Is scuba sampling a relevant method to study fish microhabitat in lakes? Examples and comparisons for three European species


Abstract – We compared fish microhabitat use patterns in the littoral zone of a lake using a new direct method (point abundance sampling by scuba, PASS) and the widely used point abundance sampling by electro-fishing technique (PASE). We collected microhabitat data for age 0+ roach (Rutilus rutilus L.), perch (Perca fluviatilis L.), and pike (Esox lucius L.). The two methods yielded different results for fish assemblage structure and microhabitat patterns. Using PASE, fish were mainly found in “shelter habitats” such as shallow waters and dense vegetation. It is likely that this behavior is caused by the disturbance of the observer stamping around. Using PASS, fish escapement behavior was rarely observed. Therefore, we concluded that this direct and nondestructive sampling technique can be used to provide an accurate microhabitat estimation of a fish community and is assumed to be more suitable than PASE for fish habitat studies.

Introduction

The cornerstone of many ecological studies is an accurate estimation of population abundance and density in various biotic and abiotic environments (Begon et al. 1996). This is easily achieved when a complete enumeration of the populations is possible; however, very few animal populations can be completely enumerated and most of the ecological explanations come from samples. Many sampling methods have been set up to try to achieve reliable estimates according to the studied organisms and communities, but each sampling method has its own shortcomings (Verner 1985; Krebs 1989; Alexander et al. 1997). Such biases are emphasized in aquatic systems, where sampling is often more complex than in terrestrial ecosystems. Numerous methods are available for estimating fish biomass, density and habitat in natural environments (Everhart et al. 1975; Nielsen et al. 1983; Meador et al. 1993; Murphy & Willis 1996) but these methods have frequently maintained a somewhat narrow perspective that is usually limited by the data provided by the sampling approach employed. However, reliably assessing population habitats and community structure requires a sampling approach with sample units comparable at all levels of ecological perception, from a large spatial scale (i.e. macrohabitat) to a narrower one (i.e. microhabitat) (Krebs 1989).

In freshwater ecosystems, although fish may be collected using a large number of sampling methods to assess density or population size (e.g. gillnets (Hamley 1975); toxicans (Davies & Sheldon 1983); electrofishing (Cowx & Lamarque 1990); and hydroacoustics (MacLennan & Simmonds 1992)), microhabitat studies require effective sampling, numerous small-scale samples and
measured the habitat features for each sample (Nelva et al. 1979). To reach this goal, the point abundance sampling theory was set up. Blonde and Elizur (1970) originally developed it for studying nesting birds. It is based on the statistical theory that many small sample units provide more precise results than a few large samples. Using this theory, two major kinds of sampling methods can be employed to define fish microhabitat. i) Sampling methods that require catching fish, such as electrofishing, are now routinely used in aquatic ecology (Cowx & Lamarque 1990). One of the most common methods, known to be efficient in freshwater research, used to define fish microhabitat, is the point abundance sampling by electrofishing (PASE) technique (Nelva et al. 1979). Even though this method provides reproducible samples, it is known to be size-selective (Copp 1989). ii) Underwater visual methods, such as diving, have been primarily applied in marine waters. These methods are currently very common and recognized for studying the relationships between reef fish assemblages and habitat characteristics (Brock 1954; Mattheus 1990; Tupper & Boutilier 1995; Charton & Ruzafa 1998). In continental hydrosystems, these methods were mainly employed in North American streams to study salmonid behavior (Ellis 1961; Keenleyside 1962) and microhabitat (Beecher et al. 1993). Scuba diving, however, has been little used in lakes. In Europe, the work of Rossier (1995) is probably the first habitat study of the two selected sites. To reach this goal, the point abundance sampling by scuba (PASS) and applied it to the littoral zone of a lake to study fish population on a microhabitat scale.

This article reports how the PASS method was set up and aims to assess the capabilities of this technique compared with PASE. We therefore investigated the microhabitat use of three fish species (Rutilus rutilus L., Perca fluviatilis L. and Esox lucius L.) during the first months of their biological cycles. The results were compared with a standard electrofishing sampling strategy (PASE). These results led us to discuss the advantages and disadvantages of direct (i.e. PASS) and indirect (i.e. PASE) sampling methods to define a species assemblage and the microhabitat use of some fish populations.

Material and methods

Study area

The study was undertaken during summer 1998 in Lake Pareloup (France). This reservoir is located in southwestern France, near the town of Rodez. It covers a total area of 1250 ha for a volume of about 168x10^6 m^3. The maximum depth is 37 m and the average depth is 12.5 m. Lake Pareloup is a warm monomictic lake that is submitted to summer thermal stratification with low oxygen content below the thermocline (located about 10 m below the surface from early June to mid-September), which prevents the fish from colonizing deep water during this period (Richeux et al. 1994). In order to obtain comparable samples we chose two restricted areas of the lake that present the same environmental and topographical characteristics. The two sampling areas were chosen for their topographical heterogeneity providing numerous kinds of habitats. Considering the environmental features of the two sites, Pujo (1995) showed that they are identical topographically. Moreover, the fish community was studied in the two bays during summer 1997 using PASE, and no statistical difference between the relative abundance of each species within the two bays was found by Wilcoxon’s nonparametric paired test (Z=−0.78, P=0.43), testifying to the identical faunistic characteristics of the two selected sites.

Sampling

Eleven transects were defined in each location (i.e. PASE in the first bay and PASS in the second). Their lengths depended on the depth and varied between 4 and 32 m. Each transect was defined by a 2-m-wide observation lane from the bank across to 1.5 m depth, marked off every 1 m. This gave 201 sampling points. For each sampling point, nine environmental variables were measured in order to assess fish microhabitat, which included: two topographical variables expressed in meters (distance from the bank and depth), one biological variable, the flooded vegetation cover expressed as the percentage of cover on the surface of each sampling point and six substratum variables expressed as the percentage of boulders, pebbles, gravel, sand, silt and mud. Both fish sampling techniques were performed weekly from spawning (early June) to the juvenile period (late August) for the three studied species (Brosse 1999) in the littoral zone of the lake (i.e. 12 weeks). In this approach, three young fish populations were taken into account to assess the ability of PASE and PASS to define fish microhabitat. These species were i) the roach (Rutilus rutilus L.), the most common fish in the lake (Angelbert et al. 1999), belonging to the omnivorous trophic guild, ii) the perch (Perca fluviatilis L.), a small predator known to be zooplanktivorous and usually ichthyophagous, and iii) the pike (Esox lucius L.) a top predator fish. The two sampling pro-
cedures were tested on these three species belonging to different trophic guilds with various behavioral traits. Moreover, young fish were chosen, as they are more abundant in the littoral areas than adults (Brosse 1999), thus allowing a better estimation of their microhabitat use and therefore a more accurate comparison between the two sampling methods.

In the first site, PASE (Nelva et al. 1979) as modified by Copp (1989) was employed to evaluate the density of each species and the microhabitat of several populations. Fish were collected using a backpack electroshocker fitted with a small 10-cm ring anode. This method is known to provide reproducible and quantifiable point samples and is efficient for the entire fish community, even if the field of attraction differs according to fish size. This technique consists of a discreet approach by foot to the sampling point. The use of a rubber-rowing dinghy was discarded because of its inability to sample shallow, gently slopping, muddy areas with this method. Upon arrival at the chosen point, the anode was swiftly immersed about 0.5 m into the water and any shocked fish were then collected with a fine-mesh dipnet. Fish specimens were preserved in 4% formaldehyde. This sampling design requires the presence of three people: the first with the electroshocker, the second with the dipnet and a third on the bank to note the results.

In the second site, PASS was set up. The swimming along of transects by a free diver was used to obtain approximate fish numbers. Fish counts were made while swimming along the transect, and the results obtained were expressed as densities or through extrapolation as estimates of total number of individuals of each species occurring in each sample according to Sale (1980). Censusing begins with the diver located far from the bank, in open waters; he then moves closer, swimming towards the bank. The observer swims in each lane, covering the full area of each point. Water clarity was sufficient to determine and count all the fish for each 2-m-wide and 1-m-long point. For each fish species, individuals recorded were sorted into two classes: young (0+) and older (≥1+) fishes. When dense fish shoals were observed (mainly young fish), counting was limited to a subsample and then extrapolated over the entire volume of the sample. This last procedure has been applied to 199 samples out of the total of 1310 PASS samples. According to Northcote & Wilkie (1963) and Ek-lov (1997), a constant speed of about 5 m/min was used in order to minimize disturbance of the fish community. This sampling design required the presence of only one person, who noted all the information on a waterproof board.

Data processing

The two data matrices (i.e. PASE and PASS) were used to develop microhabitat preference indices for each environmental variable as a measurement of habitat use by the fish population vs. habitat availability, based on the method of Ivlev (1961) and improved by Beecher et al. (1993). Similar improvements of Ivlev's electivity index are commonly used for fish habitat use studies (Copp 1990, 1992; Poizat & Pont 1996). Preference was calculated as a normalized ratio of utilization to availability for different intervals of each environmental variable. Preference indexes were obtained after dividing each variable into several modalities. Their number was defined according to the range of variation of each variable. The following formula was used:

\[ I = \frac{\text{Ob}}{\text{Ex}} - 0.5 \]

where Ob is the number of fish observed for the modality, Ex is the expected number of fish for a theoretical random distribution and \((\text{Ob/Ex})_{\text{max}}\) is the maximum value of \((\text{Ob/Ex})\) for the modality. \(I\) varies between \(-0.5\) and \(+0.5\). Positive values indicate preference and negative values indicate avoidance for a given variable. Therefore, values between \(-0.1\) and \(0.1\) can be considered as revealing indifference; from \(-0.30\) to \(-0.11\) and from \(0.11\) to \(0.30\) illustrate slight avoidance or preference, respectively; and from \(-0.5\) to \(-0.31\) and \(0.31\) to \(0.5\) reveal strong avoidance or preference, respectively. To estimate any significant differences between the two methods (i.e. PASE and PASS), we used the Wilcoxon nonparametric test according to Sokal & Rohlf (1981), which compared the two paired groups to find out whether their difference was significantly different from a nil value. This test was computed using SPSS release 8 for Windows. In the same way, the relative abundance and occurrence of every individual of each species, collected using the two sampling methods, were compared using the Wilcoxon nonparametric statistical test according to Sokal & Rohlf (1981).

Results

Within the whole data matrices, 1480 and 1310 point samples were collected, 21,049 fish were caught and 177,698 observed using PASE and PASS, respectively. The discrepancy between the amount of fish numbered using the two methods is due to the different sizes of the samples collected using each method (i.e., ca. 0.2 m² for PASE and 2 m² for PASS) and do not induce bias in the analyses, as we considered the relative values of fish abundance and occurrence. The mean abun-
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Fig. 1. Relative occurrence (a) and abundance (b) expressed as a percentage for each of the 19 fish populations (young and adults) belonging to 10 species, using the two sampling techniques. The ten species were the following: roach (*Rutilus rutilus* L.), rudd (*Scardinius erythrophthalmus* L.), perch (*Perca fluviatilis* L.), bleak (*Alburnus alburnus* L.), bream (*Abramis brama* L.), gudgeon (*Gobio gobio* L.), pike (*Esox lucius* L.), tench (*Tinca tinca* L.), carp (*Cyprinus carpio* L.) and pumpkinseed (*Lepomis gibbosus* L.).

dance of fish estimated were 71.1 and 67.8 fish per m² using PASE and PASS, respectively. For each species, young (0+) and adult fish (1+ and older) were considered as different populations to avoid bias due to behavioral and habitat differences between young and adult individuals. Moreover, this study favors the whole range of sizes of 0+ fish and therefore satisfies possible habitat changes occurring during the development of each studied species, providing in this way an overview of the main habitat characteristics of the populations considered.

Of the 15 fish species colonizing the lake (Brosse et al. 1999), 10 were recorded in our study by both sampling methods (Fig. 1). The study of the relative occurrence (i.e. percentage of samples where the considered population is captured) and abundance (i.e. numerical percentage of the considered population relative to the total number of fish captured) of each species within the fish community, using the two sampling methods, revealed almost the same results with both sampling methods (Fig. 1). The Wilcoxon's nonparametric statistical paired test showed no significant differences between the two methods for the estimation of the relative occurrence ($Z = -0.50, P = 0.62$) and abundance ($Z = -0.20, P = 0.85$) of the different fish species within the community. A more precise study of Fig. 1 showed that several populations of adult fishes (e.g. adult perch and adult roach) were found to occur more frequently using PASS than PASE (Fig. 1A). In the same way, young perch and young bleak (*Alburnus alburnus* L.) were found to be more abundant using PASE, whereas the abundance of young pike and young tench (*Tinca tinca* L.) was higher using PASS (Fig. 1B).

Concerning microhabitat data, the Pearson correlation matrix showed a strong correlation between the variables silt and sand ($\geq 0.61$ for PASE and $\geq 0.86$ for PASS) and between silt and vegetation cover ($\geq 0.75$ for PASE and $\geq 0.65$ for PASS). To avoid colinearity between variables, the percentage of silt was removed from the two data matrices. Thus, all the statistical analyses were performed on a set of eight variables (distance from the bank, depth, percentage of mud, sand, gravel, pebbles, boulders, and flooded vegetation cover). Wilcoxon's nonparametric test showed a significant difference between PASE and PASS for the microhabitat preference of each of the three young fish populations studied ($Z = -4.20, P < 0.01$ for roach, $Z = -4.29, P < 0.01$ for perch and $Z = -4.29, P < 0.01$ for pike). Thus, the fish microhabitat estimated using PASE and PASS gave different results.

Using electrofishing, roach were found to live close to the bank and generally avoided distances from the bank, which were further than 5 m (Fig. 2).
With PASS, roach were observed further from the bank (5–10 m), but they avoided distances over 15 m (Fig. 2B). The results obtained by PASE showed that roach also avoided deep water (more than 0.5 m), whereas with scuba diving, a lot of roach were observed at depths greater than 0.5 m. Muddy substratum was avoided with PASS, whereas roach collected with PASE were found on mud. Finally, considering flooded vegetation cover, PASS revealed a preference for intermediate vegetation cover (i.e. 25–75%), whereas PASE revealed a preference for dense cover.

The general trends in perch microhabitat were quite similar for the two topographical variables using both methods (Fig. 3). The same microhabitat profiles were obtained for distance from bank and depth, characterized by a preference for intermediate distances (5–10 m) and depths (0.5–1 m). Nevertheless, PASE showed that perch microhabitat choice is hardly affected by large substrata such as pebbles and boulders, whereas PASS showed perch that clearly avoided these substrata. In the same way, using PASE, perch were found inside vegetation, whereas using PASS, they were found in both vegetated areas and in open water. The two remaining substrata (mud and gravel) did not exhibit a clear difference between the two sampling methods.

For pike (Fig. 4), the microhabitat profiles showed that, using PASE, fish were always collected less than 10 m from the bank in shallow water (less than 0.5 m), whereas PASS results gave a narrower range of habitat features (between 2.5 and 10 m from the bank and between 0.25 and 0.5 m deep). Similarly, pike were found to colonize the whole range of vegetated areas using PASE, whereas PASS results showed that they colonized only intermediate vegetation cover. Finally, PASE habitat profiles revealed that pike tended to avoid large substrata, whereas such a trend was not clear from PASS.

**Discussion**

The relative occurrence and abundance showed that both methods can reliably sample the whole fish community. Nevertheless, the techniques differ due to the biases each introduces. Compared with PASS, the underestimation by PASE of the occurrence of some adult fish populations is thought to be due to the observer stamping around driving the most mobile species away. Such a bias in the electrofishing methods has already been reported (Bain et al. 1985; Copp 1989). Likewise, PASE underestimated the abundance of some young fish populations known to colonize highly vegetated areas (e.g. tench and pike), as the collection of stunned fish is limited by dense vegetation (Dewey 1992). PASS also exhibits its own shortcomings; young perch abundance could be underestimated due to errors concerning fish counts when very dense shoals were encountered. Similarly, young
bleak (Alburnus alburnus L.) abundance was underestimated by PASS. Such errors could be due to the inability of the observer to discriminate between young bleak and roach or rudd when dense shoals with both species were encountered. Thus, we can hypothesize that a large part of the young bleak population was counted as other cyprinids.

Considering microhabitat studies, fish microhabitat profiles assessed using the two sampling methods revealed different patterns for each species. Using PASE, roach were found on muddy substrata, which is unusual, as mud does not constitute a food item for young roach (Dubois et al. 1994; Angelibert et al. 1999). This species is usually strongly associated with sandy substratum (Copp 1990), and medium depths (about 0.75 m). However, habitat features concerning flooded vegetation obtained with PASS were in accordance with previous studies, revealing firstly, that roach feeding efficiency is maximal with low vegetation density and open water (Persson 1993; Eklov & Persson 1996) and secondly, that the spatial occupancy of roach located close to shelters can be related to a predation avoidance of adult perch and young pike (Mittelbach 1981; Persson & Greenberg 1990; Eklov & Diehl 1994; Eklov & Persson 1995).

Concerning perch, according to Eklov & Hamrin (1989), structurally complex habitats sustain higher macroinvertebrate biomass, which constitute one of the main feeding items for perch (Persson 1993; Eklov 1997). Consequently, perch were found close to the open waters at intermediate depths and distances from the bank using both sampling methods. Thus, perch microhabitat was reliably assessed with both sampling methods even if a significant difference was found between PASE and PASS, these general trends in perch distribution are in accordance with previous ecological studies (Diehl 1988; Macchiusi & Baker 1991). The preference of muddy bottoms and the avoidance of large substratum can be related to the search for food associated with mud (chironomids and other macroinvertebrates) and the avoidance of boulders and pebbles, which are usually colonized by large predators such as pike-perch (Stizostedion lucioperca L.) (Brabrand & Faafeng 1994) and thus could be considered as predator avoidance. On the contrary, the results obtained by PASE for large substrata seem quite irrelevant.

Concerning pike, according to Turner & Mackay (1985) and Eklov (1997), PASS results showed that young pike require at least 30% vegetation cover and are associated with dense vegetation and shallow water. This behavior is due to the feeding habits of pike; which is an ambushing predator waiting for its prey close to the bottom, inside the vegetation. Moreover, young pike colonize vegetated areas to avoid cannibalism from the larger pike (Eklov 1997). In the same way, PASS showed a preference for vegetated areas located at intermediate distances and depths. This habitat-use, assessed with PASS, can be considered as a trade-off between prey availability and predation avoidance, whereas PASE revealed that pike were found close to the bank in very shallow water. Such a habitat could characterize a refuge habitat encouraged by the sampling design. With PASS, if the observer moved slowly, the pike retreated, swam slowly around the observer and ended up at the same location as when first encountered. According to Turner & Mackay (1985), no apparent fleeing reactions to divers were exhibited.

General trends in fish microhabitat use were reliably assessed with both PASE and PASS methods, but as shown above, fish microhabitat was assessed better using PASS than PASE. Using PASE, fishes are mainly found in “shelter habitats” such as shallow water and dense vegetation. Such behavior is probably caused by the environmental disturbance of the sampling method. This hypothesis is supported by the study of substrate occupancy by the three species. Using the PASE method, substrate occupancy was usually irrelevant, as the fish escaped from their usual areas such as feeding zones (for which substrate composition is determinant) to shelters. According to Bain et al. (1985) and Dewey (1992), PASE probably induces bias due to the indirect nature of the observation: i.e., the use of a catching design and

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+++ highly affected, ++ affected, + hardly affected, 0 not affected.

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Table 1. Overview of the range conditions of use and environmental disturbances caused by direct (i.e. PASS) and indirect (i.e. PASE) sampling methods for ecological studies of fish populations and communities.
the escapement caused by the observer stamping around. However, electrofishing can be used in a wider range of situations than PASS and is less affected by turbidity and wind-induced waves, which make visual observations by scuba divers impossible (Table 1). Moreover, with PASE fish are captured and thus the number of fish and the developmental stage or length of each individual are determined accurately. Nevertheless, this catching method is inoperative in areas deeper than 1 m and is limited by water conductivity (e.g. low or high conductivity for mountain lakes or brackish waters) and by accessibility to the shore (e.g. sheer bank slope or large woody debris) (Cowx & Lamarche 1990). In the same way, temporal studies with repetitive samples during a short period are biased due to the damage caused to the sampling area (vegetation cover, substratum) by repeated stamping of the observer (Hammer 1985).

Using PASS, fish escapement behavior was rarely observed; moreover, this technique does not affect the environment or the welfare of the fish. Nevertheless, a major assumption of the census estimate is that the total number of fish observed constitutes a measure of the actual number present. The validity of this assumption depends upon various observational variables: crypticity of the fish (or the screening effect of the habitat), hiding dispersion of alerted individuals before the arrival of the diver, varying visibility of different size classes, duplicate counts, experience and speed of the observer and conditions related to weather and turbidity (Brock 1954; Northcote & Wilkie 1963; Keast & Harker 1977; Helfman 1983). According to Sale & Douglas (1981), visual censuses can display high repeatability, but they seldom (if ever) completely sample the fish present at a site especially with dense fish shoals such as young roach and young perch. Nevertheless, with good underwater visibility, divers should be able to obtain reliable estimates of fish abundance.

As shown in Table 1, which comprises a synthesis of our own results and from the literature concerning electrofishing (Bain et al. 1985; Barrett & Grossman 1988; Copp 1989; Cowx & Lamarche 1990; Dewey 1992; Perrow et al. 1996) and scuba sampling (Ellis 1961; Sale & Douglas 1981; Helfman 1983; Turner & Mackay 1985), PASS seems better suited than indirect sampling designs (e.g. PASE) to determine fish microhabitat in the littoral areas of lakes because of the accuracy of the results provided by a method that avoids physically disturbing the assemblage. We can therefore recommend this method for ecological studies of fish populations and communities. This approach appears to be relevant and more suitable than other techniques especially considering rare and endangered species due to its nondestructive nature.

### Resumen

1. Hemos desarrollado un nuevo método directo por escafandra (i.e. muestreo de abundancia puntual por observación desde escafandra, PASS) para estudiar microhabitats de peces en zonas litorales de lagos. Nuestro fin concreto fue evaluar la relevancia de este método en relación a muestreos estándar de abundancia puntual con pesca eléctrica (PASE).

2. Los muestreos se llevaron a cabo en 2 zonas litorales del Lago Pareloup (Francia) de similares características ambientales que fueron utilizadas para comparar las características de habitat obtenidas utilizando dos técnicas de muestreo distintas. Tres especies de peces representativas del grupo ecológico y, especialmente, de la cadena trófica, fueron consideradas: juveniles (O+ de *Rutilus rutilus*, *Perca fluviatilis*, y *Esox lucius*). Las dos matrices de datos (i.e. PASE y PASS) fueron utilizadas para desarrollar índices de preferencias de microhabitat para 8 variables ambientales como medida del uso de habitat por la población de peces vs. disponibilidad de habitat.

3. Test no-paramétricos de Wilcoxon revelaron diferencias significativas entre los dos métodos para cada población. Además, la estructura de la comunidad de peces y los perfiles de microhabitat que fueron evaluados utilizando ambos métodos revelaron patrones diferentes para cada población. Utilizando PASE, los peces fundamentalmente encontrados sobre habitats de “shelter” tales como aguas someras y vegetación densa. Tal comportamiento podría estar causado por las molestias ocasiones por el propio observador. Utilizando PASS, comportamiento de escape por parte de los peces fue raramente observado.

4. Concluimos que esta técnica de muestreo directa y no destructiva puede ser utilizada para obtener estimas precisas de microhabitat de comunidades de peces que asumimos más apropiada que PASE para estudios de habitat.

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### References


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