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Fish habitat selection in a large hydropeaking river: Strong individual and temporal variations revealed by telemetry

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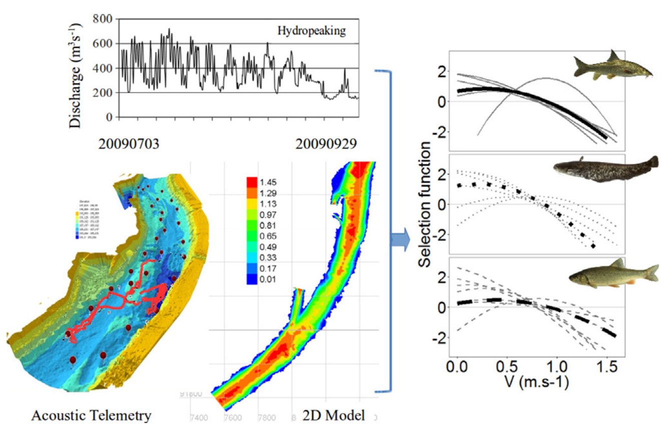
HIGHLIGHTS

- Managing hydropeaking in rivers requires understanding dynamic ecological responses.
- We continuously tracked 18 individual fish in a large hydropeaking river.
- The dynamics of hydraulic and thermal microhabitats was modeled.
- Individual habitat selection varied with time and with current and past hydraulics.
- Hydropeaking may force individuals to adopt a least-constraining strategy.

GRAPHICAL ABSTRACT



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ABSTRACT

Modeling individual fish habitat selection in highly variable environments such as hydropeaking rivers is required for guiding efficient management decisions. We analyzed fish microhabitat selection in the heterogeneous hydraulic and thermal conditions (modeled in two-dimensions) of a reach of the large hydropeaking Rhône River locally warmed by the cooling system of a nuclear power plant. We used modern fixed acoustic telemetry techniques to survey 18 fish individuals (five barbels, six catfishes, seven chubs) signaling their position every 3 s over a three-month period. Fish habitat selection depended on combinations of current microhabitat hydraulics (e.g. velocity, depth), past microhabitat hydraulics (e.g. dewatering risk or maximum velocities during the past 15 days) and to a lesser extent substrate and temperature. Mixed-effects habitat selection models indicated that individual effects were often stronger than specific effects. In the Rhône, fish individuals appear to memorize spatial and temporal environmental changes and to adopt a "least constraining" habitat selection. Avoiding fast-flowing midstream habitats, fish generally live along the banks in areas where the dewatering risk is high. When discharge decreases, however, they select higher velocities but avoid both dewatering areas and very fast-flowing

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midstream habitats. Although consistent with the available knowledge on static fish habitat selection, our quantitative results demonstrate temporal variations in habitat selection, depending on individual behavior and environmental history. Their generality could be further tested using comparative experiments in different environmental configurations.

1. Introduction

Most models of physical habitat suitability in river reaches are based on "preference" models (Johnson, 1980) that reflect microhabitat selection by fish and invertebrates (Ahmadi-Nedushan et al., 2006; Lamouroux et al., 2010; Dunbar et al., 2012). Preference models generally predict changes in abundance or occurrence of aquatic taxa (e.g. species, life stages, guilds) as a function of static hydraulic (e.g., current velocity, water depth, bed shear stress), substrate or thermal characteristics of microhabitats at the time of sampling (Lamouroux et al., 1999; Mérigoux et al., 2009). Some preference models transfer well across rivers (Lamouroux et al., 1999, 2013; Dolédec et al., 2007) and "regional" preference models, built from data collected in multiple rivers, have been successfully used to predict changes in taxa abundance in reaches after flow restoration (Lamouroux et al., 2015).

Preference models have been frequently criticized, for example because they generally do not account for biotic interactions and habitat dynamics (Lancaster and Downes, 2010) and have weak statistical bases (Guay et al., 2003). Although these aspects are less discussed, preferences also vary according to individual behavior (Enders et al., 2009) and the overall available habitat conditions at scales larger than the microhabitat (Mérigoux and Dolédec, 2004; Vilizzi et al., 2004). More generally, individual habitat selection depends on species, individual size, and type of activity (e.g., feeding, resting or breeding). Fish habitat selection may also depend on learning processes based on individual experience or observations and it is being done over a large range of spatial and temporal scales (Patton and Braithwaite, 2015). Furthermore, individual habitat selection depends on the perception of the neighboring environment (Bleckmann and Zelick, 2009) compared to the knowledge of suitable habitat conditions (e.g. refuges, feeding spots; Reebs, 1996; Braithwaite and Burt De Perera, 2006). Therefore, individual sensitivity, experience, and perception of the past and current environmental conditions should influence habitat selection.

Understanding variations in habitat selection is particularly important when the environment is spatially and temporally variable as in stream reaches subject to hydropeaking (i.e. rapid changes in discharge caused by hydropower plants) or local warming (e.g. industrial cooling water discharge). In particular, hydropeaking generates sub-daily alterations of flow magnitude, timing, durations and ramping rates (water depth changes of often several dozen cm h^{-1}; Halleraker et al., 2003; Courret et al., 2012; Schmutz et al., 2015). Such unpredictable variations strongly influence aquatic populations and communities (Lauters et al., 1996; Steele and Smokorowski, 2000; Wüest, 2012; Bruno et al., 2013; Gandini et al., 2014; Person et al., 2014). High ratios between peak and base flow during hydropeaks, high up-ramping and down-ramping rates and heterogeneous bed forms in dewatered areas generally increase the probability of fish stranding and the need of forced movements (e.g. between feeding zones and refuges) (Valentin et al., 1995; Halleraker et al., 2003; Tuhtan et al., 2012; Hauer et al., 2014). However, field evidence of individual responses to hydropeaking remains limited.

Telemetry has been used to understand individual fish habitat selection under hydropeaking environments in medium to large-sized rivers (e.g. De Vocht and Baras, 2005; Taylor et al., 2014; Li et al., 2015). In particular, acoustic telemetry is well suited for analyzing how habitat selection varies between individuals, between activity types (e.g. resting vs. moving fish) and depending on the global (e.g. direction of discharge change) or local (e.g. microhabitat hydraulics) environment. In large hydropeaking rivers, however, fixed acoustic telemetry studies remain challenging due to (1) the difficulty to implement these techniques in deep and fast-flowing conditions (Bergé et al., 2012; Li et al., 2015) and (2) the difficulty to describe unsteady (i.e. varying with discharge) two-dimensional hydraulics in these rivers, which are of major importance for understanding and mitigating the effects of hydropeaking (Hauer et al., 2014; Person et al., 2014; Schmutz et al., 2015).

This paper describes an original analysis of fish microhabitat selection in the spatially heterogeneous and temporally variable hydraulic and thermal conditions of a large hydropeaking river (Rhône River at Bugey, France) locally warmed by the cooling system of a nuclear power plant. We used modern fixed acoustic telemetry techniques to survey 18 fish individuals over a three-month period (03 July–29 September 2009), signaling their position every c. 3 s (Bergé et al., 2012). Individuals belonged to two dominant native cyprinids (barbel: *Barbus barbus*, and chub: *Squalius cephalus*) and an exotic species (wells catfish: *Silurus glanis*; hereafter, catfish; Poulet et al., 2011). The dynamics of microhabitat hydraulics and water temperature within the study reach (1.8 km long) were described using an unsteady two-dimensional hydraulic model (Capra et al., 2011), and bed particle size was mapped. We used mixed-effect models to analyze how individual microhabitat selection depended on the current microhabitat conditions (hydraulics, temperature and substrate grain size) and the dynamic history of microhabitat hydraulics over the previous 15 days. To infer temporal changes in habitat selection, we repeated our analyses for subgroups of data corresponding to different directions of discharge changes (stable, increasing or decreasing) and fish activities (resting or moving).

2. Material and methods

2.1. Study site

The Rhône River has a catchment of 98,556 km^2 and a mean annual discharge of 1720 $m^3\ s^{-1}$ at the river mouth (Olivier et al., 2009). Our study reach is 1.8 km long and 140 m wide (at a mean discharge of 465 $m^3\ s^{-1}$) and is situated 363 km upstream from the river mouth, near the Bugey nuclear power plant (45°47′44″N; 5°16′25″E; Fig. 1). The hydrological regime at Bugey is a glacial-nival regime influenced by numerous hydropower plants (nine between Lake Geneva and Bugey). The mean daily discharge is generally between 182 $m^3\ s^{-1}$ (exceeded 95% of the time) and 908 $m^3\ s^{-1}$ (exceeded 5% of the time), according to hourly data measured by the "Compagnie Nationale du Rhône" (between 1987 and 2014). Hydropower plants have a moderate influence on daily discharge but generate high sub-daily discharge variations (generally around 150 $m^3\ s^{-1}$ and occasionally >500 $m^3\ s^{-1}$) for peak hydroelectricity production (Fig. 2). Discharge is more stable during week-ends and during low flow periods (early fall). The mean annual water temperature at the upstream part of our study reach is 12.2 °C, with daily temperatures between 4.6 °C (exceeded 95% of the time) and 21.5 °C (exceeded 5% of the time) according to continuous data measured by "Electricité de France" between 1980 and 2014. Water turbidity recorded in 2009 ranged between 9.5 mg L^{-1} in February and 81 mg L^{-1} in November (Roger et al., 2010; for recent years: https://bdoh.irstea.fr/observatoire-des-sediments-du-rhone).

A nuclear power plant located on the right bank of the study reach abstracts c. 100 $m^3\ s^{-1}$ at the upstream end of our study reach to cool its four reactors, and discharges warmed water (between 7 °C and 10 °C warmer than the upstream water) at two different locations