency and percentage of Atlantic salmon studies conducted at 5 categories of temporal (Fig. 4*a*) and spatial (Fig. 4*b*) resolution. Details of the literature search and classification criteria given in text.



encompassed most of the geographic range of the Atlantic salmon in both North America and Europe (with the exception of the Baltic region) and a wide range of ecological topics (Fig. 2).

The majority of these studies of Atlantic salmon appear to trade increased resolution for reduced spatial and temporal extent. More than 75% of studies were conducted within a single river system, with fewer than 20% lasting for more than 5 years (Fig. 3). However, most studies were relatively fine grained. Greater than 85% of studies included samples taken from multiple locations within a river or single drainage system, and 44% of the studies included samples taken multiple times within the course of a single year (Fig. 4).

Implications of scale bias to Atlantic salmon research

The results of our search indicate that scale-bias is common in Atlantic salmon research. Most studies are limited in their temporal extent and rarely span the life cycle of an individual, or even the change of seasons and its associated change in physical and biological constraints. Choosing the appropriate time scale for each study requires understanding the nature of both the physical and biological features of the system. As pointed out by Frost et al. (1988) the danger lies in selecting a time frame that is either too short or too long. Inferences must be carefully evaluated within a specific temporal framework, which makes comparisons among studies even more challenging. Limitations on temporal extent (study duration) are probably linked in part to limited resources and human-imposed temporal limitations (the average duration of a graduate thesis or a funding period). However, the paucity of long-term investigation weakens inferences we can make about processes spanning longer periods and thus our ability to predict long-term trends under changing environmental and human pressures.

There is also a bias in the spatial scale of most Atlantic salmon field investigations. Most studies have concentrated on measuring particular systems (e.g., single river systems, or even single tributaries or reaches within a single tributary) using a multiple locations per river (high-resolution) approach. This emphasis probably reflects the management orientation of a great deal of Atlantic salmon research, which is often directed towards river-specific, applied problems (i.e., is a particular river good or bad for salmon, and why?), and the idiosyncratic nature of research (salmon biologists are placed somewhat haphazardly across the globe, studying the systems nearest to their home base). These intensive studies have been extremely effective at elucidating individual behaviors, genetics, physiology, and many small-scale ecological processes (Schlosser 1991). Yet they are less effective for comparing across systems where different biotic and abiotic factors prevail.

There are great differences in resolution or grain across studies. Methods for censusing populations differ greatly, and whether individuals, reaches, or entire streams are being characterized influences the appropriate spatial scale of the study. As pointed out by Grant et al. (1998), Folt and Schulze (1993), and others, small-scale patchiness, which is generally not characterized in sampling programs, may be fundamental to understanding outcome of important density-dependent interactions. This could be particularly important for understanding interactions among space holding territorial species like Atlantic salmon juveniles, where the precise numbers and sizes and nature of neighbors or food can have a strong impact on individual foraging and overall performance.

Sampling programs that miss small-scale patterns may overlook the fundamental importance of density-dependent processes in salmon population regulation. Ray and Hastings (1996) demonstrate that identifying density-dependent relationships may be especially biased by the spatial sampling design. They argue that the lack of density-dependence observed in many current studies may be an artifact of sampling programs that average over regions of widely varying population density and obscure key relationships. Further, with a study of scale-related dynamics in 79 insect populations, they found that short-time series (low temporal extent) or low test power (fewer samples) were far less important for detecting density-dependence than identifying the appropriate spatial scale.

The effect of differing spatial resolution can be illustrated by comparing predictions from two types of bioenergetic models. These models are used to examine the relationship between resources and performance. They predict fish growth rate potential as a function of both biotic and abiotic aspects of the environment, (e.g., prey density, physical habitat structure) and intrinsic characteristics of individual fish (Hewett and Johnson 1992; Ney 1993). Although they use the same input parameters and the same equations relating environment to growth, the two types of models operate at different spatial scales. "Simple" bioenergetic models are based on average conditions across a lake, river, or (at slightly higher resolution) a reach, while "spatially explicit" bioenergetic models (Brandt et al. 1992) require higher resolution information because they incorporate the actual spatial distribution of fish, their prey, and physical conditions that affect foraging and growth. Spatially explicit and site-averaged models can produce very different predictions. In a revealing example, Brandt and Kirsch (1993) found that for striped bass (*Morone saxatilis*) in Chesapeake Bay, site-averaged growth rate potential was consistently greater than spatially explicit predictions. Their explanation was that prey spatial distribution was highly patchy, and that prey densities in high density patches often exceeded densities that produce the maximum consumption rates of predators. In the spatially explicit version, this important behavioral constraint is modeled. However in the site-averaged model, behavioral restrictions on consumption are not included. In this example, a behavioral mechanism (density dependence in foraging rate) sets a ceiling on consumption, so that resolution of small-scale patchiness becomes necessary to understand the predator–prey dynamics.

Because of limited support for research, increasing sampling grain to the resolution necessary to follow individuals and their neighbors will restrict either the number of sites investigated or the number of times the samples are taken. When populations are especially patchy in space or time, it may be necessary to increase resolution no matter what the "cost." Yet, increased resolution is certainly not always required and in some cases may actually hide other large-scale processes (Frost et al. 1988). Obviously, future studies should be designed with the understanding that the resolution has a strong influence on the inferences that are drawn. A review of new methods for identifying the appropriate scale for specific systems and questions is well beyond the scope of this paper, but methods for matching variance in biological and physical processes are of growing importance to the design of research programs (Horne and Schneider 1994).

Strategies for expanding scale

As discussed above, a powerful technique for identifying the importance of scale is to conduct multiple scale studies, identify scale inconsistencies, and to use a combination of experiments or models to test the underlying mechanisms in order to extrapolate across systems. However, there are also other ways to confront scale issues that are being applied in a number of different research areas. We now address three possible methods to expand scale and test for generality across scales.

Scaling up

High-resolution, low-extent studies are valuable for certain questions. But site and time specificity comes with some costs as it limits the detection of larger scale determinants of potentially important processes. There have been a number of calls recently to "scale up," emphasizing the importance of comparing ecological processes for stream fish across larger spatial or temporal scales (Lewis et al. 1996;

Cunjak 1996). Concordance in the change in fish abundance among streams in Colorado led Gowan and Fausch (1996) to emphasize the importance of regional (large-scale) processes to fish dynamics. However, comparisons across systems or regions are problematic for a number of reasons, making it clear that scaling up is not simple.

Difficulties of scaling up are particularly apparent when increasing extent is associated with decreasing resolution (coarser grain). For example, salmonid researchers have been debating whether population density in a stream reach is determined by seasonal "self-thinning" processes in relation to some maximum carrying capacity of the environment (Grant and Kramer 1990; Grant 1993; Grant et al. 1998) or, instead, is determined by mortality during a critical period for survival early in ontogeny (Elliott 1989, 1994). Armstrong (1997) used statistical techniques to look at a single dataset (Elliott 1994) with two degrees of temporal resolution — multiple measurements over a year (fine resolution) and single estimates for each year in the dataset (coarse resolution). Armstrong found that the coarse resolution analyses could not isolate an effect of a critical period and suggested the importance of self-thinning processes to density. In contrast, the finer-resolution approach indicated that self-thinning was largely a by-product of early season mortality, which supported the critical period theory for explaining density.

Large-scale studies (e.g., watersheds) are particularly vulnerable to problems in addition to loss of fine scale resolution. Because of logistical considerations, comparable replicates are limited; they may be non-existent in the case of paired watershed studies (Power et al. 1998). At such large scales, it is not at all uncommon for unpredictable events (fires, floods) with high-magnitude impacts to affect either the "control" or the comparison watershed only, largely invalidating the study. These studies also tend to measure highly integrated "output" variables such as stream flow or total production, which are affected by a host of factors, making it difficult to understand the mechanisms by which changes occur (Lewis et al. 1996). Perhaps as a consequence of these limitations, Hicks et al. (1991) found that while watershed scale variables have been associated with salmonid abundance, no two studies have identified the same set of variables as being important, severely limiting the generality of research findings.

Despite these problems, large-scale comparisons are essential for certain questions. For example, recent large-scale studies have revealed important relationships between land use and ecological variables (see references in Schlosser 1991). An approach to conservation of Pacific salmon species has been strongly advocated that requires management of salmon at least at the basin-wide level (Allendorf et al. 1997). For basin-wide management to be effective requires an expansion from single or few sites to sites across the range of habitats and range of conditions within the basin (see Kocik and Ferreri 1998).

Another powerful tool for resolving scale issues is to "scale down" using experiments and models to explore the mechanisms underlying scale inconsistencies and patterns. A number of recent papers have dealt with the appropriate use of experiments and modeling in ecology (Frost et al. 1988; Schlosser 1991; Power et al. 1995, 1998; Osenberg et al. 1998; and others (this issue)) and emphasized their strengths and weaknesses (especially with respect to scale). Laboratory experiments have been widely used to identify a number of behavioral and physiological processes for Atlantic salmon, but field experiments are still relatively uncommon (but see Kennedy and Strange 1986; Whalen and LeBar 1994; Nislow et al. 1998). To effectively test for mechanisms driving inconsistencies or similarities at different scales we should sample at several scales, scaling up where possible and necessary, and combine these measurements with carefully designed experiments or models nested within the sampling program (see reviews by Mather 1998; Fausch 1998; Grant et al. 1998; and others (this issue) for more details on experiments with salmonids).

Synthesis across studies

One of the primary goals of all papers in this issue was to include a review of the literature in order to synthesize among studies and thereby to expand the scale of inference. Most reviews seek to expand the extent and resolution that can be obtained by comparing numerous intensive, and usually small-scale individual studies. There is a growing movement within the field of ecology to do this in a quantitative fashion (Gurevitch et al. 1992; Gurevitch and Hedges 1993; Fernandez-Duque and Valeggia 1993; Arnqvist and Wooster 1995). Different techniques are being proposed, debated, and refined in the literature, including meta-analysis and application of Bayesian statistics (Ellison 1996; Dennis 1996; Osenberg et al. 1998). These techniques appear promising for synthesizing among disparate studies of Atlantic salmon and are likely to result in some fundamental advances in the field when appropriately applied to topics currently under debate.

Meta-analysis has been used by investigators in many different systems to analyze and synthesize a number of independent studies. A key goal of meta-analysis is to extract a quantitative metric (e.g., effect size) from each study and then to apply statistical techniques to the comparison of this metric across studies (Osenberg et al. 1998). Recent meta-analyses include comparisons of the effects of selective logging on density of birds (Fernandez-Duque and Valeggia 1993), of effects of benthic versus drift feeding predators on the density of stream invertebrates (Dahl and Greenberg 1996), and strength of fish–snail interactions across lakes (Osenberg et al. 1998). A number of issues identified in this volume would be suitable for meta-analysis. One difficulty in conducting a meta-analysis arises when the investigations are run on different time or spatial scales, as shown in Osenberg et al. (1998). However, meta-analysis also can be used to test for scale inconsistencies among studies. This information can then be coupled with other approaches (field sampling, experimental manipulation, or modeling).

Following individuals over space and time

Atlantic salmon travel vast distances over time and space, which makes it logistically difficult to follow any individual over its lifetime. Okubo (1980) distinguishes two viewpoints or approaches for investigating moving populations. The first is the LaGrangian approach, which follows a population or an individual through space. The second is the Eulerian approach, which is to watch individuals or populations flow past a fixed point or through a fixed area.

Movements by Atlantic salmon impose logistic constraints on following individuals, even within a single habitat during a single life history stage (Armstrong et al. 1994). These constraints severely restrict the use of the LaGrangian technique. In studies of Atlantic salmon, it has been more common to take a Eulerian approach and to observe a number of individuals in an "instant" in time (e.g., by censusing all individuals in a reach or counting smolt moving past a counting station, etc.). Even when reaches are sampled repeatedly, individuals are rarely distinguished.

The Eulerian approach is appropriate for many questions, and carries with it the need to make many strategic decisions about extent and resolution in the sampling design, because the temporal and spatial scale of the study is essentially imposed by the researcher (as discussed previously). Adopting a LaGrangian perspective would enhance our ability to approach a number of questions in population and community ecology that cannot be addressed by Eulerian methods, in large part because LaGrangian approaches allow the organism to define the relevant scale. For example, long-term studies by Connell et al. (1997) on coral reef communities employ an essentially LaGrangian approach. He has followed individuals for more than 25 years, making it possible to examine the cumulative effects of species interactions and physical processes on growth and survival over the lifetime of an individual. This approach has been very successful in understanding the ecology of these sessile communities.

In situations where it is difficult or impossible to mark and follow individuals, modeling dispersal processes can allow researchers to simulate a LaGrangian approach for investigating habitat and population dynamics. For example, Bozek and Rahel (1991) found a scale inconsistency in habitat resource tracking in juvenile cutthroat trout. Within stream reaches, individuals preferred slow, deep microhabitats, but shallow reaches with abundant spawning gravel had the highest trout abundances. The low abundance or total absence of juvenile trout in stream reaches that seemed to contain suitable microhabitats appeared to result from spawning gravel limitation, explaining the scale inconsistency. Reaction-diffusion, or diffusion/dispersal models (Turchin and Thoeny 1993), which model distance-dependent dispersal success from a point source (such as a salmonid redd or a rearing tributary mouth) may therefore allow integration across spatial scales and improve our ability to predict salmonid abundance and survival in the context of these critical demographic events.

Even when mobile individuals can be marked and followed, the intensity of effort per individual restricts sample sizes (limits resolution) and generally forces inferences to be drawn from a few individuals in a few circumstances. Yet new techniques are being applied to the study of Atlantic salmon that will allow a more LaGrangian approach to be applied to larger samples of fish. For example, microsatellite genetic markers have been already developed to mark large numbers of individuals (Letcher and King 1997). Identity (from parentage) of an individual can be determined from a single fin clip, so individuals can be sampled repeatedly during their lives. This technique will eventually be applied to many questions (e.g., How far do individuals move during the stream phase? Which individuals (based on parentage or stocking location) are the successfully returning adults?) Fingerprinting salmon via stable isotopes of strontium and nitrogen has also been shown to be effective for following movements of groups of individuals over time (Kennedy et al. 1997; Harrington et al. 1998). Using organism structures that record the history of individuals, for example, growth rings on fish otoliths (Wright et al. 1990) is a third technique that can be used to follow an individual over time. Perhaps the most powerful developments will arise from combinations of these new techniques, which may allow large numbers of salmon to be followed from birth to death and to address questions not possible with other methods.

Summary and conclusions

The "great scale problem," as stated by Fahrig (1992) is, "what is the appropriate scale for study of a particular problem?" This is not a simple question for Atlantic salmon, because as we have seen, the mechanisms linking salmon and their environment vary over long and short times and over large and small spatial scales. We suggest that identifying scale inconsistencies via multiple scale observations and measurements is the first step for identifying the scales over which processes affecting distribution and abundance operate. Strategic use of experiments and models and expanded quantitative analysis of different studies using meta-analysis are likely to greatly enhance our understanding. Finally, application and development of new technologies that allow new approaches to old questions are certain to reveal novel insights that will contribute to the effective conservation and management of the Atlantic salmon worldwide.

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