

Ecology of stream fish: insights gained from an individual-based approach to juvenile Atlantic salmon

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Abstract – Using data from an ongoing study of juvenile Atlantic salmon growth and survival in tributaries of the Connecticut River, USA, we compare standard population-level approaches to those focusing on individuals. We highlight the potential benefits of resampling individually tagged stream fish as compared to standard approaches. Specifically we focus on growth, survival, movements and population estimation. The advantages of estimating sizes and growth rates from individual size trajectories include obtaining growth histories and the ability to perform retrospective analysis of the consequences of different life-history strategies. An example might be the patterns of growth leading to either early maturity or migration. Resampling known individuals is the only way we know to chart both short-term and long-term movements and to assign growth and mortality consequences to such movements. Finally, individual-level data permit robust estimation of survival and density/abundance using methods such as Cormack/Jolly-Seber. The results indicate that population estimates were about 10% lower using individual data than using population data, that survival from sample to sample was typically >90%, that the majority of recaptured fish did not move during the summer, that growth was rapid during spring and most fish lost mass during the summer and that growth trajectories for maturing and non-maturing fish showed substantially different patterns. An individual-based approach to stream fish ecology provides the opportunity to explore the mechanisms responsible for population-level patterns but comes at the cost of significant field effort. Tradeoffs between increased data resolution and the effort required to obtain the data must be considered before undertaking individual-based field studies of stream fishes.

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

Most studies examining growth and survival of stream fishes have focused on population-level phenomena by analyzing groups of similar individuals. While population-level approaches illuminate patterns, understanding the causes of these patterns requires an individual-level approach (Huston et al. 1988; Lomnicki 1992). Because individuals in populations are rarely identical, an individual-level approach can explicitly recognize and quantify these differences to produce a mechanistic model of population-level phenomena (Letcher et al. 1996).

There has been a variety of ways in which individual-based approaches have been applied in stream fish ecology. By far the most common is the use of simulation models in which groups of individuals are given distinct traits and followed through time (e.g. Jager et al. 1993; Clark & Rose 1997). More recently, the individual-level approach has been extended to laboratory and near-field conditions as represented by artificial streams (Berglund 1995; Duston & Saunders 1997; Armstrong et al. 1997; Utne et al. 1997). However, field studies tracking individuals, particularly juveniles, are

relatively rare in fish stream ecology (but see Le Louarin and Bagliniere 1997).

Various characteristics of stream fish make them amenable to individual-level approaches. Stream fish studies are usually conducted in relatively small areas, and many stream fish often have limited dispersal and are territorial. These traits allow for the possibility of repeated resampling of individuals which is critical for constructing individual trajectories. Stream fish studies also allow identification of the habitats occupied by the resident individuals, which can lead to useful correlations between observed habitat use and measured biological parameters.

Our goal is to highlight the potential benefits of resampling individually tagged stream fish as compared to standard population-level approaches. Data collected on individuals can easily be collapsed to provide population-level data. Although field-based data are useful as input for existing models, our focus here is on the insights gained from direct examination of empirical individual-based field-collected data. We specifically address how individual-based approaches can provide improved population estimates as well as individual movement data and growth trajectories. We also examine how we gain further insight into the causes and consequences of different life history strategies through retrospective analysis of individual histories.

Our intent is not to focus on any one aspect or benefit of individual-based approaches to fish ecology but to provide an overview of the potential insights provided by such approaches. We illustrate these approaches using preliminary data from an ongoing study of juvenile Atlantic salmon (*Salmo salar*). Salmonids are particularly well suited to individual-level study due to the importance of local interactions and their flexible life history strategies. Atlantic salmon are highly territorial (Keenleyside & Yamamoto 1962; Keeley & Grant 1995), have specific habitat requirements (deGraaf & Bain 1986; Morantz et al. 1987), several alternative life history strategies, and males can mature anywhere from age 0 to age 5 (Thorpe 1986; Mills 1989; Gibson 1993; Fleming 1996).

Methods

Our study site is located on the West Brook, a second-order stream in the Connecticut River Basin, Massachusetts, USA (42°25', 72°40'). The West Brook is stocked every spring with unfed Atlantic salmon fry at densities of 50 per 100 m² and has no natural salmon reproduction. The site also contains self-sustaining populations of brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trut-*

ta). We selected a ~1-km stretch of the stream and divided it into 48 contiguous 20-m sections. During typical low summer flows, average stream width (± 1 SE; N) is 4.7 m (± 0.1 ; 187), average stream depth is 8.8 cm (± 0.2 ; 1096) and average substrate size is 21.5 cm (± 1.1 ; 1096).

We sampled the entire area eight times at approximately 3-week intervals starting in May 1997; each sample took 6–10 day-night cycles to complete. We sampled our site using various methods; electrofishing and day and night seining. We used seining because electrofishing, while generally the most effective, can damage fish if used repeatedly (Gatz et al. 1986; Mesa & Schreck 1989). Electro-fishing samples were conducted during the day. We enclosed each section with block nets and made two removal passes with a Smith-Root model 12-A backpack electrofisher using unpulsed DC current at 500 V. Night seining samples were conducted using one-person, hand-held lip seines (73 cm wide \times 81 cm high and 6.4 mm mesh). Prior to sampling each section was enclosed with block nets. We seined each section starting at the downstream end and worked upstream, completing two passes through each section. Two people holding seines stood approximately 3 m downstream while two other people with flashlights aimed into the water walked towards the seines in a downstream direction. The walkers startled salmon into the nets, which were raised rapidly to capture fish. Sampling began approximately 1 h after sunset. We also searched for salmon in pools and slack water using flashlights. Day seining protocol was identical to night seining except that we did not search for salmon in pools and slack water and did not use flashlights. Day-seining was ineffective and was discontinued after a pass through the study reach (sample 2).

Captured salmon were anesthetized (MS-222), weighed (± 0.1 g), measured (fork length, ± 1 mm), their location was noted (± 2.5 m), the expression of milt indicated a mature male, and fish > 60 mm were tagged interperitonally with a PIT (passive integrated transponder) tag (Prentice et al. 1990) or had their tag number identified if previously tagged. PIT tags were inserted through a small incision between the pectoral fins. In this article we consider only post-young-of-year (PYOY; fish > 90 mm, age one or older) fish, although we also tagged young-of-year (YOY, < 90 mm) fish during our last two samples. Based on the occurrence of fish without tags but with incision scars, we estimated the tag loss rate to be 2.3%. An independent laboratory study indicated that growth rates between tagged and untagged fish were not significantly different (d.f. = 15, $P = 0.72$, 22 fish over a 7-month period, average growth = 3.5 g or 50%).

Population estimation

We used three population estimation methods. These methods ranged from those requiring no tagging, to batch tags to individual tags and included both open and closed population models (closed population models assume no birth, death, immigration or emigration). For the untagged situation we used the removal method, which estimates population size from two or more successive removal counts (Mahon 1980; Krebs 1989). To compute an overall estimate for all sampled sites and to reduce bias caused by catches on the second pass equaling or exceeding those on the first pass, we pooled catch data from all sites using the method outlined by Heimbuch et al. (1997). The Schnabel estimator is a closed population mark-recapture method that uses batch tags over multiple samples to arrive at one overall population estimate (Seber 1982; Krebs 1989). Finally, we used a Jolly-Seber estimator as an open population model (Pollock et al. 1990). The Jolly-Seber model also requires individual tags. We used POPAN to analyze the large data set generated (Arnason 1997).

Movement

Multiple recaptures of individual fish at 3-week or greater intervals provided a record of coarse-scale (~monthly) movement. Movement was analyzed by plotting the location of those individuals that were captured at least five times during the sampling season against date sampled. These fish represented a subsample of approximately 100 fish or about 17% of the fish sampled.

Growth

Population growth was determined by averaging the size of all captured individuals during each sample. Individual growth trajectories were estab-

lished for those individuals captured all eight times we sampled (10 fish).

Retrospective analysis and parr maturity

Because Atlantic salmon can exhibit parr maturity beginning in their first year (Myers et al. 1986; Fleming 1996), we conducted a retrospective analysis of growth to assess whether early maturity leads to unique growth trajectories. We also compared the instantaneous growth rate of individual immature and eventually-mature parr early in the season (before maturity occurred) and late in the season (after maturity was exhibited). Finally, we examined population estimates for both mature and immature parr.

Results

We completed eight samples (Table 1). A total of 657 individual PYOY salmon were tagged. The first sample was an electrofishing sample in which we captured 341 fish. The second was a day seining during which we collected 102 fish, 56% were already tagged. Samples three, four, five and six were night-seining samples, and we consistently captured about 250 fish and by sample six over 95% of the captured fish were recaptures. Samples seven and eight were electrofishing surveys, with fewer captures in sample eight most likely due to cold winter water temperatures (Table 1).

No fish expressed milt during samples one through four, but by sample seven 50% of the fish were mature males (Table 1). Assuming a 50:50 sex ratio, all males were mature by sample seven.

Population estimation

The results of the removal method estimation parallel the number of individuals captured (Fig. 1). The Schnabel estimator produced one overall estimate of 671 individuals (95% confidence interval=

Table 1. Sample number, sampling technique, date, numbers of fish caught, percentage of mature fish and average temperature in the West Brook, Whately, Massachusetts, USA 1997

Sample number	Sampling technique	Median sample date	Total number of fish captured	Total number of untagged fish captured	Percentage recaptures	Percentage mature salmon	Average temperature °C	Temperature range °C
1	Electrofishing	May 24	341	341	0	0.0	10.8	9.2–11.9
2	Day seining	June 12	102	45	55.9	0.0	12.1	11.0–14.8
3	Night seining	June 26	271	133	50.5	0.0	15.0	12.7–16.9
4	Night seining	July 19	246	64	74.0	0.0	16.9	15.3–18.2
5	Night seining	Aug 12	243	27	88.9	5.7	15.9	14.4–17.2
6	Night seining	Sept 2	252	10	96.0	23.3	15.4	14.6–16.0
7	Electrofishing	Oct 8	380	12	96.8	50.8	10.7	8.4–11.8
8	Electrofishing	Dec 21	208	25	88.0	39.4	1.1	0.2–2.0

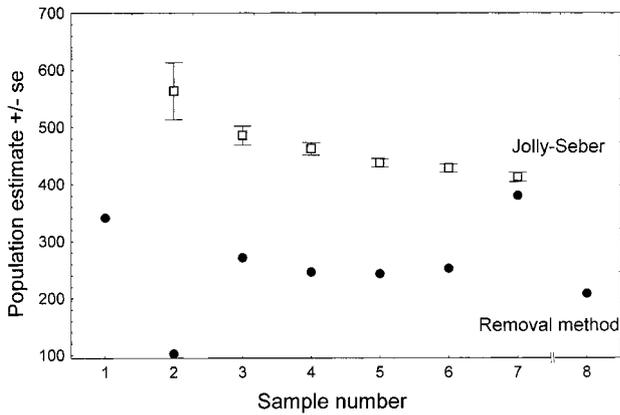


Fig. 1. Results of population estimates. Solid dots represent estimates derived from the removal method (no error estimates available). Open squares represent estimates and standard errors derived from the Jolly-Seber method.

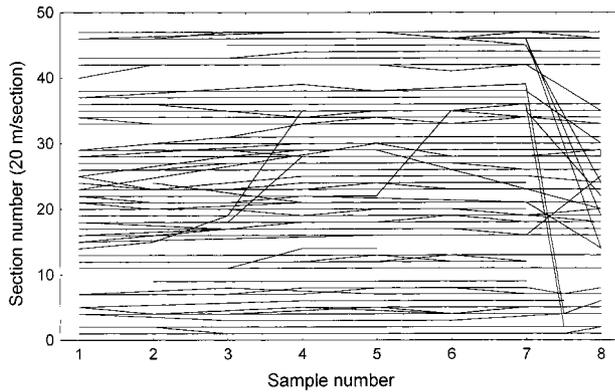


Fig. 2. Location (section number) of individual PYOY salmon captured at least five times (103 fish total). For dates of sample periods see Table 1.

637–708). The Jolly-Seber method estimated a starting population size (at time 2) lower than that estimated by the Schnabel method (for time 1) but the estimate declined through time. Both the Schnabel and Jolly-Seber estimates were within 10% of the total number of fish tagged. The high number of recaptures resulted in relatively small errors around these estimates.

Movement

We captured 103 individuals at least five times. There appeared to be little movement, with most fish usually found in the same section in consecutive samples (Fig. 2). During the first seven samples, less than 10% (10 fish of 103) of the individuals moved locations (mainly upstream), the largest movement encompassing 20 sections (approximately 400 m). A larger frequency of downstream movement is apparent between samples

seven and eight coincident with a drop in water temperature (Table 1).

Population mass

Mean mass increased rapidly through early summer (samples 1–3), declined through mid-summer (samples 4–5), increased slightly in the fall and again declined in early winter (sample 8) (Fig. 3).

Individual growth

When individual-level data are examined for these individuals that were captured during all eight samples, several tactics are apparent (Fig. 4). First, there is a wide variation in size (15–29 g) at a similar age, and this variation in size is maintained throughout the sampling period. Some individuals grow very rapidly early and then level off. Others lose weight in mid-summer. Others exhibit drastic growth spurts in late summer through autumn.

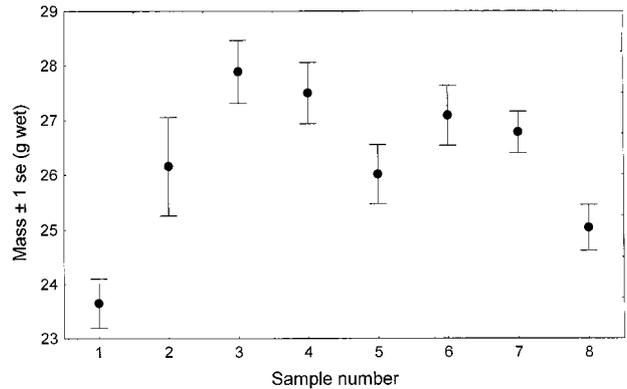


Fig. 3. Average mass (grams wet) and standard error of all PYOY salmon collected during each sample period. For dates of sample periods see Table 1.

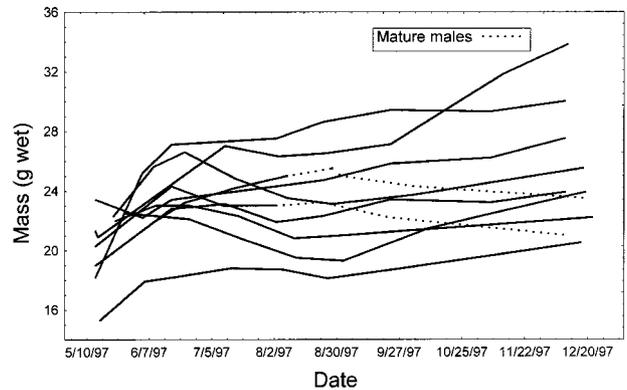


Fig. 4. Growth trajectory of individual mature and immature PYOY salmon captured eight times during the sample period

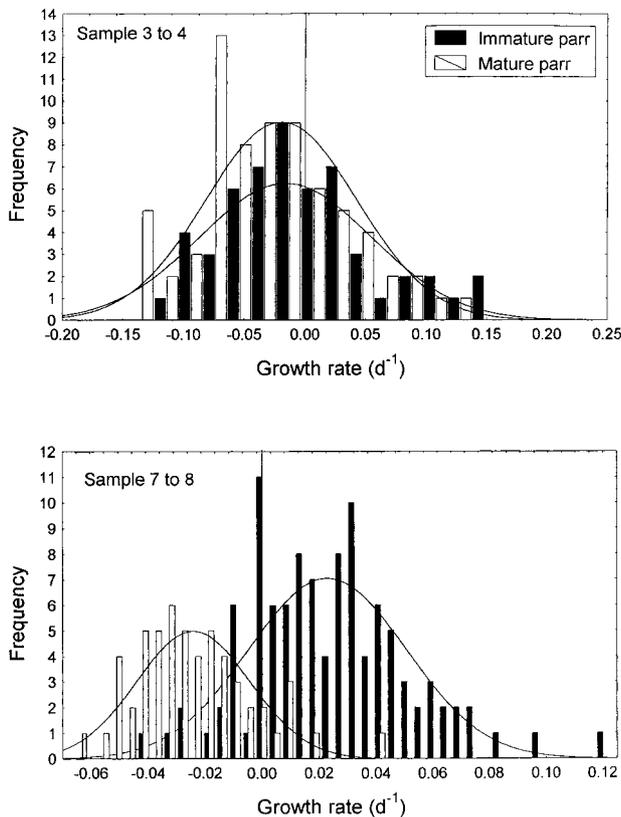


Fig. 5. Instantaneous growth rate (d^{-1}) frequency distributions of immature and mature PYOY salmon early in the season (June–July, above) and late in the season (September–December, below). Vertical solid line denotes 0 growth. Individuals to the left of the line lost weight between samples, individuals to the right gained weight.

Retrospective analysis

Individual growth. Two of the 10 fish captured all eight times were mature parr. These two individuals appear to have distinct growth trajectories exhibiting rapid early growth and a loss of weight after sample 4 (Fig. 4).

Population size. Separating the population estimates into fish that matured and those that did not reveals that the numbers of mature fish were consistently 75% of the numbers of immature fish.

Growth history. The growth histories of immature and mature parr differ considerably when comparing sample periods before and after maturity (Fig. 5). The growth rate distribution over samples three to four in early summer shows no difference between mature and immature parr with many of the fish losing weight (growth rate <0). The growth rate distribution in late fall/early winter exhibits a bimodal distribution, with the lower mode composed almost entirely of mature parr. In ad-

dition, most mature parr lost weight between samples, whereas the immature parr were mostly gaining weight.

Discussion

The results of this study demonstrate that individual-based approaches allow the use of more robust open population estimators, can produce individual growth and movement trajectories and can provide insights into the causes and consequences of alternative life history strategies through retrospective analysis. While there are clear benefits to conducting studies on individuals, considerable effort is required to collect the data. Our field survey teams consisted of 4–5 people and sampling the study site took 6–10 day-night cycles depending on weather, stream conditions and sampling method. Despite the effort involved, we believe there is great benefit in studying fish populations at the individual level and that the benefit, especially in streams, is worth the cost.

The feature that has allowed us to conduct this study efficiently is the availability of PIT tags. PIT tags are small (12 mm), allowing us to tag small juveniles (>60 mm), provide individual internal marking, and permit resampling fish non-lethally, rapidly, and without error. The non-lethal nature of PIT tags was critical in our system because all fry are stocked as part of the Connecticut River salmon restoration effort (Meyers 1994), and because adult returns remain low it was imperative to find a marking method that minimized potential mortality while maximizing information gain. A recent study using 0+ brown trout showed PIT tags to have high retention rates ($>96\%$) and no significant effect on growth or survival (Ombredane et al. 1998). There are some disadvantages to our approach. It is fairly expensive (US \$4/tag), requires an intensive effort to sample many sites frequently, and is somewhat restricted to a local scale if the goal is to maximize recapture rates.

Population estimation

Comparison of population estimation methods suggests substantial differences among methods. The removal method provided the lowest numbers and usually reflected the numbers of fish captured during each sample. Because no marks are used, this method cannot account for losses (mortality or emigration) or recaptured individuals and is therefore not very useful in situations where individual recapture is likely to be high. The removal method has been shown to consistently underestimate fish population size (Riley & Fausch 1992; Pierce 1997). The closed population method can-

not account for losses and therefore results in one overall estimate for the entire sampling period (May–September). The open population Jolly-Seber model resulted in similar estimates of original population size to those provided by the closed population model but in addition provided an estimate of loss rates through the sampling period. Estimated survival rates from sample to sample ranged from 82% in the first sampling interval to >95% through the rest of the sampling season. Survival rates can also be estimated directly from mark-recapture data using one of the many methods available (based on the Cormack-Jolly-Seber model, see review in Lebreton et al. 1992). The relative robustness of survival versus population size estimators will depend on the extent and type of assumptions that may be violated (Carothers 1973; Arnason and Mills 1987; Lebreton et al. 1992; Pierce 1997). Because mortality of larger fish is thought to be relatively low in these systems (Mather 1998), we attribute most of the loss to movement. Loss of smolts is not a factor since smolting only occurs in the early spring, a period not covered in this particular study. Future work will examine movement out of our site using permanent in-stream antennae and smolt traps.

Movement

Analysis of individual-level data is the only method by which to assess detailed movement. We could not follow individuals continuously (as might be possible if sonic tags were available or if the whole stream could be arrayed with flat bed antennae, see Armstrong et al. 1996), but were able to track the location of many individuals over an extended time period. We found surprisingly little movement exhibited by the recaptured salmon juveniles. This apparent high site fidelity could be biased if migrating fish had moved completely out of our sample site and therefore were not re-captured in subsequent sampling efforts (Gowan et al. 1994). We feel that this bias is unlikely because if such high migration rates existed, we would have captured some fish that had moved long distances within our sampling site, or would have consistently captured unmarked fish. Instead we observed almost no long-distance movements, obtained extremely high recapture rates, and by the fourth sample found few unmarked fish. Electrofishing 140 m outside our study site in each direction resulted in few (<10) recaptures of tagged fish. After depletion of a natural stream, Armstrong et al. (1994) found similarly high levels of site attachment by Atlantic salmon parr, resulting in low recolonization rates into depleted areas. Interestingly, Armstrong et al. (1994) observed that in

early summer, similar to our results, most of the movement was directed upstream.

We also observed individual differences in movement; a few individuals were apparently more consistently mobile than others. Other mark-recapture studies have shown that populations of salmonid fishes contain individuals that are particularly mobile or sedentary (Bridcutt & Giller 1993; Nakano 1995; Armstrong et al. 1997).

Movement appeared to increase between our last two samples, coincident with a decrease in water temperature. A similar increase in movements of juvenile Atlantic salmon in fall and early winter has been observed in other systems (Rimmer et al. 1983; Cunjak & Randall 1993; Whalen et al. 1999). Future work will explore whether increased movements are observed again during spring.

Growth

The mean properties of fish populations do not necessarily reflect the properties of the individuals in the population (Sharp 1987). For example, the change in mean length in a population with time may not reflect the average individual growth rate, since individual growth rate and survival probability are often linked so that slow-growing individuals suffer higher mortality. In our study, mean population growth rate showed an increasing trend in spring and early summer, reduced growth in mid-summer and zero or negative growth in autumn and winter. As an example of the lack of relationship between mean and individual growth rates, average fish mass decreased markedly between samples seven and eight (Fig. 3) yet most individual growth trajectories continued to climb (Fig. 4). We hypothesize that the loss in mass between samples seven and eight was due to larger fish leaving the study section or dying instead of mass loss of individual fish. Larger fish (>50 g) were present in samples 1–7, but were absent in sample eight.

Retrospective analysis

Various interesting insights emerge from the retrospective analyses. A retrospective analysis allows one to correlate individual histories with life history strategies. In salmon this is particularly interesting because they exhibit alternative mating strategies (Fleming 1996). For example, in our system parr mature as early as their first summer (Letcher & Terrick 1998), in later years almost 100% of the males in this and other systems mature before going to sea (Myers et al. 1986; Erkinaro & Gibson 1997; Jonsson et al. 1998; Whalen & Parrish 1999). Comparisons between population esti-

mates of mature and immature fish showed distinct differences. In our study year, numbers of mature fish were estimated to be 75% of those of immature fish. This difference may reflect a survival cost to maturing fish (Myers et al. 1986; Whalen and Parrish 1999). Because the relative numbers of mature and immature fish did not change over the course of our samples, fish destined to mature in their second summer would have had to sustain higher mortality before our sampling began (spring of second year). The generality of this result, however, must be viewed with some caution, as estimates of mature vs. immature numbers were similar to each other in the subsequent year for the same age-class (Letcher et al., unpublished data).

Our retrospective growth analysis suggests that mature and immature parr may be exhibiting different growth trajectories. Mature parr grew quickly in late spring and early summer and subsequently showed negative post-maturity growth in late summer and autumn (Figs. 4, 5). These results are consistent with those from other studies that have observed mature parr to exhibit initially greater growth than immature parr (Simpson 1992; Berglund 1995; Duston & Saunders 1997) but reduced or negative growth following maturation (Myers et al. 1986; Rowe & Thorpe 1990a, b; Herbinger & Friars 1992; Whalen & Parrish 1999). Future work will assess smolting age and size, and overwinter mortality of individual mature and immature fish.

Although previous studies have explored the extent to which individual behaviors can be extrapolated to populations and communities, most have considered small scale phenomena over short time scales rather than actual tracking of individuals (see for example Peckarsky et al. 1997). This study highlights how tracking individually tagged fish in the field over a large portion of their lives can provide insights about population-level processes and variability in life history traits.

Resumen

1. Hemos utilizado los datos de un estudio en marcha del crecimiento y mortalidad de juveniles de salmón Atlántico en los tributarios del río Connecticut, EE.UU., para comparar las perspectivas poblacionales estándares con aquellas que se centran en individuos. Hemos resaltado así los beneficios potenciales del muestreo repetido de ejemplares marcados individualmente. En concreto, nos hemos centrado en el crecimiento, la mortalidad, el movimiento y las estimas de densidad.

2. El crecimiento fue rápido en primavera y negativo en verano. Las ventajas de estimar tamaños y tasas de crecimiento a partir de trayectorias individuales incluyen la obtención de historiales de crecimiento y la capacidad de analizar a posteriori las consecuencias de diferentes estrategias vitales. Un ejemplo serían los patrones de crecimiento que conducen a migración o a madurez sexual temprana: las trayectorias de crecimiento de los ejempla-

res que posteriormente madurarían exhibieron patrones claramente diferentes de las de aquellos que no lo harían.

3. Muestrear repetidamente individuos conocidos es la única manera de detectar movimientos tanto de corto como de largo alcance e identificar las consecuencias para el crecimiento y mortalidad de tales movimientos. La mayoría de los peces recapturados no se movió durante el verano.

4. Finalmente, los datos individuales permiten estimas robustas de mortalidad y abundancia mediante métodos tales como Cormack/Jolly-Seber. Los resultados indicaron que las estimas del tamaño de la población obtenidas a partir de datos individuales fueron típicamente inferiores en un 10% a los obtenidos mediante datos poblacionales y que la supervivencia entre muestreos fue típicamente superior al 90%.

5. Un enfoque individual de la ecología de los peces fluviales permite explorar los mecanismos responsables de fenómenos que se manifiestan en las poblaciones, pero conlleva un coste en forma de un sustancial esfuerzo en el trabajo de campo. Es, por tanto, preciso considerar el balance entre la mayor resolución y el esfuerzo que se precisa obtenerla antes de emprender estudios individuales de peces de río en la naturaleza.

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