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# Exploring Population Dynamics Patterns in a Rare Fish, *Zingel asper*, through Capture-Mark-Recapture Methods

JACQUES LABONNE\*† AND PHILIPPE GAUDIN\*

\*Fish Behavioral Ecology, National Institute of Agronomical Research, Research Unit 1224, BP3, 64310 Saint-Pee-sur-Nivelle, France

**Abstract:** *We performed a capture-mark-recapture study on one of the last populations of Zingel asper, an endemic percid species of the Rhône River basin in France. The distribution of Z. asper has decreased dramatically during the last century. We sampled three sites in suitable habitats in the Beaume River. No impact of individual tagging on survival was found. The demography of the population was analyzed using capture-recapture methods that allow the estimation of survival, recruitment, and demographic growth rates. Annual survival rates were low (0.35–0.50). The level of transience was high (5% to 25%), suggesting that a significant number of individuals were highly mobile or shifted to suboptimal habitats. Seniority rates suggested random highly variable recruitment between years. The three sites had similar variation patterns in all demographic parameters, indicating broad spatial covariation in population dynamics. We found some local differences in demographic parameters, which could be linked to local habitat quality. Individual tagging allowed for the estimation of demographic parameters that improved our understanding of Z. asper population dynamics and revealed mechanisms that may affect population persistence, such as stochastic recruitment, low survival, and frequent dispersal. The fragmentation of habitat through river damming inhibits dispersal and represents a threat to the persistence of Z. asper in the Rhône basin. Our results offer evidence of the importance of dispersal in nonmigratory fishes and confirm the usefulness of individual tagging methods in rare fish demography.*

**Key Words:** dispersal, population growth rate, seniority, survival, transience

Exploración de los Patrones de la Dinámica Poblacional de un Pez Raro, *Zingel asper*, Mediante Métodos de Captura-Marca-Recaptura

**Resumen:** *Realizamos un estudio de captura-marca-recaptura en una de las últimas poblaciones de Zingel asper, una especie de pércido endémica a la cuenca del Río Rhône en Francia. La distribución de Z. asper ha disminuido dramáticamente durante el último siglo. Muestreamos tres sitios en hábitats adecuados en el Río Beaume. No se detectó impacto del marcaje de individuos sobre la supervivencia. Analizamos la demografía de la población mediante métodos de captura-recaptura que permiten la estimación de las tasas de supervivencia, reclutamiento y crecimiento demográfico. Las tasas anuales de supervivencia fueron bajas (0.35-0.5). El nivel de transitoriedad fue alto (5 a 25%), lo que sugiere que un número significativo de individuos tuvo mucha movilidad o se cambió a hábitats subóptimos. Las tasas de veteranía sugirieron reclutamiento aleatorio muy variable entre años. Los tres sitios tuvieron patrones de variación similares en todos los parámetros demográficos, lo que indica amplia covariación espacial en la dinámica poblacional. Encontramos algunas diferencias locales en parámetros demográficos, que pueden estar relacionados con la calidad del hábitat local. El marcaje individual permitió la estimación de parámetros demográficos que mejoraron nuestro entendimiento de la dinámica poblacional de Z. asper y reveló mecanismos que pueden afectar la persistencia de*

†email labonne@st-pee.inra.fr

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la población, como el reclutamiento estocástico, baja supervivencia y dispersión frecuente. La fragmentación del hábitat, mediante presas, inhibe la dispersión y representa una amenaza a la persistencia de *Z. asper* en la cuenca del Rhône. Nuestros resultados proporcionan evidencia de la importancia de la dispersión en peces no migratorios y confirma la utilidad de los métodos de marcaje individual en la demografía de peces raros.

**Palabras Clave:** dispersión, tasa de crecimiento poblacional, transitoriedad, supervivencia, veteranía

## Introduction

During the last 20 years, the study of population dynamics in wild environments has been considerably aided by the use of individual tagging and monitoring. Such technical progress allows theoretical model predictions (Bennetts et al. 2001), such as the correlation between spatial synchrony of population dynamics and dispersal intensity (Tilman & Kareiva 1997; Lande et al. 1999; Kendall et al. 2000) and the evolutionary role of dispersal processes (Dieckmann et al. 1999; Ronce et al. 2001), to be tested. There are few connections, however, between theoretical and empirical approaches (Hanski 2001). Conservation biology represents a great opportunity to apply these methodological advances (Stockwell et al. 2003), particularly to conservation of declining fish species (Collares-Pereira et al. 2002). The lack of data on fish population biology often prevents examination of questions relevant to their conservation. Precise estimates of demographic components are an essential basis for management and recovery of imperiled fishes (Sarrazin & Barbault 1996; Meffe & Carroll 1997; Sutherland 1998), but these estimates are usually lacking for fish populations. Most researchers have focused on density analysis (Gowan et al. 1994; Schlosser 1998) and have disregarded demographic rates such as survival, recruitment, and dispersal (except in highly migratory species; Northcote 1998).

Burnham et al. (1987) and Lebreton et al. (1992) provide guidelines for capture-mark-recapture (CMR) data analysis, and these methods are now generally used to estimate classical survival parameters. These protocols also allow recruitment, immigration rates, and the population growth rate to be estimated, eliminating the need for demographic modeling (Pradel 1996). Although first developed in species for which demographic parameters at young stages are known, these techniques should also be applicable to species for which demographic parameters on juveniles are not available, such as fishes and amphibians.

To use CMR modeling successfully in fish species, some obstacles must be overcome. Field experiments seldom meet the theoretical conditions required to apply demographic statistics to the data that are gathered. Recently, researchers have focused on the modeling of data that do not fit Cormack-Jolly-Seber (CJS) model requirements (the CJS approach allows use of goodness-of-fit tests to val-

idate models) and its consequences on further estimates (Pradel et al. 1997). For instance, transience leads to an underestimation of survival rate (Oro & Pradel 2000). Besides improving the reliability of survival estimates, the study of these problems may offer further insight into population-regulating processes. For instance, evidence of transience can reveal alternative dispersal strategies, providing an index of dispersal rate.

We used recently developed modeling techniques to explore the population dynamics of an endangered fish species, the “Apron du Rhône” (*Zingel asper*; IUCN [World Conservation Union] 1996). Only two known viable populations exist in the Rhône basin, France, although the presence of the species is reported in other locations. The Rhône basin is heavily disturbed by human activities (e.g., hydraulic power plants, intensive damming, discharge regulation and decrease, and eutrophication). A lack of knowledge, however, currently precludes establishment of efficient conservation strategies for this species.

We conducted a capture-mark-release study on one of the two remaining populations in the Beaume River (Mari et al. 2002). Our purpose was to provide the first estimates of demographic parameters for *Z. asper*, by quantifying survival and seniority rates, and to investigate spatiotemporal patterns of variation in population dynamics. We looked at potential spatial correlation of demographic parameters among sites and at local components of demography, and we examined specific temporal trends such as seasonal periodicity or possible decline in population growth rate. We also attempted to confirm the existence of significant movements and to evaluate dispersal rates through the study of transience. These initial findings may point to causes of the species' decline and should represent the first scientific basis for management policy and efficient riverine ecosystem restoration to maintain small relict populations.

## Methods

### Study Species

*Z. asper* is a benthic percid in the subfamily Lucioperinae endemic to the Rhône River. The species is related to *Z. streber* and *Z. zingel*, which occur in the Danube basin

(Song et al. 1998). *Z. asper* prefers run and riffle hydraulic sequences (Labonne et al. 2003). Because these habitats are usually distributed heterogeneously in rivers, they influence the distribution of fish. Usually they avoid other habitats (pools and rapids) unless preferred habitats are lacking. The species is essentially nocturnal and predatory (Cavalli & Chappaz 2003). Adults are 12 to 20 cm long. Density of the studied population (Beaume River) appears to be naturally low (20 to 40 adult individuals/ha; J.L., unpublished data). Spawning occurs in March and April, when the water temperature reaches 11° C. Mating behavior is unknown, and neither eggs nor hatchlings have been observed in the wild, but larvae in captivity are pelagic. First observations of the young-of-the-year in the wild occur in June and July, when fish are 2 to 3 months old. By this time, they have already adopted a benthic behavior. Fish appear to be mature at 1 year old and seldom live longer than 3 years (D. Danacher, unpublished data).

### Study Sites

The population is located in a 13-km reach of the Beaume River, from its confluence with the Ardèche River to the weir of Rosières (Fig. 1). Fish tend to occupy discrete riffle/pool sequences (Labonne et al. 2003) or sites in which they can complete their life cycle (Danacher et al. 2004). We selected three upstream areas of the reach as sampling sites. Previous field research showed that these areas were easy to access and presented sufficient numbers of fish for our experimental design (Fig. 1). Upstream dispersal was not possible because a weir was present. Sampling sites were 200 to 350 m in length and 25 to 50 m wide. Between these sites, habitat was unsuitable for the species (Labonne et al. 2003). Preliminary samplings showed that few individuals were present, so it was not possible to develop a feasible monitoring protocol in these areas.

### Sampling and Tagging Protocol

During each sampling campaign, each site was sampled twice within 2 hours at night by four workers using dip nets. The eyes of *Z. asper* reflect incident light and the fish remained motionless, so they were easily located with head lamps. Each campaign lasted 2 or 3 nights. Eleven campaigns were made from October 1997 to June 2000. Campaign frequency depended on in-stream conditions (i.e., stream flow and turbidity) and reproductive status (i.e., we did not disturb fish during maturation and spawning) but intervals varied from 2 to 5 months.

After performing trials on sculpin (*Cottus gobio*) and perch (*Perca fluviatilis*) in artificial channels, we implanted passive integrated transponder tags (PIT tags, Trovan, Köln, Germany) in the peritoneal cavity of anaesthetized *Z. asper* (phenoxy-ethanol, 0.2 mL). Only adult fish measuring more than 100 mm in total length ( $\geq 1$  year) were tagged. The first two sampling campaigns were undertaken to test the impact of tagging on sur-

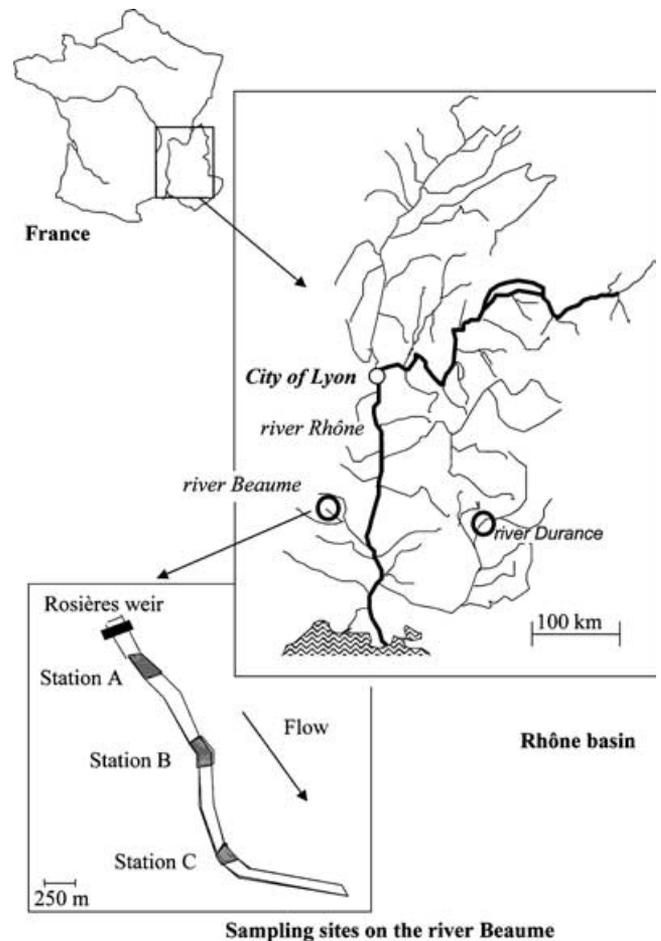


Figure 1. Location of the Beaume River in the basin of the Rhône River, southeastern France. Circles represent the known and monitored populations of *Z. asper*. Sampling sites (A, B, and C) are located downstream of the Rosières weir; the upstream limit of the population in the Beaume River.

vival and were performed only in the two upstream sites. For this preliminary experiment, we marked half the captured fish (the control group) with a fin clip, the location of which depended on the date and site of capture. The other half were anaesthetized and tagged with PIT. We assigned fish to each group randomly and kept them in a fish tank for 12 hours to control for mortality. The proportions of marked individuals from each treatment group captured during the second and third campaigns should not differ if the PIT-tagging process does not affect apparent survival (assuming that capture probability is homogeneous between groups). We therefore considered that our capture effort was reduced by 50% during these two first campaigns because fin-clipping prevents individual tagging. The modeling of the site effect on capture probability enabled us to use the results of these campaigns in other demographic analyses.

## Choice of Modeling Framework

In population studies that incorporate spatial structure, multistrata models are often used to estimate transition probabilities between strata (Brownie et al. 1993). In our study, only 16 individuals (out of 236 recaptures) represented movements among sites, so it was inappropriate to model transition probabilities with such a small number. Goodness-of-fit tests have been proposed recently for certain types of multistrata designs (Pradel et al. 2003) but are still in development. These tests need large data sets and pooling of data is usually required.

We therefore decided to analyze our data with the CJS approach, using goodness-of-fit tests to validate models (Burnham et al. 1987). The site effect in our data was used as the group effect (henceforth referenced as groups 1, site A; 2, site B; and 3, site C). We checked the data adequacy, with global trend tests, in the software U-care (Choquet et al. 2001). These tests were conducted with  $Z$  statistics and signed square roots of chi-square values of goodness-of-fit tests (tests 3SR for transience and 2CT for trap dependence). Transience tests were significant for each of the three groups (statistic for transient, two-sided test: group 1,  $p = 0.019$ ; group 2,  $p = 0.041$ ; group 3,  $p = 0.007$ ). Significant transience indicates an excess of fish that are never recaptured. Such a bias precluded using the classic CJS design for our demographic estimations, so we adopted an ad hoc modeling approach. We built a two-stage class model to exclude the effect of first capture on survival (Pradel et al. 1997). The essence of this approach is to distinguish between individuals. The first-stage class incorporates all individuals, including transient individuals. The estimate of survival rate for this stage class is biased because many individuals are considered dead only because they have emigrated. The estimate of survival rate for the second-stage class is expected to be unbiased because only individuals captured at least twice are used to estimate survival.

We estimated the proportion ( $P$ ) of transient individuals in the system as follows:

$$P(\text{transient}) = -\ln(\phi_{a1}/\phi_{a2+}),$$

where  $\phi_{a1}$  is the estimated survival rate between first and second capture and  $\phi_{a2+}$  is the estimated survival rate after second capture (which is expected to be unbiased). A high transient proportion usually reveals an excess of individuals seen only once in the sampling area. When methodological biases can be rejected (impact of tagging on apparent survival rate), one can assume that these individuals have a lower capture probability (i.e., they are mobile and evade recapture during recapture campaigns). This proportion is an index of dispersal rate or mobility for the population and includes movements at scales larger than direct movements between sites (Perret et al. 2003). To estimate survival, seniority, and demographic growth rates, we analyzed data twice, with Mark

software (White & Burnham 1999), following Pradel et al.'s method (1997). In the first analysis we obtained estimates of survival rates ( $\phi$ ). In the second analysis, capture histories were analyzed backward to estimate the seniority rates ( $\gamma$ ; i.e., the probability that an individual present at time  $t$  was present at time  $t-1$ ; Pradel 1996). The value  $1-\gamma$  thus represents local recruitment or immigration rates, or both. Seniority rates lower than 1 usually indicate an increase in local turnover. A trough is expected during the spawning season if local recruitment is successful.

Because the survival and seniority analysis could not be performed simultaneously (as in Pradel 1996), the modeling for survival did not follow the CJS design. Thus, demographic growth rate  $\lambda(t)$  was calculated as  $\phi(t)/\gamma(t-1)$ , and no confidence interval could be computed.

## Model Denomination and Hypotheses

To investigate effects of time and site in our data, we constructed the following models:

$$\{\phi(a2 * g * t), p(g * t)\} \text{ for survival, and} \\ \{\gamma(a2 * g * t), p(g * t)\} \text{ for seniority,}$$

where  $\phi$  is the survival rate,  $\gamma$  is the seniority rate,  $p$  is the capture probability,  $g$  is the group effect,  $t$  is the time effect, and  $a2$  is the transience effect, which illustrates that the model is an ad hoc method instead of the usual CJS model. From this initial structure (called the "global model"), we tested simplified models by incrementally removing interactions and factors. For instance,  $\{\phi \text{ or } \gamma(a2 + g + t), p(g + t)\}$  represents an additive model in which all interaction terms between effects have been dropped. The simplest model was  $\{\phi \text{ or } \gamma(a2), p(\cdot)\}$ , with all parameters constant through time and space.

We also tested alternative hypotheses for each demographic parameter. First, we hypothesized that capture probability was influenced by capture effort, which was reduced for the first two campaigns (because of the tagging experiment) and for the fifth campaign (because of a local pollution event that increased turbidity). We tested a nested model with dummy variables for these dates against the time-dependent model for capture probability as follows:  $\{\phi \text{ or } \gamma(a2 * g * t), p(g * effort)\}$ . Second, we hypothesized that season influenced survival and seniority rates. This hypothesis was also built as a nested model, with dummy variables (four modalities corresponding to the four seasons) tested against the time-dependent model (which considered the demographic rate variability to be stochastic) as follows:  $\{\phi \text{ or } \gamma(a2 * g * season), p(g * t)\}$ .

Models were fitted with the maximum likelihood method to estimate parameters. We used Akaike's information criterion (AIC) to select the most parsimonious models, in which lower values indicate greater parsimony and better fit (Anderson et al. 1994). Time periods

between campaigns were used to calculate demographic parameters in monthly units (e.g., 85 days = 2.83 months).

## Results

We tagged 469 *Z. asper* adults during 11 campaigns and recaptured 236 of these individuals (total of 705 capture events; site data available from authors on request). The average size of tagged fish was 134 mm, and the biggest fish was 194 mm in length. Capture numbers decreased in 1999 at the two downstream sites (B and C). Numbers were more stable at site A. The number of captures increased again in 2000 at sites B and C. Few movements were observed among the three sites, with a trend toward upstream movements (16 adult fishes, 3% of the total number marked, 6% of the recaptured fish; Fig. 2). When these fish left a site (i.e., a group) for another one, in the modeling process, we considered them as dead for the departure site and as newly marked for the arrival site.

### Impact of PIT Tagging on Survival

No postmanipulation mortality occurred during the 12 hours following tagging. Fish lengths were not different between treatments (PIT-tagged and fin-clipped fish, *t* test,  $p = 0.462$  and  $p = 0.421$  for sites A and B, respectively). Results of the tagging experiment during the first two campaigns did not show any impact of PIT tagging compared with fin clipping on recaptured numbers in either site, so the apparent survival was equal between the two groups (Table 1). As a result, we assumed that PIT tags had no impact on the survival rate of *Z. asper*.

### Model Selection

Capture probability depended on time and group and consideration of capture effort. The fifth campaign pollution event  $\{p(g + \text{effort})\}$  also improved the fit of the model (Table 2). The group effect was significant, indicating that capture probability was not homogeneous among sites. This was mainly caused by differences in capture effort

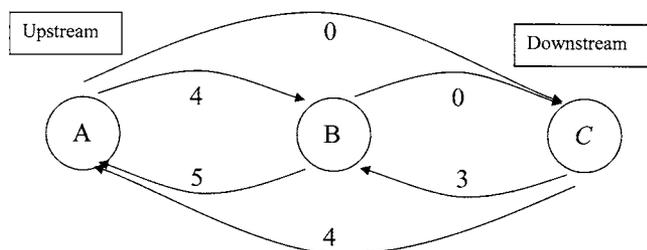


Figure 2. Number of observed movements of *Z. asper* among sampling sites A, B, and C along the Beaume River.

at the beginning of the protocol, but capture probability was consistently lower at site A (Fig. 3a). Capture probabilities were generally high ( $p = 0.65$  at site A,  $p = 0.70$  at sites B and C).

For the survival analysis, the best model showed an additive pattern:  $\{\phi(a2 + g + t), p(g + \text{effort})\}$  (AIC = 1283.72; Table 3). Survival rate was time dependent (i.e., not constant across time) but did not follow a seasonal pattern (Fig. 3b). There was a significant difference in survival rate among sites—the overall survival rate was higher in site A than in sites B and C. No interaction was significant, and variation in survival was thus spatially correlated. Low survival rates observed during spring 2000 strongly influenced other estimates for the same campaign; transience increased and growth rate decreased. Monthly survival rates fluctuated between 1.0 and 0.7. Depending on site and year, annual survival rate ranged from 0.35 to 0.50.

For the seniority analysis, the best model was  $\{\gamma(a2 + g + t), p(g + \text{effort})\}$  (AIC = 1171.37; Table 3), and it followed the same patterns as the survival model. Monthly seniority was often high (i.e.,  $\geq 0.8$ ) but seldom reached 1, which indicated regular turnover in the sampled population. Troughs were recorded during winter 1998 and winter 2000 (Fig. 3c).

### Demographic Growth Rate and Transience

Estimation of growth rate between the first and second capture occasions was not possible because an unbiased estimator for survival was not available for this period. We computed growth rates per site and through time, following the selected pattern of survival and seniority rates. Growth rates were around 1 (i.e., stable) in 1998 (Fig. 3d). In 1999 and 2000, growth rates remained below 0.95, indicating a global population decline in the sampling area. Temporal variability in growth rate appeared to differ among sites, in that site A seemed more stable than sites B and C. This finding is likely an artifact of the lower numbers of fish captured at sites B and C, resulting in higher observed variations at those sites.

To quantify population transience, we used model-selected values of survival and seniority rates (Fig. 3e). The variation pattern for transience, then, is related to the survival rate pattern. As the model retained additive effects (i.e.,  $\{\phi$  or  $\gamma(a2 + g + t), p(g + \text{effort})\}$ ), the lower the survival rate and the higher the ratio between  $\phi_{a1}/\phi_{a2+}$  and the transience estimate became. This estimate largely exceeded the observed movements of fish between sampled sites (Fig. 2) because 5% to 25% of fish exhibited transient behavior. Transience differed among sites: sites B and C had more transient individuals than site A. High but irregular transience at site C also explained important variations in number of fish and thus in growth rate.

**Table 1.** Number of *Zingel asper* captured during the first campaign and recaptured during the second and third campaigns from the control group (fin-clipped fish) and tagged group (fish tagged with passive integrated transponders).

	Site A		Site B	
	control group	tagged group	control group	tagged group
Average fish length (mm)*	127.6	129.9	132.6	136.1
Number of fish tagged (October 1997)	38	38	25	27
Number of fish recaptured (December 1997)	12	12	5	7
Number of fish recaptured (May 1998)	5	5	5	5

\*Fish lengths did not vary between control and tagged group ( $t$  test,  $p = 0.462$  and  $p = 0.421$  for sites A and B, respectively).

## Discussion

### Impact of Tagging

Our tagging experiment relied on two assumptions: first, there was no difference in capture probability between the two groups (PIT tagged and fin clipped). Second, fin clipping did not affect the survival of *Z. asper*. The first assumption is difficult to test in the wild, especially in rare and endangered species. Studies on the behavioral impact of tagging are few and are usually performed in captivity (Sharpe et al. 1998; Parsons et al. 2003). In our study, PIT tagging could reduce the mobility of fish and thus increase their capture probability, but such behavior is likely to occur in a short period of time (i.e., days). In our case, recaptures occurred 2 to 5 months later. One solution would have been to make a double-tagged group of fish, with both PIT tagging and fin clipping. We did not take such a risk because the impact of handling was not known for *Z. asper* and the double tagging could have generated a negative synergistic effect. In fact, the real impact of both tagging and handling on wild fish in the

field might not be testable, although capture-recapture methods are based on this fundamental assumption. In the literature, fin clipping is widely used, and numerous researchers have addressed the impact of PIT tagging on survival. Some studies demonstrated a negative effect (Thedinga et al. 2000; Wertheimer et al. 2002), but many studies showed no significant impact of either tagging method (Ombredane et al. 1998; Conover & Sheehan. 1999; Baras et al. 2000; Das-Mahapatra et al. 2001; Bruyn-doncx et al. 2002; Pratt & Fox 2002). These conclusions are probably highly dependent on the studied species. In *Z. asper*, our results suggest at least that there is no large effect of tagging on either behavior or survival.

### Evidence of Dispersal

Density analyses fail to incorporate dispersal processes (Fausch & Young 1995), thus closing potential research paths to understanding fish population dynamics (Gowan et al. 1994). In our study, individual tagging and monitoring through a CMR protocol allowed us to estimate several important demographic parameters, such as

**Table 2.** Model selection and values of Akaike's information criterion (AIC) for the survival ( $\phi$ ) and seniority ( $\gamma$ ) analyses given various capture probabilities ( $p$ ), including transience effect ( $a2$ ), time effect ( $t$ ), site effect ( $g$ ), season effect (season), and capture effort (effort).<sup>a</sup>

Capture probability	Survival ( $\phi$ ) and seniority ( $\gamma$ )						
	$\phi(a2 * g * t)$	$\phi(a2 + (g * t))$	$\phi(a2 + g + t)^b$	$\phi(a2 + g + season)$	$\phi(a2 + g)$	$\phi(a2 + t)$	$\phi(a2)$
$p(g * t)$	1376.18 (84)	1323.08 (55)	1312.03 (42)	1312.73 (37)	1310.69 (34)	1322.38 (40)	1322.16 (32)
$p(g + t)$	1354.10 (68)	1312.67 (42)	1290.41 <sup>c</sup> (24)	1298.84 (19)	1299.06 (16)	1313.10 (22)	1312.41 (14)
$p(g + effort)^b$	1342.77 (61)	1302.3 (35)	1283.72 <sup>d</sup> (17)	1311.59 (11)	1321.67 (8)	1305.54 (15)	1334.12 (6)
$p(t)$	1349.89 (66)	1309.81 (40)	1287.66 <sup>c</sup> (22)	1295.50 (17)	1296.12 (14)	1309.39 (20)	1313.59 (12)
$p(g)$	1352.50 (60)	1313.07 (34)	1293.08 <sup>c</sup> (16)	1321.48 (10)	1323.71 (7)	1314.28 (14)	1335.76 (5)
$p(.)$ (constant)	1348.83 (58)	1309.99 (32)	1289.68 <sup>c</sup> (14)	1317.55 (8)	1322.06 (5)	1310.93 (12)	1344.85 (3)
	$\gamma(a2 * g * t)$	$\gamma(a2 + (g * t))$	$\gamma(a2 + g + t)^b$	$\gamma(a2 + g + season)$	$\gamma(a2 + g)$	$\gamma(a2 + t)$	$\gamma(a2)$
$p(g * t)$	1243.57 (84)	1195.48 (55)	1182.49 (42)	1241.53 (37)	1240.08 (34)	1192.47 (40)	1260.32 (32)
$p(g + t)$	1224.38 (68)	1181.28 (42)	1177.52 <sup>c</sup> (24)	1251.35 (19)	1248.57 (16)	1192.52 (22)	1280.69 (14)
$p(g + effort)^b$	1223.69 (61)	1182.47 (35)	1171.37 <sup>d</sup> (17)	1267.40 (11)	1279.47 (8)	1195.70 (15)	1317.03 (6)
$p(t)$	1221.30 (66)	1178.27 <sup>c</sup> (40)	1175.05 <sup>c</sup> (22)	1248.67 (17)	1245.85 (14)	1190.19 (20)	1283.82 (12)
$p(g)$	1224.31 (60)	1183.35 (34)	1179.60 <sup>c</sup> (16)	1265.66 (10)	1281.26 (7)	1197.65 (14)	1320.58 (5)
$p(.)$ (constant)	1221.66 (58)	1180.74 (32)	1177.07 <sup>c</sup> (14)	1263.47 (8)	1278.43 (5)	1193.55 (12)	1319.65 (3)

<sup>a</sup>Number in parentheses is number of parameters in the model.

<sup>b</sup>Effects retained for the best selected model.

<sup>c</sup>AIC values indicating other potentially acceptable models.

<sup>d</sup>Lowest AIC value indicating the best selected model.

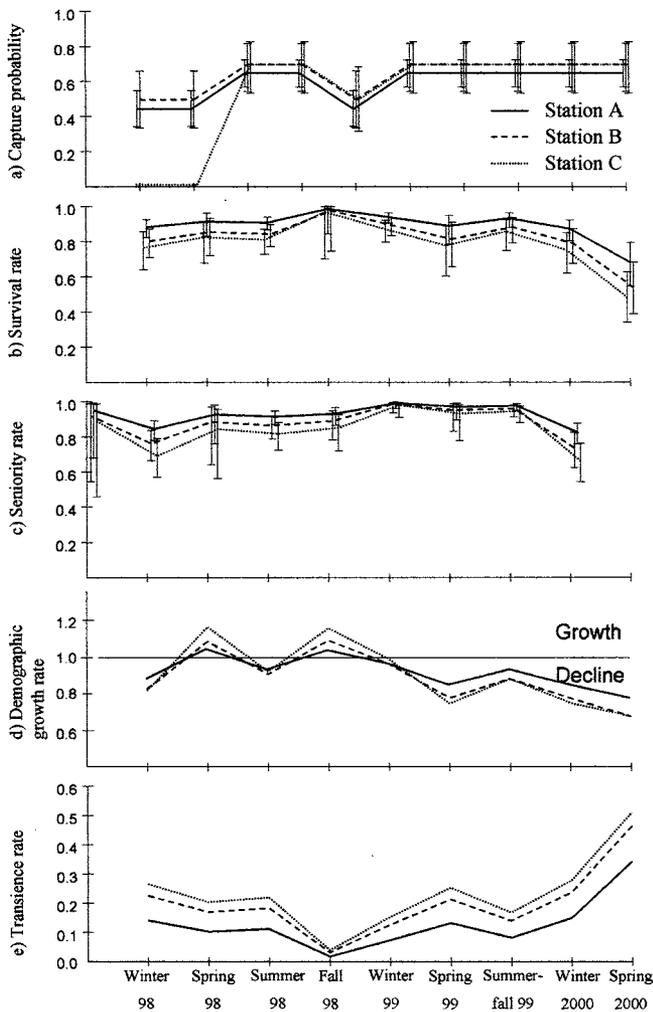


Figure 3. Variation in (a) capture probability, (b) survival rate, (c) seniority rate, (d) demographic growth rate, and (e) transience rate of *Z. asper* for the sampling sites A, B, and C along the Beaume River from winter 1998 to spring 2000. (All parameters are calculated at a monthly scale.)

dispersal rates, that are poorly estimated or not accessible through density analysis.

Even fishes that do not include extensive migration in their life cycle (*sensu* Northcote 1998) may travel far and move frequently. A multisite model (Brownie et al. 1993) seems an obvious choice to analyze our spatial framework, but goodness-of-fit tests 3G and Where Before-Where After (WBWA) described by Pradel et al. (2003) for a multistrata design failed to detect transience in our data. An exploratory analysis with multistrata models led to values between 0% to 5% for dispersal among sites (model with time-dependent survival and capture probabilities but constant transition probabilities between strata). The maximum value of these estimates matches the ratio of number of moving fish to total number of recaptured fish (15:236). This number represents the true dispersal

among sites but does not include emigration out of the study area (i.e., dispersal at the population scale). The transience approach seems better suited to detect overall dispersal in the population. It can be viewed as a turnover indicator (Gowan & Fausch 1996; Belanger & Rodriguez 2002) but this requires a more complex statistical design. Whereas turnover rate relies only on the percentage of unmarked individuals (thus mixing the effects of capture probability and immigration), transience is directly calculated from the bias in survival rates after the effect of capture probability is removed. In addition, seniority rate yields information about individuals entering the study area.

Although, to our knowledge, few researchers have addressed the question of dispersal for benthic species in riverine habitats (but see McCleave 1964; Downhower et al. 1990), our transience estimates indicate that 5%–25% of *Z. asper* individuals were nomadic. Traditional population dynamics and density studies in riverine fishes are based only on the resident fraction of populations and probably underestimate the variability of parameters or behaviors attributable to the dispersing part of the population (Gowan & Fausch 1996). We previously showed that the biological requirements of *Z. asper*'s life cycle were met within the boundaries of our sampling sites and that habitat between sites was unsuitable, at least for spawning. But the species seems to exhibit some plasticity in habitat selection (Labonne et al. 2003; Danancher et al. 2004), and originally occupied various types of rivers (Changeux & Pont 1995). Transient individuals could either have been migrating out of the study area (i.e., toward other downstream sites) or shifting to unsampled habitats between sampling sites.

The transience we detected suggests dual strategies in habitat use, where some fish remain sedentary and others disperse (long-distance dispersal) or use less-favorable habitats (short distance dispersal; Rodriguez 2002), or both. It is not possible to estimate demographic rates for the latter strategy, but they may play an important role at the river scale (i.e., population scale). Perret et al. (2003) reached similar conclusions in an exploratory analysis of the evolutionary role of the transience in populations of alpine crested newt (*Triturus cristatus*). This kind of behavioral pattern has been used in theoretical studies to predict dispersal in heterogeneous populations (Skalski & Gilliam 2003). Further investigations should focus on the behavior of transient individuals and the consequences of transience for populations.

### Patterns in Dynamics

The analysis of seniority represents an interesting tool for fish population biologists. When demographic information on juvenile stage is not available, seniority provides an inverse estimate of recruitment and immigration. The problem is to disentangle these two components, which

are fundamentally different in terms of management. In our study, we assumed that the lowest seniority values corresponded to high recruitment phases. First, newly tagged individuals were all 1 year old (based on size and scale readings). Second, these troughs occurred at the end of the winter, after spawning, when most recruitment is likely to occur. Third, seniority troughs tended to occur when large numbers of yearling fish were found at the site the year before. Seniority patterns were also correlated between sites; troughs were observed at the same times in all sites. This supports the hypothesis of local recruitment and disproves massive immigration. Mixed situations among sites remain possible, however. Genetic assignment tests will be conducted to distinguish between both hypotheses (immigration and/or recruitment) and to evaluate the contribution of local spawners to local recruitment.

Additive models were selected both in survival and seniority analyses, indicating that transience and population growth rates also follow additive patterns. We emphasize that these conclusions were drawn from the selection of the best model, which is a trade-off between best fit and parsimony. If maximizing the amount of explained variability was our objective, we would have selected the fully interactive model  $\{\phi(a2 * g * t), p(g * t), \gamma(a2 * g * t)\}$ . The model that exhibited the best AIC value required 17 parameters instead of 84 for the fully interactive model. There is thus a clear benefit to simplifying the assumptions of the additive models that explain the observed ecological patterns.

Our results provide evidence for spatial correlation of demographic mechanisms, such as survival, seniority, and immigration and dispersal rates among sites. Although this study was limited in duration (i.e., 4 years), the life span of *Z. asper* is also short: 2 to 3 years at an annual survival rate of 0.35 to 0.50. Several researchers have focused on the relationship between dispersal intensity and density fluctuations (Sutcliffe et al. 1996; Ranta et al. 1997; Lande et al. 1999) and found that correlation of densities among sites increases with the rate and distance of dispersal. Observed densities are a function of interacting demographic parameters, but apparently correlated densities can be caused by uncorrelated variations of demographic parameters. In our study, spatial correlation of demographic parameters suggests that regional environmental variation is the main factor influencing population stability, at least during the period of the study. Indeed, the linear structure of this stream system probably confers a longitudinal correlation of physical factors (e.g., temperature, discharge, and turbidity). An earlier population genetics study (Laroche & Durand 2004) determined that *Z. asper* in the Beaume River constitutes a homogeneous population. Our demographic study corroborates this result: transience was estimated as high among sites, and covariation in survival and seniority rates was common.

Although demographic variability was similar among sites, we found differences that suggest local population-regulating mechanisms. Survival and seniority rates were higher at site A than at sites B and C. Demographic growth rate was also more stable at site A. Variability in site quality may explain these differences. Belanger and Rodriguez (2002) suggest that turnover rates could be a measure of habitat quality. This explanation is congruent with our data, given that preferred habitat was more prevalent at site A than sites B and C (Labonne et al. 2003). On the other hand, upstream dispersal was not possible in site A.

Therefore the upstream site may act as a source, whereas downstream sites may act as sinks (Pulliam 1988). Also, the upstream site may constitute an artificial source because upstream dispersal is prevented by a weir.

### Contribution to Species Conservation

Our results illuminate some aspects of *Z. asper*'s life history, which may help to explain its decline. First, the species has a short life span. Second, *Z. asper* may spawn only once or twice in its lifetime. Because recruitment appears to be highly variable, the species may be especially vulnerable to stochastic events that cause year-class failure. Exact causes of recruitment failure are unknown for the species, but factors like discharge variation and algal blooms (resulting from eutrophication during summer) may be involved. Intrinsic regulatory mechanisms, such as density dependence, may also be involved. Fish seemed to require a certain minimal distance between each other, and we suspect some strong mating competition during the spawning period (Danancher et al. 2004). Finally, for unknown reasons, some gravid females (>2 or 3 years) did not lay eggs during the normal spawning periods and were found 1–2 months later still gravid (with resorbed eggs).

The associations among narrow habitat requirements, random recruitment rates, low survival rates, and naturally low density in this species suggests that local extirpation (i.e., at site scale) could be frequent. This hypothesis is supported by field monitoring, which shows unoccupied suitable habitats all along the river. High transience rates were recorded, suggesting that dispersal processes play a major role in population persistence. Although we observed stable to negative demographic growth rates in our study, theoretical results indicate that some local growth rates can be negative if overall dispersal is high enough to provide immigrants to sink areas (Hanski et al. 1996). Occasional good local recruitment also helps to ensure population persistence, as we observed during 2000, when low seniority rates may have indicated high recruitment of potential genitors. Recent population genetics results based on microsatellite loci show no genetic differentiation between sites and no deficits in heterozygosity; both observations support the notion that there

is no reproductive isolation in the population (Laroche & Durand 2004). In fact, the demographic and evolutionary consequences of dispersal behavior in *Z. asper* might be the keys to its persistence.

The basin of the Rhône River has been strongly fragmented by dam construction and hydroelectric operations during the last 50 years. This fragmentation inhibits dispersal, limiting gene flow and making local extinction a real threat for population persistence (Schlosser & Angermeier 1995; Peter 1998). *Z. asper*'s decline is likely related to these decreases in river connectivity. Although restoration projects of river connectivity are planned, they focus on migratory species (such as salmonids, eel, and shad). Fish passes are rarely designed for nonmigratory species (such as most cyprinids or percids), and benthic fishes may not benefit from such measures. Our study demonstrates that monitoring of individuals is possible for rare, nonmigratory fishes, and such approaches should be considered when trying to assess the functionality of fragmented freshwater ecosystems.

We are currently integrating our initial results and demographic data into a stochastic metapopulation model that incorporates habitat and spatial parameters to study the influence of these parameters on population viability. This model may advance our understanding of the role of dispersal in the persistence of fish populations. Although conservation biologists cannot rely solely on models to make conservation decisions (McDonald & Johnson 2001), we believe that mathematical synthesis of known data helps to identify limiting demographic factors and which ecosystem components should be managed to sustain populations.

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