

Kernel Density Estimates of Linear Home Ranges for Stream Fishes: Advantages and Data Requirements

JASON C. VOKOUN*

University of Missouri, the School of Natural Resources,
Department of Fisheries and Wildlife Sciences,
302 Anheuser-Busch Natural Resources Building,
Columbia, Missouri 65211-7240, USA

Abstract.—Kernel density estimates of linear home range can increase the information content of the home range estimate. Particularly in lotic systems, univariate kernel density estimates have desirable properties relative to simple reporting of linear ranges. Kernel density estimates are calculated from a set of relocation points (i.e., radiotelemetry contacts) that can be interpreted as a utilization distribution (UD). The UD estimates the amount of time spent at a given point within the home range. The amount of time that elapses between relocations (sampling interval), total number of relocations (sample size), and bandwidth (smoothing applied to the estimate) are important considerations when using kernel density estimates. Monte Carlo simulations using unimodal and bimodal distributions sampled randomly at sample sizes of 10–100 and three automated bandwidth selection procedures (simple normal reference, Silverman's rule of thumb, and Sheather–Jones plug-in) suggested that at sample sizes of 30 or more kernel density estimates began to level off and the largest gains in accuracy were evident for all three bandwidth selection procedures. I present example kernel density estimates for flathead catfish *Pylodictis olivaris* and use them to illustrate methods of reporting data. A literature review found relatively few examples of home range delineation for stream fishes but confirmed that the most common practice was to report the distance between the most upstream and downstream relocations. Sample size information was often inadequately reported in the reviewed literature.

Kernel density estimates of home range size have recently become popular and have been recommended in studies of terrestrial organisms (Worton 1989, 1995; Naef-Daenzer 1993; Seaman and Powell 1996; Seaman et al. 1999; Kernohan et al. 2001). Kernel home range estimates are based on a density estimate calculated from a set of relocation points (e.g., radiotelemetry contacts) that can be interpreted as a utilization distribution (UD; Van Winkle 1975). The UD assigns a second dimension to the linear home range estimate: In addition to the demarcation of the length of stream used by an individual fish, the UD is an estimate

of the amount of time a fish spent in any given area of the home range. Using kernel density estimates for stream fishes has advantages over the traditional practice of reporting linear home range as the distance between the most upstream and farthest downstream relocations of an individual fish. For instance, the kernel density estimate and the associated UD form a probability density function that integrates to one (Silverman 1986), which in turn allows objective demarcation of heavily used reaches or sections of stream, for instance, a core area in which a fish was estimated to have spent 50% of its time during the period of interest. In fact, because any point along the linear home range has an associated percentage level of use, the entire home range can be sectioned into levels of use categories for use in assessing habitat use (Mitchell 1997; Kernohan et al. 1998) with replication coming from multiple individuals. Because of the increasing use of the UD estimates of time spent in an area in terrestrial ecology and management, recent definitions of home range have begun to explicitly include the time span of interest in the definition, for example, “the extent of area with a defined probability of occurrence of an animal during a specified time period” (Kernohan et al. 2001:126).

Additionally, kernel methods estimate the extent of the home range by calculating densities based on the entire sample set of relocations during the period of interest; this is preferable to determining home range by methods that place undue emphasis on the most upstream and downstream relocation points (Kernohan et al. 2001). Kernel density estimates, when considered at the 100% or 99% use level, are typically longer than the upstream-to-downstream distance because of the nature of the estimate. It is easy to rationalize that because the study fish was located at a given point, there is some level of probability that it moved beyond that point before or after the telemetry contact. Reporting multiple levels of use such as the 95% and 90% estimates allows researchers to exclude

* E-mail: jcve18@mizzou.edu

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portions of the home range that may consist of sporadic long-range movements, which the researcher may feel uncomfortable designating as part of the home range (e.g., during flood events), while still acknowledging the movements in the calculation of home range, rather than subjectively choosing to discard certain relocations.

However, terrestrial kernel density estimates of home range are bivariate and assume that no barriers exist to prevent animals from moving in any direction across the landscape. When barriers do exist, special boundary kernels have been developed that allow for incorporation of regular boundaries (e.g., a straight line or regular arc; Silverman 1986). This scenario is almost never met for stream fishes, which are, with few exceptions, restricted to irregular wetted stream channels. Several programs and packages calculate kernel density estimates of home range appropriate for terrestrial animals (see references in Larson 2001), but they produce a home range estimate that does not respect the streamedge boundary and consequently incorrectly includes dry land inside stream meanderings. Additionally, for many stream fishes that are mobile and use a reach of linearly available channel units (pools, riffles, and so forth), a threshold exists in which the longitudinal (upstream–downstream) distances traveled overwhelm the ability of two-dimensional estimates to resolve any latitudinal (across-stream) differences in density without breaking up the associated estimate into many small, unconnected pieces of home range. Unconnected pieces of home range are perhaps acceptable for birds, but stream fishes certainly swim from one place to another through the stream channel. For fish species, a univariate kernel density estimate calculated along the midline or alternatively the thalweg of the active stream channel has many desirable properties.

Sampling considerations are important to meeting the assumptions of the UD calculation and can affect both the resulting home range boundaries and the internal structure of the home range (Seaman et al. 1999). In particular, the amount of time that elapses between relocations (sampling interval) is related to the assumption that relocations are independent, and the total number of relocations (sample size) addresses the assumption that the sample is sufficient to allow adequate estimation of the home range (Swihart and Slade 1985a, 1985b, 1997; Otis and White 1999; Garton et al. 2001; Kernohan et al. 2001). Although more initial consideration of a sampling scheme may be required when using kernel home range estimates,

the amount of data required is on the same order as that which is often collected.

No specific programs currently exist to automate the entire process of assigning relocations to the stream midline and then performing a univariate kernel density estimate of home range. I used program ArcView GIS and PROC KDE within program SAS (SAS Institute 2000). My objectives were to (1) address the data requirements of univariate kernel density–estimated home ranges by presenting original Monte Carlo simulations describing the accuracy of the estimates at sample sizes ranging from 10 to 100; (2) present example univariate kernel density–estimated home ranges in table and figure formats by using several flat-head catfish radio-tracked in the Grand River of northern Missouri; and (3) present and discuss the results of a literature review summarizing recent trends in reporting the home range of stream fishes.

Methods

Simulations.—The associated accuracy and precision of nonparametric kernel density estimators at given sample sizes are unavailable because no variance estimator exists that incorporates the variability inherent in the bandwidth selection procedure (White and Garrott 1990; Seaman et al. 1999). Researchers have used simulations to compile empirical estimates of the properties of kernel density estimates of home range (Worton 1995; Swihart and Slade 1997; Seaman et al. 1999). I used a smoothed statistical bootstrap (Efron and Tibshirani 1993) similar to Worton (1995) and Seaman et al. (1999) to generate empirical estimates of the accuracy of univariate kernel density estimates.

The UD of stream fishes was simulated with both a normal distribution and a bimodal distribution of points. The bimodal distribution was created from an equal-parts mixture of two normal distributions that maintained two distinct density modes. Both the normal and bimodal distributions were estimated with five realizations for which standard deviations ranged fourfold from 5 to 20 (Figure 1). Each realization was then randomly sampled by using Monte Carlo methods at sample sizes of 10, 20, 30, . . . 100. One hundred replicate samplings were conducted at each sample size for each realization, thus resulting in 500 simulations per sample size for normal and bimodal distributions each.

Kernel density estimates are output as smooth curves with the amount of smoothing governed by a bandwidth value used during calculation (Sil-

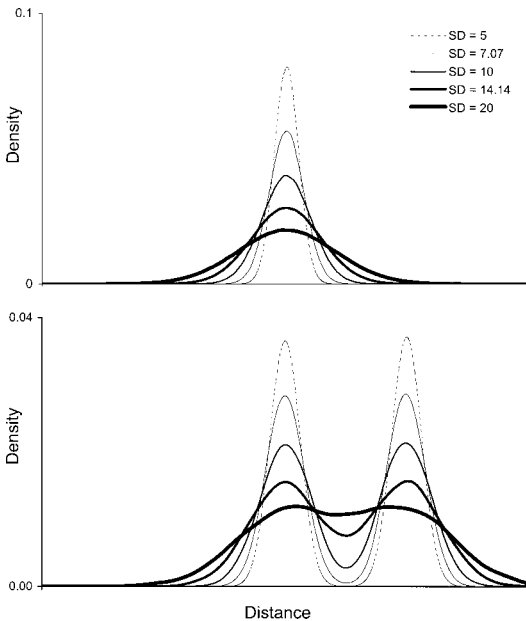


FIGURE 1.—Relative shapes of the five normally distributed unimodal (upper panel) and five bimodal realizations (lower panel) of the two distribution types used to simulate the linear home range of fishes. The distance along the x -axis simulates linear river distance; density corresponds to the density of the simulated relocation points found along the x -axis. The abbreviation SD stands for standard deviation.

verman 1986; Worton 1987). Densities are calculated by placing kernels over the distribution of data points (Silverman 1986). Kernels that overlap one another increase density values in shared areas of the distribution. The univariate kernel density estimator used in this manuscript is given by

$$\hat{f}(x) = \frac{1}{nh} \sum_{i=1}^n K\left(\frac{x - X_i}{h}\right),$$

where h is the bandwidth and $K(x)$ is the Gaussian kernel function. Two versions of the kernel density estimate exist, fixed and adaptive (Silverman 1986; Worton 1989). Fixed kernels have a constant bandwidth at each estimation or grid point. Grid points are simply evenly spaced points along the distance (x)-axis of the kernel estimate whereby the continuous kernel function can be output as a list of values that can be graphed and used in computations. Adaptive kernels have a different bandwidth applied to each grid point; this provides more smoothing in low-density areas and less smoothing in high-density areas of the data set. Research using bivariate kernels in terrestrial wild-

life studies have favored the use of fixed kernels, because adaptive kernels tend to be less predictable toward the edges of the estimate, which is an area of importance to biologists (Worton 1995; Seaman and Powell 1996; Seaman et al. 1999). Several computational methods are available for automatically choosing bandwidth, each returning different interpretations of the kernel density estimates. I incorporated two widely used methods and a third that has been recommended in the statistical literature: simple normal reference (SNR; Silverman 1986; Worton 1995), Silverman's rule of thumb (SROT; Silverman 1986; Jones et al. 1996), and the Sheather-Jones plug-in (SJPI; Silverman 1986; Marron 1989; Jones et al. 1996; Loader 1999). Additional simulations were run with each of the bandwidth selection methods, resulting in a total of 30,000 simulated home ranges.

Home-range accuracy was assessed by comparing estimates (\hat{E}) of linear home range to a home range drawn from the same distribution with an unusually large sample size (E ; $n = 5,000$) by calculating the percentage difference, which is given by

$$\frac{|\hat{E} - E|}{E} \times 100,$$

where the upright bars indicate absolute value; that is, the result will always be nonnegative. The mean percentage difference of the 500 runs at each sample size was plotted to illustrate the trend in accuracy as sample size increased. Accuracy was calculated for the 99, 95, 90, and 50% estimates.

Flathead catfish example.—Univariate kernel density estimates of home range were calculated for 10 flathead catfish radio-tracked between 15 July and 15 October 2001. This time period corresponds to a postspawning period of relatively localized activity during late summer and fall before the fish move or migrate to wintering sites. Relocations were recorded by using global positioning system (GPS) equipment in the field and later were differentially corrected. Flathead catfish were relocated approximately every 30 h on a staggered schedule (not all fish were relocated at the same time) spanning Monday to Saturday. This schedule resulted in approximately even coverage of the 24-h clock per individual fish. Events such as thunderstorms and difficulty receiving GPS signals necessitated some deviation from the 30-h staggered schedule. No fish was relocated with an elapsed time of less than 27 h.

The GPS-collected (x , y) coordinates were en-

tered into program ArcView GIS. Within program ArcView GIS, an aerial photograph data layer from 1996 to 1998 (more recent than U.S. Geological Survey topographic maps) and field observations were used to create a line that traced the thalweg of the active channel. Shareware arcscripts Add Points Evenly Along a Line (Lead 2002) and Nearest Neighbor 3.1 (Weigel 2002) were used to add points every 10 m along the thalweg line (beginning with zero at the river mouth) and then to determine which 10-m point the fish relocations were nearest to. Data were then exported from program ArcView GIS into program SAS. Within program SAS (version 7 and higher), PROC KDE was used to compute the kernel density estimate of home range. Bandwidth was chosen by SJPI. Grid points were set at 10-unit intervals corresponding to the 10-m resolution of the data set. The UD was specified to output the 99, 95, and 90% level home range estimate as well as the 50% level core area.

Literature review.—I used computer databases to search the *North American Journal of Fisheries Management* (NAJFM) and *Transactions of the American Fisheries Society* (TAFS), using key words “home range” and “movement(s).” All manuscripts studying fishes in lotic environments from 1981 to 2001 were searched for specific information about the method of home range delineation used and the level of specificity authors provided about sample size (number of relocations). Following a similar review in Seaman et al. (1999), I noted the following: (1) whether any sample size information was reported at all; (2) the total number of relocations (all animals combined); (3) the minimum number of relocations used to determine home range; or (4) the sample size for each animal or the mean and range for all animals.

Results

Simulations

The mean percentage difference decreased and leveled off as sample size increased in all cases (Figure 2). The reduction in percentage difference was substantive up to sample sizes of 30–50 for the 95, 90, and 50% estimates in unimodal distribution simulations but continued to decline for sample sizes of 60–80 for the 99% estimate. Bimodal simulations returned similar results for the 95% and 90% estimates, but the 99% and 50% estimates differed from the unimodal results. The 99% estimates had lower percentage difference values and were much closer to the 95% estimates,

whereas the 50% area estimates were much higher. The 50% estimates in bimodal distributions were the only estimates that did not level off at or below a percent difference of 5%. In all cases, the 99% estimates unexpectedly showed an increase in percentage difference from a sample size of 90–100—probably as a result of the increased probability of sampling a value far from the mean of the simulated distribution. The distributions used were theoretical and had infinite support in their tails. The effect was less pronounced in the bimodal cases, because each peak was sampled half as often to create the distribution; that is, 50 samples were in each peak as opposed to 100 in the unimodal case. Finally, the percentage difference values were similar for all three bandwidth selection methods.

Flathead Catfish Example

Linear home range estimates for the 10 flathead catfish were variable, ranging from 1,080 to 21,390 m (Table 1). The 99% kernel estimate of home range was larger than the linear home range for all fish, albeit by only 10 m in two instances. The 95% estimates were larger than the linear home range for 3 of the 10 flathead catfish, and only one 90% estimate was larger than the linear home range. The 50% kernel estimates ranged from 20 to 390 m. The 50% estimates were not a simple fraction of overall home range size, although fish with larger home ranges tended to have larger core areas. Two fish of similar size (738 and 750 mm total length; see Table 1) had similar 99% home range estimates, but their 50% estimate sizes were noticeably different.

The raw density values of univariate kernel estimates can be output in program SAS as a series of densities associated with the grid points. Specifying more or fewer grid points respectively increases or decreases the resolution at which the boundary between levels of use can be specified. Plotting densities against the grid points creates a plot of the internal structure of the home range estimate (Figure 3). The three automated bandwidth selection methods used in the simulations all selected different amounts of smoothing to the estimate: SROT applied the least smoothing, SJPI applied slightly more smoothing, and SNR applied much more smoothing to the density estimate. The different amounts of smoothing resulted in different estimates of linear distance for a given percentage level of the estimate. The home range plotted in Figure 3 shows that this individual fish (750 mm total length) had a home range with one center

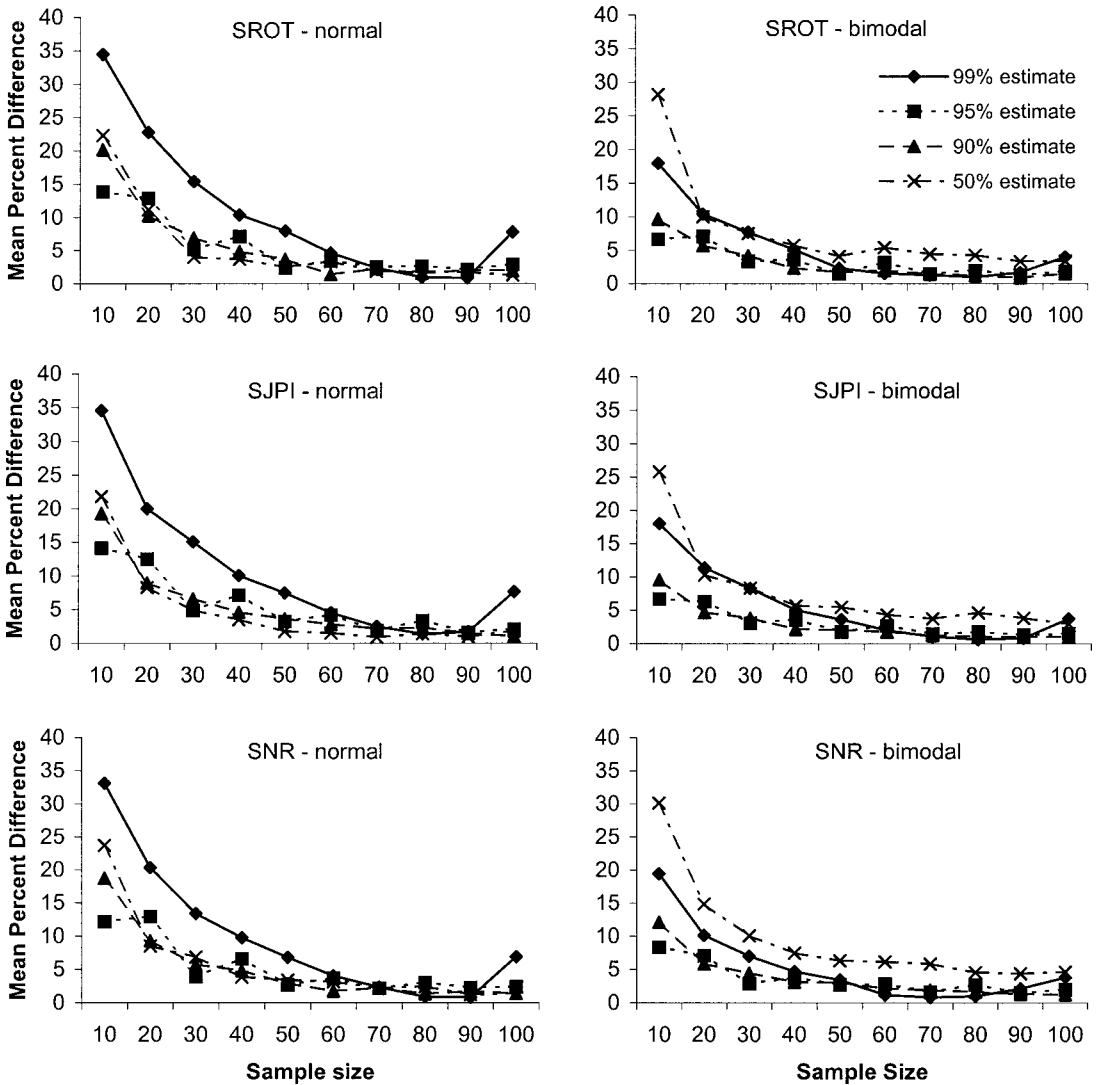


FIGURE 2.—Relation between the mean percentage difference of univariate kernel density estimates and sample size (simulated number of relocations). The mean percentage difference is calculated as the absolute difference between fixed kernel density estimates at the given sample size and a known estimate calculated at an unusually large sample size ($n = 5,000$). Bandwidth selection methods are abbreviated as follows: SROT = Silverman’s rule of thumb; SJPI = Sheather–Jones plug-in; and SNR = simple normal reference.

of activity spanning roughly 1,500 m (which included the 250-m area where the fish spent 50% of the time, as reported in Table 1) and a long tail stretching downstream. Densities were near zero in the tail and had bumps near actual places where the fish was relocated in the SROT and SJPI estimates; however, the highly smoothed SNR estimate resulted in a more constant estimate of time spent in the tail. Relocations in the downstream tail are the result of a single late July movement

that lasted 3 d and corresponded to a moderate rainfall/flood event.

The kernel estimate can also be displayed in plan view (Figure 4), and although the estimate is univariate and has no associated width, for improved clarity I have shaded the entire river corresponding to the section of the thalweg line demarcated by the kernel estimate. Distance values corresponding to those in Figure 3 have also been placed along the river section in Figure 4 to help the reader

TABLE 1.—Home range estimates for flathead catfish radio-tracked in the Grand River, Missouri, 15 July–15 October 2001. Linear home range is the distance in meters between the most upstream and most downstream relocations; the 99, 95, 90, and 50% univariate kernel estimates are the distance in meters encompassing the specified level of the utilization distribution (i.e., the percentage of time the fish was estimated to have been within the distance delineated). Bandwidth selection was by the Sheather–Jones plug-in method.

Total length (mm)	Number of relocations	Home range				
		Linear	99% kernel	95% kernel	90% kernel	50% kernel
575	50	21,390	28,390	2,780	2,300	390
595	51	1,630	1,720	1,690	1,670	40
605	37	13,500	13,710	13,700	6,840	220
628	39	1,610	1,620	1,000	800	20
668	43	2,410	2,550	1,560	1,460	160
730	44	17,040	23,040	380	80	60
738	37	7,830	7,910	7,900	1,580	90
750	50	7,680	7,810	6,790	6,760	250
810	51	1,080	1,090	620	380	30
894	46	11,030	11,280	1,260	940	140
Mean	44.8	8,520	9,912	3,768	2,281	140

visualize the transfer of the estimate from the x -axis of Figure 3 to the actual river section in Figure 4. The 50 relocations on which the kernel density estimate was calculated are also presented in Figure 4. The home range estimate has a common boundary or edge for the 90, 95, and 99% estimates on the northern upstream end.

Literature Review

Surprisingly, relatively few examples of home range delineation for stream fishes were found in NAJFM and TAFS from 1980 to 2001. Only 16 studies were identified that occurred in lotic systems and reported original data for the home range of fish species. Of those 16 studies, 7 calculated home range as the distance between the most upstream and farthest downstream relocations. Two studies used bivariate methods: the minimum convex polygon and Mohr's minimum area method. Two studies based on the same study area and species and by the same author used univariate kernel density estimates. The five remaining studies appeared to have collected data consistent with the delineation of a home range but did not do so formally. Most of the manuscripts I reviewed either described movements of fishes during seasonal periods of migration or increased movement or reported home ranges for fishes in impoundments.

Reporting of sample size was variable among the 16 studies; 4 reported the number of relocations

for each individual fish or a mean and range, none gave a minimum value used as cutoff in determining home range, 6 gave the total number of relocations without any information on the number of relocations per individual, and the remaining 6 gave no information regarding sample size at all.

Discussion

For biologists using kernel density estimates of home range for stream fishes, three issues have surfaced in the literature. First, the level of spatiotemporal autocorrelation in the relocation data set should be considered. Autocorrelation increases as elapsed time between relocations decreases (Hansteen et al. 1997). There is an inherent trade-off between increasing the number of relocations, which improves the accuracy of the home range estimates, as my simulations confirmed, and the decreased independence (and associated reduced information content) of those temporally closer relocations (Kernohan et al. 2001). It should also be noted that the simulations presented assumed independent observations at each increasing sample size. In practice, it would be difficult to estimate a seasonally defined home range such as that presented for flathead catfish and also collect 70–100 independent observations because the amount of time in the study period is finite.

The ideal elapsed time (when observations become independent) between relocations will vary by species and depends on movement patterns exhibited by the species. An approach to guide the researcher in identifying a suitable relocation interval is the time to independence (TTI) interval (Swihart and Slade 1985a, 1985b, 1997). Several authors note, however, that strict adherence to the TTI interval may not be the best choice in all cases (Reynolds and Laundré 1990; McNay et al. 1994; Kernohan et al. 2001). Especially with small species that cannot carry a heavier transmitter with a long-lived battery, the biologist will likely benefit from systematically accepting some level of autocorrelation as opposed to collecting few independent relocations (Kernohan et al. 2001). Even with larger species such as flathead catfish, the biologically defined time period in which the species maintained a postspawning seasonal home range in Missouri ultimately dictated the total amount of the time available for sampling, regardless of battery life.

The second related issue is the total number of relocations per individual. Results can vary widely for the same animal when different numbers of relocations are used (Garton et al. 2001). Simu-

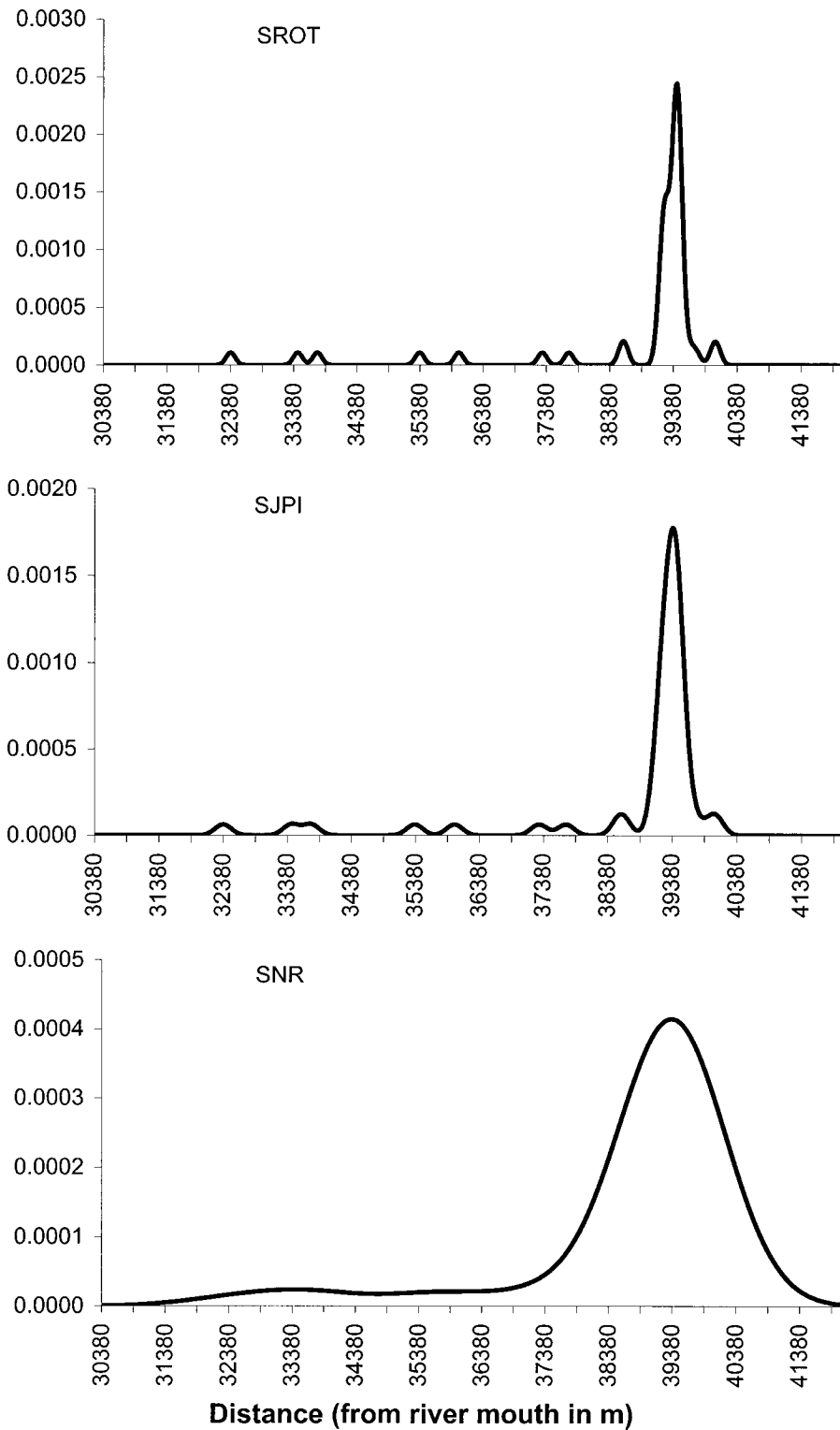


FIGURE 3.—Univariate kernel density estimates for the distribution of relocation points for a flathead catfish (750 mm total length). The sample size was 50 relocations; bandwidth selection methods were Silverman's rule of thumb (SROT), Sheather-Jones plug-in (SJPI), and simple normal reference (SNR).

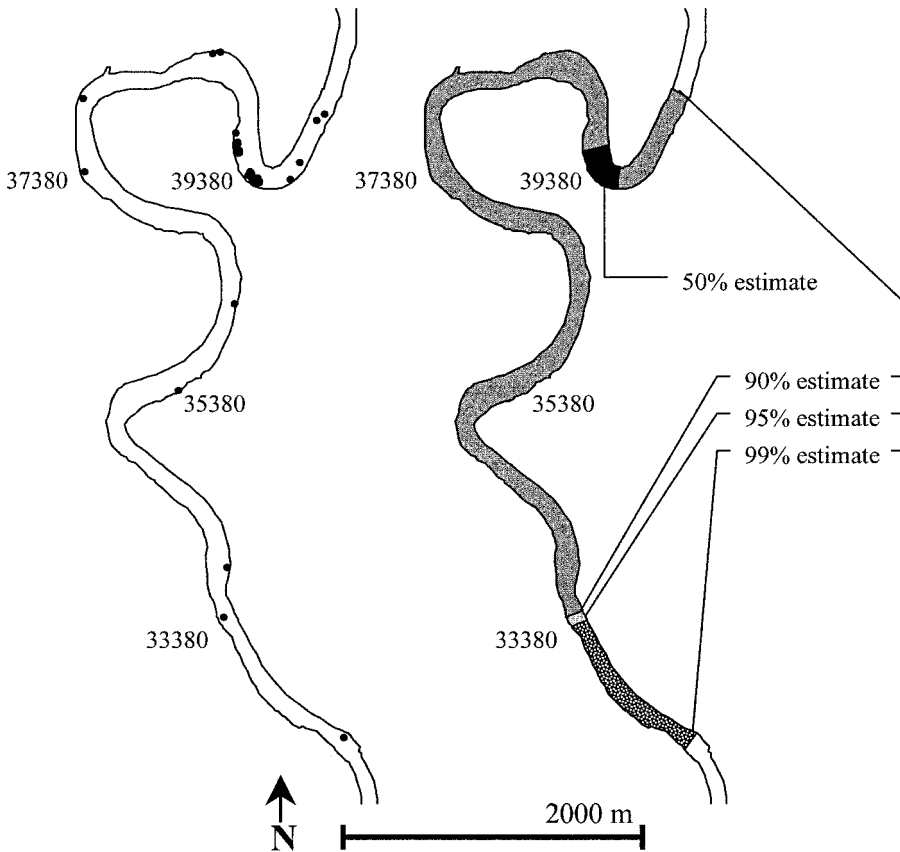


FIGURE 4.—Plan view of the distribution of relocation points for a flathead catfish (750 mm total length) in the Grand River, Missouri (left panel). The right panel contains the extent of the univariate kernel density estimate displayed in Figure 3 (SJPI only). Values are in meters for each percentage level reported in Table 1; numbers along the stream correspond to the x -axis distance in Figure 3; river flow is from north to south.

lations presented here are consistent with those presented by Seaman et al. (1999). My percentage difference values are lower than those presented by Seaman et al. (1999) at low sample sizes; however, this is not unexpected because I simulated univariate kernel estimates, whereas they used bivariate estimates. The lower percentage difference values were translated into recommendations for desired sample sizes. Where Seaman et al. (1999) recommended a minimum of 30 relocations, and preferably 50, per individual animal, I recommend collecting 30 relocations when calculating univariate kernel estimates of home range. Graphically, the relative position on the curve at 30 relocations in the univariate case presented here is analogous to the 50 relocations position on the respective curve of Seaman et al. (1999). In practice, biologists should target a sample size slightly larger than that desired. From my experience, equipment failure, holidays, family emergencies, and severe

weather contribute to accumulation of missed relocation attempts. Sample sizes reported in the literature I reviewed were commonly in the range of 20–30 per individual fish. With slightly more effort and a well-planned sampling schedule, biologists can gain the additional information and biological insight given by the kernel density estimate and associated UD. Given the large influence of sample size on reliability of the estimate, reporting the number of relocations per individual fish is important. This can easily be accomplished in a table such as Table 1, which probably would have been presented in such manuscripts anyway.

The third issue mentioned by researchers using and advocating kernel methods is the critical choice of bandwidth or automated bandwidth selection method (Silverman 1986; Worton 1995; Kernohan et al. 2001). Simulations presented here did not provide clear patterns of increased accuracy at smaller sample sizes for any of the methods

used. However, the bandwidth selection procedures did apply different amounts of smoothing to the same set of relocations (Figure 3), thus resulting in different numerical estimates of home range at all percentage levels of use. Therefore the choice of bandwidth is perhaps considered most carefully with regards to comparability among studies. Biologists using different bandwidth selection methods will find it difficult to compare results among studies. In a review and evaluation of available home range estimates, Kernohan et al. (2001) noted that kernel estimates (which were favored in the evaluation) were difficult to compare if complete information regarding bandwidth selection methods was not disclosed. Which bandwidth selection method best meets the needs of biologists estimating fish home ranges in lotic systems is an area requiring more research.

It was surprising to find so few studies reporting original home range estimates for stream fishes. The concept seems to have broad taxonomic applicability, especially for the widespread centrarchid species (Gerking 1953). Home range estimates have been reported for several species in impoundments, but estimates for their native lotic habitats are lacking. Many (if not most) stream fishes migrate to meet their life requisites; recent definitions of home range accommodate the seasonality of such animals. The estimates may be annual, seasonal, or behavior related (e.g., on the spawning grounds). Although restricted movement or home range of many stream fishes may indeed be more complicated and temporally dependent than previously believed, the concept is not wholly a "paradigm lost," as suggested by Gowan et al. (1994). The methodology described here provides a probabilistic framework within which the concept of home range may increase in utility to fisheries biologists without obviating the importance of seasonal or infrequent long-range movements. The UD concept allows investigators many opportunities to summarize and compare patterns of space use, such as the size, number, and distances among core areas. Patterns of space use among individual neighboring animals have also been investigated: the volume of intersection index (Seidel 1992) was used to describe the changes in space use among Rocky Mountain elk *Cervus canadensis* during hunting seasons by creating a kernel density estimate of hunter space use and comparing it with the home ranges of resident elk herds over the same time span (Millspaugh et al. 2000). The elk herds changed their patterns of use of space during hunting seasons in areas heavily used

by hunters. The same methods could be used to investigate patterns of space use by stream fish near and away from access points and heavily fished areas. Recent advances in battery life and reduced size, coupled with the advent of small microcontrollers that can turn transmitters on and off at preset time intervals (thereby increasing transmitter life to as long as several years), have drastically increased options for biologists designing studies. Parallel use of kernel density estimates and the UD concept should increase our understanding of and enhance our ability to manage stream fishes.

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