Université de Montréal

Habitat variability and the individual variability of juvenile Atlantic salmon (*Salmo salar*)

(La variabilité de l'habitat et du comportement individuel du saumon Atlantique juvénile (*Salmo salar*))

par

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Cette thèse intitulée :
Habitat variability and the individual behaviour of juvenile Atlantic salmon (*Salmo salar*)
(La variabilité de l'habitat et du comportement individuel du saumon Atlantique juvénile)
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Présentée par :
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Résumé

La variabilité spatiale et temporelle de l'écoulement en rivière contribue à créer une mosaïque d'habitat dynamique qui soutient la diversité écologique. Une des questions fondamentales en écohydraulique est de déterminer quelles sont les échelles spatiales et temporelles de variation de l'habitat les plus importantes pour les organismes à divers stades de vie. L'objectif général de la thèse consiste à examiner les liens entre la variabilité de l'habitat et le comportement du saumon Atlantique juvénile. Plus spécifiquement, trois thèmes sont abordés : la turbulence en tant que variable d'habitat du poisson, les échelles spatiales et temporelles de sélection de l'habitat et la variabilité individuelle du comportement du poisson. À l'aide de données empiriques détaillées et d'analyses statistiques variées, nos objectifs étaient de 1) quantifier les liens causaux entre les variables d'habitat du poisson « usuelles » et les propriétés turbulentes à échelles multiples; 2) tester l'utilisation d'un chenal portatif pour analyser l'effet des propriétés turbulentes sur les probabilités de capture de proie et du comportement alimentaire des saumons juvéniles; 3) analyser les échelles spatiales et temporelles de sélection de l'habitat dans un tronçon l'été et l'automne; 4) examiner la variation individuelle saisonnière et journalière des patrons d'activité, d'utilisation de l'habitat et de leur interaction; 5) investiguer la variation individuelle du comportement spatial en relation aux fluctuations environnementales.

La thèse procure une caractérisation détaillée de la turbulence dans les mouilles et les seuils et montre que la capacité des variables d'habitat du poisson usuelles à expliquer les propriétés turbulentes est relativement basse, surtout dans les petites échelles, mais varie de façon importante entre les unités morphologiques. D'un point de vue pratique, ce niveau de complexité suggère que la turbulence devrait être considérée comme une variable écologique distincte. Dans une deuxième expérience, en utilisant un chenal portatif *in situ*, nous n'avons pas confirmé de façon concluante, ni écarté l'effet de la turbulence sur la probabilité de capture des proies, mais avons observé une sélection préférentielle de localisations où la turbulence était relativement faible. La sélection d'habitats de faible turbulence a aussi été observée en conditions naturelles dans une étude basée sur des observations pour laquelle 66 poissons ont été marqués à l'aide de transpondeurs passifs et suivis pendant trois mois dans un tronçon de rivière à l'aide d'un réseau d'antennes enfouies dans le lit.

La sélection de l'habitat était dépendante de l'échelle d'observation. Les poissons étaient associés aux profondeurs modérées à micro-échelle, mais aussi à des profondeurs plus élevées à l'échelle des *patchs*. De plus, l'étendue d'habitats utilisés a augmenté de façon asymptotique avec l'échelle temporelle. L'échelle d'une heure a été considérée comme optimale pour décrire l'habitat utilisé dans une journée et l'échelle de trois jours pour décrire l'habitat utilisé dans un mois.

Le suivi individuel a révélé une forte variabilité inter-individuelle des patrons d'activité, certains individus étant principalement nocturnes alors que d'autres ont fréquemment changé de patrons d'activité. Les changements de patrons d'activité étaient liés aux variables environnementales, mais aussi à l'utilisation de l'habitat des individus, ce qui pourrait signifier que l'utilisation d'habitats suboptimaux engendre la nécessité d'augmenter l'activité diurne, quand l'apport alimentaire et le risque de prédation sont plus élevés. La variabilité inter-individuelle élevée a aussi été observée dans le comportement spatial. La plupart des poissons ont présenté une faible mobilité la plupart des jours, mais ont occasionnellement effectué des mouvements de forte amplitude. En fait, la variabilité inter-individuelle a compté pour seulement 12-17% de la variabilité totale de la mobilité des poissons. Ces résultats questionnent la prémisse que la population soit composée de fractions d'individus sédentaires et mobiles. La variation individuelle journalière suggère que la mobilité est une réponse à des changements des conditions plutôt qu'à un trait de comportement individuel.

Mots-clés : rivière, habitats, saumon, comportement, écoulement, échelles, turbulence, mobilité des poissons, cycles d'activité, utilisation de l'habitat.

Abstract

Spatiotemporal flow variability contributes to create a dynamic habitat mosaic sustaining ecological diversity. One of the most important topics in ecohydraulic research is to identify the relevant scales of flow variability affecting organisms at different life stages. The general objective of the thesis is to examine the links between habitat variability and the behaviour of juvenile Atlantic salmon. More specifically, three themes are addressed: turbulence as a fish habitat variable, the spatial and temporal scales of habitat selection and individual variability in fish behaviour. Through detailed field measurements incorporating a variety of sampling techniques and statistical analyses our objectives were to: 1) Quantify the causal links between standard habitat variables and flow turbulence at multiple scales; 2) Test a new *in situ* portable flume to analyse the effect of turbulent flow properties on the prey capture probability and foraging behaviour of juvenile Atlantic salmon; 3) Analyse the spatial and temporal scale dependence of fish-habitat associations within a reach during the summer and autumn; 4) Examine individual variation of seasonal and daily activity patterns and habitat use and their interaction; 5) Investigate the individual variation in seasonal daily movement behaviour in relation to environmental fluctuations.

The thesis provides a detailed characterization of turbulence in pools and riffles and showed that the capacity of 'standard' fish habitat variables to explain turbulent properties was relatively low, especially at smaller spatial scales, but varied greatly between the units. From a practical point of view, this level of complexity suggested that turbulence should be considered as a 'distinct' ecological variable within this range of spatial scales. In a second experiment, using an *in situ* portable flume and underwater videotaping of fish, we did not conclusively confirm or rule out the effect of turbulence on prey capture probability, but observed a preferential selection of locations where flow velocity was downward and turbulence intensity was lower. The selection of lower turbulence habitat was also observed in natural habitat conditions in an observational field study, in which 66 PIT-tagged fish were tracked for three months in a river reach using a high resolution network of antennas buried in the bed.

Juvenile salmon habitat selection was dependant on the scale of observations. Fish were associated with moderate depth micro-scale habitats, but also with higher depth patch-scale habitats. Furthermore, the range of habitat used by individuals increased asymptotically with the temporal scale. The scale of one hour was considered as optimal to describe the range of habitats used in a day and three days optimal to describe the range of habitat used in a month.

Individual tracking revealed high inter-individual variability in activity patterns, as some individuals were predominantly nocturnal whereas others frequently changed their daily activity pattern. Changes in activity patterns were linked to environmental fluctuations, but also to individual habitat use patterns, which might signify that lower quality habitats require fish to increase daytime activity when food intake and the risk of predation are both high. High inter-individual variability was also observed in the fish movement behaviour. It appeared that most fish exhibited low mobility on most days, but also showed occasional bouts of high mobility. Between-individual variability accounted for only 12-17% of the variability in the mobility data. These results challenge the assumption of a population composed of a sedentary and mobile fraction. Individual variation on a daily basis suggested that movement behaviour is a response to changing environmental conditions rather than an individual behavioural trait.

Keywords : river, habitats, juvenile salmon, behaviour, flow, scales, turbulence, fish mobility, activity patterns, habitat use.

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If the only tool you have is a Kraken, every
problem looks like an excuse to release it.
– Ancient proverb

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Chapitre 1: Introduction

Habitat selection is a key process governing the distribution patterns of animals. The study of habitat selection by organisms dates back to the beginning of the century (Grinnel, 1917; Lack, 1933). Since then, the question of how and why animals select a particular habitat has been of great interest to ecologists, as it provides important information on the preferences of a species for a range of environmental variables and their habitat requirements (Rosenfeld, 2003). Such information can be used as a framework to predict animal density and abundance relative to habitat availability (Bovee, 1986).

For juvenile salmonids in rivers, the patchy distribution of individuals and density-dependent growth suggest that the availability of suitable habitat is a limiting factor (Grant and Kramer, 1990). To complete its life cycle, a fish needs to survive and grow, which often depends on its ability to locate the most suitable habitats (Finstad et al. 2011). Fast growth depends on a positive energy budget, whereas high survival depends on minimizing the risk of predation. As the safest habitats do not always provide the highest growth potential, growth and avoiding predators are often viewed as a tradeoff (Metcalfe et al. 1999).

River flow is highly variable in space and time. This heterogeneity contributes to the creation of a dynamic mosaic that sustains ecological diversity in rivers (Statzner, 1981). Physical habitat is mainly characterized by the interactions between flow and bed morphology over a range of scales. Spatial scales range from micro particles to large channel morphology features (e.g. riffles and pools) and temporal scales range from flow turbulent fluctuations to seasonal floods (Biggs et al., 2005; Nikora, 2007). Many rivers are relatively hostile environments for most life, as high energetic costs are required to withstand the strong turbulent flows (Church, 2007). Stream-dwellers benefit from morphological adaptations (e.g. streamlined shapes, low-resistance surfaces) and plasticity in behaviour (e.g. mobility, activity patterns), to deal with strong flows and varying environmental conditions. Such flexibility in behaviour may also allow individuals to improve their chance of survival by balancing the tradeoff between susceptibility to predators and metabolic demands (Fraser et al. 1995).

Despite the great interest in how animals select habitats in the face of spatiotemporal habitat variability, much work remains to be done to understand how behaviour is matched to environmental fluctuations. As an example, recent field studies provide contrasting results on how fish react to fluctuations in velocity (i.e. turbulence), discharge and temperature. With the emergence of methods allowing to track individual fish at a high temporal frequency, a common result among studies is the high variability in behaviour among individuals (Okland et al. 2004; Ovidio et al. 2007; Breau et al. 2007; Heggenes et al. 2007). Because foraging decisions depend on tradeoffs experienced at the individual level, behaviour will likely vary among individuals rather than being strictly determined by large scale environmental variables such as flow stage or temperature (Bradford and Higgins, 2001). However, few studies have explicitly addressed the temporal within-individual variation in behaviour as opposed to describing general trends for groups of individuals.

The general objective of this thesis is to examine individual fish behaviour in relation to habitat variability, with a particular emphasis on the small-scale flow variability (i.e. turbulence), as there is accumulating evidence that turbulent flow properties influence fish habitat selection (Smith et al. 2005; Smith et al. 2006; Cotel et al. 2007).

Wild Atlantic salmon parr (*Salmo salar* L.) was selected as a study species, because of its growing status as a model species for examining fundamental relationships between animals and their environment (Findstad et al. 2011). Furthermore, despite its long-standing cultural and economic importance, Atlantic salmon populations are declining over large portions of its range due to the loss and degradation of fluvial habitats (Parrish*, et al.*, 1998). This alarming situation has generated a need for a better understanding of how wild Atlantic salmon interact with habitat during their freshwater life stage. Ultimately, this knowledge will help to provide management tools to assess potential impacts of stream restoration projects. Through innovative fish tracking and habitat sampling techniques, this thesis is an attempt to advance current knowledge of how habitat and, more specifically, flow spatial and temporal variability at the scale of turbulence and flow stage influence the individual behaviour of Atlantic salmon parr.

The thesis comprises eight chapters. An overview of the existing literature on juvenile salmonids behaviour in relation to habitat over a range of spatial and temporal scales is presented in Chapter 2. This literature review presents and discusses the scales of habitat variability in rivers and several aspects of fish behaviour: habitat selection, foraging, diel activity patterns and mobility. This chapter provides a broad context to understand the relevance of the objectives and results of this thesis. In Chapter 3, the objectives are stated and the general methodology is presented, as the main challenges related to data acquisition and analyses are discussed. The main results of this thesis are found in chapters 4 to 8.

Chapter 4, 6, 7 and 8 are written in journal article format for submission to internationally recognized research journals while Chapter 5 is written in the form of a classic thesis chapter.

In Chapter 4, we quantify the relationships between ‘standard’ fish microhabitat variables and turbulent flow properties in morphological units (i.e. pools and riffles) at multiple scales using a novel statistical technique. We show that the spatial coherence of turbulent flow properties is higher in pools than in riffles. However, the capability of standard habitat variables to predict turbulent properties was low, and variable among units of the same morphological type. Therefore, from a practical point of view, turbulence should be considered as a distinct fish microhabitat variable. This article is now published in *River Research and Applications*.

In Chapter 5, we examine the effect of velocity and turbulent flow pattern on the foraging behaviour of Atlantic salmon parr using an *in situ* portable flume. This study combines experimental and field-based approaches in order to develop a new methodology for the study of the foraging behaviour of fish. The relation between turbulent flow properties and behavioural measures were examined: time spent near the river bed; capture and attack time; and, capture probability, as well as preferential focal positions across turbulent flow treatments.

The results presented in Chapter 6, 7 and 8 are based on the use of a large array of antennas buried in the bed of a river reach to monitor the position of Atlantic salmon parr tagged with passive integrated transponders (PIT) over a period of three months from the summer to autumn seasons. To our knowledge, this system provided one of the most extensive spatial and temporal resolutions of fish tracking ever accomplished, allowing us to examine the individual variability of habitat selection, diel activity patterns and movements in a natural river.

In Chapter 6, we examine the spatial and temporal scales of habitat selection of parr. The results reveal the importance of an intermediate spatial (patch scale) and temporal scale (1 hour, 3 days). We show that scale-dependent habitat selection is more important for mean flow velocity and depth than for bed roughness and turbulence.

In Chapter 7, individual patterns of diel activity and habitat use were examined. Results show a predominantly nocturnal and crepuscular activity pattern. However, a fraction of the fish showed a high temporal variability in activity patterns: some days being diurnal; some days being nocturnal; and, other days being active both day and night. This article has been submitted to *Canadian Journal of Fisheries and Applications*.

In Chapter 8, we quantified individual patterns of parr daily mobility. We found that within-individual variability in daily movement accounted between 84 and 87% of the mobility variability. These results challenge the assumption of a population composed of a sedentary and of a mobile fraction. Individual variation on a daily basis suggested that fish movements respond to changing environmental and biotic conditions rather than being an individual behavioural trait. This article has been submitted to *Canadian Journal of Fisheries and Aquatic Sciences*.

Finally, Chapter 9 discusses the key findings, outlines the general contribution of the thesis, and proposes research pathways for future studies.

Chapitre 2: Background

Rivers are heterogeneous and complex environments. The interactions between flow and the river bed result in a wide range of flow depths and velocity. Stream-dwellers benefit from such heterogeneity, as it provides for various life functions such as feeding, resting and sheltering. For juvenile salmonids, behaviour is flexible, allowing individuals to select particular habitats and to adapt to temporal changes in environmental conditions (Slobodkin and Rapoport, 1974). Herein, we broadly define behaviour as every action made by organisms in response to their environment, thus including the preferential selection of a particular habitat over another one (Wooton, 1990).

Fish behaviour is governed by a range of factors that are interdependent (Armstrong et al., 2003) and interacting over a range of spatial scales (Roy et al., 2010). This chapter reviews the literature focusing on how physical habitat influences the tradeoff between growth (g) and predation risk (μ) and how it affects in turn juvenile salmon behaviour in terms of habitat selection, activity and mobility patterns (

Figure 2.1). Despite the importance of intra- and inter-specific competition on salmonid ecology and habitat selection (Nislow et al., 2011), a full treatment of this biotic issues is beyond the scope of this thesis and this review. Nevertheless, the role of some biotic habitat factors is discussed, as physical habitat effects on fish are often mediated through biotic habitat.

The review is composed of six sections (

Figure 2.1). The first section provides a brief overview of juvenile Atlantic salmon ecology, including foraging behaviour and habitat selection. The second section describes the range of spatial and temporal scales of physical habitat in rivers. The third section reviews the various effects of habitat on the components of fish energy budget and on predation risk over a range of scales.

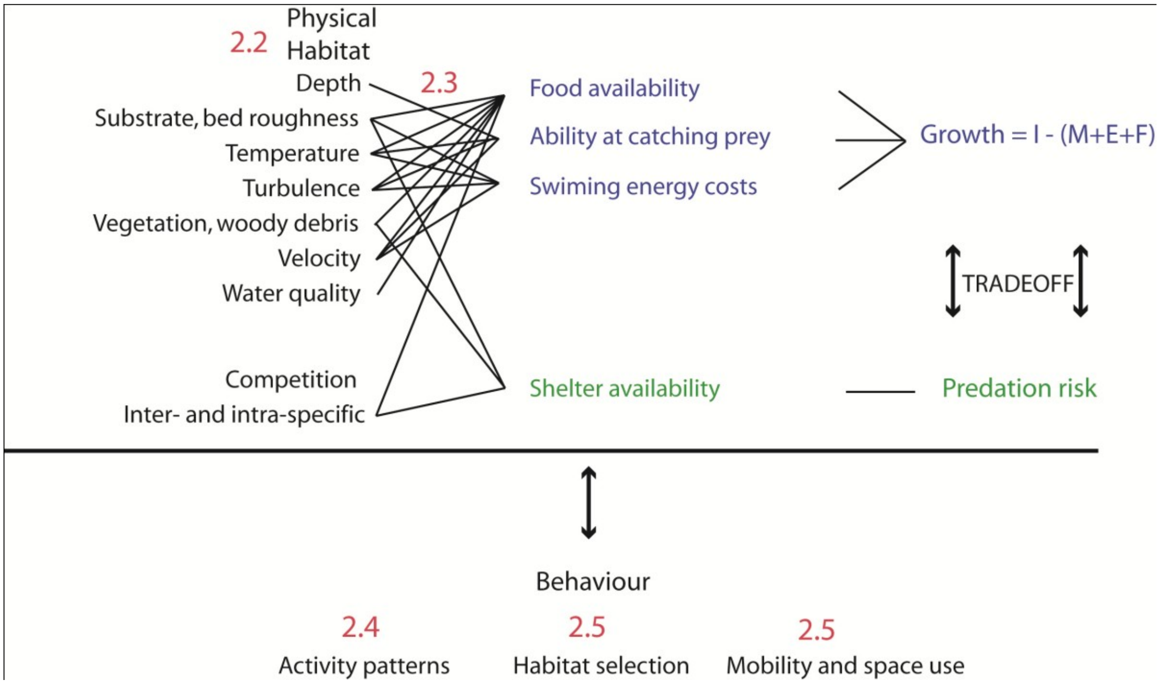

Figure 2.1 Schematic representation of how competition and different physical habitat variables affect growth (blue) and predation risk (green) of juvenile Atlantic salmon. Topics of each section of this chapter are identified (red).

The fourth and fifth sections will address the question of the effect of flow variability and activity patterns on habitat selection and on mobility respectively.

2.1. Juvenile Atlantic salmon ecology and habitat selection

2.1.1. Atlantic salmon life cycle

Atlantic salmon (*Salmo salar L.*) is an anadromous species. Individuals spend a part of their life in the ocean and come to rivers and streams to reproduce (Figure 2.2). In the late fall, during the spawning season, female lay their eggs in redds, in the substrate where they stay for the winter. In early spring, the eggs hatch and the alevins feed on a nutrient rich yolk sac during the first weeks of their life. After about four weeks, the fish emerge from the substrate and move to shallow, low-velocity habitats, called nursery areas (Armstrong et al., 2003).

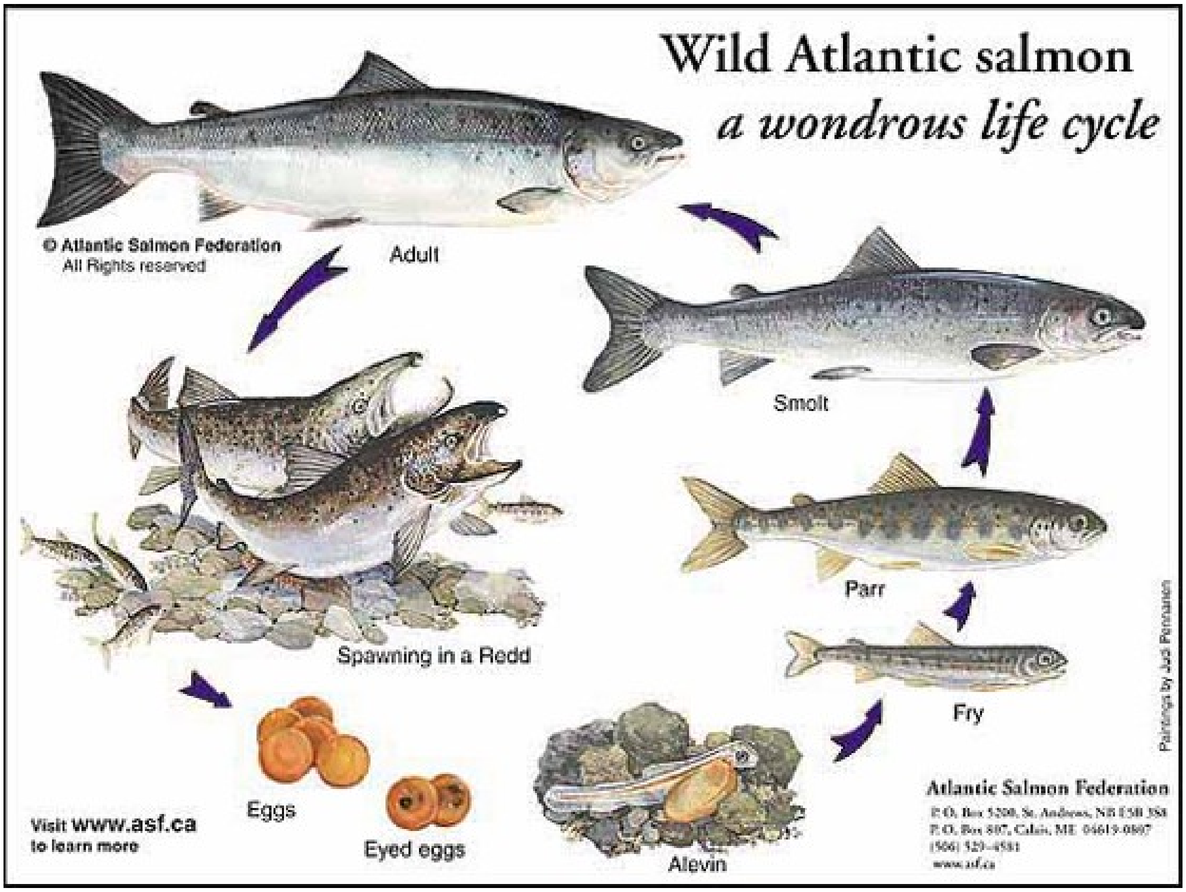

Figure 2.2 Atlantic salmon life cycle. See text. (Source: Atlantic salmon federation www.asf.ca)

By the end of the year, they will grow to become parr. At this stage, they are easily recognizable by their vertical dark spots and their pattern of red dots that is unique to each individual (Figure 2.3). The juveniles grow in the river for a period of two to three years. This period can occasionally extend to up to five years. At the end of this period, parr undergo morphological changes called smoltification in preparation for a life in saline water. After one to three years in the ocean, mature salmon will return to spawn in their natal river. As opposed to Pacific salmon, a significant portion of individuals survive after spawning and can reproduce more than once (Bernatchez and Giroux, 1991). In this thesis, we are interested in the parr life stage, as it corresponds to a freshwater life stage during which the fish actively forages.

Figure 2.3 Atlantic salmon parr. Art by J.O. Pennanen. Approximately life size.

2.1.2. Juvenile salmon foraging behaviour

During the first years of their life, juvenile Atlantic salmon spend most of their time foraging in order to maximize their growth. When they are not foraging, they shelter in the interstices of the substrate to avoid predation (Armstrong et al., 2003; Finstad et al., 2011). Juvenile salmonids are visual foragers (Hughes and Dill, 1990). The majority of their diet comes from drifting macroinvertebrate (Metcalfe et al., 1997), but they can also feed on benthic organisms, especially at low light levels or when drifting prey are not abundant (Nislow et al., 1998; Amundsen et al., 2000). Parr frequently exhibit a fidelity to a specific rearing micro-habitat, often referred to as a ‘home rock’, ‘home stone’, ‘feeding station’ or 'foraging station'. Their feeding behaviour involves performing 'attacks' on prey as they drift on the water surface or in the water column, or simply by a head-jerk movement when the drifting prey is close by. After each foraging movement, parr tend to come back to their home rock to "sit and wait" for the next prey (Stradmeyer and Thorpe, 1987; Figure 2.4). Like most of the sit-and-wait predators, they must visually detect their prey and have a finite detection range (Piccolo et al., 2008a). While they sit on their home rock, parr deploy their pectoral fins to maintain a position that minimizes their swimming energy expenditures (Kalleberg, 1958).

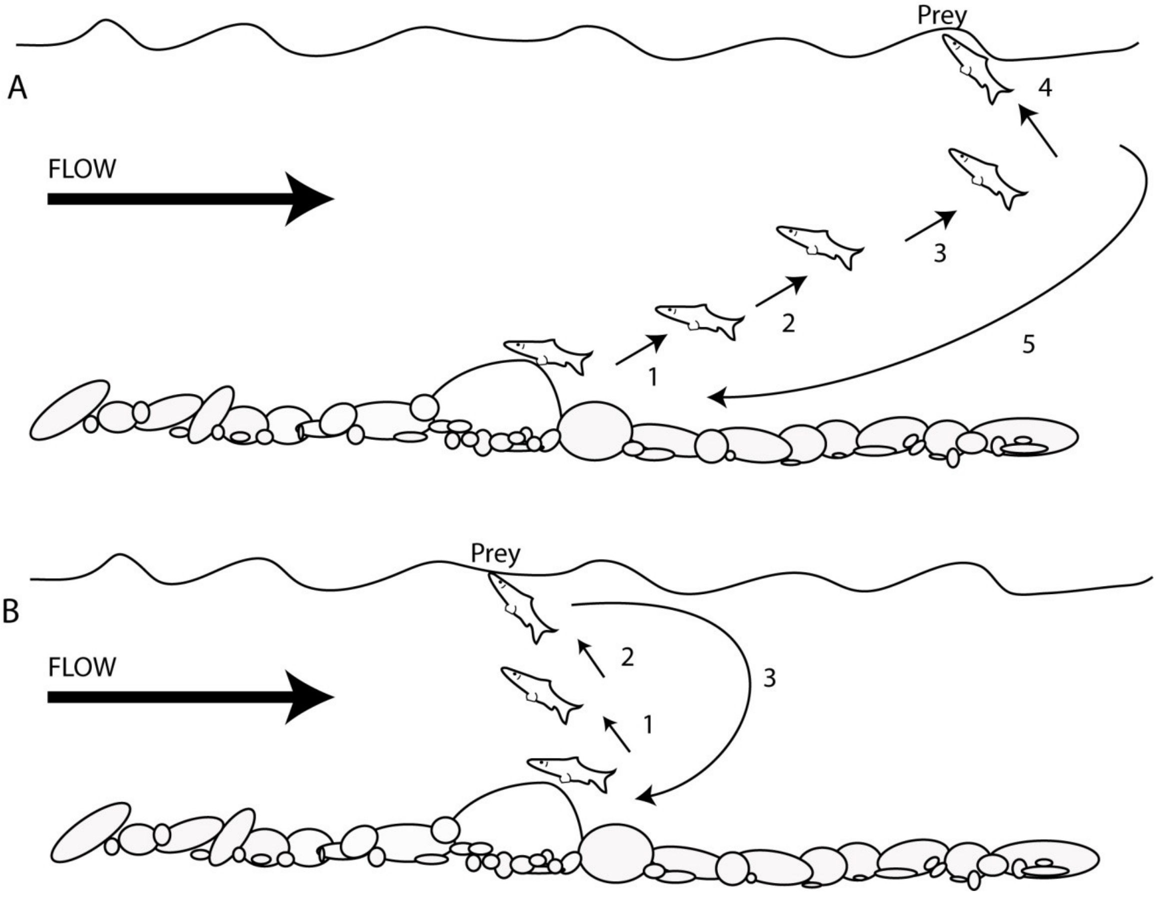

Figure 2.4 Juvenile salmon surface drift feeding: A) passive indirect. B) Direct. Modified from Stradmeyer and Thorpe, (1987).

The fins act as hydrofoils generating a negative lift. Typically, parr contact the substrate with the tips of their extended pectoral fins while upstream at an angle of 10 to 15 degrees (Arnold, 1991). This oblique posture decreases parr reaction time when initiating feeding movements. At higher velocities, to prevent dislodgement, the angle decreases and the dorsal fin retracts to reduce drag. The presence of negative velocity (countercurrent) on the lee of the home rock also helps to reduce the cost of maintaining position (Facey and Grossman, 1992). However, despite this morphological adaptation, maintaining posture may imply significant energy costs (Webb, 2002).

2.1.3. Juvenile salmon habitat use and habitat selection

Numerous studies have detailed the habitat use and habitat selection of Atlantic salmon parr in relation to physical habitat variables (e.g. Rimmer et al., 1984; Degraaf and Bain, 1986; Heggenes et al., 1990). Early studies described parr rearing mesohabitat as a riffle area with a gravel or cobble substrate (Symons and Heland, 1975). It has been reported, however, that parr are also observed in less typical habitats including pools (Saunders and Gee, 1964), ponds and lakes (Erkinaro and Gibson, 1997) and slow moving, often weedy areas.

Most often, juvenile salmonid habitat selection is characterized at the microhabitat scale through snorkelling observations or electrofishing. The method consists in measuring habitat features at the precise location of a fish caught by electrofishing or observed by snorkelling and comparing them to random values of ‘available’ habitat. Physical habitat is routinely characterized using three variables: streamwise flow velocity (U), flow depth (Y) and substrate size (D). Flow velocity is generally either sampled at a depth of 0.6Y or close to the bed at the focal point (snout velocity). Parr habitat preference varies considerably among studies (Table 2.1). For example, Symons and Heland (1978) observed a preference of parr for a narrow range of velocities (50-65 cm s^{-1}) whereas Heggenes et al (1990) estimated a much wider range of preference (10-65 cm s^{-1}). Such differences highlight the importance of indirect biotic factors interacting with habitat selection, such as fish density and food availability (Finstad et al., 2011).

Table 2.1 Habitat use values reported in the literature for Atlantic salmon during the fry stage and parr stage (Armstrong et al. (2003)).

Stage	Habitat variable	Measures	Values	Reference
Fry				
	Snout velocity	Range	5-15 cm·s^{-1}	Morantz et al. (1987)
		Range	10-30 cm·s^{-1}	Morantz et al. (1984)
	Mean column velocity	Range	20-40 cm·s^{-1}	Crisp (1993)
		Minimum	>5-15 cm·s^{-1}	Heggenes et al. (1999)
		Maximum	<100 cm·s^{-1}	Heggenes (1990)
		Range	10-30 cm·s^{-1}	DeGraff and Bain (1986)
	Water depth	Maximum	<10 cm	Heggenes et al. 1999
		Range	20-40 cm	Morantz et al (1987)
		Preference	<25 cm	Symons and Heland (1978) Kennedy and Strange (1982) Morantz et al (1987) Heggenes et al. (1987) Heggenes (1990) Crisp (1993)
		Range	5-65 cm	Heggenes (1990)
		Max	<100 cm	Morantz et al. (1987) Heggenes (1990) Heggenes et al. (1999)
	Substrate size	Range	16-256 mm	Symons and Heland (1978)
Parr				
	Snout velocity	Range	5-35 cm·s^{-1}	Morantz et al (1987)
		Range	0-20 cm·s^{-1}	Heggenes et al. (1999)
		Range	10-50 cm·s^{-1}	Rimmer et al. (1984)
	Mean column velocity	Maximum	>60 cm·s^{-1}	Heggenes et al. (1999)
		Maximum	<120 cm·s^{-1}	Morantz et al. (1987)
		Minimum	<20 cm·s^{-1}	Heggenes et al. (1999)
		Preference	50-65 cm·s^{-1}	Symons and Heland (1978)
		Preference	10-65 cm·s^{-1}	Heggenes (1990)
	Flow depth	Range	25-60 cm	Symons and Heland (1978 Rimmer et al. (1984 Morantz et al. (1987) Heggenes et al. (1990)
		Range	20-70 cm	Heggenes et al. (1990)

Substrate	Range	64-512+ mm	Symons and Heland (1978) Heggenes (1990) Heggenes et al. (1999)

As these factors vary from site to site, the transferability of habitat preference curves among sites is difficult (Maki-Petays et al., 2002).

Flow velocity is an important factor of habitat selection, as it generates a tradeoff between drifting prey availability and energy costs related to swimming (Fausch and White, 1981; Fausch, 1984; Heggenes et al., 1999). Therefore, in order to maximize energy intake and minimize energy expenditures, parr should select micro habitats where velocity is moderate, yet close to fast currents. Generally, moderate-velocity hydraulic refuges are provided by bed roughness elements, such as protruding boulders. In general, young-of-the-year fish tend to use lower velocity habitats than parr (1+ and older) (Table 2.1), presumably because of their lower capability of catching prey in fast currents (Nislow et al., 1999).

Substrate composition, another important habitat feature, is closely linked to bed roughness, as larger particles are more likely to protrude than smaller particles. Besides affecting the availability of low velocity areas, bed composition also influences the availability of shelter from predation. Hence, parr tend to prefer habitats where the bed is mainly composed of clasts in the cobble to boulder class (64-512 mm) (Heggenes et al., 1999). As parr become larger, they tend to use larger sized rocks as rearing habitats (Mitchell et al., 1998). This preference could also be partly due to an increase in spatial flow heterogeneity providing a greater density of varied habitat types (resting, feeding, sheltering). Recently, it was also shown that the addition of large cobble and boulders could increase visual isolation, which could lead to an increase in parr density in a given reach (Dolinsek et al., 2007a). Substrate use may vary according to fish size and period of the day. Mitchell et al. (1998) have reported that parr used larger home rocks during the day than at night, possibly to benefit from a better cover against diurnal predators. Cover from predators can also be provided by vegetation on the banks or surface turbulence (Heggenes et al., 1993).

As reported in previous studies, flow depths most frequently selected by parr ranged between 25 and 60 cm (Degraaf and Bain, 1986; Morantz et al., 1987). Parr also tend to use deeper flows than YOY fish (Table 2.1). However, a recent study reported that parr were present in deep pools in large rivers where bottom velocity remained moderate (Linnansaari et al., 2010).

While information about habitat use is valuable, no studies have attempted to link fitness to the use of specific microhabitats in their natural environment (Finstad et al., 2011). Such an approach has been problematic because individuals use a variety of microhabitats within their home range over short time scales (Ovidio et al., 2007) and exploit different foraging patches that vary on a diel and seasonal basis. Furthermore, inter-individual variability in behaviour, life history or foraging strategy might lead to using similar habitats in different ways (Finstad et al., 2011).

2.1.4. Behaviour

Juvenile Atlantic salmon have long been regarded as sedentary and territorial animals (Kalleberg, 1958; Keenleyside, 1962; Saunders and Gee, 1964). As they grow, they may develop a clear social hierarchy where dominant fish select the most profitable foraging sites (Hughes and Dill, 1990). It was proposed that the juxtaposition of the foraging sites could create a fixed mosaic of adjacent territories (Jenkins, 1969; Dill, 1978). The size of each territory could vary with fish size (Grant and Kramer, 1990) and fish density (Dolinsek et al., 2007b) and the number of available territories could determine the carrying capacity of a particular reach (Grant and Kramer, 1990).

This view of a fixed mosaic of territories has, however, been revisited if not seriously questioned by subsequent studies. Pucket and Dill (1984) characterized fish behaviour in three categories: territorial fish, which defend the most profitable habitats, non-territorial fish, which appeared to use the lower quality habitats such as pools and margins, and ‘floaters’, which constantly moved in between the territories, mostly as a result of being chased. Using underwater cameras and PIT tagging to document the movements of fish, Armstrong et al. (1999) have observed in a relatively small and narrow enclosure (45 m^2, 1-3 m wide) that parr showed overlapping home ranges at high and low densities. They also reported a great variety in space use patterns. During the experiment, 80% of the fish established a home range within the first 8 days of the experiment (settlers), while the remaining never settled and continuously moved throughout the length of the enclosure (non settlers). While non settlers were expected at high densities where all profitable habitats were occupied, they were also observed at low density. Overlapping parr home ranges have been confirmed in two subsequent radio-telemetry studies of non-captive fish in large natural rivers, which suggests a more complex behaviour than the fixed mosaic of territories (Okland et al., 2004; Ovidio et al., 2007). These results also question the idea of parr habitat carrying capacity being limited by the number of territories (Okland et al., 2004).

For young fish, rapid growth is crucial to ensure survival and fitness (Hutchings and Jones, 1998; Letcher et al., 2002). Therefore, it is assumed that the selection of a home rock or territory will favour a net energy maximizing foraging strategy. Because of that, juvenile salmonids are a popular model for investigating 'central place foraging' decisions (Stephens and Krebs, 1986). By extension, because of their propensity to defend their territories from conspecifics, juvenile salmon behaviour is similar to a central-place territorial model (CPTM). In a recent study, Steingrímsson and Grant (2008) proposed a new model that takes into account the greater mobility of juvenile salmon. They observed YOY Atlantic salmon foraging from multiple central places (foraging stations) (Figure 2.5) rather than being stationary as described earlier (Kalleberg, 1958). This study is consistent with the majority of the most recent studies on fish movements that suggest that fish are more mobile than previously expected.

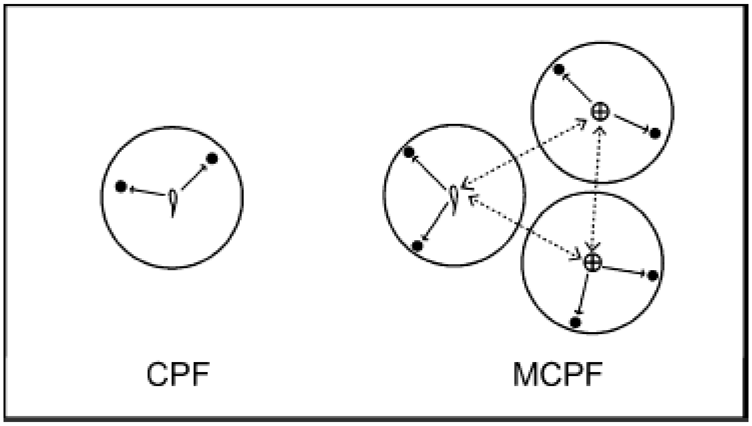

Figure 2.5 Schematic representation of space use of a central place forager. The central stations are represented by a fish. Solid circles and arrows reprensent foraging or aggressive

acts whereas arrows with dashed lines represent shift between stations (Steingrimmson and Grant, 2008).

Habitat selection theory suggests that dominant fish should select the most profitable foraging sites and defend them against intruders (Fausch, 1984). Indeed, several studies have shown that dominant juvenile salmonids grew faster than subordinates in laboratory experiments (Metcalfe, 1991) and in the wild (Hojesjo et al., 2002). Nevertheless, other studies have reported that dominant fish might not always grow faster than others (Martin-Smith and Armstrong, 2002; Harwood et al., 2003). This inconsistency could be due to the spatio-temporal variation of drifting invertebrates and fish densities. In reaches where food is consistently more abundant in a limited number of territories, dominant fish might grow faster. In contrast, when the food is more randomly distributed across the section by turbulent flow, a non territorial cruising foraging strategy could be more profitable in terms of growth (Leung et al., 2009). Further work is needed to clarify the relationship between behaviour and fitness of individual fish in natural environments.

2.2. The scales of habitat variability in streams and rivers

Fluvial habitats stretch over a continuous gradient from the scale of micropatches to the scale of watersheds (Maddock, 1999; Figure 2.6).

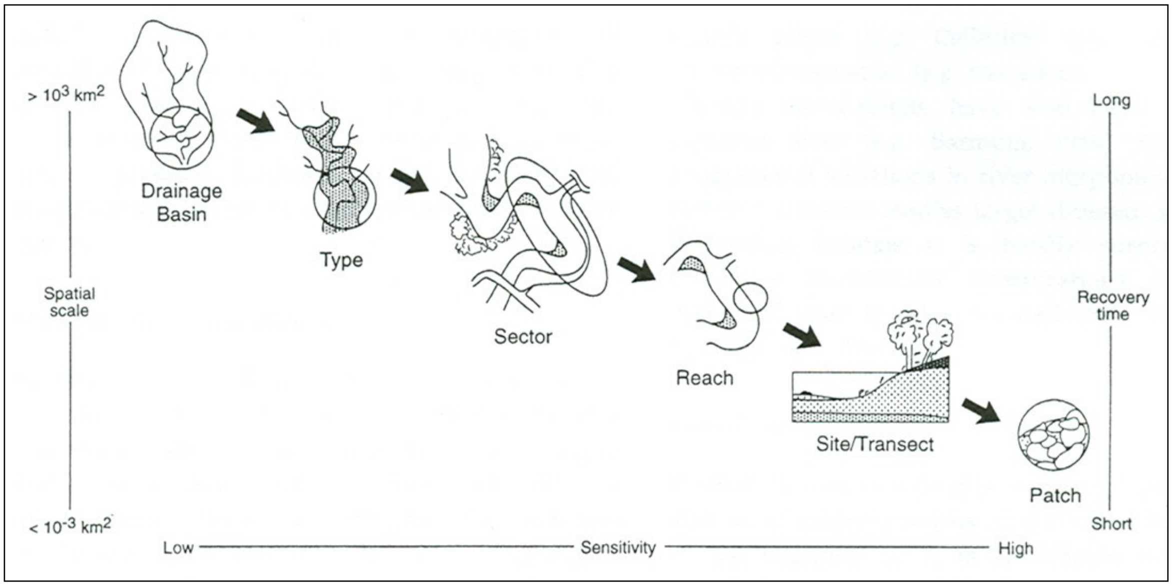

Figure 2.6 Functional classification of river habitats based on spatiotemporal hierarchy (Maddock, 1999, after Frissell *et al.* 1986; Petts, 1984).

As the scales are nested, heterogeneity at one scale results from the interaction occurring at a lower level (Poole, 2002; Figure 2.7).

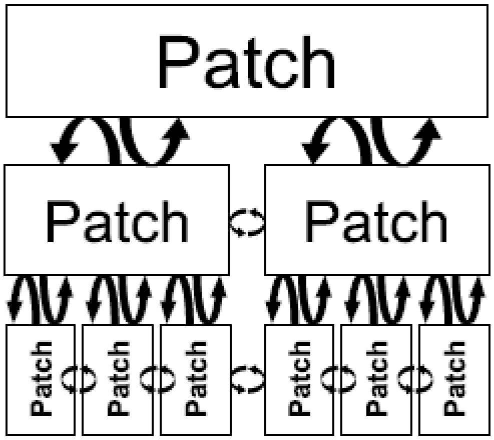

Figure 2.7 Hierarchical dynamics of river habitats. Each line represents a landscape scale divided into patches at different spatial scales. The arrows represent the processes that create interactions between the patches at the same scale and between the scales (Poole, 2002).

The hypothesis that the biotic structure of ecosystems is linked to habitat heterogeneity is regarded as one of the keystones in ecology. This hypothesis assumes that structurally complex habitats provide a greater number of niches and means of exploiting resources (Grace, 1991; Power, 1992). For juvenile salmonids, heterogeneity could mean a higher habitat density serving different life functions, such as resting, reproduction, feeding, etc. (Inoue and Nunokawa, 2002). Fish are affected by multiple interacting abiotic variables (

Figure 2.1). Physical habitat can be characterized by the combination of characteristics of the geomorphological properties of the river bed and of the properties of flow on a range of scales. Temperature might present a lower spatial variability in small streams than velocity and depth, but it has a major effect on fish metabolism and on habitat physical structure in the winter, when ice forms (Linnansaari and Cunjak, 2010).

2.2.1. The scales of bed morphology

The spatial scales of habitats are strongly controlled by bed geomorphology, which could be represented on a continuum. However, three scales of roughness are typically distinguished: the grain scale, the scale of sedimentary structures and the large scale form of the channel (i.e. morphological units; (Brayshaw et al., 1983; Robert, 1990). These scales of roughness are one of the major attributes of fish habitat. First, morphology indirectly influences fish habitat by interacting with other important habitat variables. At the reach scale, velocity at a given discharge is controlled by the morphological characteristics of the channel through hydraulic geometry (slope, width, height) (Leopold et al., 1964). At the larger scales, variation takes the form of pool and riffle sequences, which are important for fluvial fish (Inoue and Nunokawa, 2002), as they are responsible for the most important depth variation in the river.

Second, morphology directly influences parr habitat quality. For example, fine sediments can have a negative effect, by filling the interstices between large bed particles, thus blocking access to refuges. In contrast, the abundance of large cobbles and boulders provide home rocks (Coulombe-Pontbriand and Lapointe, 2004). At a larger scale, the organisation of sedimentary structures, such as lateral structures and pebble clusters, can also provide good quality habitats (Lacey and Roy, 2008b). Morphological features provide more stability to the bed, which is occasionally disorganised by important flood events through sediment transport. Following a flood, the river bed tends to reorganise itself (Lamarre and Roy, 2008).

2.2.2. The scales of flow variability

In fluvial environments, flow velocity is often regarded as the single most important variable, as it structures habitat and is generally the best predictor of fish distribution (Hart and Finelli, 1999). Flow variability can be observed at multiple temporal and spatial scales, ranging from millisecond to decades and from millimetres to tens of kilometres (Biggs et al., 2005).

Generally, the amplitude of fluctuations is scale dependent. This relation can be illustrated by the power spectrum of instantaneous velocity (Nikora, 2006; Figure 2.8A) and space (Figure 2.8B). By illustrating the entire range of flow variability on a continuum, this schematic spectrum provides a context to link turbulent flow variability to ecological processes and habitat selection. Nikora (2006) proposed to differentiate between two main scales of temporal flow variability: turbulence and hydrological.Turbulence can then be distinguished in three subscales, from micro (milliseconds) to macro (seconds) scales. Microturbulence is associated with energy dissipation at the molecular scale, whereas macro-turbulence is associated with large scale eddies that have periods of several seconds. In between, the mesoscale illustrates coherent flow structures (1-3 seconds) ubiquitous in river flow. At the hydrological scales, flow variability is related to discharge fluctuations. The stage variability is directly a function of the meteorological regime and typically presents strong seasonal patterns (intra-annual variability) in temperate regions. Inter-annual variability is also important, as low recurrence extreme floods can make drastic changes to fluvial habitats. Nikora (2006) has underlined the gap of knowledge of hydraulic variability occurring between the scales of flow variability associated with climate and the variability associated with turbulence (Figure 2.8A). Marquis and Roy (2011) have recently examined flow variability at the scales of hours and found large-scale flow pulsations that could correspond to this intermediate scale. However, this inherent property of the flow would have little effect on fish habitat selection. Spatial flow variability has also been divided in two major scales: turbulence and geomorphological (Nikora, 2006; Figure 2.8B).

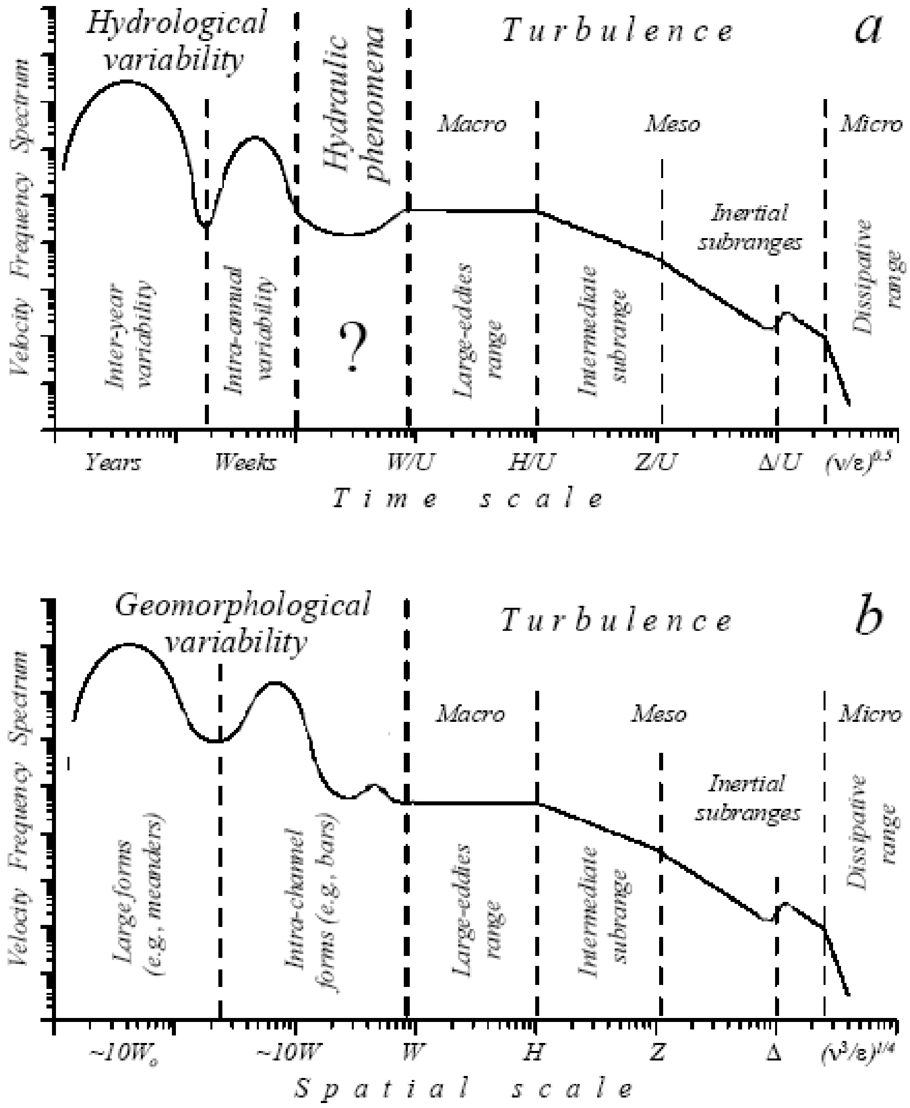

Figure 2.8 Schematic representation of a A) temporal and B) spatial velocity power spectrum in a gravel-bed river. W_o abd W and are channel width and channel depth respectively,H is mean flow depth, Z is distance from the bed and Δ is roughness size (Nikora, 2006).

The small-scale spatial patterns are induced by turbulence processes, whereas the larger scale coherent structures are associated with secondary circulation at the scale of channel width (e.g. meanders, recirculation zones in pool margins).

2.2.3. Small-scale river hydraulic variability

In gravel-bed rivers, where Atlantic salmon live during their freshwater life stages, flow is typically shallow and the relative submergence of clast (flow depth / roughness height) generally ranges from 10 to 20 during flood and around 5 at base flow (Hardy et al., 2009). In such shallow and rough flows, turbulence is ubiquitous (Carling, 1992). Turbulence is defined as an unstable state of a fluid, in which pressure and velocity varies in time and space. When a flow is turbulent, fluid particles move on irregular trajectories, causing an exchange of momentum from one particle to another (Bradshaw, 1985). Micro turbulence occurs just above the molecular scale (energy dissipation), while meso- and macro – turbulence take the form of coherent flow structures. Macroturbulence can be induced by roughness elements, but also take the form of ubiquitous alternating pulses of decelerating and accelerating flow.

Turbulent flow can be sampled using high frequency velocity probes such as an Acoustic Doppler velocimeter (ADV). This type of probe typically records high frequency (25 Hz) velocity time series (Figure 2.9) in three dimensions (u, v, w).

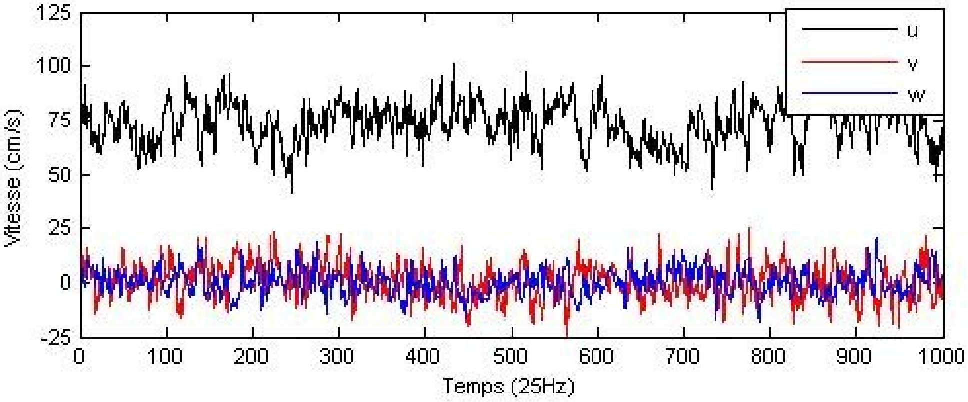

Figure 2.9 Example of an instantaneous flow velocity time series recorded with an ADV for a period of 1000 s at a frequency of 25 Hz. u (upper) represents downstream velocity fluctuations, v represents the lateral component and w the vertical component.

However, flow meters currently available on the market impose a tradeoff between sampling frequency and sampling volume. As a high sampling frequency is crucial to characterize turbulence (Buffin-Belanger and Roy, 2005), it is currently only possible to sample turbulent flow in a small volume at the time (1 cm3).

Turbulence can be characterized using two specific approaches (Roy et al., 2004). First, it can be described using the moments of the statistical distribution. The second approach consists of building metrics based on the duration and frequency of turbulent events at variable thresholds. By using spatial and temporal autocorrelation functions on a time series of instantaneous velocity measurements, researchers have been able to identify three types of turbulent structures in rivers: burst-sweeps motions, vortex shedding and large scale flow structures (Figure 2.10; Buffin-Bélanger and Roy, 2000). Bursting motions are thought to develop in the sub-viscous sublayer. The term bursting is part of a cycle of upward and downward fluid movements.

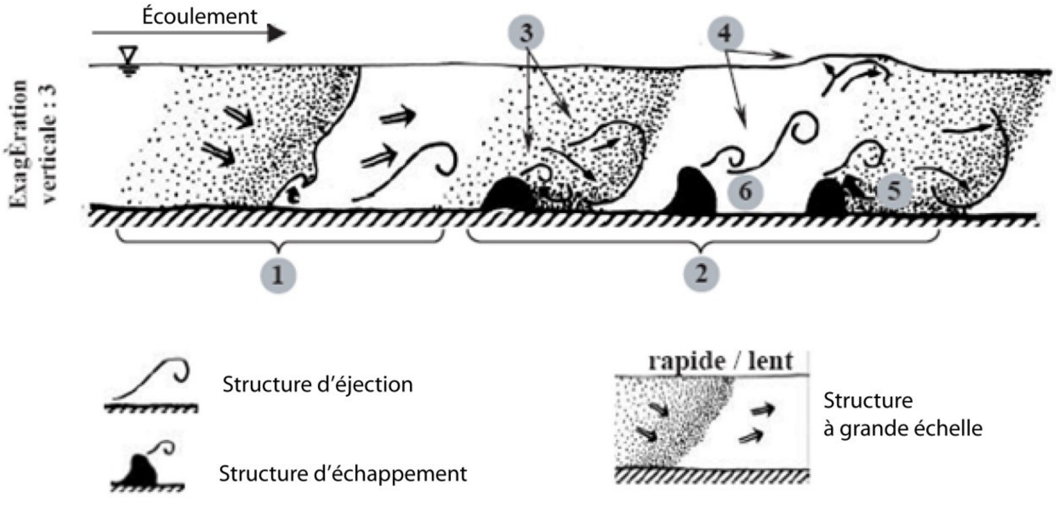

Figure 2.10 Schematic representations of the three types of turbulent flow structures in a straight section of a gravel-bed river. Vertical exaggeration: 3. Legend: Ejection: burst/

sweep cycle. Echappement : vortex shedding, structure à grande échelle : Large scale flow structure (Buffin-Bélanger et al. 2000)

The first part of the cycle consists of an ejection of a slow portion of fluid moving from the bed towards the surface, whereas the second part is a fast movement originating from the surface towards the bed (sweep).The duration of this ejection-sweep cycle is relatively short (<1 s) and has been observed on both smooth (Kline et al., 1967) and rough beds (Defina, 1996).

In contrast, a second type of structure is specifically associated with the presence of protruding roughness elements such as pebble clusters (Lacey and Roy, 2008a). Vortex shedding is created by the interaction between the recirculation zone located in the lee of an obstacle and the streamwise flow. Buffin-Belanger and Roy (1998) identified six distinct flow zones (Figure 2.11). First, flow accelerates over the pebble cluster. Immediately downstream from the obstacle, a recirculation zone is created by flow separation. The interaction between the recirculation zone and the streamwise flow induces vortex shedding. Then, downstream from the bed protuberance, at the reattachment point, the flow is slowed down and progressively elevates towards the surface (upwelling zone). The size and frequency of these structures is a function of flow velocity and obstacle size (Acarlar and Smith, 1987). These turbulent structures are of particular interest, as they occur specifically in the presence of large roughness elements, which serve as home rocks for parr. The third type of flow structures exist without the presence of large bed roughness elements (e.g. Kirkbride and Ferguson, 1995; Roy et al., 2004; Hardy et al., 2009). *Large scale flow structures* consist of a succession of high and low-speed oblique wedges that extend over the entire water column (Buffin-Belanger et al., 2000 Figure 2.10).

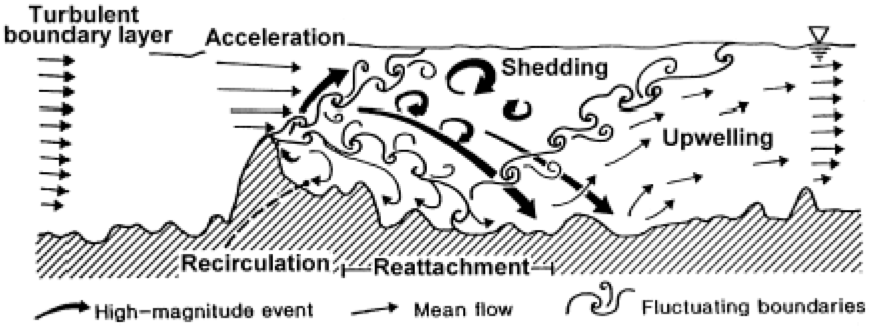

Figure 2.11 Six flow zones related to the presence of a pebble cluster in a gravel-bed river. Vortex shedding results from the interaction between the recirculation zone and the streamwise flow (Buffin-Bélanger et Roy, 1998).

As imagined by (Yalin, 1992), large scale flow structures alternate both laterally and longitudinally (Figure 2.12). The studies that have investigated large scale flow structures have reported spatial and temporal periodicities (Clifford et al., 1992; Lapointe, 1992), except for (Nikora et al., 1997) who suggested that coherent flow structures were randomly distributed in space and time. Using a detailed *in situ* characterisation of turbulent flow, Roy, et al (2004) have observed that large scale flow structures have an elongated shape, with a length ranging from 3 to 5 times the flow depth (Y) and a width ranging from 0.5Y to 1Y.

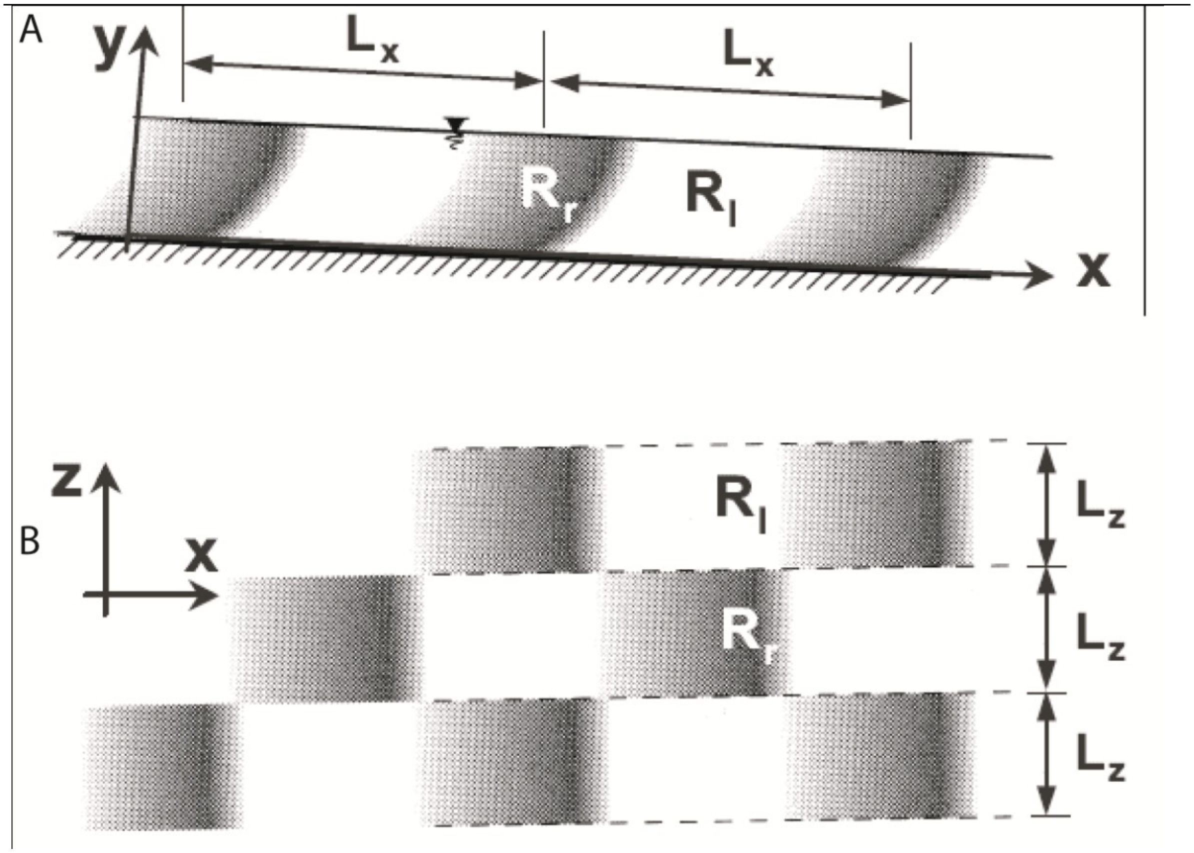

Figure 2.12 Snapshot representation of the spatial organisation of the succession of high and low-speed wedges. Lx: Length, Lz: Width, Ri:low speed, Rr: high speed. A Side view of the water column. B. Plan view of the river survace (Yalin, 1992).

Large scale turbulent flow structures interact with the other structure types. For example, high speed wedges could be triggering powerful ejections (megabursts) (Roy et al., 2004). Similarly, (Lawless and Robert, 2001a) suggested that the vorticity created upstream from a flow obstacle could be responsible for the generation of large turbulent flow structures. This hypothesis was quantitatively demonstrated in a recent study showing that large-scale flow structures owed their origin to bed-generated turbulence and were the result of flow-topography interactions in the near-bed region (Hardy et al., 2009).

Although the spatial distribution of turbulent flow properties at the micro-habitat scale (i.e. around a pebble cluster), have been previously described in detail (Brayshaw et al., 1983; Buffin-Belanger and Roy, 1998; Tritico and Hotchkiss, 2005; Lacey et al., 2007), only a few studies have examined larger scale flow properties, in morphological units and reaches. At the reach scale, Lamarre and Roy (2005) tested the hypothesis that the spatial patterns of turbulence properties were dominated by shedding induced by individual roughness elements. However, they only observed a very local effect of large bed roughness elements. This suggests that the flow properties were dominated by patterns induced by large scale turbulent flow structures that are mostly independent from protruding bed elements. Lacey and Roy (2008b) have also shown that pebble clusters have a very local effect on the structure of the turbulent flow. These results were confirmed in a similar study, suggesting that a large portion of turbulence spatial variability would be controlled by the gross morphology of the channel (Legleiter et al., 2007).

The morphological unit scale, such as pools and riffles may also influence the relative effect of bed roughness elements on flow. For example, Smith and Brannon (2007) observed that the presence of cover for fish (i.e. protruding roughness elements) changed the mean turbulent properties in the pools, but not in the riffles. The difference between the flow properties in various morphological units could be associated to the types of flow structures that are present (Harvey and Clifford, 2009). For instance, Clifford and French (1993) observed higher magnitude contributions for pool than riffle samples suggesting that these flow characteristics may vary between morphological units. This idea was explored further by Harvey and Clifford (2009), who observed that glides were the hydraulically simplest morphological unit in terms of hydraulic properties, possibly because of the flume-like shape of these channels and of the dominance of burst-sweep structures (Figure 2.13). Glides also have the least spatial heterogeneity. The riffle would be a more complex morphological unit, with a higher relative roughness and associated vortex shedding. Pools could be the most complex habitats, with flow dominated by a combination of burst-sweep structures and shedding from both smaller particles and from flow obstructions such as large woody debris. However, relative depth heterogeneity could be less important. However, these findings are based on only seven to ten flow measurements in four morphological units.

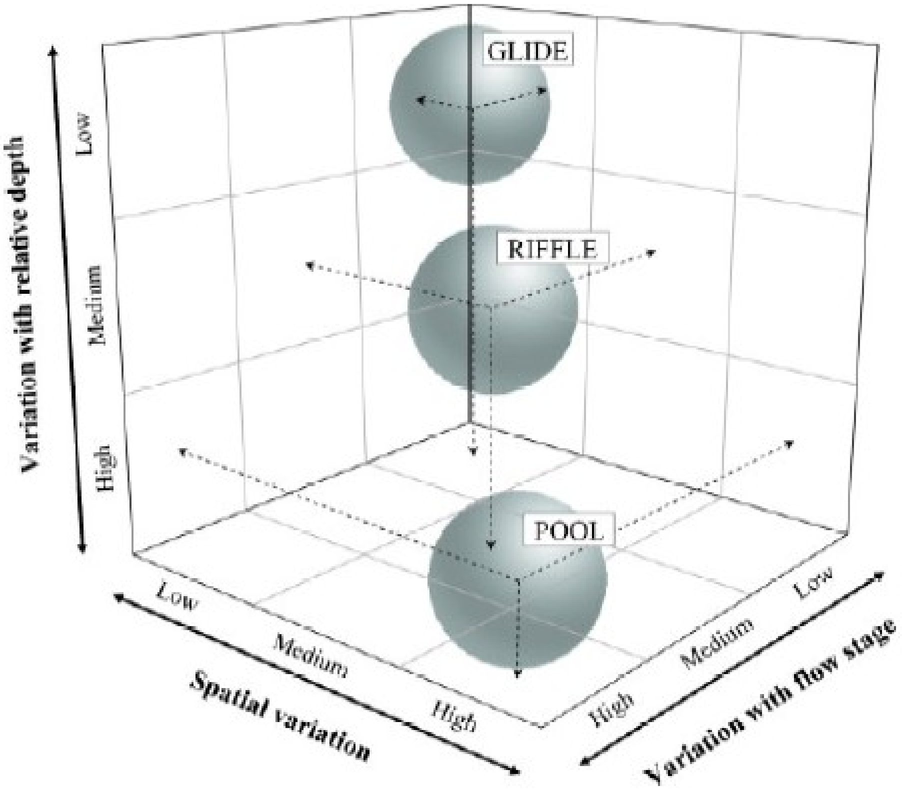

Figure 2.13 Conceptual diagram illustrating the levels of internal heterogeneity identified in glide, riffle and pool biotopes in terms of variation in hydraulic parameters spatially, with relative depth of the measurement and with flow stage (Harvey and Clifford, 2009)

Indeed, observations we made from more detailed surveys at base flow in pools and riffles suggest that the scales of spatial flow variability are not always consistent with morphological unit types (Roy et al., 2010), which suggests a need for a more detailed subtype habitat typology.

2.3. The effect of habitat on juvenile Atlantic salmon growth and survival

In rivers, the wide range of temporal and spatial scales structures the availability and the spatial arrangement of fish habitats. For individuals, the selection of microhabitat (flow velocity, depth, substrate and cover) and larger scale environmental fluctuations (i.e. flow stage and temperature) will influence directly and indirectly the parameters of the energy budget, thus affecting growth and survival of juvenile salmon (
Figure 2.1). Roughly, growth is determined by:

$$G = I - (M+L)$$

where G stands for growth, I is energy intake from food, M for metabolic costs, which include basal metabolic rates and metabolic costs of activity and L stands for energy losses, which include faecal and ureic wastes from ingested food (Kemp et al., 2006) . Habitat variability over a range of scales directly influences the energy budget through energy costs related to swimming (M) and indirectly the energy intake from food (I) by affecting the abundance and distribution of prey and by modulating the ability of juvenile to catch drifting prey.

2.3.1. Metabolic activity costs

For fish, locomotion is responsible for around 40% of the energy budget (Boisclair and Leggett, 1989). Fish swim to feed in the water column, move within and among foraging patches, and escape predators and competitors. Therefore, any habitat feature that influences the presence of predators or competitors can indirectly be expected to affect swimming costs (Finstad et al., 2011). More directly, flow velocity and temperature are the most important factors affecting swimming energy costs (Elliott, 1976). Numerous studies have quantified and modeled the effect of mean flow velocity on the energy costs of various fish species using swimming respirometry chambers (Hill and Grossman, 1993). Such models from laboratory experiments can be extrapolated to estimate the swimming costs under various flow stages (e.g. Nislow et al., 2000). Swimming energy costs can also be estimated indirectly using growth rates in experimental channels, by controlling food intake while varying flow discharge (Kemp et al., 2006). In experimental conditions, higher discharge reduces performance (i.e. growth and lipid content) (Kemp et al., 2006).

The variability at a smaller scale, turbulence, is an important factor influencing fish energy costs related to swimming. However, results from various studies appear mixed. On one hand, turbulence is viewed as a benefit. Fish can take direct advantage of turbulent structures by capturing the energy present in discrete vortices by adapting its mode of locomotion. Liao *et al.* (2003) showed that rainbow trout (*Oncorhynchus mykiss*) altered their swimming motions by deforming and translating their body in accordance with periodically alternating Karman gait vortices. The use of electromyogram sensors showed that trout muscle activity was decreased when swimming in the wake of demi cylinders in comparison with swimming in steady flow (Figure 2.14). Fish were using the momentum of vortices by swimming tightly in between them. However, this type of behaviour could be uncommon in natural environments, as a periodic Karman gait might not develop at a high flow Reynolds number. Furthermore, the ability of fish to capture the energy from the vortices depends on a specific ratio of vortex diameter to fish length, which might not be available in rivers (Liao, 2007).

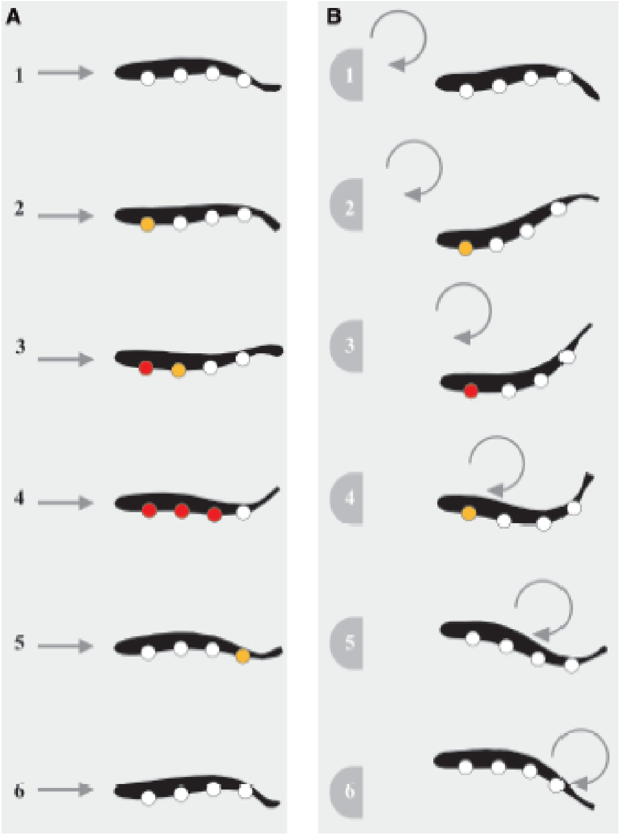

Figure 2.14 Time series illustrating that axial red muscle activity differs between trout swimming in free stream flow versus trout holding station behind a cylinder. Circles denote electrode positions with no (open), intermediate (orange), or high (red) muscle activity. (A) A propagating wave of muscle activity for a trout swimming in the free stream. (B) Muscle activity for a trout behind a D-section cylinder with estimated locations of a clockwise vortex (Liao et al., 2003)

In more ‘unpredictable’ flows, turbulence has been shown to impose an energetic constraint on fish by increasing the cost of locomotion. Using a respirometry technique on

Atlantic salmon parr, Enders et al. (2003) found that increasing turbulent intensity at a constant mean velocity was matched with an augmentation of the swimming costs.

The metabolic costs (oxygen consumption) of parr increased by 1.3 to 1.6 times when swimming in turbulent flow compared to steady flow (Figure 2.15). Similarly, Pavlov et al (2000) found that the maximum sustained swimming speed of fish decreased with turbulence intensity, suggesting an increase in swimming costs at higher turbulence. Moreover, in a study using underwater cameras in a natural stream, brook trout swimming kinematics (e.g. tail beat frequency, amplitude, etc.) was drastically different from previous laboratory experiments in steady flow (Mclaughlin and Noakes, 1998).

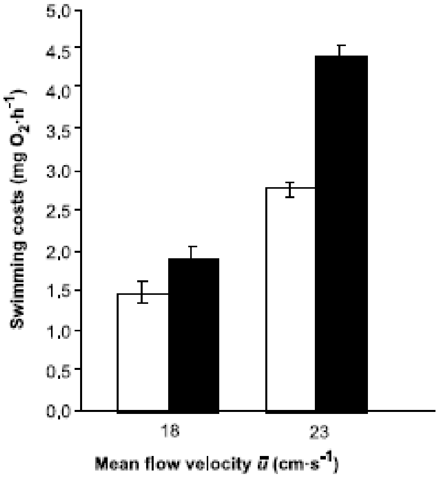

Figure 2.15 Energetic cost values of juvenile Atlantic salmon under four flow conditions combining (U) and turbulent intensity (RMS). Empty bars represent the energetic costs under low turbulence (5 cm/s) black bars reprensent high turbulence conditions (8 cm/s). Vertical lines represent standard errors (Enders *et al.* 2003)

The studies presented above illustrate well a duality between the vision of turbulence as a benefit and as a constraint for fish. Despite the lack of studies undertaken in the field, it appears that the effect of turbulence mostly depends on the type of turbulence being imposed on the fish. Besides the random versus predictable character of turbulent flow structures, the ratio of fish size to eddy size was suggested as a factor influencing whether or not turbulence could be 'felt' by a fish. Nikora et al. (2003) concluded that turbulence had no effect on time-to fatigue of *Galaxias maculates* in a circular flume. Biggs et al. (2005) speculated that turbulent eddies would have an effect on fish if they were 0.001 to 10 times a fish's body length. To test this hypothesis, Tritico and Cotel (2010) subjected fish (*Semotilus atromaculatus*) to horizontal and vertical eddies created by cylinders of various sizes. The authors observed that eddy size corresponding to 76% of fish body total length led to losses in postural control (spill) that coincided with a reduction in critical swimming speed. This reduction was of 10% and 22% in turbulent flows dominated by large vertical and horizontal eddies respectively (Figure 2.16).

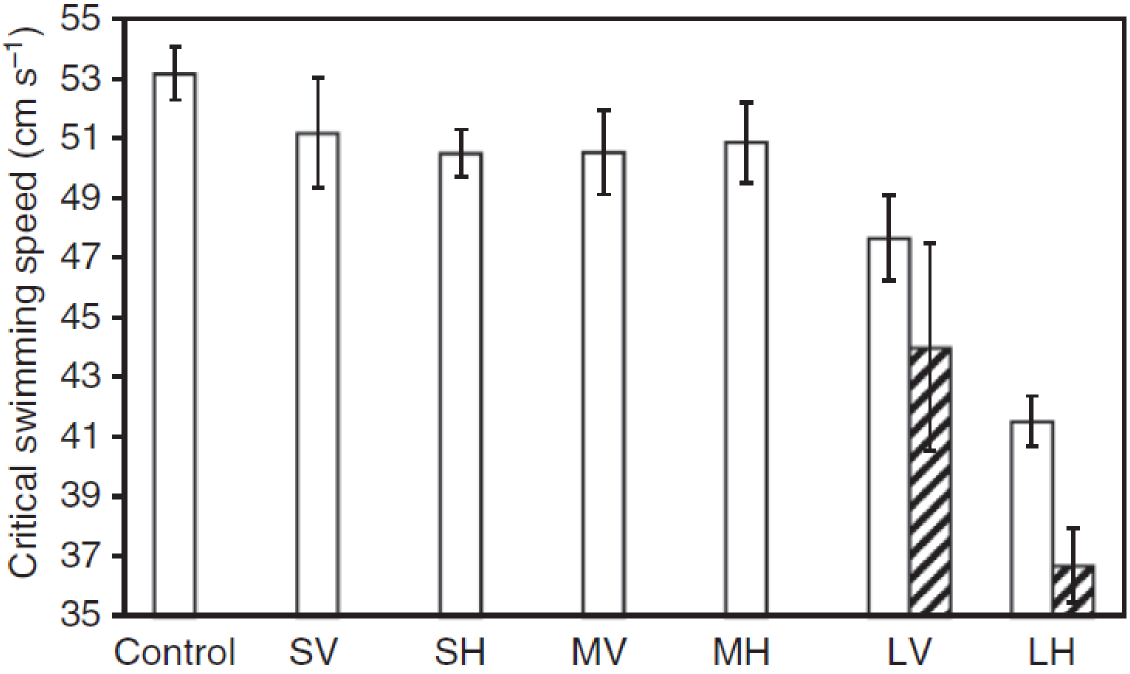

Figure 2.16 The critical swimming speed (open bars) and speed of first spill (hatched bars) varied across flow treatments. The bars represent the mean while the whiskers represent ±2 s.e.m. Spills (defined as head rotations followed by downstream body translation) were not observed for fish swimming in the control, small cylinder or medium cylinder array flow treatments. SV, MV, LV – small, medium and large vertical; SH, MH, LH – small, medium and large horizontal. (Tritico and Cotel, 2010)

Temperature also strongly influences metabolic costs (Elliott, 1976). The growth rate and food consumption are the highest between 16 and 20^{o}C (Elliott and Hurley, 1997), but growth can occur between 0 and and 25^{o}C (Jonsson et al., 2001). However, the energy costs related to swimming tend to increase with temperature. For instance, in a laboratory experiment, Enders *et al.* (2005a) estimated an increase of 12-18% in energy costs associated with an increase from 5 to 15 ^{o}C.

2.3.2. Prey availability and distribution

For juvenile salmonids, food resources are largely composed of downstream transport of invertebrates in the water column (Keeley and Grant, 1997; Hayes et al., 2000; Hayes et al., 2007). The spatial and temporal variation of drift therefore leads to changes in net energy intake and fish growth. Studies in controlled conditions showed that an increase in food abundance led to an increase in growth rates (Rosenfeld et al., 2005). Research on invertebrate drift in rivers has mainly focused on the temporal variation in relation to photoperiod, water temperature, predators and life-cycle stage (for a review, see Brittain and Eikeland, 1988). So far, the spatial variability of drift has received limited attention.

Drift is generally assumed to vary with mean flow velocity (Fausch, 1984). The rate of drifting prey increases with velocity and that beyond a threshold, benthic invertebrates can be dislodged by scouring (Mackay, 1992). The assumption that food availability increases with velocity is commonly used in energetic-based habitat models (Puckett and Dill, 1985). However, Leugn et al. (2009) recently questioned the link between drift and velocity in natural rivers. By performing a nested scale sampling of invertebrate drift, the authors did not find a significant relationship between drift concentration and velocity at the micro-habitat scale sampled within pools and riffles. These results suggest that small scale flow heterogeneity (short distance between low and high velocity) and turbulence may homogenize drift concentration. Nevertheless, at a larger spatial scale, they found that the drift concentration was higher in the riffles than in the pools. Besides providing energy intake for salmonids, resource distribution influences habitat selection (Giroux et al., 2000; Hayes et al., 2007). The ability of fish to predict the drift distribution within a stream could help it identify the most energetically profitable feeding habitat in a stream (Hansen and Closs, 2007). However, more research on resource distribution in relation to a spatially explicit characterization of turbulent flow in natural environment would most likely help to shed light on this problem and improve drift foraging models (Hayes et al., 2007).

2.3.3. Efficiency at catching drifting prey

For salmonids, velocity habitat selection is based on a tradeoff between food availability and swimming energy costs. A third factor complicates this tradeoff: the ability to catch prey decreases with flow velocity. With the increasing interest in drift foraging models (Hayes et al., 2007), several recent studies have explicitly addressed the question of prey capture probability in controlled laboratory settings (Piccolo et al., 2007; Piccolo et al., 2008a; b; Watz and Piccolo, 2011). Velocity may influence the distance at which the prey can be detected as well as the probability of capture (O'Brien et al. 2001). These data were recently confirmed for juvenile Coho salmon and steelhead using 3D video analysis. Piccolo et al. (2008b) reported a velocity-dependent decrease in capture probability (from 65% to 10%) with an increase of velocity from 0.29 to 0.61 $m \cdot s^{-1}$ (Figure 2.17). Velocity also had no effect on prey interception speed. Prey interceptions were consistently made at maximum sustainable speed (Vmax) for both salmonid species. The authors concluded that the reduction in prey capture probability was due to both a reduction in prey detection distance and to a decline in detection probability within the prey capture area (Figure 2.17). Nevertheless, our understanding of the effect of flow velocity on prey capture probability may be incomplete.

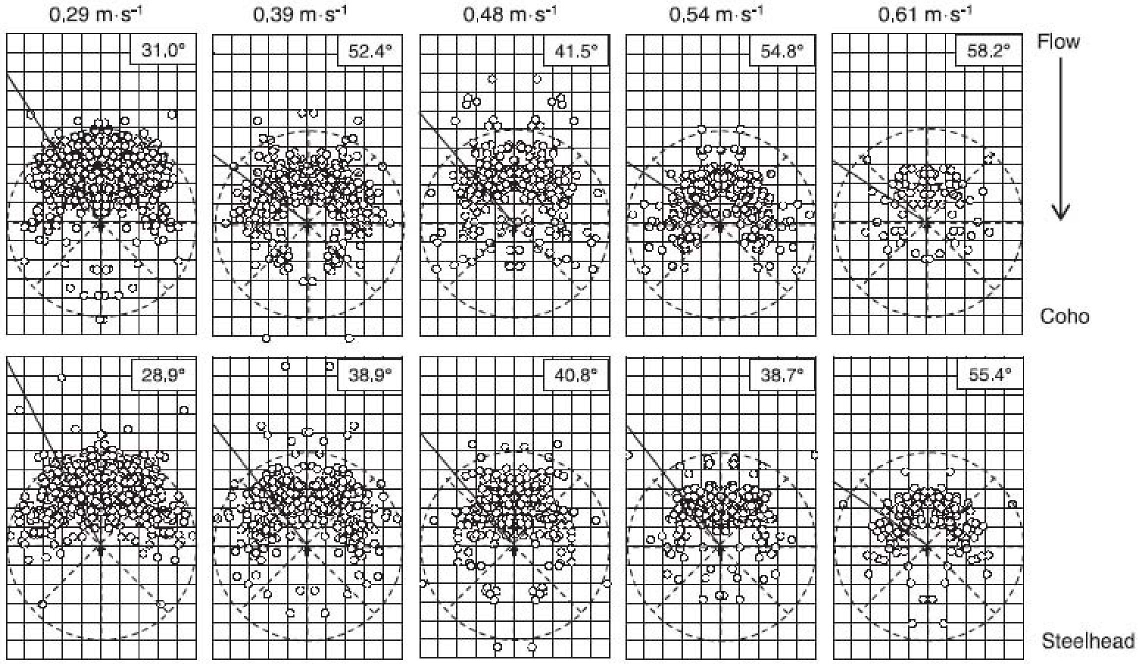

Figure 2.17 Top view of prey detection location for coho and steelhead at five different mean flow velocity. Data are pooled (N= 5 fish) for each species. Each circle represent a prey capture. Water flows from the top to the bottom of the figure. Solid lines are mean prey detection angles with 0^o upstream of fish and 180^o downstream (Piccolo et al. 2008a).

For the same reason that drifting prey are transported in an unpredictable manner throughout the water column by turbulent flow structures, they might also be harder to detect and catch as turbulence increases. Furthermore, as turbulence intensity is generally correlated with flow velocity, we hypothesize that a part of the decrease in capture efficiency might be attributed to turbulence. In the only study examining the effect of turbulence on fish feeding, Enders et al. (2005b) tested the hypothesis that Atlantic salmon parr could adjust their feeding behaviour in accordance with the occurrence of large-scale turbulent flow structures. They hypothesised that parr would initiate attacks on drifting invertebrates during low-speed wedges in order to minimize swimming energy expenditures. However, the results of the study did not confirm such behaviour. Interestingly, the parr initiated significantly fewer attacks when turbulent intensity was higher (Figure 2.18). However, this study was performed using a small number of individuals (n = 8), which makes it questionably representative. Moreover, it was not possible to distinguish between a decrease in the number of attacks related to a decrease in detection distance and a lack of prey.

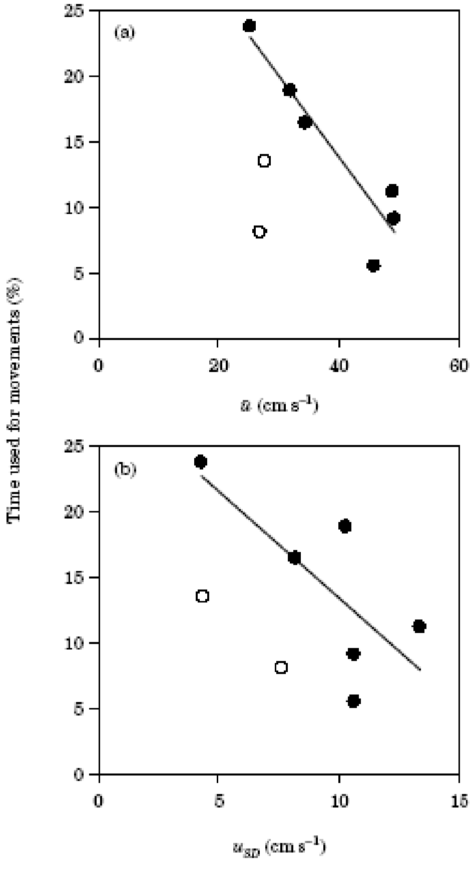

Figure 2.18 Proportion of time used by the fish for feeding movements in relation to a) mean flow velocity and b) standard deviation of mean flow velocity (i.e. turbulence). Measurements were taken during two sampling period 1 (empty) and 2 (full). The curves (only the data from sampling 2 were considered. (Enders et al. 2005b)

Nevertheless, Kemp et al. (2005) observed that the feeding rates of parr differed between 'complex' and 'simple' habitats in a laboratory flume. Although complexity here referred to the addition of boulders, it could indirectly be assumed to increase flow heterogeneity and turbulence. The authors suggested that flow complexity can result in costs for parr, which can be expected to offset to some extent the benefits related to flow refuges. It could also be hypothesized that turbulent flow mixing could decrease the ability of parr to detect and catch their prey.

Temperature is also associated with the ability of juvenile *Salmo trutta* to capture prey (Watz and Piccolo, 2011). The authors observed a decrease of prey capture probability from 96% to 53%, as temperature decreased from 14°C to 5.7°C (Figure 2.19). Conversely, capture maneuvre time and proportion of time resting on the substrate increased with decreasing temperature.

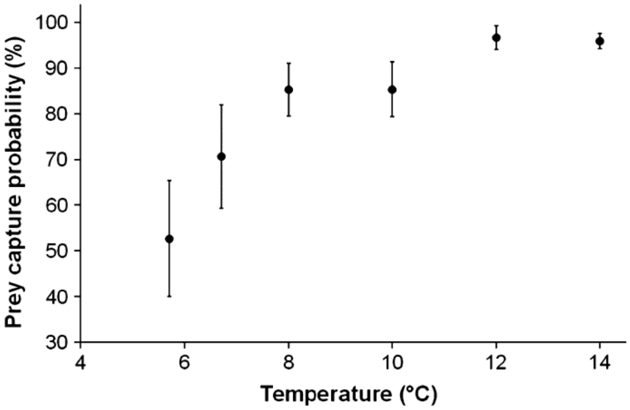

Figure 2.19 The mean (±SE) prey capture probabilities of drift-feeding juvenile brown trout foraging on chironomid larvae at different temperatures (Watz and Piccolo, 2011).

2.3.4. Predation risk

When juvenile salmon are not feeding, they tend to find shelter to minimize the risk of predation. Habitat spatial structure determines the availability of shelters, which take the form of interstices in the substrate. The presence of surface standing waves produced by turbulence can also provide shelter from predators. Illumination also plays a major role in modulating predation risk, as the fish become less visible at low light levels (Valdimarsson and Metcalfe, 1998). The minimization of the ratio between predation risk (μ) and growth rate (g) has been used to explain the switch between diurnal to nocturnal activity pattern in the winter, when food is scarcer and escape reactions are diminished in cold water (Fraser et al., 1993). Because of environmental fluctuations inducing changes on μ *and* g, plasticity in behaviour appears to be crucial.

2.4. Habitat variability and daily activity patterns

Early work described juvenile Atlantic salmon as a diurnal forager, feeding from spring to autumn by intercepting drifting prey from feeding stations where they maintain position just above the substrate (Kalleberg, 1958). Surveys carried out during the winter reported that few juvenile salmon could be seen during the day, with most finding shelter in the interstices of the substrate, which led to the conclusion that juveniles were dormant during winter (Rimmer et al., 1983). However, stomach content observations suggested that parr were feeding at night during the winter. This seasonal switch from diurnal to nocturnal activity was further documented by several field studies carried out mainly in eastern North America and Scandinavia, first for brown trout, *Salmo trutta* (Heggenes et al., 1993), then for Atlantic salmon (Fraser et al., 1995), as well as for other salmonid species (Table 2.2). In parallel, laboratory studies attempted to understand the mechanisms underlying such behavioural plasticity, by isolating concomitant biotic and abiotic interacting factors (Table 2.3).

Water temperature is thought to be the key factor responsible for the switch from diurnal to nocturnal activity, independently of photoperiod and season (Fraser et al., 1993). In the summer, when food is more abundant, juvenile salmon tend to maximize growth. As the water gets colder, below 8 to 12°C, parr escape reaction time drops, so they become nocturnal in order to avoid diurnal predators (Rimmer et al., 1985). However, because parr are visual predators, feeding efficiency also decreases when light level is low (Valdimarsson et al., 1997). Higher food availability at night might offset the decrease in efficiency (Fraser and Metcalfe, 1997), but it still remains unclear if nocturnal foraging leads to a decrease in growth in natural environments (Finstad et al., 2011). Nevertheless, in cold water, metabolic and digestion rates become lower, which could make a reduction of feeding rate less damaging in the winter (Fraser et al., 1993).

Gries et al. (1997) observed nocturnal behaviour in temperatures ranging from 13 to 23°C, with Post-YoY (PYoY: 1+ and up) exhibiting almost a strictly nocturnal behaviour. Further studies confirmed the occurrence of such nocturnal activity for PYOY and suggested a size-dependent tradeoff between growth and predation risk (Imre and Boisclair, 2004; Johnston et al., 2004; Breau et al., 2007). Larger fish with higher levels of accumulated fitness assets should be less willing to take risks to forage during the day. In contrast, YOY need to forage as much as possible, especially during the day when foraging efficiency is higher in order to survive the first months after emergence (Imre and Boisclair, 2004).

Table 2.2 Field studies examining activity patterns of juvenile salmonids showing differences between the summer and the winter and between young of the year (YOY) and older juveniles (PYoY). *Day*, *Night* and *both* indicate a predominance of nocturnal, diurnal activity and no particular activity pattern. * Survey carried out during the day only. (I) Individualy tagged

Author	year	Location	Species	Summer		Winter		Temperature	Other Factors	Observation
				YoY	PYoY	YoY	PYoY			
(Heggenes et al.)	1993	Norway	*Salmo trutta*				Night	1 to 15		Snorkelling count
(Fraser et al.)	1995	Norway	*Salmo salar*				Night	3.5 to 8.4		Snorkelling count
(Gries et al.)	1997	Vermont	*Salmo salar*	Both	Night			12 to 23		
(Gries and Juanes)	1998	Vermont	*Salmo salar*	Both*	Day*			17 to 23		Snorkelling count
(Amundsen et al.)	1999	Norway Finland	*Salmo salar*	Both	Night			8to15		Stomach content
(Amundsen et al.)	2000	Norway	*Salmo salar*		Both		Night	0 to 13		Stomach content
(Bremset)	2000	Norway	*Salmo salar* *Salmo trutta*		Day		Night	0 to 18		Snorkelling
(Bradford and Higgins)	2001	British Colombia	*O. mykiss* *O. tshawytscha*	Both	Day	Night	Night		Low Flow	Snorkelling count
			O. Mykiss *O. tshawytscha*	Night	Night	Night	Night		High Flow	
(Hiscock et al.)	2002	New-Foundlan	*Salmo salar*				Night	0 to 3		Radiotelemetry (I)
(Imre and Boisclair)	2004	Quebec	*Salmo salar*	Both	Night			14to21		Snorkelling count
(Johnston et al)	2004	Quebec	*Salmo salar*	Day	Night	Night	Night	0 to 14		Snorkelling count
(Breau et al)	2007	New Brunswick	*Salmo salar*	Day	Night			12 to 28		Snorkelling and marking (I)
(Cromwell and Kennedy)	2010	Idaho	*O. tshawytscha*	Day	Day			10.8	region1	Snorkelling obs
				Day	Both			15.6	region2	Snorkelling obs

Table 2.3 Laboratory studies examining the effect of various factors on the diel patterns of juvenile salmonids. *Day*, *Night* and *both* indicate a predominance of nocturnal, diurnal activity and no particular activity pattern. (+) or (-) indicates the direction of the main effect on activity pattern. *Twilight activity unchanged.

Authors	**Year**	**Species**	**Activity**		**Factor under observation**	**Method**	**Temp**	**Width**
			PYOY	**YoY**				
(Fraser et al.)	1993	*Salmo salar*	Both	Night		video observations		1
(Harwood et al.)	2002	*Salmo salar* *S. trutta*		Night	No interspecific competition	Visual, refuges	4.3 to 6.1	0.6
				Night (-)	Intersp. Comp.			
(Linnansaari *et al*.)	2008	*Salmo salar*		Night	Low ice thickness	PIT	0 to 5	0.95
				Night (-)	High ice thickness			
(Metcalfe *et al*.)	1999	*Salmo salar*	Night		Low food avail	PIT, refuges	5.5	1
			Night (+)		High food avail			
(Orpwood *et al*)	2006	*Salmo salar*	Both		Low food avail	PIT, refuges	12 to 21	1
			Night (+)		High food avail			
(Orpwood *et al.)*	2010	*Salmo salar*	Both	Both	No cover	PIT, refuges	5 to 18	0.6
			Night (+)	Night (+)	High cover avail			
			Both	Both	food availability			
(Blanchet et al.)	2008	*Salmo salar*		Day	No inter-sp. comp.	Visual (*in situ* cages)	15 to 20	0.6
		O. mykiss		Day (+)*	inter-sp. comp.			
(Reeves et al)	2011	*O. mykiss*	Night	Both	Moutain origin	Visual	2 to 16	0.76
			Both	Both	Coastal origin			

Continued...

Authors	Year	Species	Activity PYOY	Activity YoY	Factor under observation	Method	Temp	Width
(Alanara and Brannas)	1997	*O. mykiss*	Both		High food avail	PIT self feeders	10 to 14	0.5
			Day		Low food avail			
		S. alpinus	Day		High food avail			
			Day		Low food avail			
(Brannas and Alanara)	1997	*O. mykiss*	Dualism		Competition	PIT self feeders	10	0.5
			Dualism		No competition			
(Fraser et al)	1995	*Salmo salar*	Day	Night		Video	2 to 18.5	0.3
(Valdimarsson et al.)	1997	*Salmo salar*	Both	Night (+)	Early migrant	Visual	2 to 12	0.6
			Both	Night	Delayed migrant			
(Valdimarsson and Metcalfe)	1999	*Salmo salar*		Day	Early migrant	Visual	4.6	0.6
				Night	Delayed migrant			

Fish of the same species from different regions might also display different adaptative strategies. Reeves et al (2010) observed the diel pattern of 1+ steelhead trout from a mountainous region and from a coastal region on the West Coast of the United States. They found that mountain fish were diurnal during both summer and winter, whereas coastal fish switched to a nocturnal activity pattern in the winter. Then, in a laboratory stream, while fish from both regions were subjected to the same decreasing temperatures, the sheltering response was significantly greater for the fish originating from the mountain region than for fish from the coastal region. This suggests that the diel activity pattern is at least partly genetically based. Geographic provenance might therefore explain the divergence between previous studies. Some previous field studies, mostly carried out in Scandinavia have reported PYoY salmon being diurnal during the summer (Table 2; Amundsen et al., 2000; Bremset, 2000) while other studies, mostly performed on the East Coast of North America have found them diurnal (Amundsen et al., 1999; Imre and Boisclair, 2004; Johnston et al., 2004). The reason for such difference remains unclear. Perhaps the differences could be site specific or could be associated with differences in climate regimes, food or predator abundance. Furthermore, patterns might differ among salmonid species, as larger *Oncorhynchus tshawytscha* individuals also forage during both day and night during the summer, while smaller ones are strictly diurnal (Cromwell and Kennedy, 2011).

Laboratory experiments have also confirmed that food abundance can influence the daily activity pattern of juvenile salmonids (Metcalfe et al., 1999; Orpwood et al., 2006). Metcalfe et al. (1999) reported that a change in food density led to a parallel change in sheltering, with a 16% reduction of nocturnal foraging and 98% reduction of daytime foraging, thus minimizing the mortality risk to food gained ratio (Figure 2.20). Those results were confirmed using a similar experimental setup by Orpwood et al. (2006), who also reported that fish remained nocturnal at a high water temperature in high food density conditions rather than switching to diurnal foraging. When responding to variation in food availability, parr showed no differences in growth but rather modulated the amount of time they were active.

In a subsequent experiment testing the interaction between food supply and riparian cover availability, Orpwood et al. (2010) reported no effect of food availability on activity patterns. They attributed the increase of *Salmo salar* activity at night to a higher overhead cover availability.

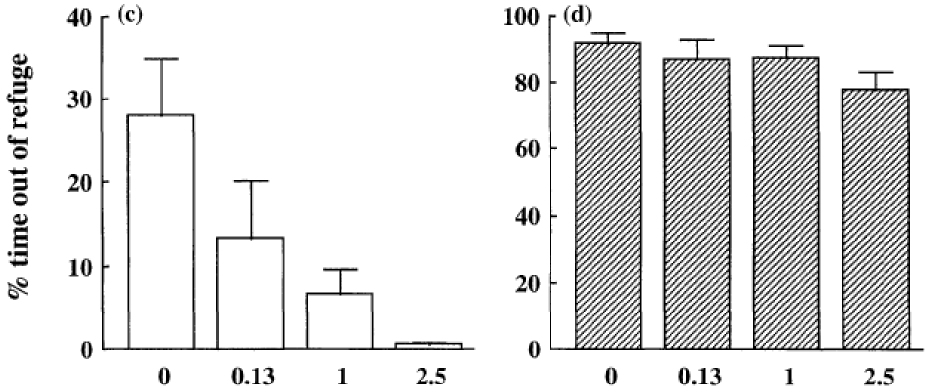

Figure 2.20 Diel activity patterns of juvenile salmon (n=12) in relation to food availability. Mean (+SE) % of time out of refuge during (left) each day and (right) each night. Food availability expressed as percentage of the wet weight of the fish provided per 24h. (Metcalfe et al. 1999).

These results were consistent in both seasons, although fish were generally more nocturnal in the winter. This finding seems counterintuitive, because the presence of cover should reduce predation risk and increase nocturnal foraging, which was thought to be less beneficial in terms of growth. However, the presence of cover and increased nocturnal activity did not induce differences in growth rates. Therefore, they concluded that the presence of overhead cover allowed fish to reduce foraging efforts during the most risky part of the diel cycle and to forage longer at night to compensate. The maintenance of growth rates during night foraging might be caused by a reduction in the resting metabolic rates due to reduced stress (Millidine et al., 2006) and by an associated reduction in food demands. In the winter, when riparian cover sometimes vanishes in northern regions, ice cover can provide protection against predation. In contrast with the previous study and using outdoor experimental channels, Linnansaari et al. (2008) found that even if juvenile salmon were predominantly nocturnal in the winter, diurnal activity significantly increased as surface ice became thicker. This suggests that μ/g may become slightly more favorable in these circumstances.

Besides temperature and cover, the effect of physical habitat on salmonid activity patterns has rarely been investigated. In a field study carried out in British Columbia, Bradford and Higgins (2001) compared the activity patterns of two genetically similar groups of *Oncorhynchus mykiss* and *O. tshawytscha* located in two reaches of a regulated river system with contrasting flow stages. In the reach with high flow, most fish were nocturnal year-round, whereas in the reach with low flow, during the summer an important fraction of the group of fish was active during daytime and switched to nocturnal activity in the winter. Despite the fact that flow stage was the main difference between the two study reaches, the high temporal variation in fish activity patterns between the surveys suggests that flow, which remained at a constant level, was not the sole factor in play. Bradford and Higgins (2001) suggested that the effect of flow stage on activity patterns required further investigation. They also hypothesized that activity patterns adopted by individuals are likely to be governed by proximate factors rather than large scale environmental variables. This idea was supported by Breau et al. (2007), who examined the variability of activity patterns of juvenile salmon at the level of individuals. Results revealed a high inter-individual variability in activity patterns and in how fish responded to water temperature and seasonality. This high variability among fish evolving in similar temperature and light conditions suggests that microhabitat use is likely to influence activity patterns. The inter-individual variability in fish activity patterns and how it relates to microhabitat use and environmental fluctuations deserves further study (Johansen et al., 2011).

2.5. Habitat variability and habitat selection and mobility

For juvenile salmonids, environmental fluctuations may lead to temporal variability of habitat suitability through changes in growth rates and susceptibility to predation. As presented in the previous section, modulating activity patterns constitutes one way of minimizing μ/g. In the same way, habitat selection and foraging modes may constitute a behavioural adaptation to environmental fluctuations. In turn, such changes in behaviour should also be seen in the mobility of individuals. Movements occur over a range of scales, from microhabitat foraging stations to mesohabitat movements between pools and riffles to large-scale movements between major habitats such as smaller stream to larger rivers or lakes. One of the key questions is whether fish are able to track the relative quality of adjacent habitat patches in the context where food availability or flow velocity can change over a short time scale (Martin-Smith and Armstrong, 2002). Becoming mobile and adopting a larger home range might be a way to adapt to such changes (Armstrong et al., 1999).

The effect of variation in discharge on wild fish habitat selection and growth has become an important centre of attention in the last decade, in the context of an increasing number of flow regulated streams. For instance, in Quebec, the number of harnessed rivers has increased by 400% in the last 15 years (BAPE, 2009). One of the main questions related to regulated flows is whether or not fish will adapt to flow changes by moving to lower velocity habitats as discharge increases in order to maintain a similar velocity range. To answer this question, Kemp et al. (2003) performed a laboratory experiment in which they made available both low and high velocity habitats with constant food availability. Their results showed that fish were not consistently selecting 'optimal' low flow habitats when flow stage was increased. However, in a later study, the authors observed a certain level of plasticity, as fish decreased their activity and mobility in high flows (Kemp et al., 2006). This result is consistent with the hypothesis that parr should forage over shorter distances, thereby reducing foraging costs per prey consumed (Kemp et al., 2006; Scruton et al., 2008). However, in natural streams, drifting prey availability tends to correlate positively with discharge (Rosenfeld et al., 2005), which explains why fish growth often increases with discharge (Nislow et al., 1999; Davidson et al., 2010; Teichert et al., 2010). Nevertheless, episodes of very high discharge can have a negative impact on growth (Arndt et al., 2002; Arnekleiv et al., 2006) and survival rates (Jensen and Johnsen, 1999), possibly because high flow events can induce a decrease of food availability, as invertebrates can experience increased mortality (Hildrew and Giller, 1994).

In the context of a sudden high discharge caused by hydropeaking, other authors have found no effect on habitat use and mobility in relation to discharge (Robertson et al., 2004; Heggenes et al., 2007). In contrast, Berland et al. (2004) reported restricted movements during stable low and high stage, but increased movement during decreasing flows. Flow discharge might also influence diel patterns in mobility, most likely by influencing activity patterns. For instance, Riley et al. (2009) observed greater mobility at night under summer low flow and greater by day under normal flow.

One possible reason explaining the differences in mobility observed across studies is the difference in reach-scale spatial heterogeneity of habitats. For instance, Heggenes et al. (2007) reported a higher mobility of brown trout in homogenized habitats than in heterogeneous natural ones. Similarly, a positive relationship between habitat heterogeneity (i.e. density of boulders) and density of juvenile Atlantic salmon has also been observed and associated with a decrease in visual isolation (Dolinsek et al., 2007a). However, flow heterogeneity could as well be important in increasing density, by providing drift availability close to flow refuge.

At the micro-habitat scale, several field and laboratory studies have indirectly shown that fish can reduce energy costs related to swimming by exploiting ‘unsteady flows behind instream structures or generated by the movements of other fish (Liao, 2007). This can be achieved in two ways. First, fish can benefit from the reduced mean flow velocity that is found behind flow obstacles. These habitats are commonly referred to as flow refuges. These areas are typically pebble clusters and boulders, but other natural and artificial structures such as logs, T-structures (Fausch, 1993), cones, half-spheres (Sutterlin and Waddy, 1975), cylinders (Webb, 1998) and prismoidal shapes (Smith et al., 2005) also have a great potential in attracting fish. However, despite the reduced velocity, these obstacles typically generate vortex shedding through flow separation and therefore can cause higher levels of turbulence intensity (Smith et al., 2006). This type of flow exploitation is the most documented in the literature, although quantitative characterization of turbulence is only rarely achieved.

To our knowledge, the only study to investigate habitat selection while explicitly taking into account and characterizing turbulence was performed in a 90 cm wide laboratory flume (Smith et al., 2006). A first set of experiments revealed that juvenile rainbow trout selected low turbulence micro-habitats across a range of mean flow velocities (Figure 2.21).

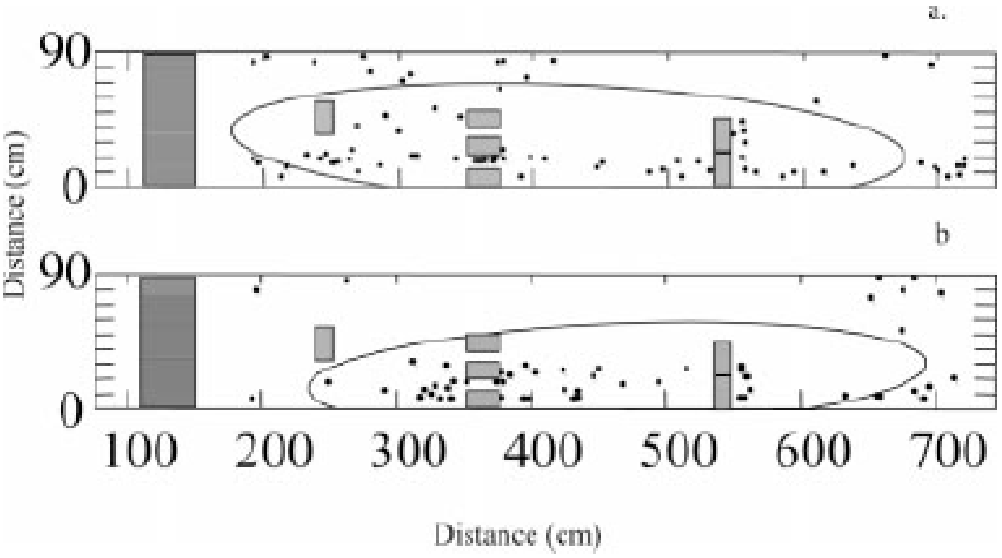

Figure 2.21 Fish position in the experimental flume (Black circles) at a discharge of a) 0.030 $m^3 \cdot s^{-1}$ and b) 0.111 $m^3 \cdot s^{-1.}$ Ellipses represents 65% fish presence confidence interval for each discharge treatment. Flow is from left to right (Smith et al. 2005).

They only occupied higher turbulence micro-habitats when excessive mean flow velocity was reached (Smith et al., 2005). In a second experiment, turbulent kinetic energy was able to better predict fish density across three discharge treatments than mean flow velocity

(Figure 2.22; Smith *et al.* (2006). Such a selection of low turbulence habitats could minimize swimming energy costs. However, flow variability in the flume was induced by the presence of prismatoidal shapes and movement was restricted. Therefore, it remains unclear if such behaviour would be adopted in natural environments. Nevertheless, there is accumulating evidence that fish select habitat not only based on average flow velocity, but also on the degree of spatio-temporal variability of the flow. Hence, previous studies made it clear that physical habitat models should try to incorporate turbulence metrics when estimating and modelling the cost of locomotion in turbulent flow (Liao, 2007; Smith and Brannon, 2007). This is especially relevant for mobile species. However, more work is needed to determine which flow feature is responsible for the increase in swimming costs. Furthermore, the effect of turbulence on prey capture efficiency remains to be explored.

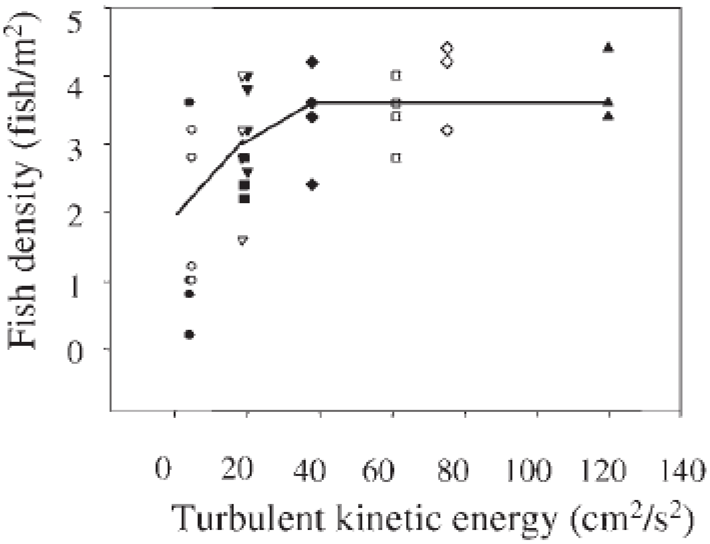

Figure 2.22 Relation between Turbulent kinetic energy (TKE) and fish density in a flume experiment in which juvenile rainbow trout were exposed to different discharges and covers. Closed circles, open circles and inverted closed triangles represent no cover, moderate cover, and full cover, respectively for a discharge of 0.06 m^3/s. Closed diamonds, open diamonds and closed triangles represent no cover, moderate cover, and full cover for a discharge of 0.06 m^3/s. (Smith et al. 2006)

Water temperature also has an important effect on habitat selection and behaviour. Across much of its geographic range, Atlantic salmon experience temperatures below optimal for more than half of the year. As temperature declines in the autumn and winter, juvenile salmon increase their use of cover and often remain sheltered in the interstices of the substrate, particularly during the day. Low temperature has the effect of lowering fish swimming capabilities (Webb, 1978) and ability to catch prey (Watz and Piccolo, 2011). However, studies carried out at the seasonal scale have provided contrasting results. Bremset et al. (2000) observed that Atlantic salmon parr activity decreased gradually along the season with temperature. However, recent telemetry studies have not confirmed these observations, as no difference in mobility between the summer and autumn was observed for *Salmo salar* (Okland et al., 2004) and *Salmo trutta* (Heggenes et al., 2007). Conversely, Riley et al. (2006) observed higher movement rates during the autumn than during the summer. The lack of concordance between activity levels and movements among studies suggests that temperature interacts in a complex manner with other abiotic and biotic factors to influence fish mobility. For example, spawning activity generally occurs at low temperatures and might generate higher mobility for precocious male parr (Riley et al., 2006).

The apparent contradictions in field research investigating fish behaviour in relation to environmental conditions suggest that these relationships are highly complex. A considerable portion of our knowledge of fish behaviour comes from laboratory studies allowing control on environmental variables. However, several aspects of behaviour have not been examined in the field. Furthermore, the often low sample sizes and differences in spatial and temporal scales of sampling make comparison between studies difficult. More studies adopting a holistic approach to studying fish behaviour might improve our knowledge of the effect of multiple fluctuating variables characterizing real habitat conditions.

Chapitre 3: Objectives and methodological approach

3.1. Problem statement and methodology

For juvenile salmonids, habitat selection affects the growth and mortality risk of individuals (Figure 3.1). Because the best feeding habitats are not always the safest, choosing where and when to forage, find shelter or move often implies a tradeoff (Figure 3.1). For individual fish, such decisions will affect patterns of habitat selection, diel activity and mobility, which represent important aspects of fish behaviour. Chapter 2 suggested that previous field studies have provided contrasting and somewhat inconsistent results in how fish respond to spatio-temporal changes in habitat.

In a broad perspective, the overall objective of this thesis is to quantify the linkages between habitat variability and juvenile salmon behaviour. Figure 3.1 illustrates the functional framework in which each habitat variable interacts to influence one or several components of the energy budget and/or the susceptibility to predation. In turn, combined with biotic processes (e.g. competition, prey population dynamics), these mechanisms will influence fish behaviour. As fluvial habitat varies over a range of spatial and temporal scales, fish may benefit from adopting a dynamic habitat selection strategy including adjusting diel activity and mobility patterns, both at the population and individual levels.

Specifically, three aspects of habitat and behaviour are addressed: 1) turbulence as a significant fish habitat variable; 2) spatial and temporal scales of habitat selection and 3) individual variation in fish behaviour (i.e. habitat selection, activity patterns and mobility).

In combination, these three themes forge specific research objectives that will be addressed in the following chapters.

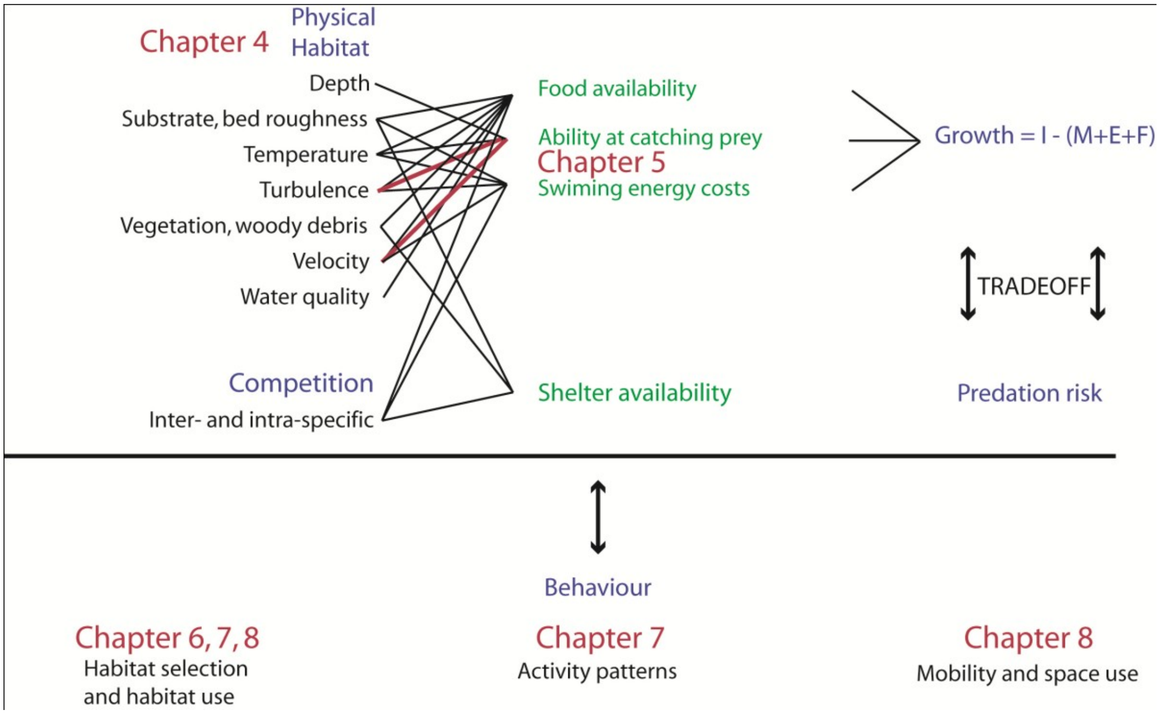

Figure 3.1 Functional framework within which each of the thesis chapters addresses specific aspects of juvenile salmon ecology. Physical habitat variables and competition affect the tradeoff between growth and predation risk through components of the energy budget. In turn, behaviour interacts with this tradeoff in order to maximize fitness. Chapter 4: The relations between standard habitat variables and turbulent properties. Chapter 5: The effect of turbulence on the ability at catching prey. Chapter 6: Multiscale habitat selection. Chapter 7 Individual variability in activity patterns and habitat use. Chapter 8: Individual variability in mobility. Interactions between physical habitat variables not shown.

3.1.1. Turbulence as a fish habitat variable

Several laboratory studies have revealed that flow turbulence affect swimming energy expenditures (Enders et al., 2003; Liao, 2007), maximum swimming speed (Pavlov et al., 2000), and posture stability (Tritico and Cotel, 2010), all of which might affect growth rates. Turbulent flow properties might also have an effect on fish density and habitat selection (Smith et al., 2005; Smith et al., 2006). Such results suggest that turbulence could improve physical habitat models (Liao, 2007; Smith and Brannon, 2007; Lacey et al., 2012), especially mechanistic individual-based models (Hayes et al., 2007). However, among the main challenges facing researchers investigating the effect of turbulence on ecological processes is the difficulty of isolating its effect from those of other intercorrelated variables commonly used in fish habitat models (mean flow velocity (U), depth (Y) and substrate size (D)) (Smith et al., 2005). While mean flow velocity powers turbulence intensity (Hardy et al., 2009), bed roughness elements also induce vortex shedding and increase turbulence (Lacey and Roy, 2008a). Furthermore, large-scale turbulent-flow structures tend to scale with flow depth (Roy et al., 2004). In spite of the observed correlation between mean flow velocity and turbulence intensity, the portion of turbulence variability explained by mean flow velocity, depth and bed roughness is currently not well known, as the relationships between these variables might change as a function of the spatial scale. By considering the links between standard habitat variables and turbulence, it might be possible to show that turbulence is a redundant descriptor of microhabitats. Moreover, the causal links between habitat variables and turbulent flow properties might be scale-dependant. At present, a detailed description of microflow hydraulics in fish habitat for different morphological units is still lacking.

With the increasing interest in individual-based bioenergetic models (Hayes et al., 2007; Jenkins and Keeley, 2010), the question of how habitat affects the efficiency of detecting and capturing prey has received more attention. A succession of laboratory experiments reveal that prey capture probability decreases as light intensity (Fraser and

Metcalfe, 1997) and temperature decrease (Watz and Piccolo, 2011) and as mean flow velocity (Piccolo et al., 2008b) and flow depth increase (Piccolo et al., 2007). In this perspective, by inducing unpredictable prey trajectories, turbulence might have a negative effect on prey detection and capture. This hypothesis is based on the observation that parr feeding rates are lower in 'complex' habitats (presumably more turbulent) than 'simple' habitats (Kemp et al., 2005). However, the effect of turbulence on the ability of prey capture remains to be explicitly addressed.

3.1.2. Spatial and temporal scales of habitat selection

The characterization of habitat across scales is of particular interest, as habitat heterogeneity has been shown to influence salmonid mobility and behaviour (Kemp et al., 2005; Dolinsek et al., 2007a; Dolinsek et al., 2007b; Heggenes et al., 2007). Characterizing habitat selection is routinely performed by snapshot surveys at the micro- or at the meso-habitat scale. Although juvenile salmonids have long been considered sedentary, recent studies have revealed that they are mobile and that they use a variety of habitats. From such observations, we hypothesize that parr might select their habitat based on the properties of microhabitat (foraging station), but also on the properties of the surrounding microhabitats, or even at the scale of morphological unit. Furthermore, the importance of different physical habitat variables might vary with the scale of observation. Moreover, in spite of our knowledge that some individuals use a variety of different habitats over a few days (Enders et al., 2009), the individual range of habitat use has not been explicitly quantified. Information about the range of habitats used by individuals as a function of the temporal scale might reveal an important aspect of fish habitat requirements.

3.1.3. Individual variability of behaviour

When examining fish behaviour in response to environmental fluctuations, my aim is to extract trends to describe the general behaviour of the population. Chapter 2 highlighted how recent literature based on experiments with marked fish tracked over time has provided contrasting results in how habitat selection, activity patterns and mobility respond to habitat fluctuations. The low number of marked individuals tracked in each study, combined with a high variability among individuals might be responsible for such variability among studies (Heggenes et al., 2007). In order to estimate an average population response from a number of individuals, it is crucial to quantify how much variability is attributed to individuals over time (Heggenes et al., 1999). However, our understanding of how individual behaviour varies with time in response to microhabitat use is incomplete.

3.2. Objectives

The overall objective of this thesis is to quantify the link between habitat variability and juvenile salmon behaviour. Through detailed field measurements incorporating a variety of sampling techniques and statistical analyses juvenile salmon behaviour and its natural habitat were examined to address the following objectives:

1. Quantify the causal links between standard habitat variables and flow turbulence at multiple scales in different morphological units of a gravel-bed river (Chapter 4).
2. Testing a new *in situ* experimental method to analyse the effect of turbulent flow properties on the prey capture efficiency and foraging behaviour of juvenile Atlantic salmon (Chapter 5).

3. Analyse the scale dependence of fish-habitat associations within a reach during the summer and autumn (Chapter 6).
4. Examine individual variation of seasonal and daily activity patterns and habitat use and their interaction (Chapter 7).
5. Investigate the individual variation in daily movement behaviour during the summer and autumn in relation to environmental fluctuations (Chapter8).

This thesis provides insights on the role of turbulence as an important fish habitat variable (Chapters 4, 5 and 6), the scales of habitat (Chapters 4 and 6) and individual variability of behaviour (Chapters 5, 7 and 8). The results will describe the impact of habitat variability on fish behaviour and will therefore be useful to elaborate appropriate strategies to manage salmon habitat.

3.3. General methodology

The main findings presented in this thesis are based on detailed field data sets on physical habitat and fish behaviour (Figure 3.2). To meet our five objectives, I carried out field work at two study sites which provided three distinct data sets. The first data set, presented in Chapter 4, is strictly composed of detailed hydraulic and geomorphic measurements in morphological units of a gravel-bed river. The second data set, analysed in Chapter 5, results from an experiment in which fish were submitted to four different velocity and turbulence treatments using an *in situ* portable flume. Data consist of underwater videos of fish drift feeding and of detailed hydraulic measurements.

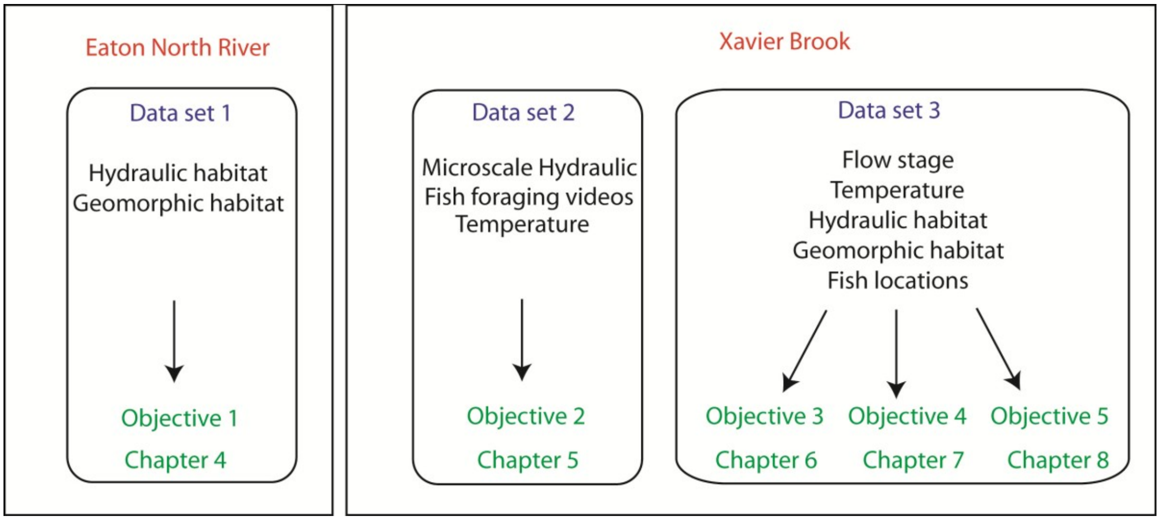

Figure 3.2 Data sets contents (rounded rectangles), obtained at two study sites (rectangles), used to address the objectives addressed in Chapters 4-8.

The third data set, the most extensive one, is analysed in Chapters 6, 7 and 8, includes high resolution fish tracking data over three months from July to November in a river reach. We acquired Data set 1 in the summer of 2005 on the Eaton North River, but the analysis presented in Chapter 4 was carried out in 2008. Data set 2 and 3 were obtained in 2009 and 2008, respectively, at two nearby locations on Xavier Brook, Saguenay. The Eaton North river (Study site 1) is located in the Eastern Townships, 30 km from Sherbrooke (Québec), whereas Xavier Brook (Study site 2) is situated at the boundary between Côte Nord and Saguenay region (Québec) (Figure 3.3). Although both sites are located far from each other, they present many similarities. Both sites are gravel-bed river reaches of approximately 15 m in width. Substrate is generally coarse, with the presence of boulders.

Figure 3.3 Location of the study sites in Southern Québec. Study site 1, Eaton North River is located in the Eastern Townships. Study site 2, Xavier Brook is located at the border between the Saguenay and the Côte Nord region.

Both rivers have been studied extensively in the last decade, Eaton North River for fluvial dynamics studies (Buffin-Belanger et al., 2000; Lacey and Roy, 2008a) and Xavier Brook for Atlantic salmon population dynamics research (Tucker and Rasmussen, 1999; Garant et al., 2000)

Experimental approach to the objectives

Throughout the thesis, research objectives and their associated methodology represent a gradient of increasing spatial and temporal scales in terms of extent and duration (Figure 3.4). This is matched with an increase in complexity in terms of concomitant variables at play (Figure 3.2).

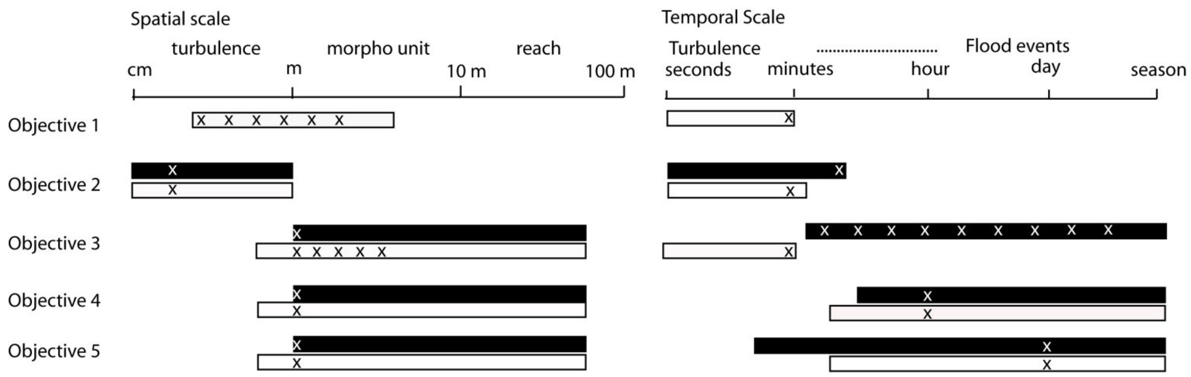

Figure 3.4 Range of scales covered by sampling protocol adopted for each objective. White bar represent physical habitat sampling and black bars fish sampling. Left side of bars are delimited by grain size (sampling frequency) and right side by extent/duration. “X” indicate the scales of the study (i.e. the window at which the data were averaged). For Objective 3, the temporal scale of minutes represent the duration of sampled velocity measurements. We assumed velocity to remain relatively constant during the study period, as periods of high flow events were removed from the analysis, which explains the lack of correspondence between the fish and the habitat sampling scales for Objective 3.

In Chapter 4, we examined the relationships between physical hydraulic properties in morphological units of a gravel-bed river. Without being carried out in a controlled environment, data were recorded in restricted areas (≈ 20 m^2) under constant flow stage. Flow velocity times series were sampled close to the bed on a systematic sampling grid. Although this approach does not explicitly control for covariates (e.g. discharge), the sampling methodology allowed me to isolate and describe a small temporal and spatial fraction of the fluvial system. In Chapter 5, we used an experimental approach to examine the effect of flow properties on drift feeding while controlling for food availability. Each fish was individually submitted to four 20-minute flow-turbulence treatments in a 1.2 m long tank. In contrast, in Chapters 6, 7 and 8, we recorded the locations of multiple interacting fish in a 65 m long reach of a natural gravel-bed river for three months. We adopted a more holistic approach as we monitored a natural and complex system without imposing any control on the numerous concomitant variables.

In this thesis, a field research approach in a natural river was considered most appropriate to provide a rich source of information on the relationship between individual behaviour and environmental variables. Our approach provides a realistic description of wild fish behaviour resulting from the interrelations in an inherently complex ecosystem. While experiments with captive fish might make it easier to discriminate the effect of a single environmental variable, artificial settings are rarely large enough to provide a free range to juvenile salmon, given their relatively high mobility (Okland *et al*. 2004, Ovidio et al. 2007). Furthermore, artificial environments and the absence of predators might influence fish behaviour, therefore limiting the representativeness of results. However, a field approach also involves greater difficulty in isolating the effect of one particular variable, considering the countless external variables that may be influencing the target behaviour under investigation. In this context, we combined both experimental (Chapter 6) and observational approaches (Chapter 7) to address the question of the effect of turbulence on fish.

Although the detailed methodology for each experiment is described in their respective chapters, we present here the critical methodological aspects of each of the three data sets used in the thesis. This presentation discussed the originality of the approach, the choice of study sites, the instrumentation and data analysis techniques.

3.3.1. Data set 1: The relationships between 'standard' habitat variables and turbulent properties in pools and riffles.

In Chapter 4, we describe the planimetric spatial structure of flow properties in two pools and two riffles of a gravel-bed river, the Eaton North River in the Eastern Townships (Figure 3.5). The main criteria while selecting the site were the availability of wadable and clearly defined morphological units typical of gravel-bed rivers and their accessibility. Flow velocity time series were sampled at 1932 locations using acoustic Doppler velocimeters (ADV) on a systematic sampling grid.

Figure 3.5 Study site 1. Eaton North river. Picture taken in August at low flow.

Velocity spatial coordinates as well as microtopographic measurements were recorded using a total station. From these data, standard habitat variables (mean flow velocity, depth and bed roughness) and 19 turbulent properties were estimated for each location using a variety of statistical analyses (parametric statistics, correlation, quadrant, U-level analyses).

We introduce bed roughness as a likely habitat feature to substitute for more classical measurements of substrate particle size. Bed roughness is quantified as the spatial standard deviation of bed elevation in a moving window. We suggest that bed roughness may give a better description of the availability of hydraulic refuge and shelter from predators that substrate size, as large particles are likely to be imbricated with protrusions not much higher than for smaller particles from the average bed level. These variables and the general field sampling protocol were used in each of the subsequent chapters of the thesis to characterize fish habitat.

To analyse spatial patterns of turbulence and their links with standard habitat variables, we used a combination of multivariate statistical techniques. Principal components of neighbour matrices (PCNM) and variation partitioning through a series of redundancy analysis (RDA) allowed extracting the main features of turbulent flow on a range of spatial scales. Chapter 4 confirms the potential of the PCNM technique to extract scale-dependent spatial patterns of turbulence, as previously shown by Lacey et al. (2007). To our knowledge, for its resolution and extent, Data set 1 represents the most detailed empirical description of *in situ* planimetric hydraulic spatial pattern available in the literature.

3.3.2. Data set 2: The effect of turbulent flow properties on prey detection and capture probability of juvenile salmon

In Chapter 5, we recorded underwater videos of drift feeding juvenile salmon under four velocity and turbulence treatments. Besides improving our knowledge of the effect of turbulence on feeding, we tested the potential of a portable flume to investigate *in situ* fish behaviour. Our portable flume was inspired by a flume designed by Vericat et al. (2007) that was used to study invertebrate drift (Gibbins et al., 2007; Gibbins et al., 2010) and sediment transport (Vericat et al., 2008). Slightly larger, our portable flume was composed of a straight section (observation section), preceded upstream by hinged doors (wings) (Figure 3.6).

Figure 3.6 Portable flume installed in the ‘open’ doors position in Xavier Brook, Saguenay in the summer 2009. Superimposed aluminum graduated frame holds acoustic Doppler velocimeters.

The portable flume was designed to be assembled and installed in the field, aligned parallel to the flow streamlines. When the wings are open, the water is funnelled inside the flume. Opening the wings larger than the width of the flume increased flow velocity in the observation section. A preliminary study carried out in the Eaton North River by Laurence

Chaput-Desrochers in the context of a BSc honor thesis quantified the turbulent properties in the flume under various settings. Results showed no obvious effect of the flume on turbulent properties while doors were kept parallel to the width of the flume. With doors open at 55°, an increase of up to 52% in mean streamwise flow velocity was estimated. However, the differences in velocity and turbulence properties between the treatments were lower in the experiment involving fish carried out in the Xavier Brook. This is most likely due to differences in the bed morphology of the site and to the addition of a supple net preventing fish from escaping the flume. In addition to adjusting the wing opening, we added bricks stacked in a pyramid shape at the entrance of the observation section. Each of 30 individual fish were submitted to a combination of turbulence and mean velocity levels and filmed for 20 minutes while being fed on brine shrimp distributed at a constant rate (Figure 3.7).

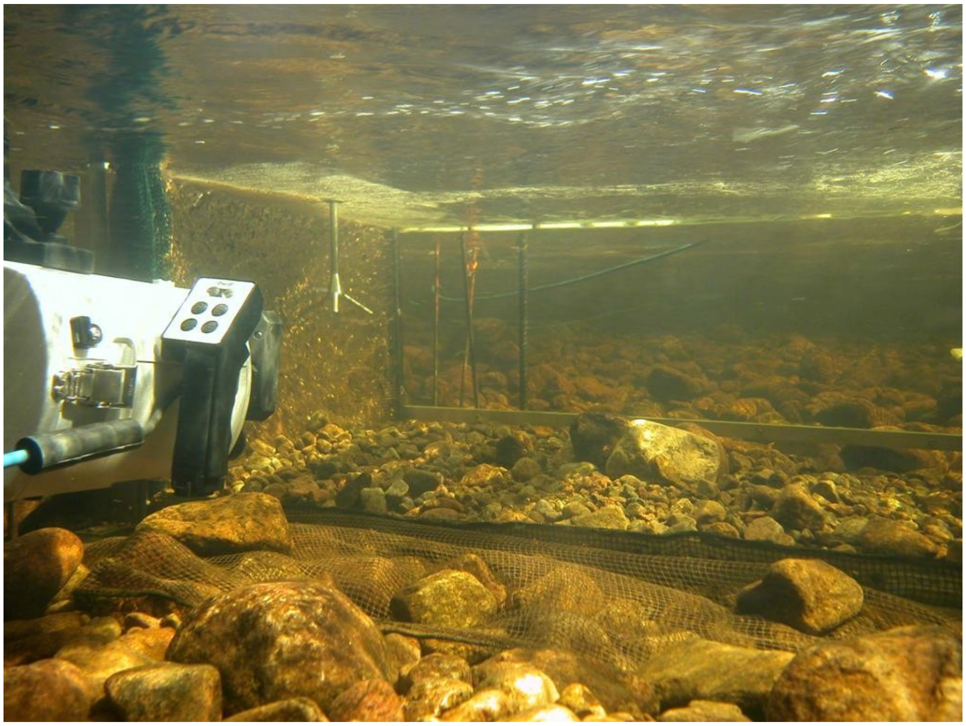

Figure 3.7 Underwater view of the observation section from camera side. Flow from right to left.

Foraging videos were then analysed to extract prey detection and capture probabilities as well as preferable focal positions in the four treatments. Data were analysed using repeated measures ANOVA. As one of the specific objectives of the experiment was to assess the usefulness of this new experimental flume, further methodological details such as issues with missing data and the limitations related to the use of the portable flume will be discussed in Chapter 5.

3.3.3. Data set 3: Individual fish positions and detailed habitat characterization of a reach

In a reach of Xavier Brook, we monitored the individual location of 66 juvenile salmon for three months using a flatbed passive integrated transponder antenna grid (Figure 3.8). The tracking system was composed of 149 antennas buried in the river bed.

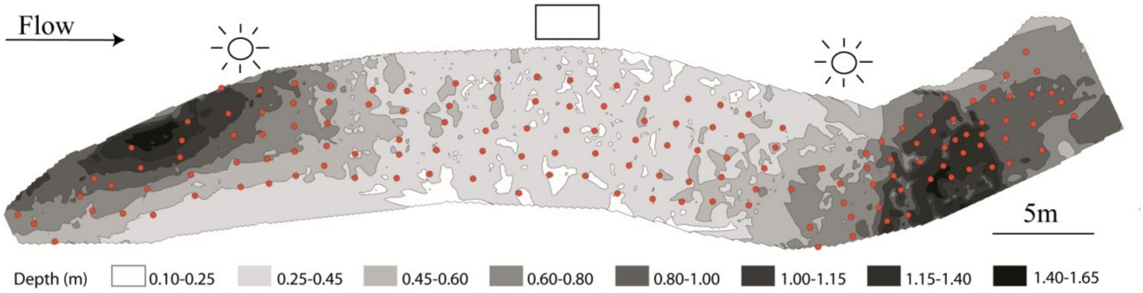

Figure 3.8 Study site, Xavier Brook, where a flatbed antenna grid buried in the river bed was installed. Red spots indicate antenna, suns indicate solar panel and rectangle the location of the controller. Contours illustrate bathymetry at median flow during the summer and autumn 2008.

The antennas were buried in the river bed using a small excavator at low flow along transects at equal distance to each other across the site (Figure 3.9). Each transect was connected to a tuning capacitor unit with 5 m long twin-axial wires (Figure 3.9) The tuning units are then connected to a CYTEC multiplexer, which is linked to a custom made controller (Technologie Aquartis). The controller contains a reader, a datalogger and a controller unit. Power was provided by two 110 W solar panels linked to rechargeable batteries. Antennas of the network were sequentially interrogated every 34s.

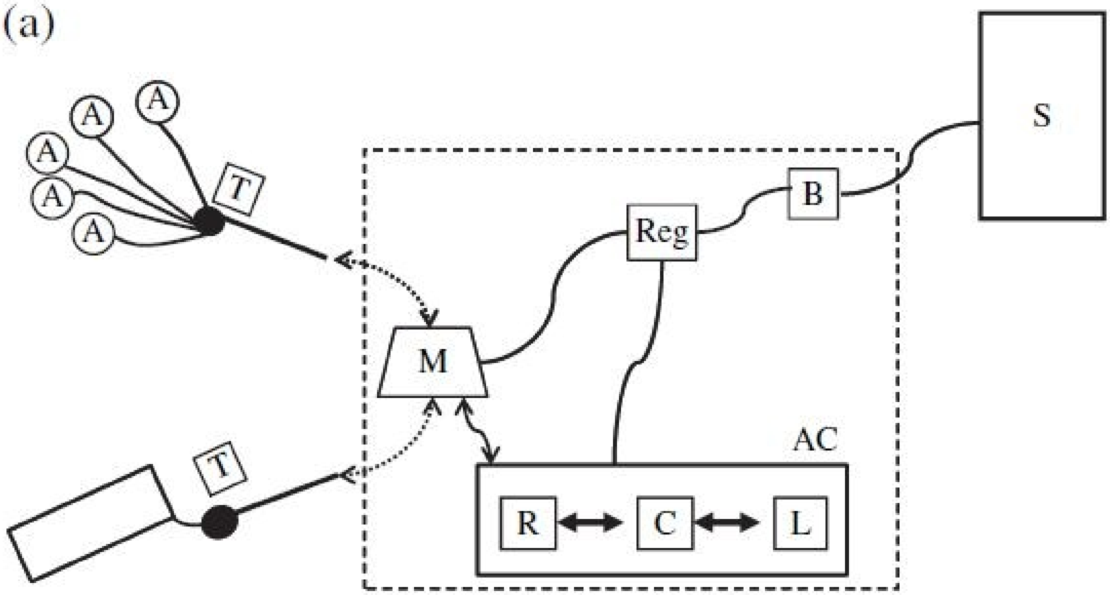

Figure 3.9 Schematic diagram of the electronic system. Round and rod antennas (A) are connected in groups of five to a tuning capacitor unit (T), while rectangular antennas have their own tuning units, which are in turn connected to a multiplexer (M). The multiplexer (M) is linked to the Aquartis controller (AC) containing an Aquartis controller (C), a TIRIS reader (R) and a datalogger (L). The multiplexer and the controller are both connected to a DC converter (Reg) linked to the batteries (B) and solar panels (S). The multiplexer, controller, DC converter and batteries are housed inside a shelter (dotted box). Arrows indicate the flux of information (Johnston et al. 2009)

The system was built and tested by Johnston et al. (2009) in the summer 2007 in Xavier Brook. The stream is a 4 km long second order tributary of the Sainte-Marguerite River. The study site is a 100 m long section located 425 m upstream from the confluence with the main river. The site comprises a main and a secondary channel separated by a central gravel bar (Figure 3.10). The site was chosen for its high habitat diversity, with a clear pool-riffle sequence providing important variation in flow depth, substrate and flow velocity. Furthermore, the site was inhabited by juvenile salmon and was accessible by road, with a nearby wildlife officer cabin. Prior to the installation, fish were caught by electrofishing and held in fish tanks, then released on site at the end of operation.

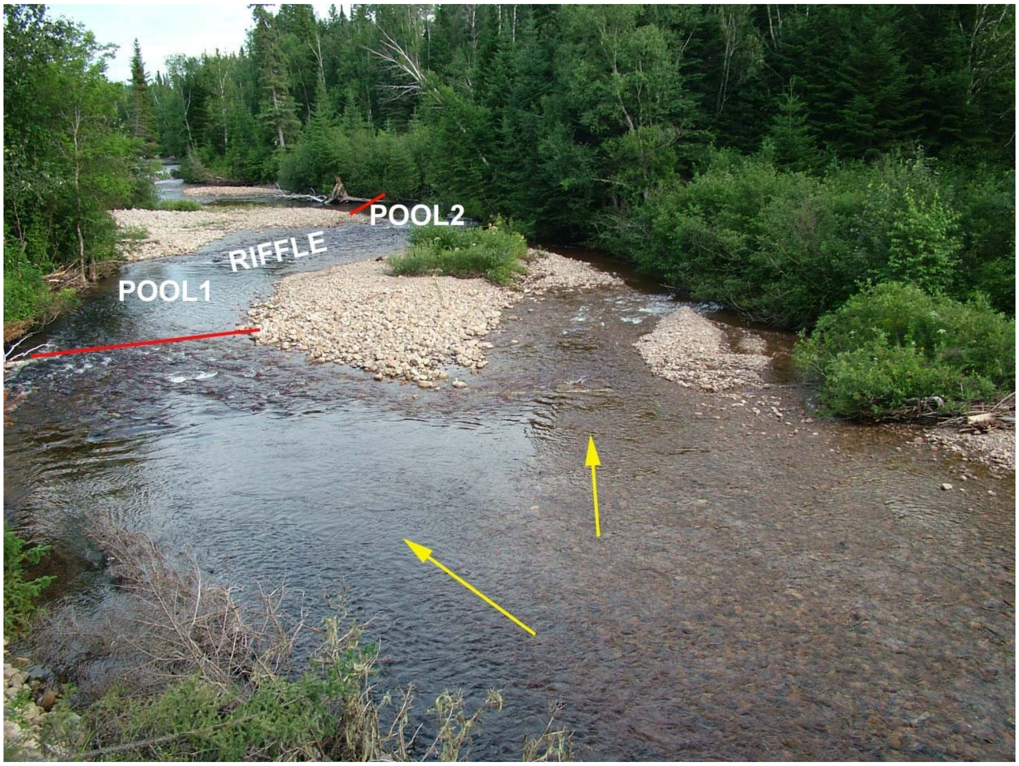

Figure 3.10 Reach of Xavier brook where the network of antennas was installed. Study site delimited by red lines. Yellow arrows indicate flow direction. Picture was taken in June at high flow.

Originally, the network consisted of 242 antennas, including 160 round antennae, 22 rectangle antennas and 60 ferrite rod antennas (Figure 3.11). In addition to the systematically displayed antenna grid, two other sets of five antennas were installed, one in the side channel and one downstream, where fish had been detected with portable PIT antennas (Figure 3.11). The rectangle antennas were 3 x 1 m in size and were built to achieve a larger detection range than the round antennas and were installed on the gravel bars. The ferrite rod antennas were designed for an easier installation in coarse substrate, but they also have a smaller detection range. However, preliminary tests in 2007 revealed interference problems.

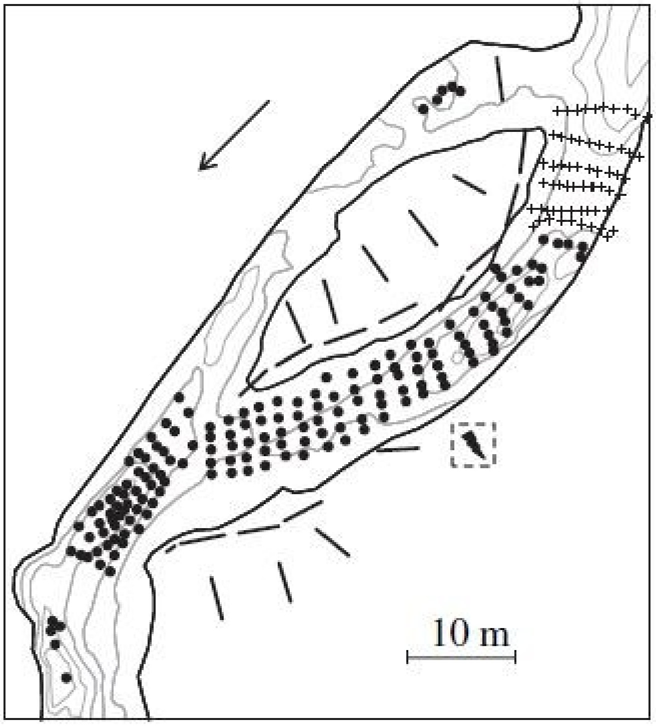

Figure 3.11 Network of antennas, as built by Johnston et al. (2009), with locations of the round antennas (black circles), rectangle antennas (lines) and rod antennas (cross). Arrow indicates flow direction. For the study included in this thesis, the round antennas downstream and in the side channel, the rectangle and the rod antennas were not used.

In November 2007, the controller and multiplexer were removed to a storage facility. In the spring 2008, prior to fish tagging, two consecutive high discharge events caused important damage to the system. A few wires were found severed and antennas exposed. Although we welded the wires and buried back some antennas, sixteen antennas were destroyed and could not be repaired, including the rectangular antennas, and those displayed in the side channel and in the downstream section. As a result, only the functional round antennae were activated and tested. This resulted in a final number of 144 working round antennas. Once the system was operational, the maintenance of the antenna grid was minimal. Every 5-7 days, data were downloaded and two of the batteries were changed for charged ones in order to avoid power failures.

The detection range of each antenna was about 1 m^2 and the detection field of the entire antenna grid covered 27% of the wetted area at base flow (Johnston et al., 2009). The antenna grid provided a large data set composed of a time series of approximately 100 000 fish detections. All antennas considered operational recorded fish positions during the study period. The number of fish detections decreased through time after the release of the first group of fish (n=42), likely caused by a high flood (stage over bankful) that occurred two days after the first release. Following this observation, we added the second group of fish at the end of August (n=23). All fish were tagged with passive integrated transponders (PIT). PIT tags allow the individual identification of fish, tagging of small fish, and tracking of fish for an indefinite period of time. A midventral incision was made 5.0 to 7.5 mm anterior to the pelvic girdle and a PIT tag was inserted and the incision was closed with surgical glue (Figure 3.12; Figure 3.13).

Previous studies have also achieved the monitoring of individual fish activity by tagging individuals with color markers and performing snorkelling observations (Breau et al., 2007) or by using portable passive integrated transponder (PIT) tracking (e.g. Johnston and Bergeron, 2010). These approaches can provide high spatial resolution data over a large spatial extent at the cost of being relatively invasive and time consuming, thus limiting the temporal frequency of surveys. In contrast, radio-telemetry can provide continuous data at a high temporal resolution over a very large spatial extent. The size of the spatial sampling units is generally large and do not provide details at the microhabitat scale, particularly when fish positions are recorded by fixed stations from the banks.

Figure 3.12 Passive integrated transponder (22mm)

Figure 3.13 Tagging a juvenile Atlantic salmon with a passive integrated transponder. Closing incision with surgical bound while irrigating gills with water.

Our antenna grid provided a small grain size, allowing the observation of microhabitat use ($1m^2$) and a resolution of 1 antenna per 5 m^2 over an extent of 65 m (Figure 3.14for sampling definitions). Combined with a high temporal frequency of detection (every 34 s), long duration (3 months), and a large number of individual fish (65) makes this network an ideal tool to investigate fish-habitat patterns across a range of scales (Johnston et al. 2009). In comparison with other networks of antennas previously used, our system provided us with the most extensive data set in terms of stream area covered in comparisons with published tracking systems (Armstrong et al., 1996; Castro-Santos et al., 1996; Burns et al., 1997; Greenberg and Giller, 2000; Riley et al., 2003). Furthermore, this is the first system to be used in a completely natural stream.

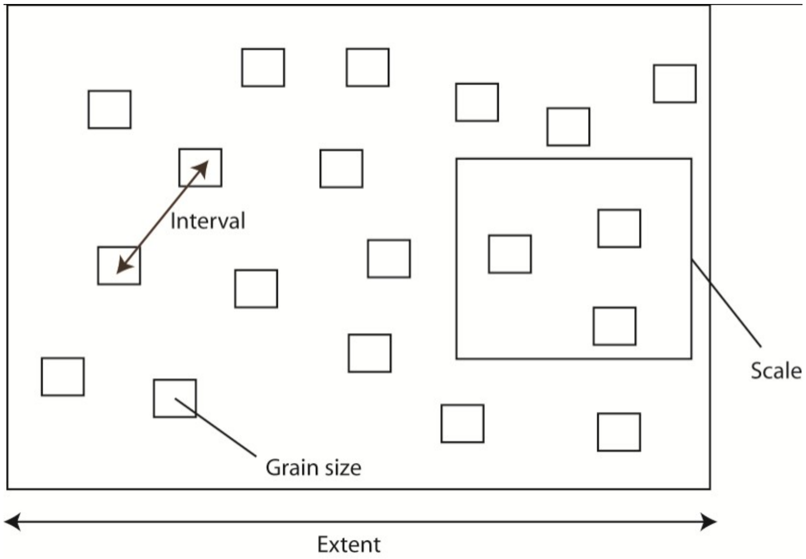

Figure 3.14 Definition of components of sampling design. Grain size, interval, extent and scale. Sampling units are represented as squares and the scale is defined as the area over which values are averaged (Legendre and Legendre, 1998).

The network of antenna did, however, present some limitations. First, inherent to the PIT technology is the incapacity to detect different tags located on the same antenna (Armstrong et al., 1996). Second, despite a relatively high spatial and temporal resolution, with each antenna being activated every 34s and 27% of the reach being covered by the detection range, we detected only a fraction of every fish's locations and the proportion of time detected varies per individual. Nevertheless, although not providing a systematic temporal sampling such as radio-telemetry, it is the only available tool to obtain automated and continuous microscale movements and microhabitat use of individuals.

In Chapter 5, juvenile salmon activity is compared between daily periods using individual detections based on the assumption that active fish are engaged in movement and are more likely to be detected by the antennas than sheltering fish. In parallel, when a fish was detected at a single antenna without interruption for 30 min, it was considered sheltering and was removed from the data set. While it is likely that some individuals were undetected by the system while being active, as the grid provided a systematic spatial sampling, we postulate this error to be a minor issue. This study represents the first assessment of individual parr activity pattern in the wild, with the exception of Breau et al. (2007), which observed 35 YOY and 8 parrs by snorkelling over two months during the day and evening in the summer.

The nature of the data guided and in some cases constrained certain choices in the data analysis. First, the high frequency of fish detection led to high temporal autocorrelation in the data. Therefore, for most analyses, a data repetition filter was applied, which involved removing all consecutive detections recorded at the same antenna within windows of 30 minutes or 1 hour. Furthermore, because of the longitudinal study design and the irregular sampling frequency (i.e. individuals being sometimes detected, sometimes not), we used methods for repeated measurements of the same individual over time (generalized linear models autoregressive covariance structure and generalized linear equations). While these statistical methods are useful for comparing different ‘treatments’, the visual representation of the data can represent a challenge.

Data set 3 also includes a detailed characterization of physical habitat, including downstream flow velocity, turbulence, depth and bed roughness, carried out using the methodology presented in Chapter 4. Using four ADVs, a flow velocity time series at median flow stage were measured throughout the reach, from which we estimated mean downstream velocity and turbulent kinetic energy. ADV measurements were recorded using a 1.5 X 1.5 m aluminum graduated support frame with transverse movable bars. Each corner of the frame was referenced using a total station and the individual location of each measurement was determined. A sampling density of three measurements$\cdot$m^{-2} was achieved, which is slightly below the sampling density of four measurement/m^2 considered optimal for a spatial interpolation with errors below 10% (Roy, 2006).

Flow velocity time series were measured at 10 cm above the bed, not often used in the fish literature (but see Enders et al., 2009). Therefore, it limits some direct comparisons with previously published velocity habitat use values. However, the decision to measure at this height rather than at the bottom (nose velocity) or at average column velocity (0.4Y) was made considering several sampling issues as well as ecological relevance. Sampling with ADVs over large areas in natural rivers is quite time consuming. Therefore, sampling efficiency is an important issue (Roy, 2006). Sampling at a single point thus allowed us to cover the extent of the study reach on three occasions while remaining at a constant flow stage. Measuring at 10 cm above the bed rather than bottom velocity with ADVs prevented excessive echo noise arising from the pulse signals rebounding off the river bed, which can be quite important and can lead to low quality data. Because of the high spatial heterogeneity of the bed substrate, morphology, and flow , accurately describing the bottom velocity in a large reach would require a too many measurements given currently available equipment. Furthermore, when active, Atlantic salmon parr spend most of their time foraging. Given the low velocity close to the bed, juvenile salmon spend an important part of their energy budget on burst movements in the water movement to catch prey (Hughes and Dill, 1990). In this regard, velocity at 10 cm above the bed might be more relevant than bottom velocities, which are generally low. Furthermore, the height of the flow measurements was within 0.2Y for 60% of the flow measurements. Our decision to sample at 10 cm is also justified by the fact that turbulence properties are relatively stable in the near-bed region, as the mean and turbulent flow properties show consistent patterns in spite of the bed heterogeneity (Buffin-Belanger and Roy, 1998). This inconsistency is caused by the dominance of energetic large scale turbulent flow structures that occupy the entire width of the water column (Roy et al., 2004). Furthermore, in a wide range of bed material, velocities measured at 10 cm above the bed have shown a great potential at estimating thresholds for particle movement and were favored over velocities measured 1.5, 2.5 or 5.0 cm above the bed. Therefore, it is assumed that measuring at 10 cm above the bed is an adequate method to capture the signature of near-bed turbulence as well as the large scale turbulent flow structures (Enders et al., 2009).

Considering the effort that necessitates the characterization of the flow field and the relatively low duration of flood events, it was not possible to repeat flow sampling at different flow levels. Therefore, in Chapters 5, 6 and 7, when we describe or compare habitat use, we excluded the periods of higher flow events (i.e. flow stage > 20 cm above minimum). We assumed that during minor flow stage fluctuations, at most locations, velocity ranks will remain relatively unchanged. Similarly, flow depth was not adjusted to fluctuations in flow stage. This choice was justified by the desire to interpret the selection of depth habitat relative to each other rather than to specific values of depth. For instance, while adjusting depth used with flow stage, use of high depth habitat could be associated with lower flow and glide use at higher flow. In contrast, by not adjusting depth to flow stage, we can more easily interpret depth use to specific locations in the reach.

Many studies have described habitat selection, activity patterns and mobility of juvenile salmon. However, few have explicitly addressed the questions of turbulence as a physical habitat variable, the scales of habitat selection and the importance of individual variability of behaviour in the wild. Our data set is among the most detailed description of physical hydraulic habitat and fish behaviour, allowing us to quantify juvenile salmon foraging behaviour, habitat selection, activity patterns and mobility.

3.4. Linking paragraph

As explored in Chapter 2, fluvial habitat is often characterized by highly turbulent flow conditions and these fluctuations affect fish energy costs and behaviour. Therefore, it was suggested that habitat models might benefit from including turbulence metrics. Considering that sampling turbulence in rivers is time consuming and that turbulent properties are correlated with “standard” fish habitat variables (mean flow velocity, substrate and depth), their addition to habitat models would likely contribute redundant information. However, to date, a detailed description of turbulence properties in morphological units is lacking. The aim of the following chapter[1] is to investigate the spatial structure of turbulent flow and the relationships between ‘standard’ habitat variables and turbulent flow properties in pools and riffles of a gravel-bed river at multiple spatial scales. We use a novel statistical technique to model the multivariate turbulence spatial structure and quantified its association with habitat variables. This chapter differs from the thesis chapters that follow, as it does not directly address the question of fish behaviour, but rather explores the complexity of the hydraulic habitat and discusses the relevance of turbulence as a fish habitat variable.

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[1] Roy, M. L., Roy, A. G. and P. Legendre. 2010. The relations between ‘standard’ habitat variables and turbulent flow at multiple scales in morphological units of a gravel-bed river. River Research and Applications, 26: 4, 439-455 (Reprinted with permission from John Wiley and Sons).

Chapitre 4: The relations between ‘standard’ fluvial habitat variables and turbulent flow at multiple scales in morphological units of a gravel-bed river

4.1. Abstract

Fluvial fish habitat is often characterized by highly turbulent flow conditions. Several laboratory experiments suggest that unpredictable turbulent fluctuations can increase the swimming energy costs of fish. At the scale of fish habitat models, it can be hypothesized that turbulence can be captured by the combined effects of the standard habitat variables: depth, velocity and substrate. However, recent studies conducted at the reach scale suggest that turbulent properties are more controlled by the large scale bed morphology than by individual roughness elements. In this study, we investigate the spatial structure of turbulent flow and the potential relationships between ‘standard’ habitat variables and turbulent flow properties in pools and riffles of a shallow gravel-bed river. The study explores these relations at multiple spatial scales. Mean turbulent properties and turbulent flow structures statistics were computed from 1932 near bed velocity time series sampled with acoustic Doppler velocimeters on a regular grid in four morphological units (two pools and two riffles) presenting a gradient of complexity. We used a novel multivariate variation partitioning analysis involving principal coordinates of neighbour matrices (PCNM) to partition turbulent flow properties into six significant spatial scales (VF: 0.35, F: 0.75, M: 1.25, L: 2, XL: 2.5 and XXL: 3 m). Between 45 and 70 % of the variance of the turbulent flow properties were explained by the spatial PCNM. In the four units, turbulent properties exhibited a spatial dependence across the entire range of scales.

However, the proportion of variation explained by the larger-scaled PCNMs was higher in the most homogeneous units. In general, the spatial dependence of turbulent flow was lower in the riffles than in the pools, where the mean flow velocity was slower. The capacity of 'standard' fish habitat variables to explain turbulent properties was relatively low, especially in the smaller scales, but varied greatly between the units. From a practical point of view, this level of complexity suggests that turbulence should be considered as a 'distinct' ecological variable within the range of spatial scales included in this study. Further research should attempt to link the spatial scales of turbulent flow variability to benthic organism patchiness and fish habitat use.

4.2. Introduction

Understanding the linkages between organisms and their hydraulic environment is a critical step in developing predictive models regarding the structure of fluvial ecosystems (Hart and Finelli, 1999). The temporal and spatial scales of flow variability are among the main drivers of numerous fluvial ecological processes (Biggs et al., 2005). One of the important issues in ecohydraulics research is to identify and match the proper fluvial scale to the ecological process or organism distribution of interest. At the smaller end of the spatio-temporal range of scales (mm to tens of meters, milliseconds to minutes), turbulent fluctuations can have direct and indirect effects on stream biota (Church, 2006). Three dimensional rapid and often extreme velocity fluctuations occur around the time-averaged velocity across multiple scales (Hart et al., 1996). Velocity fluctuations are organized into coherent turbulent flow structures occupying the entire water column (Buffin-Belanger et al., 2000). Turbulence has an effect on the physical processes near the bed and on the forces applied to the particles composing the substrate. Turbulent forces play a role in sediment transport and as a consequence on bed morphology (Best, 1993). Turbulence also affects directly or indirectly numerous ecological processes such as resource distribution (Frechette et al., 1989), nutrient absorption by periphyton (Labiod et al., 2007), predator-prey interactions (Weissburg and Zimmerfaust, 1993) and agglomeration and destruction of algae (Stoecker et al., 2006). It also provides hydraulic habitat diversity, which could increase the abundance of ecological niches. Recent studies have also revealed that turbulence could affect fish swimming energy costs (Enders et al., 2003; Liao et al., 2003), habitat selection (Smith et al., 2005; Cotel et al., 2006; Smith et al., 2006) and capture efficiency (Enders et al., 2005b). Turbulence can also provide a refuge from predators when water surface is skimming, affects water temperature and turbidity spatial distribution by means of mixing and could be responsible for the patchy distribution of benthic organisms (Quinn et al., 1996).

The effect of turbulence on the habitat selection of mobile organisms is complex as it may change as a function of scale and life functions (feeding, resting, reproduction, etc.). Moreover, the effect of turbulence at different scales could be conflicting. For example, a large scale mixing layer could provide a positive abundance of nutrients whereas small scale intense fluctuations could cause a dislodgment of the organism. Furthermore, the effect may change with the type of physical habitat. For example, Liao *et al.* (2003) showed that fish were able to change their manner of swimming in the presence of artificially created periodic vortices in order to decrease their muscle activity. The fish were then able to capture the energy from the vortices. In contrast, in more natural and unpredictable flows, fish exposed to higher levels of turbulence presented higher swimming energy expenditures (Enders et al. 2003). These results suggest that the ‘type’ of turbulence might influence fish energetics differently and may therefore affect habitat selection (Liao, 2007).

However, the question of the effect of turbulence on fish habitat use in rivers remains to be explored.

Among the main challenges facing researchers investigating the effect of turbulence on ecological processes is the difficulty to isolate the effect of turbulence from the effect of other intercorrelated variables such as standard habitat variables commonly used in fish habitat models (mean flow velocity (U), depth (Y) and substrate size (D)). That is caused by the complex relationships between the variables that may change as a function of spatial scales (Moir and Pasternack, 2008). The spatial distribution of turbulent flow properties at the micro-habitat scale around a pebble cluster or boulder have been previously described in detail (Brayshaw et al., 1983; Buffin-Belanger and Roy, 1998; Tritico and Hotchkiss, 2005; Lacey et al., 2007). Downstream from a roughness element, shedding motions are present, which results in an increase in turbulence intensity (Buffin-Belanger and Roy, 1998). However, the effect of roughness elements on flow properties is local. At the scale of pools and riffles, spatial patterns of turbulence properties might be controlled by the gross morphology rather than by individual boulders or pebble clusters (Lamarre and Roy, 2005; Legleiter et al., 2007). Smith and Brannon (2007) investigated the effect of roughness elements (fish cover habitats) on mean turbulent flow properties in riffles and pools and they observed a significant difference between turbulent kinetic energy in pools presenting abundant cover (high roughness) and without cover (low roughness) for juvenile salmonids. In contrast, they found no significant difference in the riffles, suggesting morphological units influence the effect of roughness on flow properties. Furthermore, at this scale, water depth could have an important effect on turbulence. For instance, the length and width of large-scale turbulent flow structures tend to scale with water depth (Roy et al., 2004).

Moreover, these structures are accountable for at least 50 % of the total turbulent kinetic energy (Liu et al., 2001). Mean flow velocity is often correlated with turbulent intensity and turbulent flow structure properties. As mean flow velocity increases, the standard deviation of the fluctuations (RMS_U) tends to increase (Nikora, 2006).

Several authors have proposed that future work should attempt to add turbulence metrics to fish hydraulic habitat models (Enders et al., 2003; Smith et al., 2006; Smith and Brannon, 2007). However, as turbulent properties might be strongly correlated to 'standard' habitat variables (velocity, depth and substrate size), their addition to habitat models may predominantly contribute redundant information. Furthermore, with the tools currently available, a characterization of turbulence in the field is costly and time-consuming. Nevertheless, habitats often present similar mean flow velocity and very different levels of turbulence. In spite of the observed correlation between mean flow velocity and turbulence intensity, the portion of turbulence variability explained by mean flow velocity, depth and bed roughness is currently not well known, as the relationships between the variables might change as a function of the spatial scale. Only a few studies have focused on the spatial distribution of turbulent flow properties at the scale of pools and riffles. To this date, we still lack a detailed description in different morphological contexts.

The quantification of the spatial structure of ecological processes and habitat is a major issue in current ecological studies. The spatial structure of ecological processes or species distribution can be attributed to two different sources. The first source is the inherent nature of the ecological process itself through the interrelations between neighbouring locations or individuals that cause autocorrelation (Legendre, 1993). A second source of spatial structuring on ecological processes is the effect of environmental or habitat variables which also have their own spatial structure. Similarly, environmental variables can also be structured by other environmental variables and the relationships between the variables can change according to the spatial scale at which it is described. For example, a relationship between two variables can be negative at a fine scale but positive at a larger scale. The most common tool used to describe the spatial structure of habitat and to link it to ecological processes is the combination of trend surface analysis with variation partitioning (Legendre and Legendre, 1998). Although this technique has proved successful and is widely used, trend-surface analysis only allows the broad-scale spatial variation to be modelled and does not allow to discriminate between the scales as the different polynomials are intercorrelated (Borcard and Legendre, 2002).

Borcard and Legendre (2002) have developed a spatial modelling method that provides a way to identify all the relevant spatial scales present in a data set: the principal component of neighbour matrices (PCNM). This statistical technique achieves a spectral decomposition of the spatial relationships among the sampling sites, creating variables that correspond to all the spatial scales that can be found. This technique is analogous to Fourrier analysis, but provides a broader range of signals and can be used with irregularly spaced data (Borcard and Legendre, 2002). PCNM is a flexible tool as opposed to autoregressive models or trend surface, as these spatial variables can easily be incorporated into regression or canonical analysis models (Dray et al., 2006). Although PCNM was designed to describe and explain the spatial structure of ecological data, it is applicable to several other domains. For instance, it has been used to partition the spatial variability of vertical turbulent flow field at the micro-scale around a pebble cluster in a gravel-bed river (Lacey et al., 2007).

In this study, we investigated the planimetric spatial structure of turbulent flow close to the bed obtained from a 1932 velocity measurements sampled across a systematic sampling grid in diverse morphological units. First, PCNM and canonical analysis were used to characterize the spatial structure of turbulent flow within two pools and two riffles in a shallow gravel-bed river. Then, we examined the potential causal relationships between standard habitat variables and turbulent flow properties at multiple scales using variation partitioning.

4.3. Materials and methods

4.3.1. Study site

Data were collected at the end of the summer 2004 on a section of the Eaton North river, located in the Eastern townships, approximately 200 km East of Montréal, Québec, Canada. At base flow, the width of the river ranged from 10 to 20 m and maximum flow depth was 1.5 m. The hydraulic and morphological properties of two pools and two riffles were characterized and mapped in detail. The four units presented a variety of morphological characteristics. Riffles 1 and 2 were located in a straight portion of the river, upstream from Pools 1 and 2. Pool 1 was located in a meander bend whereas Pool 2, a constriction pool maintained by a bedrock outcrop, was located 150 m downstream. The semi-alluvial context of Pool 2 created a much steeper slope than the other units (

Table 4.1). The units covered an area ranging from 20 to 32 m^2.

Table 4.1 Morphometric characteristics of the units and discharge at the time of flow velocity sampling. D50 : median size of B-axis (Wolman, 1954).

	Slope (%)	**D_{50}**	**Area (m^2)**	**Discharge (m^3/s)**
Riffle 1	0.2	55	20	2.49
Riffle 2	0.3	30	28	2.31
Pool 1	0.5	28	32	1.20
Pool 2	3	35	28	2.05

4.3.2. Field measurements

In every morphological unit, micro-topography and three-dimensional velocity measurements were sampled and mapped in detail. Micro-topography was mapped using a robotic total station (Trimble 5600DR) by combining a systematic sampling by transect to a characterization of individual roughness elements with a break of slope approach. We characterized each particle or cluster of particles that was protruding at a height of approximately 15 cm or higher above the mean bed level. The average sampling densities in the four morphological units ranged from 29 to 36 points/m^2. From the micro-topography surveys, digital elevation models (DEMs) were created using a triangle irregular network interpolation. The topography sampling and the river bed DEM were carried out according to guidelines outlined by Lamarre (2006).

A pressure transducer was used to record water level fluctuations and discharge was repeatedly estimated from cross-section flow measurement throughout the summer. Discharge values were then derived from a stage-discharge curve. The water level did not decrease by more than 1 cm within any of the flow measurement sessions. However, the discharge ranged from 1.2 to 2.5 m^3/s among the flow measurement sessions (

Table 4.1). Pool 2 was sampled at a discharge clearly lower than the three other units.

The 3-D instantaneous streamwise, lateral and vertical velocity fluctuations were recorded in each morphological unit using two acoustic Doppler velocimeters (*ADV*, *Sontek* ®, San Diego). Each ADV was attached to a steel wading rod. In the stream, the ADVs were moved between measurements and levelled by two operators. Velocities were measured at 10 cm above the bed. This height was determined in consideration of the difficulty to quickly obtain good quality data closer to the bed and the large number of samples required in this study. Flow velocity was sampled every 25 cm on a systematic sampling grid (16 points/m^2). Metal rods and strings were used as markers to build the sampling grid. The sampling grid of each unit was oriented towards the main downstream direction of flow. The locations close to the bank where depth was lower than 20 cm were not characterized because of the ADV instrumentation limitations.

4.3.3. Velocity time series quality check

Instantaneous velocities were recorded at each location for 80 s at 25 Hz, resulting in 2000 measurements per time series, which is higher than the optimal record length recommended by Buffin-Bélanger and Roy (2005) for similar experimental protocols. A total of 1932 velocity time series were recorded in the four units. Each time series was plotted and visually inspected for obvious anomalies. As suggested by Lane et al. (1998) and the manufacturer, series presenting a correlation signal lower than 70% were rejected from further analysis. Low correlation signals can be caused by insufficient seeding in the clear water and echo noise arising from the irregular river bed (Lacey and Roy, 2007). Doppler noise is inherent to all Doppler-based backscatter system signals. It is typically present over all frequencies. The removal of Doppler noise at high frequencies prevents biases in the estimation of turbulent statistics (Lane et al. 1998). Spectral analysis was also used as a means to detect noise in the data. The slope of the power spectra within the inertial subrange was compared to the Kolmogorov -5/3 law. The series that exhibited a flat slope were removed from further analysis. This process resulted in the rejection of one to two percent of the series. Similarly, spikes in the velocity times series associated with instantaneous low signal correlations were detected using a phase-space thresholding filter (Goring and Nikora, 2002). As spikes in the signals are extreme values, their presence can bias the estimation of turbulence statistics. To ensure data quality, data were removed when more than five percent of the series was modified by the filter. Less than one percent of the series were removed. Then, the data were filtered with a 3rd order Butterworth filter where the half frequency was equal to fD/2.93 = 4.1. For further details on this data quality check procedure, see Lacey and Roy (2007).

4.3.4. Habitat variables

From the microtopography and flow velocity data, 22 variables were created: three habitat variables (Table 4.2; variables 1 - 3) and 19 turbulent flow variables (variables 4 - 22). Mean flow velocity (U) was derived from the longitudinal component of ADV time series. Water depth (Y) was obtained by subtracting the water level from the bed elevation values and a bed roughness (k) index was computed by applying a standard deviation 65 X 65 cm moving window on the DEMs. Hence, a value is attributed to the center point of the window. A characterization of bed roughness based on bed elevation is less common in the

Variable	Description	Riffle 1		Riffle 2		Pool 1		Pool 2	
		Avg	Std	Avg	Std	Avg	Std	Avg	Std
Spatial									
(x,y) (m)	Geographic coordinates (x,y)								
PCNMs	Spatial Eigenvectors								
Habitat									
1- U ($cm \cdot s^{-1}$)	Mean streamwise velocity	77.16	8.39	64.07	16.01	27.47	10.36	22.84	13.03
2- Y (m)	Depth	0.44	0.03	0.38	0.03	0.37	0.07	0.64	0.12
3- k (m)	Roughness index	0.02	0.01	0.03	0.01	0.03	0.02	0.05	0.02
Turbulence									
4- RMS_U (cm/s)	Root mean square streamwise velocity	11.64	1.64	12.98	2.97	6.93	1.63	7.99	2.72
5- RMS_V (m/s)	Root mean square – lateral	8.56	0.99	9.94	2.09	5.72	1.33	7.71	2.36
6- RMS_W (m/s)	Root mean square – streamwise	5.93	0.82	7.23	1.63	3.72	1.19	5.30	1.72
7- τ (N/m^2)	Mean Reynolds shear stress	26.17	10.49	35.20	21.87	8.55	6.10	10.73	11.09
8- TKE (cm^2/s^2)	Turbulent kinetic energy	124.10	30.63	167.60	69.03	50.14	23.65	84.14	50.73
9- ITS_U (s)	Integrated time scale – streamwise	0.41	0.13	0.24	0.05	0.72	0.38	0.66	0.46
10- ITL_U (cm)	Integrated length scale – streamwise	31.94	11.10	15.07	4.52	18.58	9.66	12.31	7.23
11- ITS_V (s)	ITS –lateral	0.16	0.08	0.13	0.03	0.34	0.21	0.60	0.50
12- ITS_W (s)	ITS- vertical	0.13	0.02	0.12	0.02	0.32	0.23	0.38	0.27
13- ITL_W (cm)	ITL –vertical	9.90	1.69	7.39	1.62	7.17	2.79	6.48	2.91
14- Q1-p (%)	Proportion of time high speed outward	9.69	1.02	9.02	1.70	8.25	1.76	6.68	2.11
15- Q1-d (s)	Mean duration of events –Q1	0.11	0.01	0.10	0.01	0.13	0.04	0.14	0.04
16- Q4-p (%)	Mean propotion of time occupied by incursions	2.08	0.62	2.39	1.25	2.54	1.11	3.90	1.95
17- Q4-d (s)	Mean duration of events -Q4	0.07	0.01	0.07	0.01	0.08	0.02	0.11	0.04
19- HS-N	Frequency of HS events (U-level)	65.39	8.38	73.45	11.78	71.45	18.37	58.86	16.28
20- HS-P (%)	Proportion of time- high speed events (U-level)	10.40	0.71	10.00	0.80	9.66	0.96	9.43	1.16
21- HS-D (s)	Mean duration of HS events (U-Level)	0.13	0.02	0.11	0.02	0.12	0.04	0.14	0.04
22- HS-Max (s)	Maximum duration of HS events	0.70	0.23	0.53	0.17	0.73	0.38	0.90	0.52

Table 4.2 All variables of the study in three categories: spatial variables, standard habitat variables and turbulence variables. Velocity measurements were taken 10 cm above the bed. Spatial average and standard deviations are presented.

ecological literature than the more traditional approach based on particle size distributions (e.g.Wolman, 1954). The latter makes the assumption that bed arrangement and particle shape, orientation, packing, spacing, sorting and clustering are homogeneous (Nikora et al., 1998). However, this assumption is not always appropriate. For example, it is common to observe large particles buried in the bed that do not protrude above the bed higher than smaller particles. In contrast, our index based on bed elevation provides a direct measure of bed roughness that might be more relevant in affecting flow properties and providing cover for fish.

From the velocity time series, several types of turbulence variables were created (Table 4.2). Time averaged turbulent statistics were estimated at each measurement point. These included turbulent intensities, the root mean squared streamwise, lateral and vertical velocities (u', v', w'), the mean Reynolds shear stress (τ=-ρuv), where ρ is the water density and uv the covariance of the streamwise and vertical velocity and the turbulent kinetic energy, a combination of the turbulent intensities in the three dimensions (TKE = 0.5 (u'^2 + v'^2 + w'^2)). Integral timescales (*ITSu*, *ITSv*, and *ITSw*) were derived by integrating the autocorrelation functions of the streamwise, lateral and vertical velocity components over time.

$$ITS_x = \int_{t=0}^{T=t} Rxx(\Delta t)dt \tag{1}$$

ITSu, ITSv and ITSw therefore represent the length of time over which each velocity component presents a significant positive autocorrelation. This variable is sometimes referred to as *eddy length*. The integral length scale (*ITL*), obtained by multiplying the *ITS* by *U*, was used to estimate the spatial extent of the turbulent structures.

Turbulent properties were also estimated using two types of turbulent event detection techniques. First, we used quadrant analysis as described by (Lu and Willmarth, 1973) with a threshold value of Th = 2, which means that only the strong events remained in the analysis (Table 4.2 variables 14 to 17). The proportion of time (p) and the duration (d) of the events were estimated for quadrant 1 (*Q1*) and 4 (*Q4*). *Q1* and *Q4* are associated with the streamwise high-speed events. The events in *Q4* are related to the occurrence of sweep structures known to be accountable for shear stress generation whereas *Q1* is related to high speed outward interactions (Buffin-Belanger and Roy, 1998). Second, we used the modified U-level technique to detect the occurrence of macroturbulent flow structures (Luchik and Tiederman, 1987). This method tracks changes in the longitudinal velocity components as follows. The beginning of a turbulent event begins when $|u'| > ks_u$ and ends when $|u'| < pks_u$, where u' is a velocity fluctuation around the average, k is a threshold and s_u is the standard deviation of the velocity fluctuations and p takes a value between 0 and 1. Here, a threshold of k = 2 and p = 0.25 were used. In the present study, the variables associated with low-speed, *Q2* (ejections) and *Q3* (inward interactions), were very strongly correlated to the high speed variables (*Q1* with *Q3* and *Q2* with *Q4*). Therefore, we chose to focus on the high speed events rather than on the low-speed, as we suppose in many cases they may have a stronger impact on biota, such as dislodgement of organisms.

Turbulent flow variables were tested for normality (K-S test) and transformed when it was necessary using a Box-Cox (1964) normalisation procedure. As all turbulence variables did not bear the same physical units, they were also centred and standardized.

4.3.5. Morphological units

The four sites presented a wide range of hydraulic environments. Table 4.2 summarises the statistics of the four units. Space averaged mean flow depth (*Y*) did not vary greatly between the units. However, the pools presented a higher standard deviation than riffles, which illustrates the wider range of depth values. Furthermore, mean bed roughness (k) was higher in the pools than in the riffles, Pool 2 presenting the roughest bed and Riffle 1 the smoothest. The average mean streamwise velocity (*U*) ranged from 21 to 62 cm/s and was two to three times higher in the riffles than in the pools (Figure 4.1, Table 4.2). Similarly, the mean values of turbulent properties (*RMS*, τ and *TKE*) in the riffles were higher than in the pools. In general, the four units presented a gradient of hydraulic heterogeneity. The gradient from the most heterogeneous to the most homogeneous unit is Riffle 2, Riffle 1, Pool 1 and Pool 2.

4.3.6. Turbulent flow spatial scale partitioning: PCNM analysis

The PCNM method developed by Borcard and Legendre (2002) allows the determination of the proportion of the response variables' variation explained by spatial patterns at each spatial scale. Based on the spatial coordinates, the PCNM analysis creates a set of explanatory spatial variables (eigenvectors), further referred as *PCNMs*, which represent the range of spatial frequencies that can be perceived on the sampling grid, given the sampling design (Borcard et al., 2004). These distance-based eigenfunctions are orthogonal to one another and therefore do not present intercorrelations (Dray et al., 2006). The *PCNMs* are constructed through a series of operations presented in Figure 4.2. For regular sampling designs, *PCNMs* are sinusoidal and of decreasing periods. We grouped them into six spatial scales. The four morphological units were processed separately. The following will briefly describe the five steps involved in the PCNM analysis. In the sixth step, PCNM-turbulence model outputs will be linked to standard habitat variables. For further details on the method, see Borcard *et al.* (2002) and Borcard *et al.* (2004).

Step 1 Euclidian distance matrix

A pairwise Euclidian distance matrix was computed from all the geographic coordinates of each velocity measurement.

Step2 Truncation of the distance matrix

A threshold value (t) was chosen and used to build a truncated distance matrix as follows.

$$D^{*} = \begin{Bmatrix} dij \ if \, dj \leq t \\ 4t \ if \ dj > t \end{Bmatrix} \tag{2}$$

For all four morphological units, the threshold value was set to 0.25 m, a value corresponding to the sampling interval, as recommended for regular sampling design because it keeps all the sampling locations connected in a single network (Borcard et al. 2004).

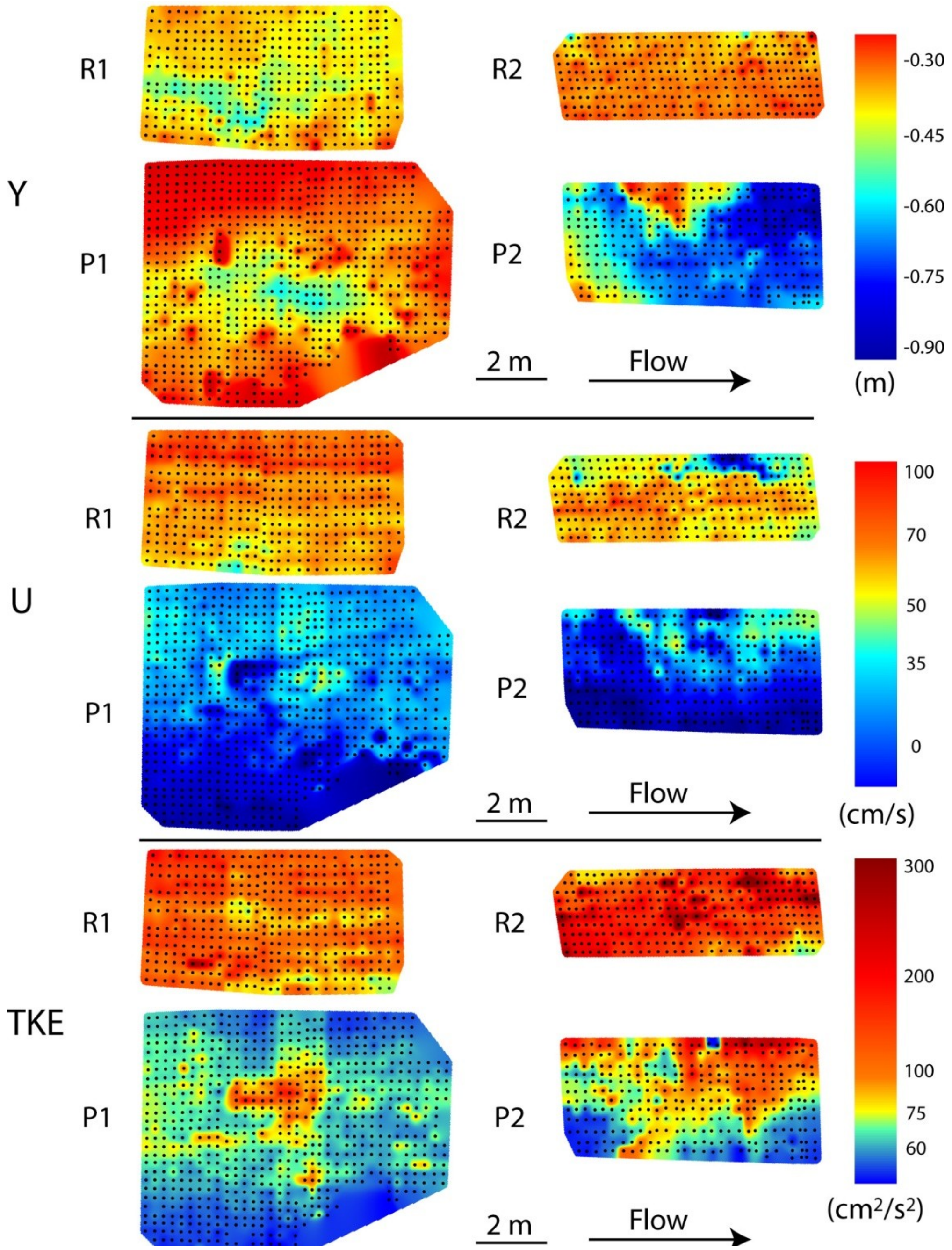

Figure 4.1 Color plots of Depth (Y), Mean streamwise flow velocity (U) and turbulent kinetic energy (TKE) for the four morphohygraulic units Riffle 1 (R1), Riffle 2 (R2), Pool1 (P1) and Pool 2 (P2). Flow velocity was sampled every 25 cm on a regular sampling grid (points).

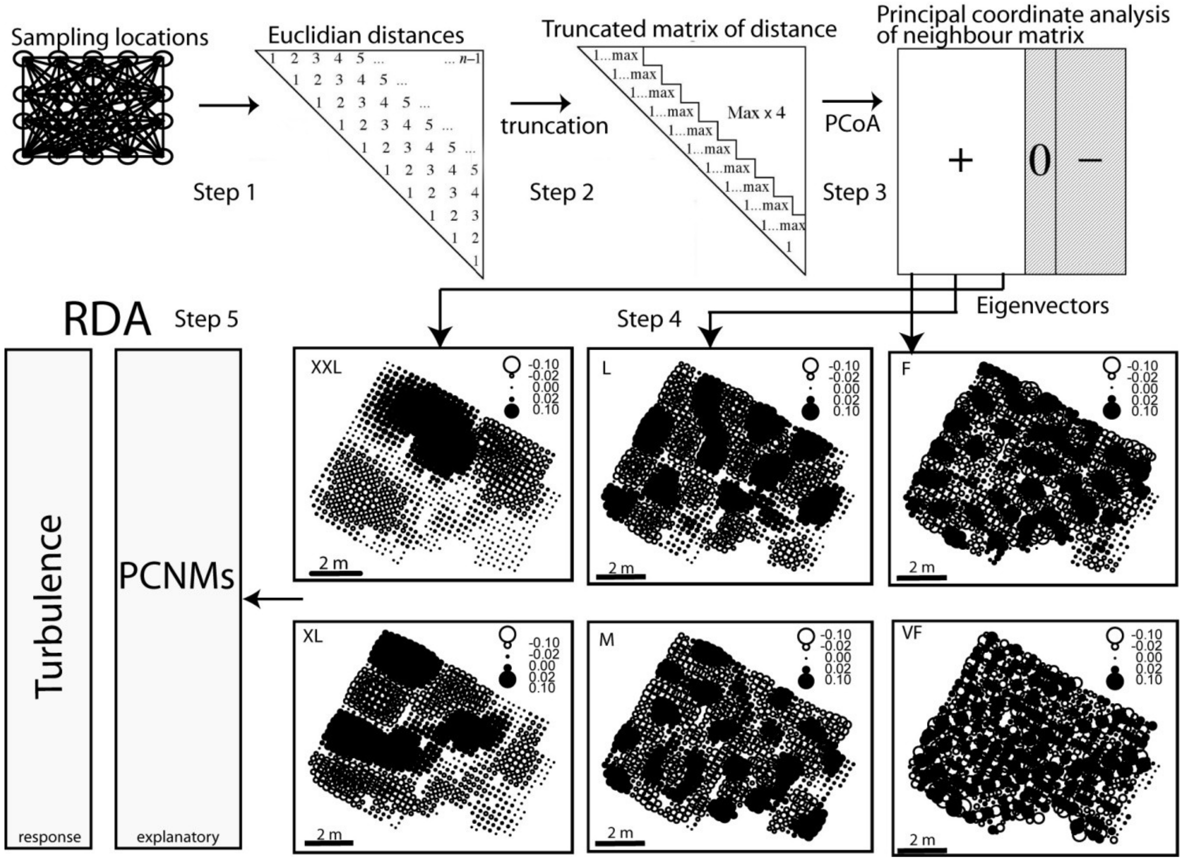

Figure 4.2 Schematic diagram of Principal component of neighbour matrices (PCNM) methodology. Step 1: From the spatial coordinates, a matrix of the Euclidian links between the samples was built. Step 2: The distance matrix was truncated at a distance (0.25 m). Step 3: A matrix of eigenvectors was obtained by Principal coordinates analysis of the truncated matrix. Step 4: All positive eigenvectors (*PCNMs*) were mapped and grouped in spatial scales. The figure presents six examples of *PCNMs* constructed from the coordinates of Pool 2, selected from each of the spatial scales. XXL: 3-4 m, XL: 2.5-3 m, L: 1.5-2.5 m, M: 1-1.5 m, F: 0.5-1 m, VF: 0.25-0.5 m. The size of the circles is proportional to the magnitude of the *PCNMs* values. Step 5: Each group of *PCNMs* associated to a specific scale were used as explanatory variables in canonical analysis (RDA) to explain the variability of turbulent flow variables. Modified from Borcard *et al*. (2004)

Step 3 Generating *PCNMs* : Principal coordinate analysis (PCoA) on the truncated distance matrix

A set of eigenvectors was obtained by performing a principal coordinate analysis (PCoA) on the truncated distance matrix (D*). PCoA, also known as 'classical scaling', is a common ecological ordination method based on linear scalings (Gower, 1966). The

PCNMs, the positive eigenvectors, include all the spatial scales that can be analysed in each sampling grid. Eigenvectors associated with large eigenvalues contain the larger-scale variability whereas the lower eigenvalues represent the fine-scale variability. Because the distance matrix was truncated, a portion of the eigenvectors had negative eigenvalues. These were removed from the analysis. For each morphohydraulic unit, the number of positive eigenvectors was approximately equal to two-thirds of the number of samples (Borcard et al. 2004). Therefore, Pool 1 presented much more *PCNMs* than the other units. All PCNM analyses were carried out using the R language software (Comprehensive R Archive Network, http://cran.r-project .org/) and the spacemakerR package (Dray et al., 2006).

Step 4 Defining relevant spatial scales

A forward selection permutation method was used to determine which PCNMs were explaining a significant portion of the variability of the turbulent flow variables. Between 20 and 30% of the *PCNMs* per unit significantly explained turbulent flow variability and were therefore selected (Table 4.3). For each spatial scale, the *PCNMs* were used as explanatory spatial variables to explain the variability of turbulent flow properties using canonical redundancy analysis (RDA). RDA is the direct extension of multiple regression to model multivariate data sets (Legendre and Legendre, 1998).

All significant *PCNMs* were mapped on the geographic coordinates and visually inspected. Figure 4.2 illustrates examples of *PCNMs* maps for Pool 1. Selecting the number of PCNM submodels is a subjective process.

Table 4.3 Classification of PCNM variables (*PCNMs*). Number of variables in each spatial scales. The physical scale ranges were subjectively set, based on the half periods of the *PCNMs*.

Scales			**Morphohydraulic units**			
		Physical (m)	Riffle 1	Riffle 2	Pool 1	Pool 2
Number of sig. PCNMs	+ Extra large (XXL)	3.0 - 4.0	6	3	9	4
	Extra large (XL)	2.5 – 3.0	5	6	17	8
	Large (L)	1.5 – 2.5	12	7	27	12
	Medium (M)	1.0 – 1.5	11	13	29	17
	Fine (F)	0.5 - 1.0	11	18	34	25
	Very fine (VF)	0.25 - 0.5	9	19	36	22
	Total		54	66	152	94
Total PCNMs			302	214	561	232
Number of samples			432	307	800	343

We divided the spatial eigenfunctions in six submodels corresponding to spatial scales: Very large + (XXL), Very large – (XL), Large (L), Medium (M), Fine (F) and Very fine (VF). The physical scale associated with these arbitrary spatial scales was set by inspecting the half-periods of the *PCNMs* (Table 4.3). The minimum scale size is restricted by the sampling interval (0.25 m) and by the extents of the morphohydraulic units (4 m). In order to compare between the units, we set the maximum spatial scale to be the largest scale of the smallest unit. Any variability occurring beyond the range of scales will not be taken into account by the analysis.

Step 5 Spatial scale partitioning of turbulent flow properties: Canonical redundancy analysis (RDA)

For each spatial scale, RDA was used to determine the proportion of variability of the 19 turbulence variables explained by the *PCNMs* associated to that specific scale. R^2 is an indicator of the importance of the contribution of *PCNMs* to the variation of turbulent flow variables. R^2 values were adjusted for the explanation that would be provided by the same number of random explanatory variables measured over the same number of objects (Ezekiel, 1930).

Step 6 The relationships between turbulence and standard habitat variables at all spatial scales: variation partitioning

In this step, the relationships between habitat variables (*U*, *Y* and *k*) and turbulent flow properties at each spatial scale was assessed with a variation partitioning procedure using the function 'varpart' of the Vegan R-language package (Oksanen et al., 2007). Habitat variables were used as explanatory variables to explain the variability of the first canonical axis of the RDAs previously obtained for each scale in step 5. In this process, habitat variables were run successively in multiple regression models as co-variables and subsequent variables need to explain a significant amount of the residual variance (Monte Carlo, 999 permutations). This procedure, automated in the ‘varpart’ function, allowed us to discriminate between the fractions of variation explained by a single habitat variable from the portion explained by two or three intercorrelated variables. Finally, multiple regression models were used to investigate the spatial structure of single turbulence variables and to break down the variation into contributions from each spatial scale.

4.4. Results

In each morphological unit, an important proportion of turbulent flow variability was explained by the spatial component of the data. The canonical redundancy analyses based on the *PCNMs* at each spatial scale explained a significant portion of variation of turbulent flow properties with adjusted coefficients of determination (R_a^2) ranging from 0.44 to 0.70 (Figure 4.3; Table 4.4). R_a^2 values were higher for the pools than the riffles. Six successive RDA revealed the proportion of variation explained by each spatial scale. In general, turbulent flow variables showed a spatial structure across multiple scales at all four sites. The six spatial scales explained a minimum of 7% and a maximum of 42% percent of the total explained turbulent flow variability.

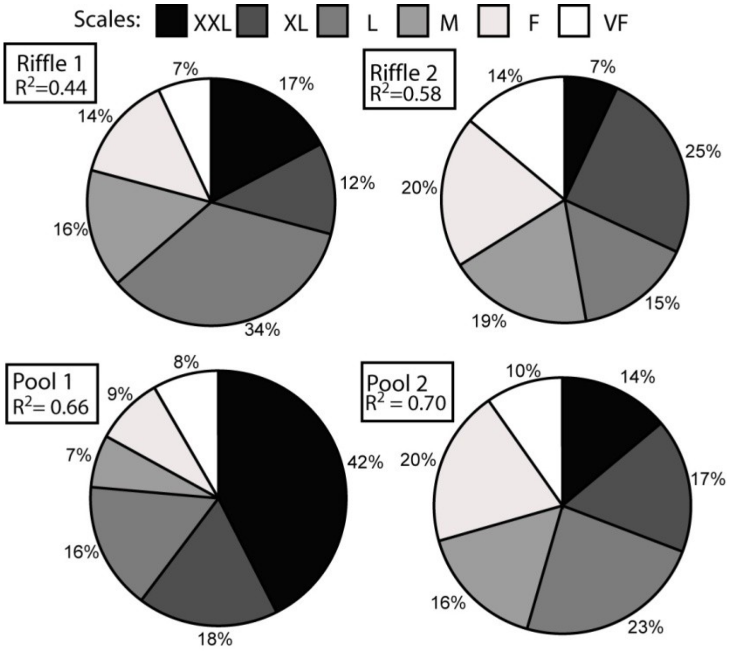

Figure 4.3 The values in rectangles express the total variance explained by all scales (adjusted R^2). Pie charts present the break down of explained variance per PCNM spatial model (XXL: 3-4 m, XL: 2.5-3 m, L: 1.5-2.5 m, M: 1-1.5 m, F: 0.5-1 m, VF: 0.25-0.5 m).

In Riffle 1, the L scale (1.5 - 2.5 m) was dominant, with 34% of the variation explained by all scales. Similarly, the spatial structure in Pool 1 was dominated by one spatial scale, with XXL *PCNMs* explaining most variability (42 %). In contrast, the variability of turbulent flow in Riffle 2 and Pool 2 was divided more evenly across the spatial scales.

Table 4.4 Classification of PCNM variables (*PCNMs*). Number of variables in each spatial scale. The physical scale ranges were subjectively set, based on the half periods of the *PCNMs*.

	Riffle 1			Riffle 2			Riffle 3			Riffle 4		
Scales	λ_1	λ_2	R^2	λ_1	λ_2	R^2	λ_1	λ_2	R^2	λ_1	λ_2	R^2
XXL	0.03	0.02	0.06	0.03	NS	0.04	0.13	0.09	0.27	0.05	0.04	0.10
XL	0.03	0.01	0.04	0.08	0.04	0.14	0.05	0.04	0.11	0.05	0.04	0.11
L	0.09	0.02	0.12	0.05	0.01	0.08	0.06	0.02	0.10	0.07	0.06	0.17
M	0.03	0.01	0.06	0.04	0.03	0.10	0.02	NS	0.04	0.05	0.03	0.11
F	0.03	0.01	0.05	0.05	0.02	0.11	0.02	NS	0.06	0.07	0.03	0.13
VF	0.01	0.01	0.02	0.03	0.02	0.08	0.03	NS	0.05	0.03	0.02	0.07

Multiple regression models show that the behaviour of each variable presented a great variability between the sites (Figure 4.4). In general, the variables did not exhibit much difference between each other in the smaller scales (M, F, VF). The spatial structure observed in the larger scales (L, XL, XXL) was more important in distinguishing the variables in Riffle 1, Riffle 2 and Pool 1. For instance, in Riffle 1, where spatial dependence was the lowest in general, the variables related to turbulence intensities (Rms_u, Rms_v, Rms_w and *TKE*) and the length and duration of turbulent flow structures (*ITS* and *ITL*) were the most spatially structured. In contrast, the turbulent structure variables (*Q* and *HS*) showed a low spatial dependence in the range of scales. The main difference between the variables was the contribution of the L-scale (1.5 - 2.5 m), which was more important for mean turbulent variables (*Rms*, τ, *TKE*) than for the turbulent event variables. A similar spatial structure was observed in Pool 1, except for one scale, the XXL scale (3-4 m), and in Riffle 2, where a strong spatial coherence in the XL scale (2.5 – 3 m) was observed. In contrast, Pool 2 showed very low variation in spatial structure between the turbulence variables and scales.

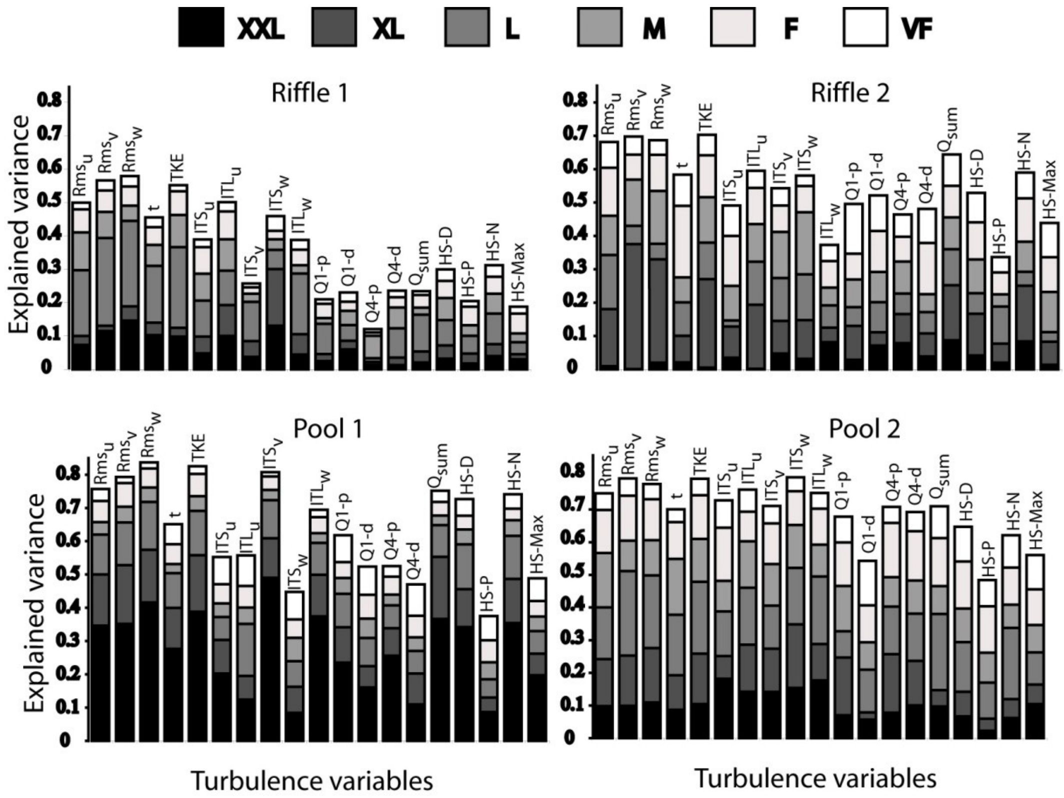

Figure 4.4 Fractions of explained variance (adjusted R^2) for each turbulent flow variable per spatial scale. PCNMs models: XXL: 3-4 m, XL: 2.5-3 m, L: 1.5-2.5 m, M: 1-1.5 m, F: 0.5-1 m, VF: 0.25-0.5 m.

In each morphological unit, *Rms* and *TKE* were always among the most spatially structured variables and mean Reynolds shear stress was slightly lower. Variables describing the turbulent flow events obtained from quadrant analysis generally presented the lowest spatial coherence, except in Pool 2. Similarly, the proportion of time and maximum duration of high-speed turbulent events (*HS-P*, *HS-Max*) presented the lowest R_a^2. In contrast, the duration and frequency of high speed events (*HS-d*, *HS-N*) presented a spatial structure across a range of scales: mainly larger scale in Pool 1, mainly finer scales in Riffle 2 and all scales in Pool 2.

The relationships of standard habitat variables with turbulent flow variables at each scale were investigated using a variation partitioning procedure. The fraction of variation explained by mean flow velocity, flow depth, bed roughness and the fraction shared by two or more variables are presented in Figure 4.5.

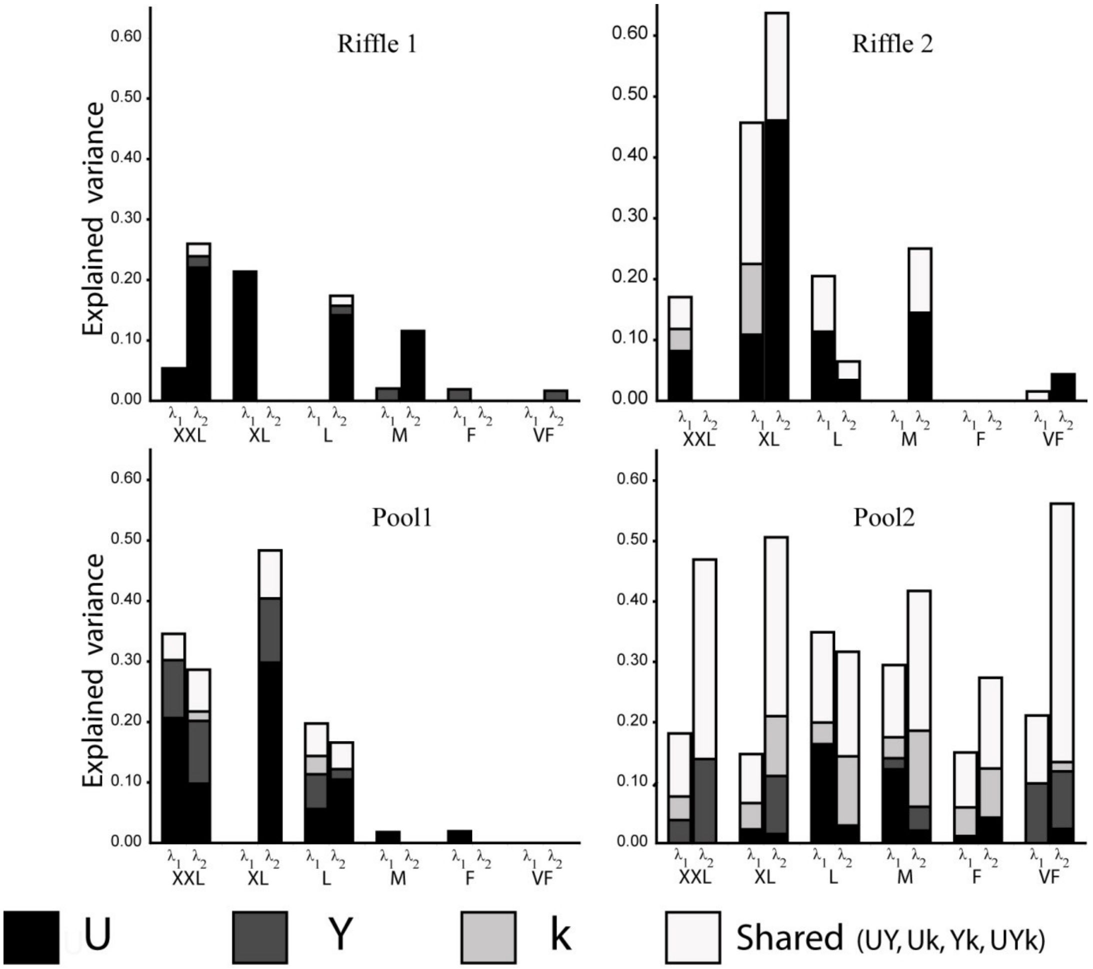

Figure 4.5 Fraction of variance (adjusted R^2) of 'scaled turbulence' explained by habitat variables (Y: depth (m), U: mean streamwise velocity (cm/s), k: bed roughness index (m)). 'Scaled turbulence' represents the first (λ_1) and second (λ_2) canonical axis of each spatial scale (PCNM models).

The coefficients of determination are shown for significant canonical axes only. In all morphological units, the proportion of variation explained by standard habitat variables for the combined scales ranged from 0.25 to 0.65. It was considerably lower in Riffle 1, in which the range of habitat values was lower (Table 4.2).

The single variable explaining the largest fraction of variation was mean flow velocity, especially in Riffle 1, Riffle 2 and Pool 1. In Pool 2, mean flow velocity also explained a large fraction of turbulent flow properties, but in interaction with flow depth and bed roughness. Flow depth and bed roughness alone did not explain a major fraction of turbulent properties, except for the XXL and XL scales in Pool 1. However, Y and k had a shared effect in the XL scale in Riffle 2 and in all the range of scales in Pool 2. The fraction of variation explained by multiple variables was very low in Riffle 1 and Pool 1. Generally, in three of the four morphological units, habitat variables explained turbulent flow properties in the larger spatial scales ranging from 1 to 4 m and not much in the finer spatial scales. In Riffle 2 and Pool 1, turbulent flow properties were more strongly affected by U, Y and k at the XL scale. In contrast, turbulent properties in Pool 2 were explained by habitat variables at all scales. However, the first canonical axis (λ_1), which represents the major part of turbulence variability, was better explained by habitat variables at the L and M scales.

4.5. Discussion

4.5.1. Spatial scale partitioning of turbulent flow variables

In this study, the extensive high resolution measurements and a PCNM analysis provided a way to estimate the proportion of turbulent flow variation (R_a^2) associated with six spatial scales ranging from 0.25 m to 4.0 m. In the four morphological units, turbulent properties exhibited a spatial dependence across the entire range of scales. However, they showed a substantial variability among the units, partly because the units were selected in order to portray the range of hydraulic properties at base flow. In two of the four units, the smaller spatial scales (< 1.5 m) explained less variability than the larger scales (> 1.5 m). In previous studies that have examined in detail the variability of turbulent flow properties at the reach scale in shallow gravel-bed rivers, Lamarre and Roy (2005) and Legleiter *et al*. (2007) have reported the presence of large spatial patterns of mean turbulent flow properties and the localized effects of individual bed roughness elements on turbulence. The overriding effect of large scale patterns over the smaller scales could be caused by the presence of large scale coherent turbulent flow structures that are highly energetic and are not much affected by individual roughness elements such a boulders and pebble clusters (Roy et al., 2004; Lacey and Roy, 2007). Even though they were larger in size, the reaches presented in previous studies (Lamarre and Roy, 2005; Legleiter et al., 2007; Peterson et al., 2007) were more similar to Riffle 1 and Pool 1 as they were relatively homogenous in terms of the streamwise mean flow velocity (*U*). These sites do not include patches of high velocity flow with others of very slow flow such as the two more heterogeneous units of this study, Riffle 2 and Pool 2. These two units showed a larger fraction of variance explained by the smaller scales (0.25 to 1.5 m) than the other units. This scale is typically associated to the turbulent processes such as flow separation and eddy shedding induced by large roughness elements. The spatial heterogeneity of turbulent flow was previously examined at this scale over a replica of a natural gravel patch (2 m^2) at three heights close to the bed on a 0.05 x 0.10 m systematic sampling grid (Buffin-Bélanger *et al*,. 2006). At 0.1 m above the bed, the authors observed a relatively low spatial heterogeneity of *RMS* and *TKE*. Furthermore, semi-variance analysis revealed a very low spatial autocorrelation, suggesting that the small variations observed at the patch scale occurred within scales finer than their sampling grid (Buffin-Belanger et al., 2006).

In this study, between 30% and 55% of the variability was not explained by PCNM spatial models. A large part of that unexplained variability could be related to the processes occurring at scales smaller than those taken into account by the sampling scheme. At the small scale, turbulent intensities can present very high spatial heterogeneity. For example, at 5 cm above the bed, Stone and Hotchkiss (2007) typically observed variations of as much as 100% over 144 cm^2 of bed surface in a riffle, a run and a pool. Similarly, several studies have shown a very high spatial and temporal heterogeneity of turbulent flow at the centimeter scale (Hart et al., 1996; Dancey et al., 2000). However, flow measurements at this very fine scale were recorded at a few millimeters above the bed. This suggests a high variability of turbulent flow properties at the scales of bed particle size and of river sections, but a relative homogeneity at the intermediate morphological unit/patch scale.

In this study, the choice of sampling velocity at a height of 10 cm was a tradeoff between sampling efficiency and ecological relevance. Even if a significant part of river biota is benthic and rarely leaves the first few centimeters from the bed, turbulent flow properties at 10 cm above the bed are of great importance. For example, fish such as juvenile salmonids spend most of their time sitting and waiting on the river bed and the major part of their swimming energy expenditures is related to burst movements in the water column to catch drifting preys (Hughes and Kelly, 1996). Sampling closer to the bed would most likely have resulted in a higher spatial heterogeneity of the flow variables as spatial flow heterogeneity increases with height above the bed. It appears that streamwise velocity becomes spatially homogeneous at a distance varying between two to four times the median bed roughness height (Buffin-Belanger et al., 2006).

Our results show that the total portion of variability of turbulent flow explained by the spatial scales was higher in the pools than in the riffles. This could be a consequence of the higher mean flow velocity in riffles than in pools. Previous studies have suggested a decrease of spatial flow heterogeneity associated with an increase of discharge or mean flow velocity, both at the reach scale (Moir et al., 2006; Legleiter et al., 2007) and at the patch scale (Buffin-Belanger et al., 2006). However, the proportion of variation explained by the larger scales (XXL, XL, L) was not higher in the pools. Nevertheless, the spatial organization of near-bed flow may remain similar, as suggested by a strong covariation of hydraulic variables for individual sampling locations at different levels of flow (Buffin-Belanger et al., 2006).

The spatial scale partitioning of the variability of 19 individual turbulence variables exhibited a high inter-site variability. However, in general, the mean turbulent flow variables like *RMS* and *TKE* displayed a stronger spatial structure than turbulent event variables obtained from quadrant analysis. Q_1 events are often associated to the reattachment point in a separation zone in the lee of obstacles and Q_4 to the frequent low magnitude fast downward events induced by the presence of protruding roughness elements (Buffin-Belanger and Roy, 1998). In a recent study, Lacey *et al.* (2007) used the PCNM analysis to quantify the spatial scales of flow variability of a vertical flow field around a pebble cluster (1.5 x 0.4 m). Even at this smaller scale, quadrant based variables were less spatially structured than the mean turbulent statistics such as *RMS*. However, in the present study, the great variability between the sites prevented us from making any generalization on the spatial scalings observed between the variables. In Pool 2, most flow variables showed a high similarity of both total R_a^2 and the proportions of variation explained by each scale. However, the variability contained in each spatial scale might be differently related to habitat variables.

4.5.2. The link between 'standard' habitat variables and turbulence at multiple scales

In the present study we investigated the relationships between 'standard' fish habitat variables *U*, *Y* and *k* and the variation of turbulent flow variables in four different hydraulic contexts. The explanatory power of 'standard' fish habitat variables at each scale varied greatly between the four morphological units. It was not surprising that mean flow velocity explained the largest proportion of the turbulent flow variation, as the Reynolds number increases linearly with *U*. However, results revealed that correlations were mainly limited to the scales larger than 1.5 m (XXL, L and L). That may be due to the relatively low heterogeneity of *U* in the smaller scales across the reach at a height 0.1 m above the bed, as reported at the patch scale by Buffin-Bélanger *et al*. (2006). In contrast, *Y* generally explained low proportions of turbulent flow variation at all scales. This is relatively unexpected, since turbulent coherent flow structures tend to scale with flow depth (Shvidchenko and Pender, 2001; Roy et al., 2004; Nikora, 2006). The length of these structures generally ranges from two to six times the flow depth. Thus, an increase in depth could be associated with an augmentation of the magnitude of the variables describing the duration of turbulent structures such as *ITS* and *Q-d* variables. The weak explanatory power of depth in three of the four morphological units may be partly explained by the relative homogeneity of depth in these units. Indeed, in Pool 2, where the range of depth values was higher, *Y* explained a larger proportion of variation. However, that portion of variation is shared with the effect of U and k as they are highly intercorrelated. Similarly, the effect of substrate, represented by the bed roughness index, was also relatively low. Numerous studies have previously quantified in detail the spatial distribution of turbulence properties around bed roughness elements (Brayshaw et al., 1983; Lawless and Robert, 2001b; Lacey and Roy, 2007). Even though pebble clusters and other individual roughness elements cause an increase in turbulent intensity through shedding, this effect is local (Legleiter et al., 2007). Although the complex bed configuration is not reflected in the mean turbulent flow properties at the reach scale (Lamarre and Roy, 2005), it was expected that k would explain turbulent flow variability at the smallest scales in this study. However, in three of the four units, it was not the case. This is most likely because the footprint of roughness elements was occurring at a scale smaller than the one detected by the VF scale and because the measurements were sampled at 0.1 m above the bed, which represented sometimes as much as $0.25Y$. Furthermore, in this study, the roughness at a sample site was characterized using the spatial standard deviation of the elevations in a 65 cm square around a measurement point. However, the magnitude of turbulent properties might be inherited from roughness element located further upstream rather than produced by local shear stress, especially at a few centimeters above the bed. Therefore, the roughness upstream from a micro-habitat might also be considered when describing fish habitat.

The difficulty to isolate turbulence properties from standard habitat variables has been pointed out as a main issue in ecohydraulics research (Enders et al., 2005b; Smith et al., 2006). In general, in this study, the standard habitat variables had a relatively low capacity to explain turbulent properties using simple correlations, especially at the smaller scales. That was partly caused by the complex river dynamics system. For instance, within the morphological units, patches of coarse cobble could be found in slow deeper flow presenting low turbulence magnitude as well as in fast shallow flow associated with high turbulence levels. From a practical point of view, this level of complexity suggests that turbulence should be considered as a 'distinct' ecological variable within the range of spatial scales included in this study.

Understanding the linkages between organisms and their hydraulic environment is a critical step in developing predictive models regarding the structure of fluvial ecosystems (Hart and Finelli, 1999). The temporal and spatial scales of flow variability are among the main drivers of numerous fluvial ecological processes (Biggs et al., 2005). One of the important issues in ecohydraulics research is to identify and match the proper hydraulic scale to the ecological process or organism distribution of interest. As shown in this study, PCNM analysis is an efficient way to identify relevant spatial scales of flow variability. These hydraulic scales could potentially be setting the boundaries of fluvial organisms and territory size or structuring their mobility patterns. For instance, XXL-scale turbulence patterns are affecting drifting invertebrate spatial distribution, as drifting macroinvertebrate concentration is correlated with velocity at the morphological unit scale rather than at the fish micro-habitat scale (Leung et al., 2009). In contrast, individual turbulent structures occurring at the M- and VF scales could affect fish feeding movements (Enders *et al.*, 2005). Organisms living in more heterogeneous habitats (variability poorly explained by spatial scale variables), such as Riffle 1 and 2 could be less mobile than organisms living in more homogeneous environments, as they could find complementary habitat types (resting, feeding, etc.) closer apart. However, such links between spatial turbulent flow variability and organism behaviour remain to be explored.

Both the spatial scale of turbulent structures and the size of the organisms of interest might be important factors to consider when examining the effect of turbulence on biota (Nikora et al., 2003). For instance, bacterial growth is affected by microturbulent flow (Bergstedt et al., 2004), the distribution of macroinvertebrates is influenced by coherent structures associated to individual cobbles and boulders (Bouckaert and Davis, 1998) and large scale flow structures can affect the bioenergetics of juvenile fish (Enders et al., 2003). Biggs *et al*. (2005) have hypothesized that the scale of the variations would have to be comparable to the organism size (i.e 0.01 – 10 times body length) to be felt. The size and magnitude of the acceleration/deceleration in the abrupt boundaries between high and low-speed structures might also play an important role. The size of coherent structures is generally obtained by substituting space for time using time series analysis such as autocorrelation functions, *U-Level* and quadrant analysis. It is still difficult to determine which turbulence statistics are the most relevant to use in different ecological contexts. Except for the autocorrelation functions, the variables associated to turbulence structures used in this study have not been used in ecohydraulics studies. However, the use of turbulent event detection techniques in future research could possibly reveal new aspects of the effect of flow on organisms. Indeed, results showed that they were generally less spatially structured than the mean turbulent statistics (Rms, Tke) and less correlated with mean flow velocity, which could be an advantage in the context of adding turbulence metrics to physical habitat models. The question of the effect of turbulence on organism habitat use remains to be explored.

4.6. Linking paragraph

The previous chapter highlighted and discussed the role of turbulence as a fish habitat variable and suggested that future work should attempt to improve our understanding of various turbulent properties on fish. Most studies have examined the direct impact of turbulence on energy expenditures or on swimming performances. However, we hypothesize that turbulence might influence the energy input as well as the expenses. Therefore, Chapter 5, presented as a classic thesis chapter, examines the effect of turbulence on juvenile salmon prey capture rates. The effect of turbulence on fish is often investigated in laboratory flumes, in flows that are generally less turbulent than most natural rivers. In this regard, the objective of the next chapter is to test the use of a portable flume allowing control over flow properties to study juvenile salmon drift feeding. The portable flume is designed to be assembled in the field and fixed on the river bed. It allows one to control the flow properties in the transparent observation section to facilitate underwater filming of fish behaviour. The preliminary results in the following chapter do not conclusively confirm or rule out the effect of turbulence on prey capture probability. However, we consider that the new portable flume methodology is a promising way to reconcile the strengths of observational studies in natural habitat and the experimental control provided by laboratory conditions.

Chapitre 5: The effect of flow properties on the capture probability of juvenile Atlantic salmon in a portable flume

5.1. Introduction

Stream salmonids often forage using a sit-and-wait tactic, which consists of performing attacks on drifting prey delivered by the current and returning to a specific central position (Hughes and Dill, 1990). The selection of a high velocity foraging position implies a tradeoff between energetic costs and prey encounter rates (Fausch, 1984; Hill and Grossman, 1993). The profitability of a foraging position also varies with the ability to catch prey in relation to the hydraulic properties of microhabitats (Hughes and Dill, 1990; Guensch et al., 2001). These tradeoffs are integrated in individual-based foraging models, which have gained in complexity, integrating an increasing number of habitat quality parameters (Hayes et al., 2007; Jenkins and Keeley, 2010). Because such an approach relies on a mechanistic understanding of underlying processes, it provides a robust structure to develop general predictive models (Finstad et al., 2011). In order to better understand salmonid behaviour and to calibrate foraging models, recent laboratory studies have examined the effect of individual habitat variables on prey capture probability. These studies have revealed that capture probability is not affected by depth (Piccolo et al., 2007), but decreases with decreasing water temperature (85 to 52 from 8 to 5.7 ^{o}C; Watz and Piccolo 2011) and increases with decreasing flow velocity (65% to 10% from 29 $cm \cdot s^{-1}$ - $61 cm \cdot s^{-1}$; Piccolo et al. 2008).

In rivers and streams, turbulence causes flow velocity variation at the millisecond scale (Roy et al., 2004). Turbulent flow influences ecological processes through multiple pathways (Hart and Finelli, 1999). For juvenile salmonids, turbulence has been shown to influence individual energy budget (Enders et al., 2003; Liao et al., 2003; Enders et al., 2004; Standen and Lauder, 2005) and habitat selection (Smith et al., 2005; Smith et al., 2006; Enders et al., 2009). Turbulence might also be an important driver of resource distribution. For instance, in rivers, where turbulence is generally high, drift distribution within morphological units (i.e. pools and riffles) cannot be predicted by downstream flow velocity at the microhabitat scale, which suggests prey might be mixed throughout the water column (Leung et al., 2009). The unpredictability of prey trajectories might have an impact on the ability of fish to catch prey. Kemp et al. (2005) conducted an experiment testing for the effects of 'complex' (boulder rich) and 'simple' habitats on juvenile salmon feeding rates and found a significant decrease in feeding rates in complex habitats. It was hypothesized that this decrease in feeding rate was attributed to a reduced visual field and/or to a "chaotic flow pattern". However, the influence of turbulence on prey capture probability was not explicitly assessed.

The methodology used to examine prey fish capture probability generally consists of video analysis of fish foraging in laboratory flume settings (Piccolo et al., 2007; Piccolo et al., 2008b; Watz and Piccolo, 2011). Generally, the flow generated in laboratory flumes is less heterogeneous, with lower turbulence levels than in typical juvenile salmonid habitat (Lacey et al., 2012). Therefore, if turbulence influences the ability to detect and capture prey, values reported from laboratory experiments might be overestimated.

In this study, we combined a field and experimental approach to examine the foraging behaviour of juvenile Atlantic salmon in various flow conditions. We used an *in situ* portable flume, which consisted of a transparent enclosure (observation section) equipped with hinged doors upstream to funnel the water inside and modify flow properties. Portable flumes have been developed to simulate benthic invertebrate drift (Gibbins et al., 2010) and sediment transport during floods (Gibbins et al., 2007; Vericat et al., 2008) and were recently used to study the interaction between sediment transport and aquatic vegetation (Harvey et al., 2011).

Our specific objectives were to investigate the effect of velocity and turbulence on prey detection and capture of juvenile Atlantic salmon and to assess the value of using a portable flume methodology. We will test the predictions that 1) capture probability declines with turbulence, 2) the number of attacks and the proportion of time spent on the substrate will decrease with turbulence and 3) parr will select focal positions with lower turbulence than random locations across the observation section.

5.2. Materials and methods

We designed and built a portable flume to be assembled and disassembled in a day in the field and fixed on the river bed at any wadable location using steel rods. Flume length and functioning was based on Vericat et al. (2007). The flume is composed of two parts: the downstream observation section, and the upstream hinged panels, referred as the wings (Figure 5.1). Both the observation section and the wings are made of translucent lexan panels and are joined together by stainless steel screws and polymer transverse bars. The entire flume is 2.4 m long, 0.6 m high and adjustable in width, which was set to 0.75 m for the current experiment. The observation section is 1.2 m long and is closed at both ends with mesh (1 cm) to prevent fish from getting out.

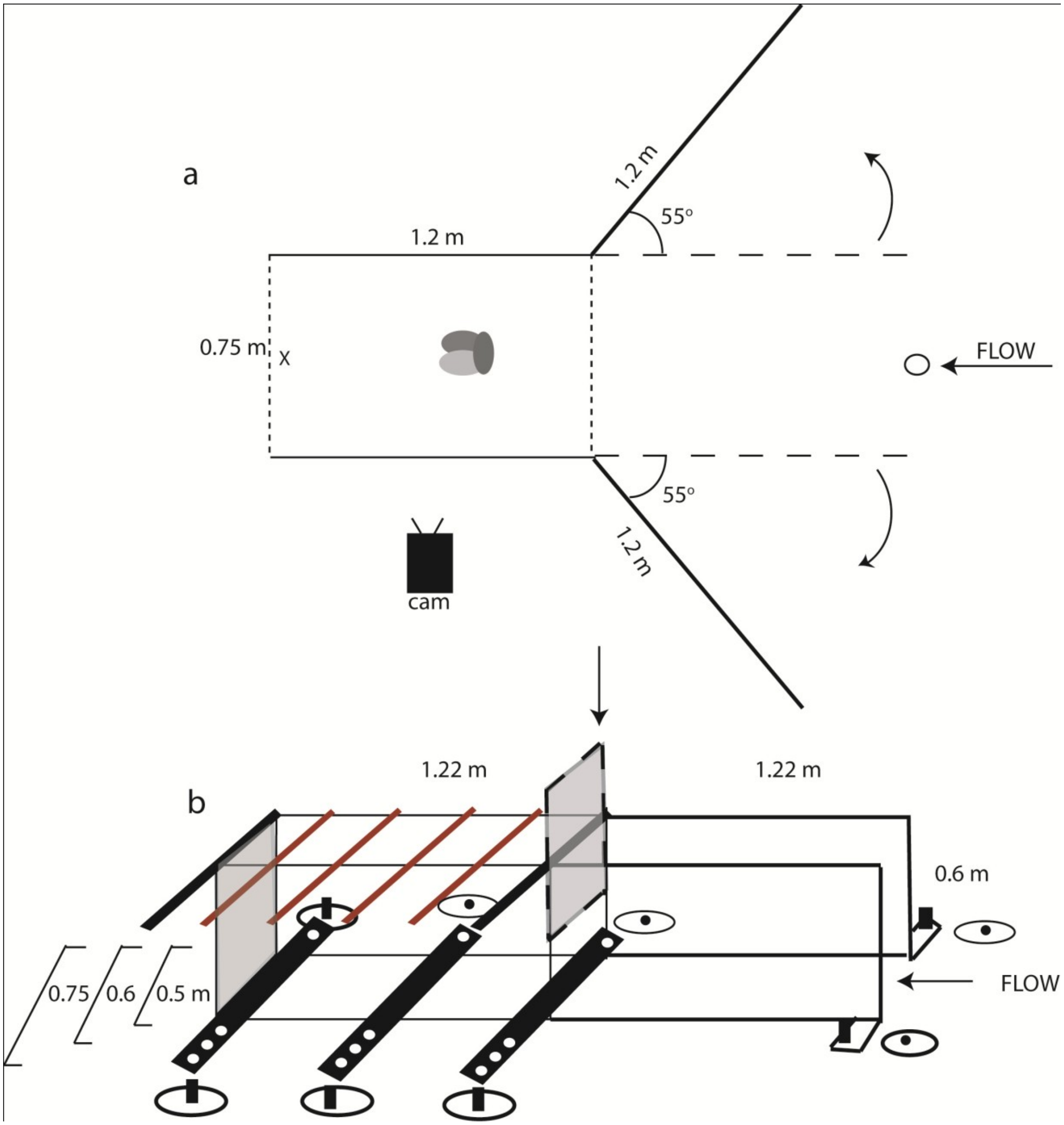

Figure 5.1 a) Plan view of portable flume. Dashed lines represent the positions of wings in open positions. Camera is held by a support underwater. “O” represents the location of food delivery at mid water column height. X defines the location of a continuously recording ADV. b) Side view of the portable flume with wings closed. For the experiment, width was adjusted to 0.75 m. Removable nets were installed at both ends of the observation section (shaded rectangles). Transversal bars (red) are attached in order to strengthen the flume structure.

When the wings are ‘closed’ (i.e. parallel to the observation section) and the flume is installed on a river bed that is relatively symmetrical on both sides of the wings, the flow characteristics within the observation section are similar to those observed in the absence of the flume (preliminary testing, Chaput-Desrochers, 2011). When the wings are displayed in an open position, more water is funnelled inside the observation section, thus creating an increase in velocity (Figure 5.1). To induce turbulence, six bricks (203 × 102 × 57 mm) were piled at the entrance of the observation section forming a pyramid (Figure 5.2). After several preliminary tests, this structure using bricks was favoured over other objects as it appeared to be a tradeoff between the efficiency of creating a turbulence pattern relatively similar to natural pebble clusters and ease of replication.

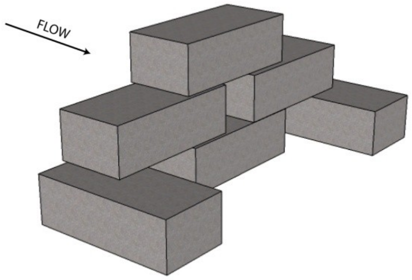

Figure 5.2 Added flow obstacle formed with standard American size bricks (203 x 102 x 57 mm) used to generate turbulence at the entrance of the observation section.

A camera (Sony, DCR-TV18) placed in a waterproof case (Amphibico) was fixed by a support on the left hand side of the flume, oriented perpendicular to the observation section (Figure 5.1). The camera was wired to a computer located on the river bank that allowed real-time observations (Figure 5.3 & 5.4).

Figure 5.3 Portable flume installed in Xavier Brook. Camera and velocity probes were wired to a computer on the bank. Four Acoustic Doppler velocimeters (ADVs) were used to characterize hydraulics within the observation section. ADVs were removed during feeding trials.

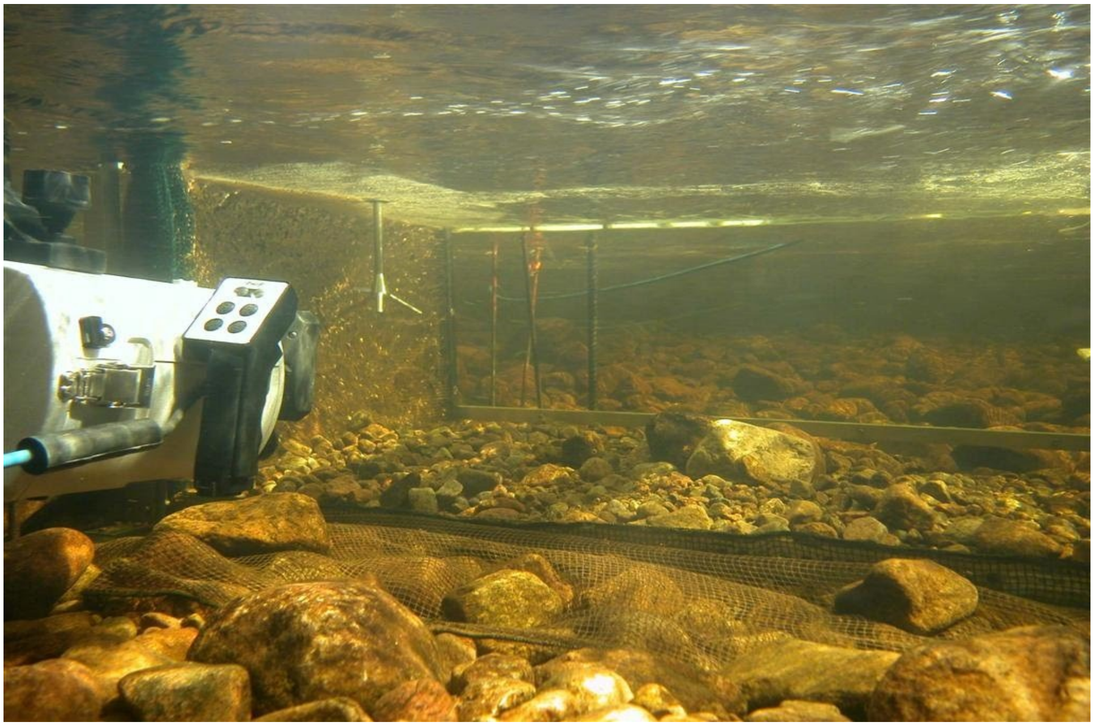

Figure 5.4 Underwater view of the observation section from beside the video camera. Flow is from right to left.

5.2.1. Experimental protocol

The experiment took place in Xavier Brook, Saguenay, Québec, which is a gravel-bed stream of approximately 15 m in width with a generally coarse substrate and clear riffle-pool morphology in its downstream section. A week preceding the experiment, the flume was installed in a glide (Figure 5.3), over a heterogeneous bed composed of a mix of 60% cobbles and 40% gravel. Several fish were caught by electrofishing and put in a fish tank. One at the time, the fish were put in the observation section of the flume and fed manually by releasing prey 1.5 m upstream from the observation section. During these tests, fish actively fed, but frequently escaped from under the panels of the observation section. Therefore, we added substrate along the observation section to block the cracks, thus altering the natural structure of the river bed and reducing the median substrate size (D_{50}) to 11 mm. The observation section was centred on a cluster of cobbles (B-axis:), to serve as a focal point as in previous laboratory studies (Piccolo et al., 2008b; Watz and Piccolo, 2011). Four flow treatments were generated, resulting in two levels of mean flow velocity (i.e. wings parallel and open) and four levels of increasing turbulence (LVT1: wings parallel without bricks. LVT2: wings parallel with bricks, HVT3: wings open without bricks, HVT4: wings open with bricks). When open, wings were placed at 55° from the parallel position (Figure 5.5).

Between 22 July and 15 August 2009, 29 juvenile Atlantic salmon were captured and used for feeding trials. The first 17 were captured by electrofishing and the remaining 12 were captured using small aquarium nets while snorkelling. Six fish were used for pre-trial testing. The experiment relied on 23 individuals, with an average weight and fork

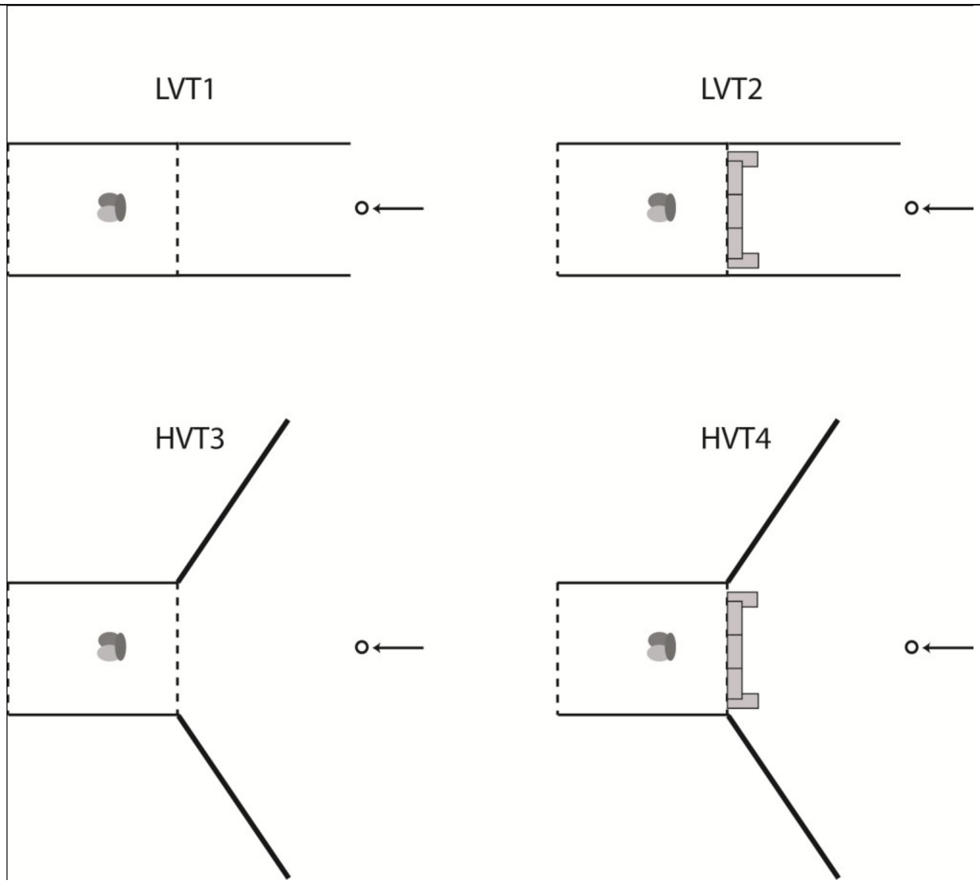

Figure 5.5 Four flow treatments carried out in the portable flume: Low velocity Turbulence 1 (wings parallel); Low velocity turbulence 2 (wings parallel with obstacle); High velocity turbulence 3 (wings opened); and, High velocity turbulence 4 (wings opened with obstacle). Flow is from right to left.

length of 13.7±0.9 g and 104±2.2 mm, respectively. One fish length and six weights could not be measured because one fish escaped from the flume and because of a scale malfunction at the end of the experiment. Four to six fish were captured and held in individual fish tanks in the river for a maximum of three days. The fish were starved for a minimum period of 24 hours before the feeding trials. Each fish was submitted to a feeding trial in each of the four flow treatments. Then, fish were released and new fish were captured in a new location. Each feeding trial consisted in placing a single fish in the observation section for 20 minutes to acclimatize, after which it was fed periodically with drifting rehydrated brine shrimps (*Artemia sp.*). Fish were observed ten meters away from the bank using the camera feed to a computer. When the fish started feeding, the trial began and the camera started recording for a period of 20 min. A feeding trial consisted of 80 prey releases. Each release delivered with a dropper consisted of 1 ml of rehydrated brine shrimps, typically containing one to three individual preys. On several occasions, when a fish sheltered in the interstices or laid inactive on the substrate for an extended period, the fish was removed and put back in the observation section later in the day or the next day for a second try. After three unsuccessful attempts, inactive fish were removed from the trial and released in the river. The order in which flow treatments were given was randomized. Prey were released 1.5 meters upstream from the observation section, in the mid-water column.

Water temperature was greater than 13°C for all treatments, well above 6.7°C, the temperature at which capture probability starts to decrease (Watz and Piccolo, 2011). Flow depth within the flume at minimum flow stage ranged from 32 in the center over the pebble cluster to 46 cm (Figure 5.6).

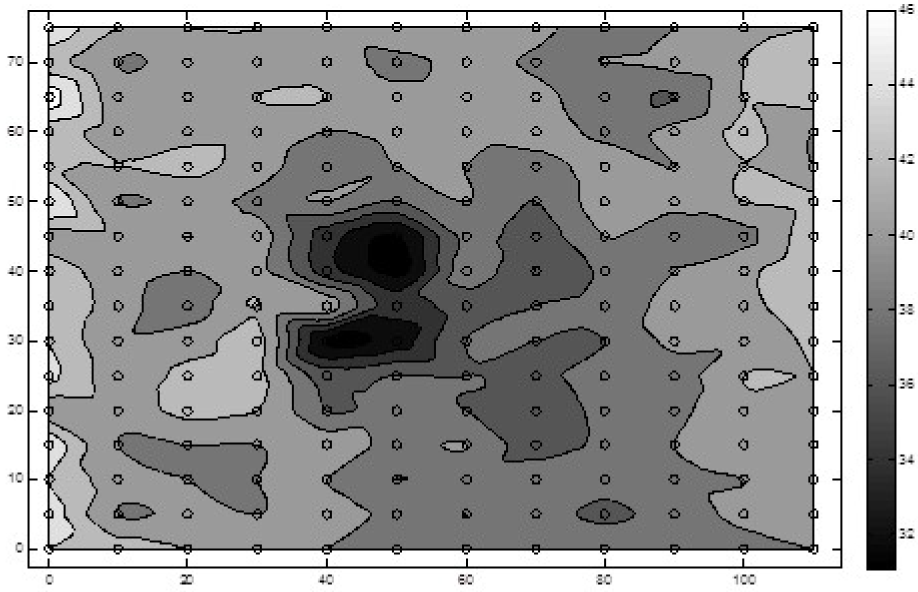

Figure 5.6 Bathymetry contour map (cm) in the observation section.

Flow stage variation, estimated from the depth measured every day within the observation section varied by only 3 cm among all trials.

5.2.2. Flow characterization and flow treatments

Flow velocity was measured every day using a propeller velocimeter at the upstream end of the wings ($30\ cm \cdot s^{-1} \pm 1.3\ cm \cdot s^{-1}$). Flow characteristics in the observation section were characterized in detail on August 8 at three heights above the bed: close to the bed (Y= 5 cm), at 0.4Y (15 cm) and at 0.6Y (25 cm). Four acoustic Doppler velocimeters (ADVs) mounted on a leveled graduated aluminum frame were used to sample 90 s velocity time series. This duration of recordings corresponds to the optimal record length for the estimation of turbulence statistics (Buffin-Belanger and Roy, 2005). ADVs provide velocity fluctuations at a frequency of 25 Hz for the three velocity components of the flow. For each flow treatment, 36 point measurements were sampled close to the bed and at 0.4Y and 72 points measurements were taken at 0.6Y. Each time series was inspected for obvious visual anomalies. Four to five measurements over the pebble cluster close to the bed were rejected for bad data quality. Time series data quality check and filtering was carried out using a methodology described in Chapter 4. Six flow variables were estimated and mapped. Mean downstream flow velocity (U) and mean vertical velocity (W) were estimated from averages of the longitudinal and vertical components of velocity time series. Time average turbulent statistics included mean Reynolds shear stress ($\tau = -\rho \langle u'v' \rangle$), where u' and v' denotes longitudinal and vertical velocity fluctuations from the mean and <> an average, ρ water density and turbulent kinetic energy ($TKE = 0.5 * (\langle u'^2 \rangle + \langle v'^2 \rangle + \langle w'^2 \rangle)$), where w' denotes vertical velocity fluctuations.

Each fish was subjected to four treatments (Table 5.1). Repeated measures ANOVA and multiple comparisons performed for each height for *U*, *TKE* and τ showed significant differences for all treatments.

Table 5.1 Spatially averaged statistics of downstream velocity (U), Reynolds shear stress (τ) and turbulent kinetic energy (TKE) per flow treatment

	LVT1	LVT2	HVT3	HVT4	RM-ANOVA
U 0.6Y(cm·s^{-1})	38.1	38.2	46.1	46.7	$F_{3,105}$=327, p<0.001
U 0.4Y(cm·s^{-1})	35.7	34.4	49.3	42.6	$F_{3,105}$=323.53, p<0.001
U bed(cm·s^{-1})	25.7	20.9	37.5	28.1	$F_{3,81}$= 41.758 p<0.001
τ0.6Y(N·m^{-2})	1.2	1.1	3.1	3.8	$F_{3,105}$=27.16, p<0.001
τ 0.4Y(N·m^{-2})	1.1	3.2	4.0	7.3	$F_{3,105}$=31.17, p<0.001
τ bed(N·m^{-2})	4.7	4.9	9.3	8.8	$F_{3,81}$= 5.099 p=0.003
TKE 0.6Y(cm·s^{-1})	18.1	18.9	34.4	36.1	$F_{3,105}$=17.28, p<0.001
TKE 0.4Y(cm·s^{-1})	20.1	26.3	27.4	40.3	$F_{3,105}$=53.03, p<0.001
TKE bed(cm·s^{-1})	39.5	47.8	54.0	65.5	$F_{3,81}$= 5.721 p=0.001

Spatially averaged streamwise flow velocity (*U*) at 0.6Y was of 38 cm·s^{-1} for the low velocity treatments (LVT1 and LVT2) and 46 cm·s^{-1} for the high velocity treatments (HVT3 and HVT4). However, closer to the bed, the added obstacle for treatments LVT2 and LVT4 induced an area of lower velocity in the lee of the obstacle, thus reducing the spatially averaged values of *U* for these treatments. In terms of turbulence, the four treatments represented an increasing gradient of TKE close to the bed with values ranging from 40 to 66 cm^{2}·s^{-2}. However, at 0.4Y (mean column height) and 0.6Y, TKE was lower when wings were parallel than open. Similarly, shear stress was higher in treatments HVT3 and HVT4 than LVT1 and LVT2, but differences among treatments with doors parallel and doors closed were low. However, although it was not quantitatively described, prey trajectories might be more diverse and unpredictable when the obstacle was placed at the entrance of the observation section (LVT2 and HVT4) than in treatments without obstacle (LVT1 and HVT3).

5.2.3. Video analyses

Videos were recorded at a frequency of 30 frames·s^{-1} and had a duration of 20 min. Each video was observed to extract fish foraging characteristics using VirtualDub video capture and processing utility (General public license). When other wild fish, mostly adult brook charr (*Salvelinus fontinalis*) approached the flume and were visible in the video, those parts were subtracted from the video, assuming competition might have modified the behaviour of the individuals under observation. From each video, five foraging variables were examined: 1) *prey capture probability* was estimated from the number of prey captures out of the 80 prey deliveries; 2) *proportion of aborted attempts* was obtained from the number of times fish initiated an attack on a drifting prey, but turned back in mid-course; 3) *prey attack time* was defined as the duration between the moment the fish left the substrate to attack a prey and the time when it closed its jaws around the prey; 4) proportion of *time resting on the substrate* was obtained by subtracting the duration of all feeding movements and non-feeding movements to the total duration of the trial (non-feeding periods were characterized by any time fish spent swimming for extended periods in the water column or by the switching between focal points); and 5) *height of prey capture* was defined for each attack as (0-10 cm), medium (10-25 cm) and high (25+ cm). We carried out data transformation (Log_{10}+0.5) to obtain normality of the frequency distribution and to homogenize variances.

Fish foraging characteristics between treatments were compared using mixed models accounting for repeated observations on the same individuals and using flow treatments as fixed effect. Best covariance structure was selected based on lowest AIC values (Burnham et al., 2011). In order to assess the preferential focal positions adopted by fish within the flume, the location of the fish nose when it was laying on the substrate was noted as a proportion of use per minute on a 10 X 10 cm grid using Matlab(c) image processing toolbox. For each hydraulic variable, frequency of use and availability were used to obtain estimates of preference based on Jacobs (1974) Index

$$D = \frac{r - p}{r + p - 2rp}$$

where r is the proportion of a range of hydraulic values used by the fish and p is the proportion available in the flume.

5.3. Results

From the total of 92 feeding trials, fish were considered actively feeding (i.e. more than 5 prey) in 49 trials (52%) (Figure 5.7). Only five individuals were considered active during all four treatments. Fish were not interested in feeding in 14 trials (15%), as they mainly rested on the substrate and performed fewer than 5 prey captures. The remaining 29 trials (31%) were not recorded because the fish never started feeding.

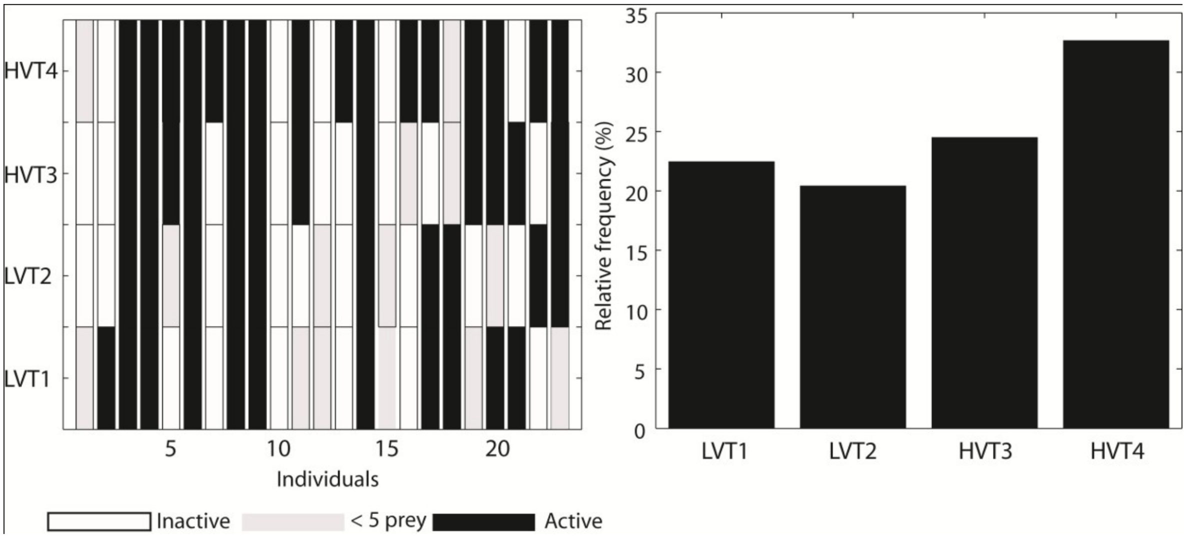

Figure 5.7 A) Feeding trials per individual, for which fish were inactive and never started feeding (fish showed low interest in feeding and performed fewer than 5 feeding excursions) and trials in which individuals were actively feeding. B) Frequency of successful trials (i.e. fish actively feeding) per treatment.

From the 49 effective feeding trials 22% to 24% were LVT1, LVT2 and HVT3 treatments. Thirty-two percent of treatments were HVT4 and difference in frequencies among treatments were not significant (χ^2= 1.694, df=3, *p*=0.638) (Figure 5.7).

5.3.1. Effect of flow manipulation on fish foraging

High inter-individual variability was observed within each treatment for the four foraging variables (Figure 5.8). Despite differences in means, no significant difference was observed between treatments for any variable (Table 5.2). Average capture probability ranged between 0.25 and 0.4 and was higher for the low velocity treatments LVT1 and LVT2, although not significantly, and capture probability was more variable between individuals. No difference in capture probability was observed among the treatments with and without a flow obstacle.

Table 5.2 Mixed models testing effect of flow treatment on four fish foraging variables.

		df	F	p
Capture probability	Intercept	1, 15.5	71.17	<0.001
	Treatment	3, 31.4	1.55	0.221
Aborted excursion	Intercept	1,16.0	65.5	<0.001
	Treatment	3,36.4	2.45	0.079
Prey attack time	Intercept	1,17.1	80.95	<0.001
	Treatment	3,30.0	1.6	0.210
Resting on the substrate	Intercept	1,16.8	604.04	<0.001
	Treatment	3,29.0	0.82	0.492

In contrast, the average observed probability of aborted foraging excursion seemed lower for the treatments without obstacle than with obstacle. Average proportion of aborted excursions ranged between 0.04 and 0.08.

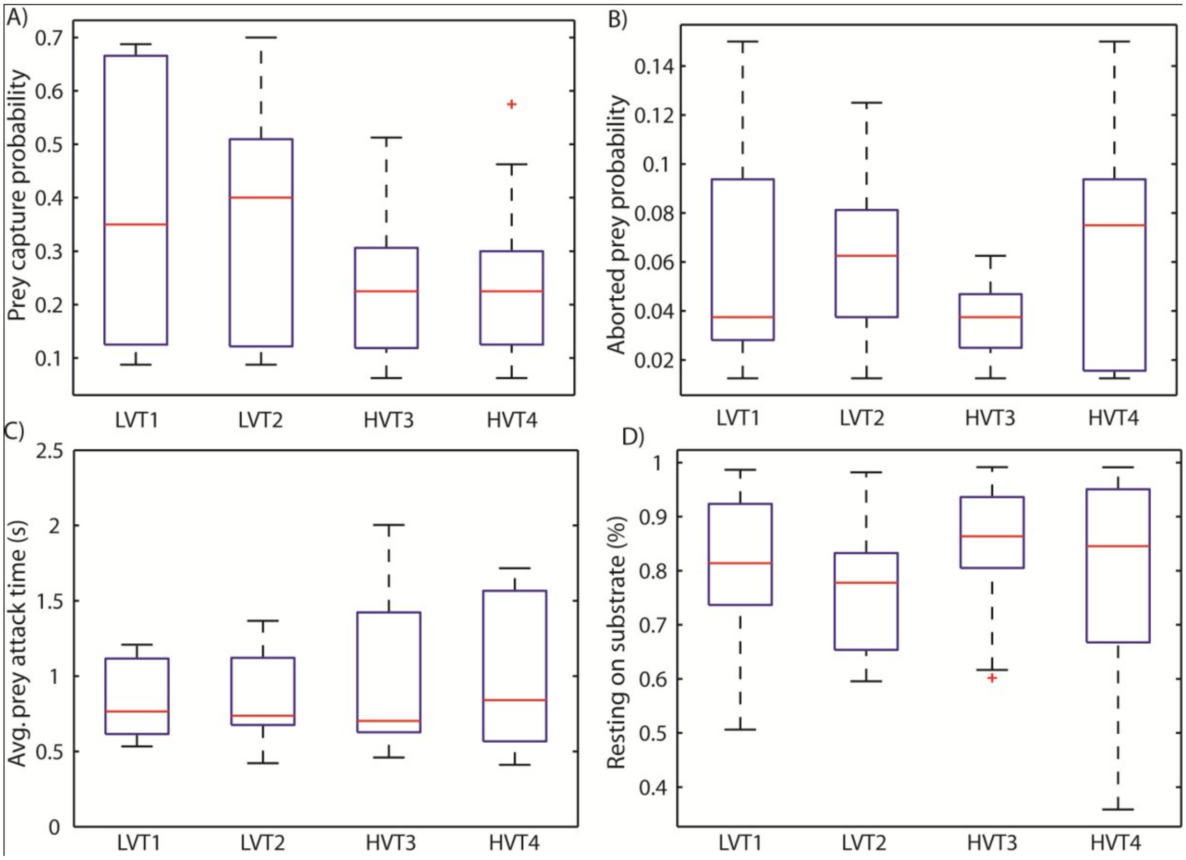

Figure 5.8 Boxplot of A) prey capture probability, B) aborted prey probability, C) average attack time of prey drifting at 10-25 cm and D) proportion of time resting on the substrate per flow treatment. LVT1: low speed low turbulence, LVT2: low speed high turbulence, HVT3: high speed low turbulence, HVH4: high speed high turbulence.

Average prey attack time ranged between 0.7 and 0.8 s and was consistent across treatments. Except for a few exceptions, fish rested on the substrate most of the time in all treatments, with averages ranging between 75 to 85%. The proportion of attacks at low height (0-10 cm) ranged from 49-63%, medium height (10-25 cm) attack proportions ranged from 30-42% and high attacks (25 cm+) ranged from 2 – 13%. Differences in average proportion of attacks per height did not differ significantly for any height (mixed model Low height $F_{3,29.98}$=1.13, p=0.354; medium height, $F_{3,32.73}$=1.246, p=0.309; high height $F_{3,29.27}$=1.398, p=0.264) (Figure 5.9).

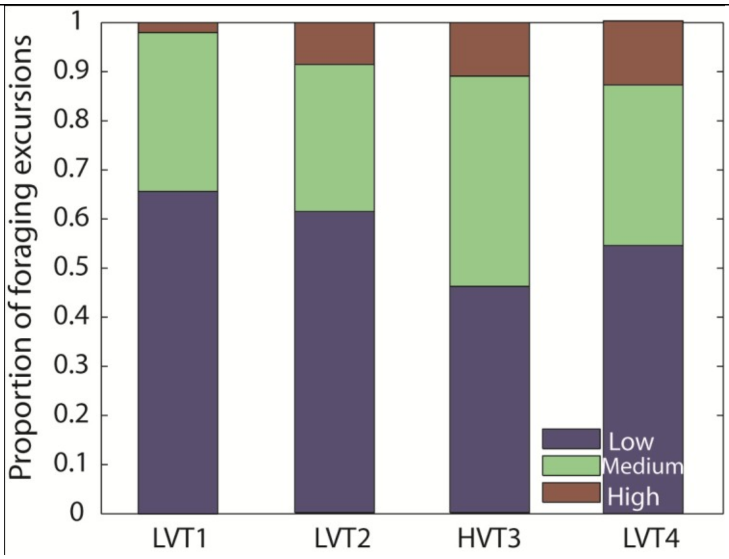

Figure 5.9 Proportion of attacks at low (0-10 cm), medium (10-25 cm) and high (25-40 cm) height per treatment.

5.3.2. Flow manipulation

Average flow properties differed between flow treatments (Table 5.1). However, there was considerable overlap in flow properties values between treatments caused by high spatial flow heterogeneity in the observation section (Figure 5.10 and Figure 5.11). For downstream flow velocity (*U*), at 0.6Y, flow velocity was relatively homogeneous and lower for the treatments with the wings parallel than closed (Figure 5.10). However, at 0.4Y and close to the bed, the spatial heterogeneity was more similar between the treatments with or without the flow obstacle.

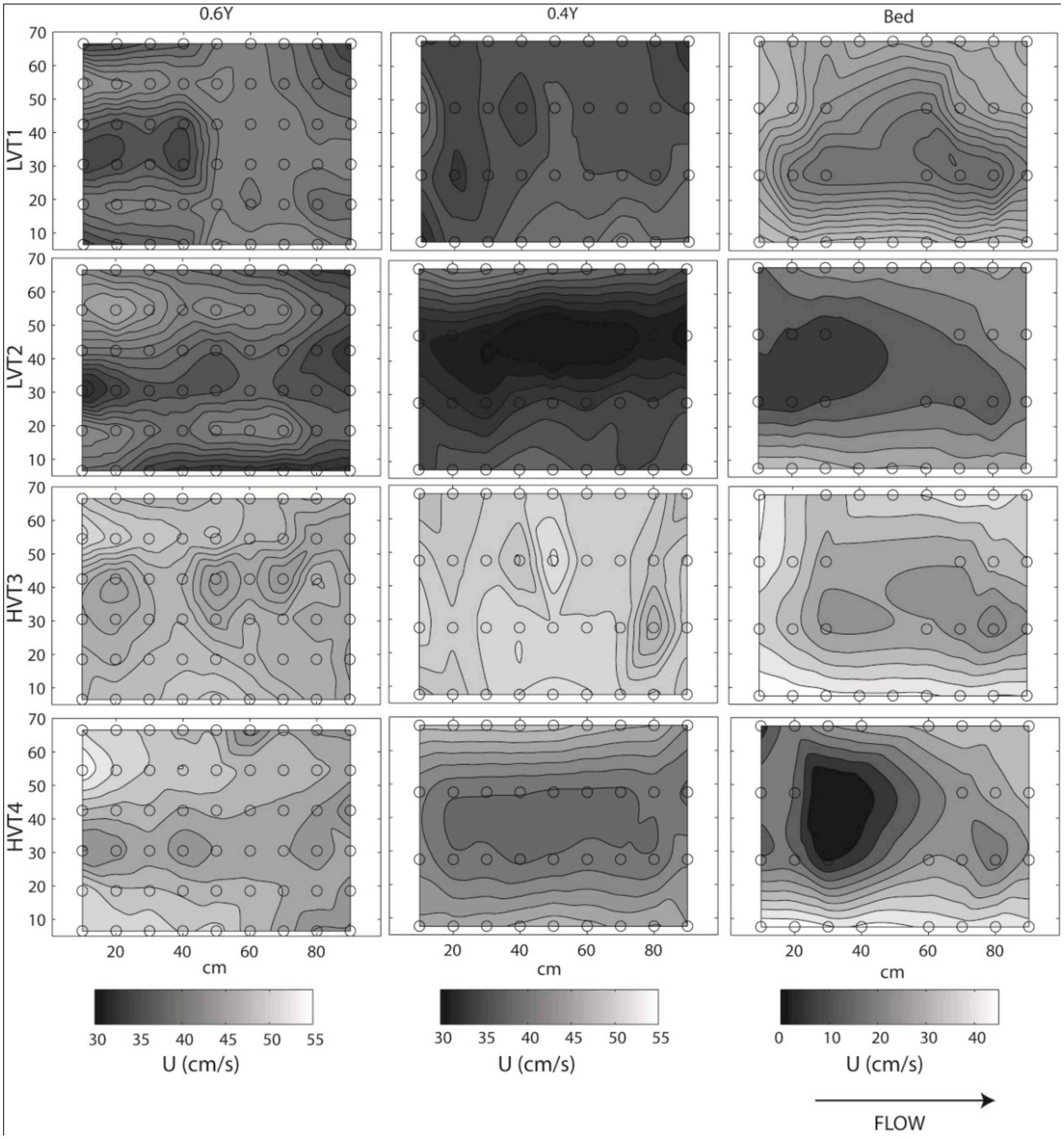

Figure 5.10 Maps of streamwise velocity (cm/s) A) close to the bottom (5 cm above the bed) B) at mean column velocity (0.4Y) C) and at 0.6Y (25 cm above the bed) for the four flow treatments.

At 0.4, *U* spatial structure was relatively homogeneous for LVT1 and HVT1, and with a transverse gradient with lower *U* in the center, caused by the presence of the obstacle, than closer to the wall for LVT2 and HVT4. Closer to the bed, a longitudinal pattern was created by the central pebble cluster for all treatments although this pattern was clearer for treatments with the added obstacle.

Turbulence, described in terms of Reynolds shear stress (τ), also overlapped greatly between the treatments (Figure 5.11).

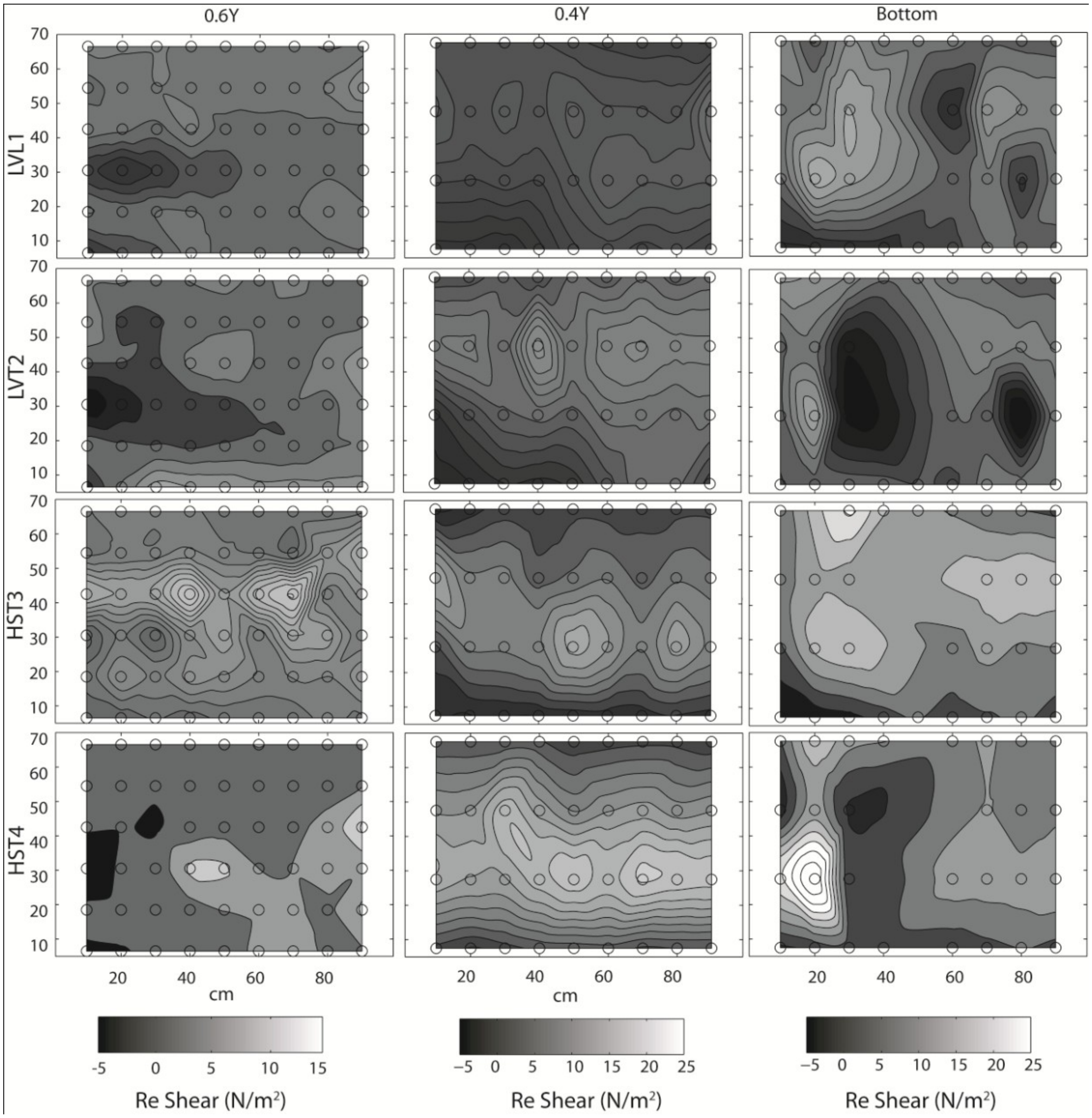

Figure 5.11 Maps of Reynolds shear stress ($N \cdot m^{-2}$ $X10^{-1}$) A) close to the bottom (5 cm above the bed) B) at mean column velocity (0.4Y) C) and at 0.6Y (25 cm above the bed) for the four flow treatments.

For all treatments, average τ was higher close to the bed and decreased towards the surface (Table 5.1). At 0.4Y, average τ increased from treatment LVT1 to HVT4 and spatial patterns were relatively similar, with higher τ in the middle than closer to the walls. Close to the bed and at 0.6Y, the wing display created more difference in average Reynolds shear stress than the addition of the obstacle. However, the added obstacle caused larger differences in spatial patterns between treatments. Treatments LVT2 and HVT4 presented the widest range of τ values, with negative values around the pebble cluster and values reaching 25 $X10^{-1}$ $N \cdot m^{-2}$ in the lee of the obstacle in HVT4.

5.3.3. Preferential focal positions within the flume

Juvenile salmon selected specific locations in the observation section, which were characterized by a narrow range of hydraulic values. No fish used the pebble cluster in the center of the observation section that was expected to serve as fish focal point. Instead, they selected the area located in the most downstream 20 cm cross-section of the observation section (Figure 5.12). Fish did not adapt preferential focal positions to changes in the hydraulic spatial structure within the flume but generally selected the same locations. In treatment HVT3, fish spatial distribution was slightly wider.

Across flow treatments, preferred focal positions were typically characterized by the highest values of U available in the flume and avoided the low velocities (Figure 5.12). Also, fish were more often found in areas of downward velocity (negative W) and avoided areas of upward velocity (Figure 5.13).

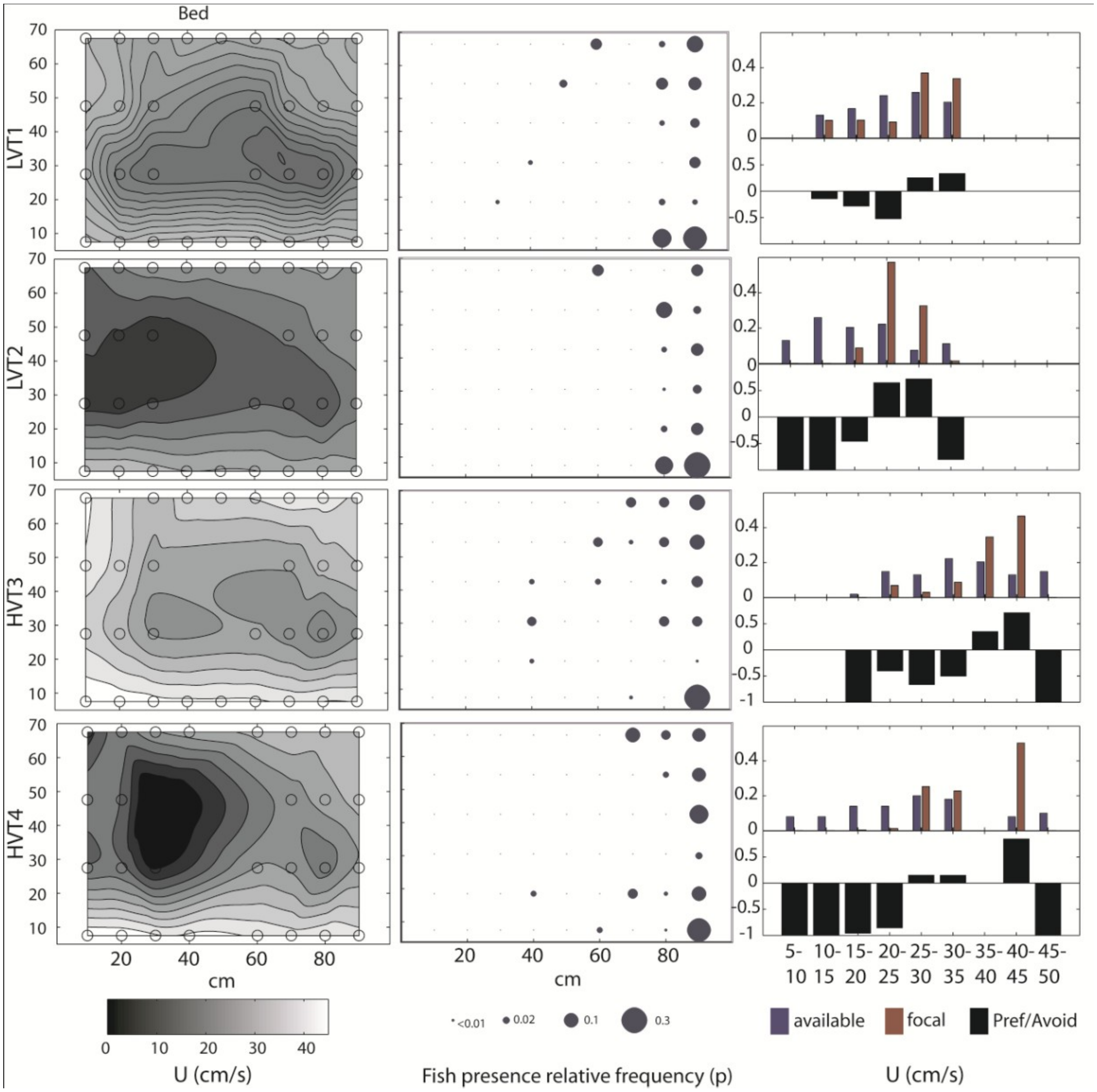

Figure 5.12 Maps of bottom downstream flow velocity. (Center) Relative frequency maps of fish locations (datum =individuals). Flow is from left to right. (Right) Relative frequency of available and used focal mean flow velocity and associated preference index. Positive and negative values illustrate preference and avoidance respectively

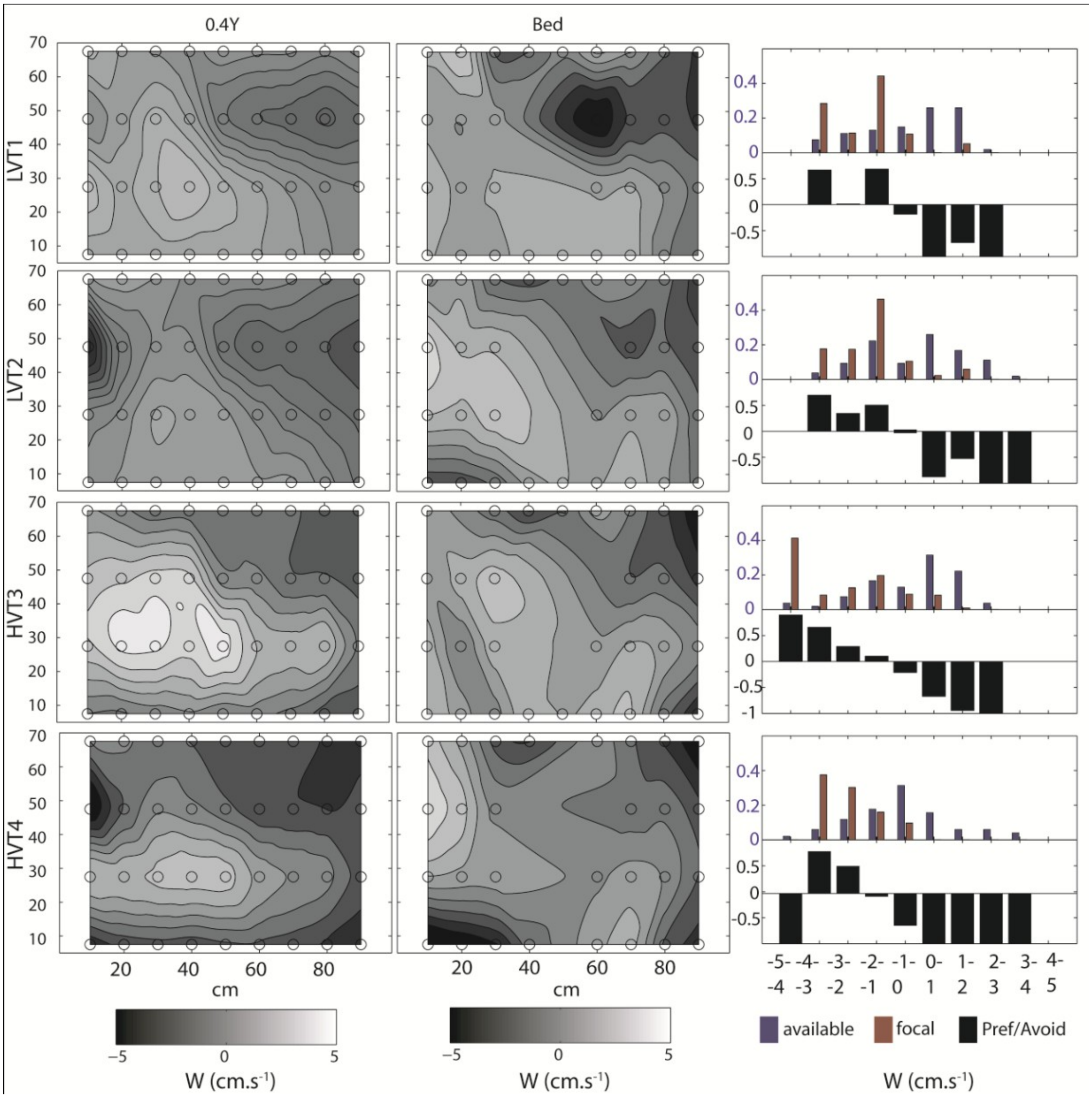

Figure 5.13 (Left) Maps of bottom vertical velocity (W). (Center) Maps of longitudinal Integral time scale (ITSU) at 0.4Y. Flow is from left to right. (Right) Relative frequency of available and used focal vertical velocity (positive values =upward, negative = downward) and associated preference index. Positive and negative values illustrate preference and avoidance respectively.

In terms of Reynolds shear stress, fish avoided areas where τ was negative and where it was over 10-25 X10^{-1} N·m^2 (Figure 5.14). They preferred focal positions where τ was 0-5 X10^{-1} N.m^{-2} in the treatments without obstacle and 5-10 N·m^{-1} in the treatments with obstacle.

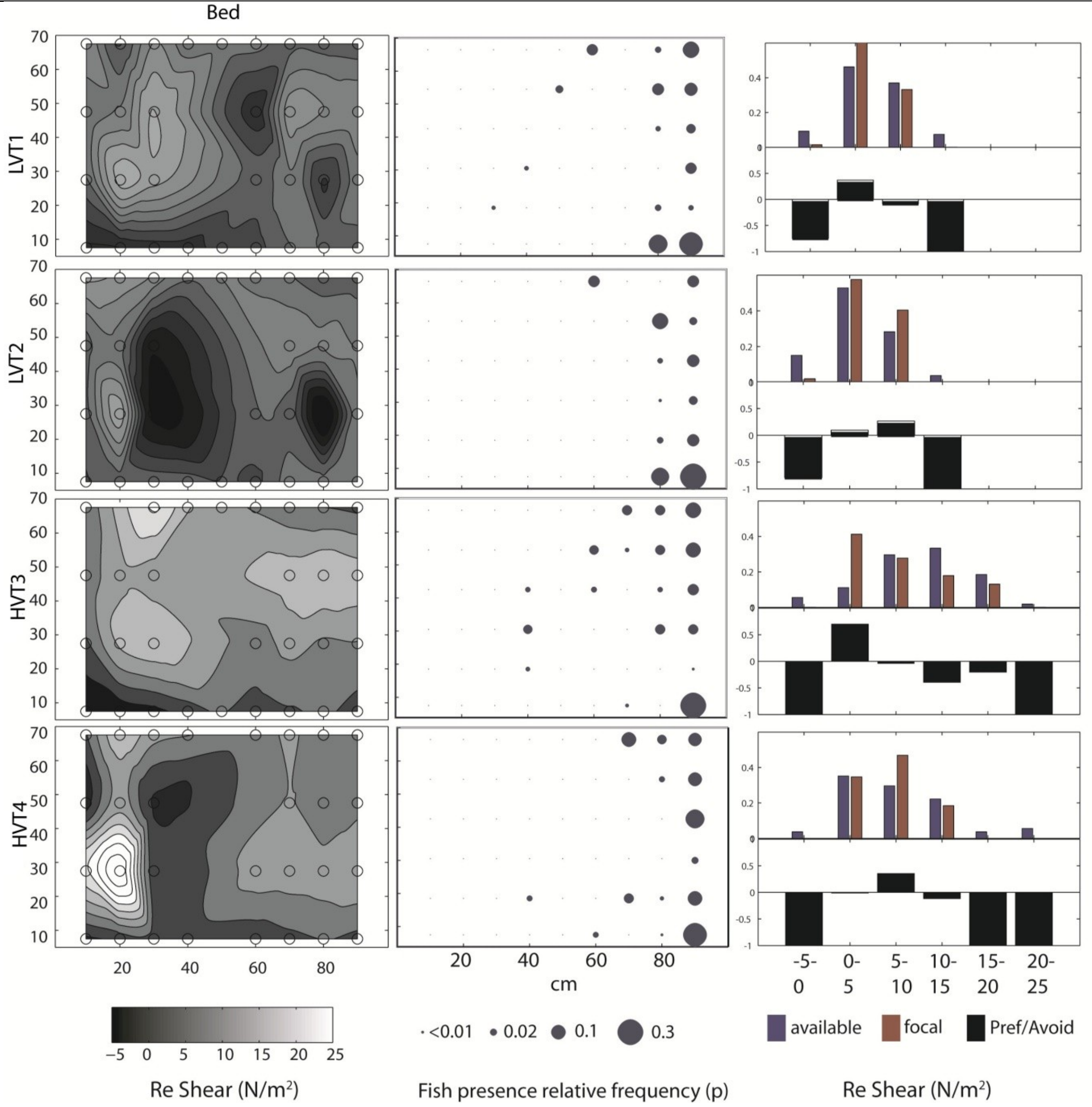

Figure 5.14 (Left) Maps of bottom Reynolds shear stress. (Center) Relative frequency maps of fish locations (datum =individuals). Flow is from left to right. (Right) Relative frequency of available and used focal Reynolds shear stress and associated preference index. Positive and negative values illustrate preference and avoidance respectively.

Similarly, preferred focal positions were characterized by low TKE values ranging from 0-50 $cm^2 \cdot s^{-2}$ and high turbulence locations were avoided (Figure 5.15).

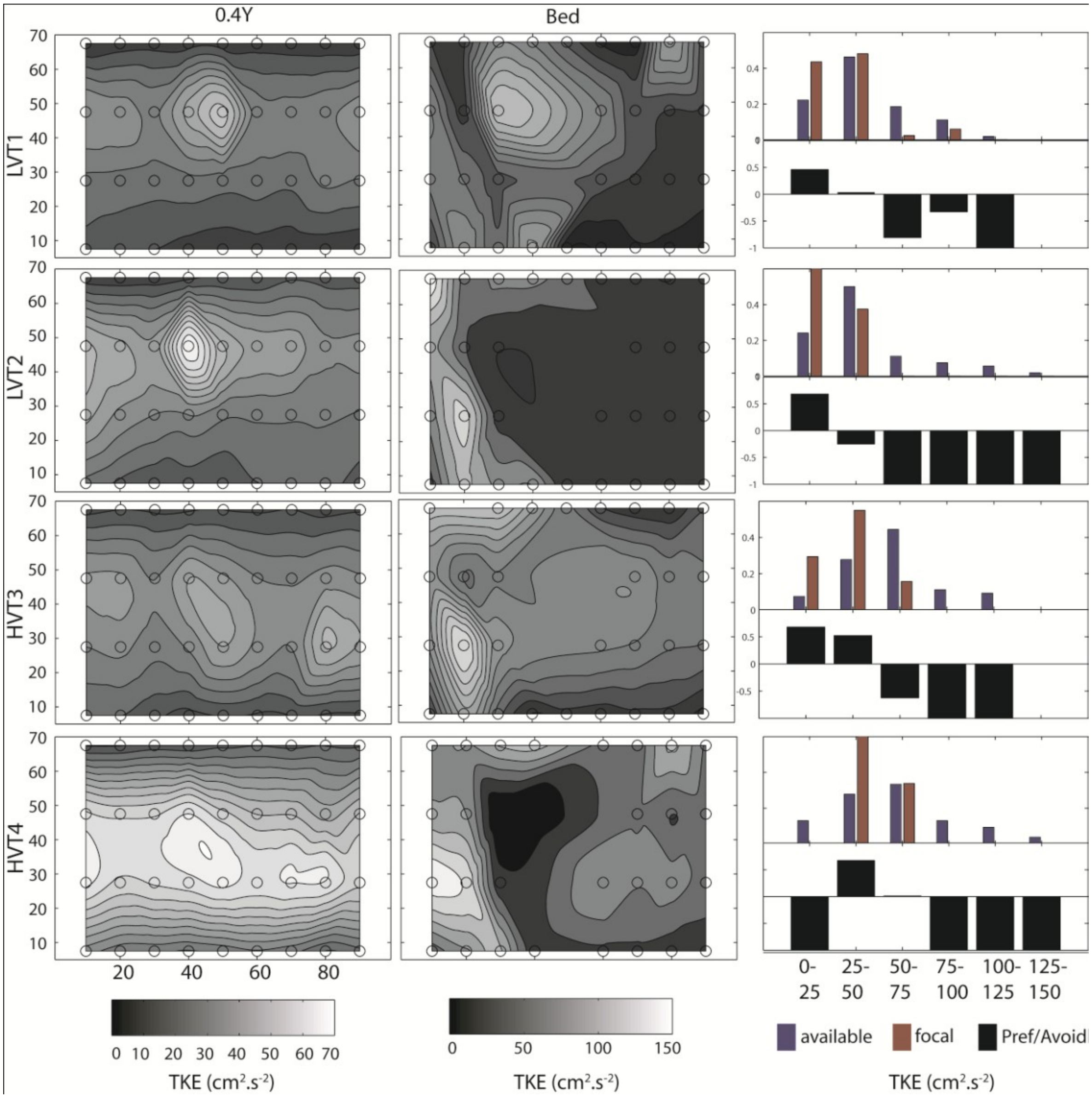

Figure 5.15 (Left) Maps of bottom turbulent kinetic energy (TKE). (Center) (Left) Maps of TKE at 0.4Y. Flow is from left to right. (Right) Relative frequency of available and used focal TKE and associated preference index. Positive and negative values illustrate preference and avoidance respectively.

5.4. Discussion

Our results showed high inter-individual variability in the foraging success and time budget within each flow treatment. Therefore, no clear effect of average hydraulic properties on the ability to catch prey was observed. However, the average prey capture probability for the two lower velocity treatments (U0.6Y: 34-36 $cm \cdot s^{-1}$) was higher than that for the two higher velocity treatments (U0.6Y: 42-49 $cm \cdot s^{-1}$) by 25%. Although this difference was not statistically significant due to high variability, this capture probability values are similar to those observed at comparable levels of average velocity for *Oncorhynchus mykiss* (Hill and Grossman, 1993, decrease of 0.35 to 0.10) and *O. kiysutch and O. mykiss* (Piccolo et al., 2008b, decrease of 0.52 to 0.3).

The inverse relationship between flow velocity and prey capture probability could be due to a diminution in prey detection distance (i.e. faster moving prey are detected closer to the fish) and to a decrease in detection probability (Piccolo et al., 2008b). One might expect a similar rationale to apply to turbulence, as higher turbulence might lead to more unpredictable prey trajectories that might affect fish prey detection ability. However, this hypothesis was not confirmed, as prey capture probability was similar between the two treatments of comparable velocity, even though they had contrasting levels of turbulence at mean column height.

Fish preferentially selected focal positions in moderate velocity, and low turbulence areas and avoided the highly turbulent locations. This behaviour, previously observed for juvenile salmonids in a laboratory flume (Smith et al., 2005) and in the field (Cotel et al., 2006), could be attributed to higher swimming costs in higher levels of turbulence (Enders et al., 2003). Similarly, the selection of average downward velocities and avoidance of upward velocities might be associated with the ease of maintaining position. Parr resist downstream displacement by balancing the drag with the friction force (Arnold, 1991). While downward velocity adds to the friction force, upward velocity contributes to the lifting force, hence imposing a stress on the fish and possibly higher energy expenditures associated with maintaining position. Average vertical velocity might be an important feature driving microhabitat selection.

The choice of a semi-experimental approach using a portable flume to observe fish feeding behaviour involved multiple tradeoffs. While it allowed examining fish feeding in an environment close to a natural one, the experimental controls were relatively limited and several causes might have obscured the process under observation.

During the study period, fish showed a generally low interest in feeding. Among 92 possible trials, 42 were rejected because fish were inactive or sheltering in the substrate. Furthermore, in the retained trials, it was not possible to distinguish missed prey due to undetected prey or due to a low interest in feeding. The low activity during the day might be explained by the dominant nocturnal activity pattern of parr (Imre and Boisclair, 2004). The difficulty in distinguishing inactivity from prey capture probability was also an issue for Watz and Piccolo (2011), who observed fish foraging at temperatures below 8^{o}C. Furthermore, the clear effect of velocity on prey capture probability previously shown was for smaller juvenile salmonids (Piccolo et al. 2008; 75-80 mm).

Flow treatments generated in the portable flume and the addition of the obstacle provided a relatively small range of spatially averaged velocities and turbulence (at 0.4Y U 35 to 49 $cm \cdot s^{-1}$, TKE: 20-40 $cm^2 \cdot s^{-2}$), but a wide range of hydraulic values within each flow treatment. Therefore, hydraulic values were overlapping between the treatments, particularly higher above the bed. Perhaps turbulence would have a clearer effect below or above the range of average values tested in this study.

Our hypothesis that turbulence would decrease prey capture probability was based on the assumption that higher average turbulence statistics causes unpredictable prey trajectories. However, this assumption needs testing, because spatial structure might also play a role. For instance, treatment LVT2, a treatment with the added obstacle, caused lower turbulence magnitudes than HVT3, without the added obstacle. Furthermore, although it was not a significant effect, there was a slight difference in the frequency of aborted excursions between the treatments with and without the added obstacles. The overlap between hydraulic characteristics across treatments was also caused by the positive correlation between the magnitude of average turbulence statistics and downstream flow velocity (Nikora, 2006). However, in morphological units of gravel-bed rivers, velocity is only moderately correlated with turbulence statistics, as locations with similar velocity sometimes show contrasting levels of turbulence (Roy et al., 2010), particularly as a function of bed roughness and protruding roughness elements (Buffin-Belanger and Roy, 1998).

Previous use of portable flumes in rivers (Gibbins et al., 2007; Vericat et al., 2008) have not explicitly characterized the flow field within the observation. Flow maps revealed a generally symmetrical downstream flow velocity pattern, with regions of lower velocity in the centre resulting from the presence of the pebble cluster and the added obstacle. Velocity increased away from the obstacle in a gradient towards the walls, which might be expected in natural flows. However, the presence of a clearly downward velocity in the downstream corners is atypical and these were the favoured focal locations of the juvenile salmon. These vertical velocities might have been induced by the addition of a downstream net used to prevent the fish from getting out of the section. Nevertheless, the treatments with the wings placed in an open position created conditions of higher velocity and turbulence without creating obvious changes in the flow spatial structure. However, preliminary flume testing in higher flow velocities (60-90 $cm \cdot s^{-1}$) in a different river has shown a strong modification of the flow structure in the first half of the observation section caused by the funnelling, which suggests a need to increase the observation section length (Chaput-Desrochers, 2011). Such flow patterns, untypical of natural high flows should be described while using a portable flume in stream invertebrate and sediment transport studies. Furthermore, several aspects related to the use of portable flumes remain to be assessed. For example, using the flume in locations with various slopes and bed morphology might provide different effects on flow treatments. With respect to velocity, perhaps using the flume in locations with contrasting habitat features without opening the wings could be a valuable approach guaranteeing the preservation of flow conditions that are fully representative of what the fish experience in nature.

Early process-based foraging models were based on the assumption that fish catch 100% of their prey in a given reaction volume (Hughes and Dill, 1990). Taken together with other studies, our results confirm that this is not the case. Our experiment did not show a significant effect of velocity and turbulence on the ability of fish to catch prey. Our results do not rule out the effect of turbulence on fish foraging but rather highlight the need to investigate this question further with a wider range of hydraulic values in order to possibly implement a turbulence–dependent prey capture function that might be useful to mechanistic foraging models.

5.5. Linking paragraph

The previous chapter examined the effect of turbulence on prey capture ability. Despite the absence of a clear effect of turbulence on drift feeding, fish preferred positions within the portable flume that were located in areas of lower turbulence intensity. In a natural habitat, juvenile salmon use a variety of habitats and can move between foraging stations. Therefore, it is possible that they might select microhabitats based on their hydraulic properties, but also based on the properties of surrounding adjacent areas. In the following chapter, we test this hypothesis by examining the scales of habitat selection of juvenile salmon in a natural river reach during three months. This chapter highlights scale-dependent habitat selection, and supports the importance of the *patch* spatial scale and the temporal scales of one hour, to describe the range of habitat used in a day, and three days, to describe the range of habitat used in a month. Chapter 6 introduces Data set 3, by describing the habitat use of tagged fish in the reach and average trends of habitat selection, which will be dissected in more detail in Chapters 7-8.

Chapitre 6: Spatiotemporal scales of habitat selection of juvenile Atlantic salmon

6.1. Abstract

Habitat preferences of Atlantic salmon were quantified using a large array of passive integrated antennas at high resolution during three months in a natural stream reach over spatial scales ranging from *micro* ($0.28 m^2$) to *meso*-scale ($78\ m^2$) and over temporal scales ranging from 5 minutes to 24 days during day, night, summer, and autumn. Fish exhibited an overall preference for moderate and high classes of flow depth (0.45-0.90 m), flow velocity ($0\text{-}50\ cm \cdot s^{-2}$), low turbulence ($TKE = 0\text{-}200\ cm^2 \cdot s^{-2}$) and high bed roughness (>0.05 m) at the *micro*-scale, but were also positively associated with higher depth and velocity at the *patch*-scale (1.35-1.65 m and $25\text{-}75\ cm \cdot s^{-1}$). These data suggest that fish take into account both the properties of their *micro*-habitats, but also the depth and velocity in the surrounding area. The range of habitat used increased asymptotically with the temporal scale of observation. On average, individuals used close to 10% of the range of available habitats in 5 minutes, 20% in one hour and over 60% in three days. A period of 1h was identified as a minimum duration required to characterize the daily habitat range of an individual and a period of three days the minimum duration to characterise the seasonal habitat use range. This high resolution data set illustrates the ecological relevance of the *patch*-scale habitat sampling and the considerable temporal variability of the mean daily habitat used by a group of individuals in a reach.

6.2. Introduction

The questions of how and why fish select their habitat are critical, as they lead to the identification of habitat requirements and to improved resource management plans

(Rosenfeld, 2003). Because fish habitat selection is influenced by processes interacting over a range of spatial and temporal scales, the implications of studies are influenced by the chosen scale of investigation (Folt et al., 1998). Therefore, detailed knowledge of how habitat selection changes over the range of scales could enhance habitat restoration initiatives where fish populations are declining.

Numerous studies have detailed the habitat preferences of wild juvenile salmonids in relation to physical habitat variables using correlative habitat associations (Armstrong et al., 2003). The vast majority of habitat selection studies have focused on the *meso*-scale (morphological units, i.e. pools and riffles) (e.g. Grant and Kramer, 1990; Armstrong et al., 1998; Stickler et al., 2008) and the *micro*-scale (i.e. point measurement where fish is observed) (e.g. Rimmer et al., 1984; Degraaf and Bain, 1986; Heggenes and Saltveit, 1990). During their juvenile stages, Atlantic salmon spend most of their time feeding or sheltering from predators. At the *meso*-scale, preferred salmon parr habitats are characterized by large areas of gravel and cobble substrate, typically found in riffles (Keenleyside, 1962; Symons and Heland, 1978). However, parr are also present in less typical habitats such as pools (Saunders and Gee, 1964) and slow moving waters (Gibson and Coté, 1982). At the *micro*-scale, habitat selection is routinely characterized by building preference curves of physical habitat variables using the IFIM (Bovee, 1982). However, ranges of habitat use can vary importantly between rivers or study sites (Maki-Petays et al., 2002). This complexity may be due to temporal variability of habitat selection patterns or be induced by multiple factors such as fish density, spatial structure of habitat availability, or region-specific fish behaviour (Reeves et al., 2010).

Although juvenile Atlantic salmon have long been regarded as sedentary and territorial (Kalleberg, 1958; Saunders and Gee, 1964), more recent studies have revealed that parr are more mobile, use a variety of habitats, and occupy overlapping home ranges (Okland et al., 2004; Ovidio et al., 2007). Furthermore, the properties of surrounding habitats could play a role in providing complementary functions such as feeding and cover (Durance et al., 2006; Johnston and Bergeron, 2010). From this dynamic spatial behaviour, we can hypothesise that parr select their habitat based on the properties of *micro*-habitats, but also on the properties of the surrounding *meso*-habitats – i.e. at the scales of morphological units. Therefore, the size of habitat sampling units might be important in the accurate description of salmonids habitat selection.

The awareness of the importance of scale on the interpretation of habitat selection has increased the interest in conducting spatially explicit methods to explore juvenile salmonid habitat selection. Bult et al. (1998) developed a technique to describe spatial scaling and habitat selection in fluvial habitats. As an example application of their technique, they showed how daytime depth preference of young-of-the-year (YOY) Atlantic salmon changed with the scale of investigation. Fish preferred intermediate depths at the reach level, but preferred shallow depths at larger spatial scales, which suggested a preference for intermediate depths located close to riffles rather than pools. Similarly, Guénard et al. (2010) investigated the habitat association of 1+ and 2+ juveniles over larger scales, ranging from 0.2 to 6.0 km, using a new complex statistical spatial analysis. Parr abundance was mostly associated with river bed composition at the 0.4-4.1 km scales whereas channel depth was more influential at the 0.2 to 0.3 km scales. Both studies reported scale-dependant patterns of habitat selection and underlined the importance of identifying the scales relevant to fish to better interpret fish behaviour.

Habitat selection might also vary with the temporal scale of observation. At the temporal scales of a few minutes, mobile individuals might use both medium-velocity habitats to “sit-and-wait” and high-velocity habitats where they perform brief foraging movements (Fausch and White, 1981). At the scale of a few hours during daytime, juvenile young-of-the-year salmon tend to use multiple central place territories (Steingrimsson and Grant, 2008). Such space use may or may not lead to variability in habitat use in a short period of time. At the daily time scale, older juvenile Atlantic salmon tend to select habitats with lower velocity at night than during the day, to offset a decrease in their ability to catch drifting prey in the darkness (Metcalfe et al., 1997). As parr get older, they are more active at night than during the day (Imre and Boisclair, 2004; Johnston et al., 2004), although not all individuals behave this way (Chapter 7). Activity patterns might also change at the seasonal scale, as a result of a complex trade-off between susceptibility to predation and meeting metabolic demands (Fraser et al., 1993). During the summer, Atlantic salmon parr are active during the day, but also at night (Gries et al., 1997). However, as the temperature decreases below 8-12°C, parr suppress their daytime activity to become mostly nocturnal (Valdimarsson et al., 1997; Johnston et al., 2004). Such behaviour can be accompanied by a stronger preference for large-substrate-size *micro*-habitats, providing shelter at night, and riffle *meso*-habitats during the day (Heggenes et al., 1996; Mitchell et al., 1998). Changes in habitat use occurring at the scale of multiple days might result from competitive interactions or fish exhibiting “wandering” behaviour, characterized by the absence of a fixed territory (e.g. Armstrong et al., 1999; Chapter 8).

The most important *micro*-habitat features are flow velocity (*U*), flow depth (*Y*) and substrate size (*D*) (Heggenes and Saltveit, 1990). Flow velocity is often regarded as the most important physical *micro*-habitat variable, as it affects food drift rate and fish energy expenditures (Hughes and Dill, 1990). However, velocity fluctuations, or turbulence, has also been identified as a relevant physical variable. Turbulence is associated with a decrease in maximum sustained swimming speed (Pavlov et al., 2000), an increase in swimming energy costs (Enders et al., 2003), and the spatial heterogeneity of drifting prey (Leung et al., 2009), which influences fish habitat selection dynamics (Hojesjo et al., 2007). Several studies also revealed a negative association between turbulence metrics and habitat selection (Smith et al., 2005; Cotel et al., 2006; Smith et al., 2006).

Common approaches to surveying parr *micro*-habitat selection include using electrofishing, snorkelling observations or portable PIT tag antenna systems. Although these approaches are intrusive, they can provide high spatial resolution habitat selection data over large spatial areas. However, they are time-consuming, thus limiting the temporal frequency of the surveys. In contrast, radio-telemetry provides continuous habitat selection surveys at a high temporal resolution, but for a short duration due to battery limitations on small fish (Ovidio et al., 2007). Furthermore, the size of sampling units is often relatively large and does not provide a precise location of the animals. Recently, developments in flat-bed PIT tag antenna grid provided ways to monitor fish positions continuously at both high temporal and spatial resolutions over extended periods of time, even in low light conditions (Armstrong et al., 1999; Greenberg and Giller, 2000; Riley et al., 2003; Johnston et al., 2009). Therefore, this type of tracking system is an ideal tool to investigate the question of small scale fish habitat selection within a river reach.

The first objective of this study was to determine how parr habitat associations change with the spatial and temporal scales of investigation. We examined at what spatial scales fish select their habitat and to what spatial extent fish respond to the properties of the surrounding habitat when selecting a *micro*-habitat. To achieve this, we applied a habitat frequency analysis adapted from the method developed by Bult et al. (1998). The second objective was to investigate the variation in the range of habitat use in relation to temporal scales of observation ranging from 5 minutes to 24 days, during the day and night and the summer and autumn. These results will provide information on the average time period required for parr to use a variety of habitats that could be useful in developing successful habitat management and conservation strategies.

6.3. Materials and methods

6.3.1. Study site

The study site is located in Xavier Brook, a tributary of the Ste-Marguerite River in Saguenay, Québec, Canada (48°2591799 N; 69°5394899 W). The study reach is approximately 100 m long and 15 m wide. A central bar divided the channel into a primary channel of 65 X 10 m and a side channel, which was not included in the study. The main channel was composed of two pools separated by a steep riffle (Figure 6.1). At low stage, flow depth was approximately 1.65 m in the deepest portion of the pools and 0.30 m on average in the riffle.

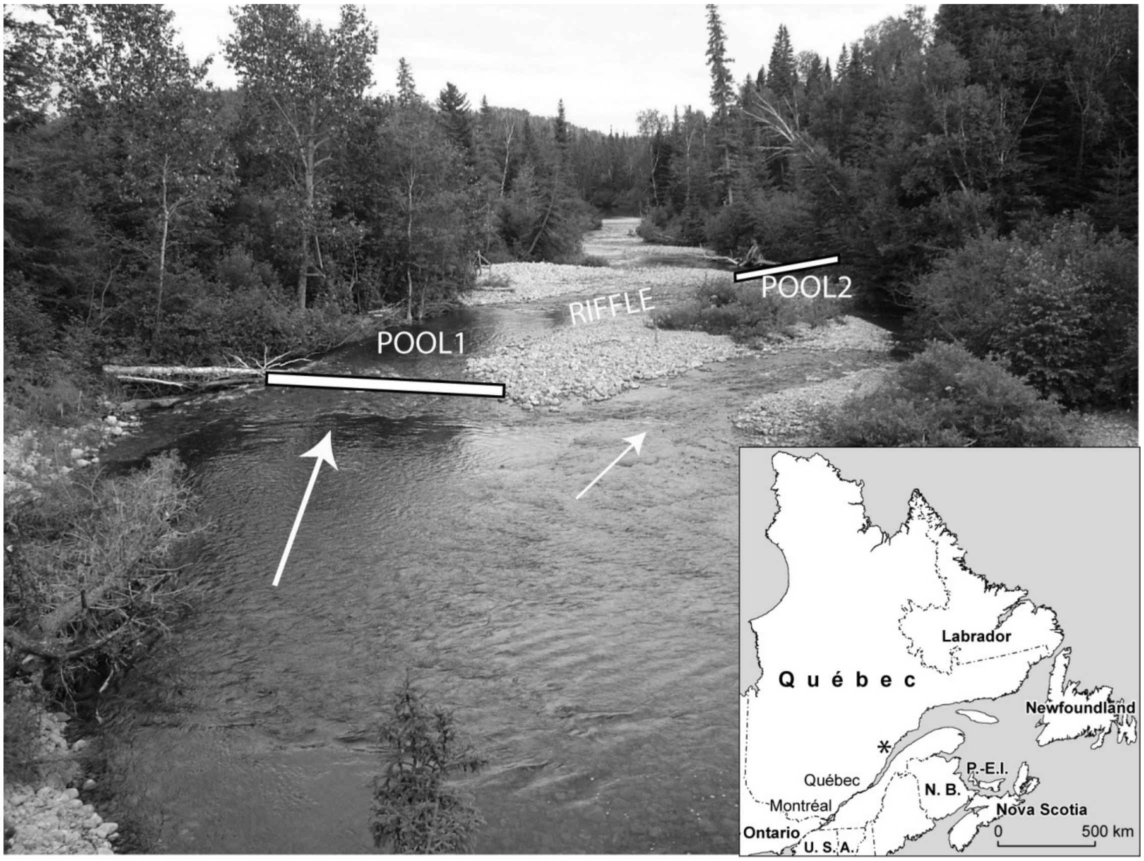

Figure 6.1 The study reach, delineated by the white bars , on Xavier Brook, Saguenay, Qc, Canada (location shown by star on inserted map). Bed morphology was characterized by a clear riffle-pool sequence. Maximum bankful width is approximately 35 m.

Substrate size varied from cobble-boulder in the riffle to gravel-cobble in the deep portion of the pools and gravel-sand in the pool recirculation zones.

6.3.2. Flatbed antenna grid

The flatbed antenna grid was installed in Xavier Brook in the summer of 2006 and tested in 2007. Our study was undertaken during the summer 2008. The antenna system monitored fish locations in the reach using PIT tags at a high temporal frequency (34 s) and over a three month field season (98 days: 24 July to 1 November 2008).

The system consisted of an array of 149 circular antennas (50 cm in diameter) buried within the river bed and designed to detect the presence of 23mm PIT tags (Texas Instruments TIRIS model RI-TRP-RRHP, 134 2 kHz) and other tags complying with the ISO 11784/11785 international standards. The antennas were distributed along cross-channel transects composed of five antennas. Overall, the detection field of the antenna grid covered 19% of the wetted area of the site at a discharge of 0.4 $m^3 s^{-1}$.

Each transect was linked to a tuning capacitor, which was linked to a CYTEK multiplexer (JX/256 series, mercury wetted 256 single poles relay, www.cytec-ate.com). The multiplexer was connected to an *Aquartis* controller (custom made by Technologie Aquartis; www.aquartis.ca) made of a TIRIS S-2000 reader, a datalogger and a custom-made controller unit. The system was powered by three solar panels connected to four 6 V batteries plugged in series and two 12 V batteries plugged in parallel. Each antenna was activated successively for the detection of PIT tag presence every 34s. When a PIT tagged fish was detected, the date (dd/mm/yy), time (hh/mm/ss), antenna ID (multiplexer card and port number) and fish ID (tag number) were recorded. Detection range varied from 300-400 mm in height and 600-700 mm in diameter. During the study period, all antennas detected at least one fish. For more technical details on the antenna grid, see Johnston et al (2009).

6.3.3. Habitat survey

Flow stage and temperature fluctuations were recorded every 15 min using a pressure transducer (*Level logger*) for the duration of the experiment in a L-pipe installed in the river bank. Water stage was estimated by correcting the recorded pressure values for changes in atmospheric data obtained from the closest meteorological station.

The spatial physical characteristics of the study reach were characterized in detail. Micro-topography was surveyed using a robotic total station (Trimble 5600DR) by combining a systematic transect sampling to the characterization of individual roughness elements that protruded by more than 10 cm above the local mean bed elevation. This strategy optimized sampling effort, as sampling point density increased proportionally with bed complexity. From the microtopography survey, we created a digital elevation model (DEM) using a triangular irregular network (TIN) interpolation with pixel size of 10 cm. Sampling and interpolation were undertaken following the guidelines outlined by Lamarre (2006).

Flow velocity measurements were sampled extensively along the reach on three occasions during low flow periods (stages of 13, 14 and 16 cm over minimum summer flow). Three-dimensional flow velocity measurements were sampled using four acoustic Doppler velocimeters (ADVs, Sontek, San Diego) simultaneously at 10 cm above the bed. The density of samples was $3 \cdot m^{-2}$. An aluminum frame was used as a support and reference grid for the ADV measurements. Each corner of the frame was referenced using the total station in order to map the location of all flow velocity measurement point. Velocities along the bank edges, where depth was lower than 20 cm, could not be characterized due to instrument limitations. At each location, velocity time series were recorded for 80 s at 25 Hz, which is higher than the optimal length suggested by Buffin-Belanger and Roy (2005) for similar data. Rigorous data quality inspection was undertaken following a procedure (see Lacey and Roy, 2008a) that included 1) plotting and visualising the velocity time series to detect obvious anomalies, 2) assessing the signal correlation

(Lane et al., 1998), 3) Doppler noise filtering (low-pass), 4) detecting and replacing spikes using “phase-space thresholding” filtering of ambiguities (Goring and Nikora, 2002) and spectral analysis.

6.3.4. Fish capture and tagging

A total of 69 Atlantic salmon parr were captured in the study reach by electrofishing on 24 July (N_A=44) and 28 August 2008 (N_B=25). Parr of body length < 84 mm and juvenile *Salvelinus fontinalis* were immediately released at capture locations. Minimum size for tagging was selected in order to minimize mortality (Roussel et al., 2000) and growth rates (Tatara et al., 2009). The fish were then anesthetised in a clove oil solution (3 ml/10 L) and implanted with 23-mm PIT tags (*Texas Instruments*) in the abdominal cavity. Tagged fish were allowed a recovery period of approximately 2 hours in a fish tank before being released on the study site. A total of three fish were lost during tagging. Average fork length (L ± SD) and average mass (M ± SD) of tagged fish were: L_A: 98 ± 7.4 mm; M_A= 9.7 ± 1.7 g; L_B: 109 ± 8.3 mm; M_B: 10.7 ± 2.3 g.

6.3.5. Data analysis

From the spatial habitat survey, we characterized four habitat variables: flow depth (Y), bed roughness (k), mean flow velocity (U) and turbulent kinetic energy (TKE). Topography was detrended for mean thalweg slope and water surface at median flow was subtracted to obtain flow depth. Areas with depth lower than 0.2 m were cropped, as no velocity measurements were available at these locations. *Bed roughness (k)* was characterized by computing an index based on the estimate of local bed elevation variability. Bed roughness represents the spatial standard deviation of bed elevation values of the DEM pixels included in a 0.65 m square moving window. The size of the window was determined in order to characterize the roughness of most of the largest particles present in the reach. Although frequently used in stream ecology and hydraulics, bed roughness is not a very common variable in studies of fish habitat, which generally describe variables related to the particle size distribution (e.g.Wolman, 1954). However, protuberance from the bed might be more important in creating flow refuge and cover than particle size. For instance, it is common to observe large particles buried in the bed that do not protrude higher above the bed than smaller particles (Nikora et al., 1998). In contrast, an index of bed elevation variability provides a direct estimate of bed roughness that might be more relevant to fish habitat. Mean flow velocity was estimated by the average of all velocity fluctuations of the longitudinal component of the ADV time series. Velocities were rotated so the magnitude of the longitudinal component *U* would become 100% of the total magnitude and the lateral component would become null. Turbulent kinetic energy (TKE), a measure that combines the variance of the three components of the velocity fluctuations was also obtained from the velocity time series as $\mathrm{TKE} = 0.5(u^2_{sd} + v^2_{sd} + w^2_{sd})$. *Depth*, *bed roughness*, *mean flow velocity* and *TKE* were interpolated in 0.30 m cells using a natural neighbour algorithm (*Vertical Mapper 3.l in MapInfo*). Further analyses on habitat matrices were carried out in *Matlab (c)*.

6.3.6. Habitat selection analyses

To examine habitat selection in relatively stable environmental conditions, fish locations recorded when the stage was higher than a threshold of 20 cm above the minimum flow stage and 10 cm above the median flow stage were removed from further analysis, representing 16% of the duration of the study period corresponding to five rainfall events (Figure 6.2). Furthermore, the high temporal frequency of fish detections (every 34s) induced temporal redundancy in the habitat selection data. Hence, for individual fish, consecutive detections recorded at the same antenna within one hour were removed. Next, we computed the frequency of different individuals and the total number of fish detections observed at each antenna during the entire study period in order to map and visualize the overall habitat selection spatial patterns.

Fish habitat relationships were analysed using a frequency analysis that consisted in subsampling habitat matrices to estimate the average proportion of a habitat class that was available and to compare it with the average proportion of the habitat frequency that was used by the fish. This method allowed us to investigate fish-habitat relationships at various spatial scales in order to determine which scales were the most relevant. This was achieved through the following steps:

First, we divided the habitat variables into eight ordinal classes (Table 1). As minor fluctuations of flow depth, velocity and turbulence occurred during the study period, ordinal classes (1-8) seemed preferable to interpret habitat selection than actual values. We assumed that *Y*, *U* and *TKE* habitat ranks would remain reasonably similar across low amplitude stage fluctuations, so that a low velocity habitat would remain a low velocity habitat in comparison to other available habitats.

Second, for each variable and habitat class, we subsampled each habitat matrix using circle shaped sampling units of increasing radius following a method proposed by Bult et al. (1998).

Table 6.1. Class ranges used to compute habitat associations of four variables: Y: water depth, k: bed roughness, U: downstream flow velocity and TKE: turbulent kinetic energy. Classes were divided evenly over the range of values measured at a stage of approximately 17 cm.

Habitat Classes	1	2	3	4	5	6	7	8
Y (m)	0-0.23	0.23-0.45	0.45-0.68	0.68-0.9	0.9-1.13	1.13-1.35	1.35 1.58	1.58-1.65
k (m)	0 0.015	0.015 0.030	0.030 0.045	0.045 0.060	0.060 0.075	0.075 0.090	0.090 0.105	0.105-1.2
U (cm·s^{-1})	-25 0	0 25	25 50	50 75	75 100	100 125	125 150	150-165
TKE (cm^{-2}·s^{-2})	0 100	100 200	200 300	300 400	400 500	500 600	600 700	700-1200

The method can be used to sample habitat using any number of sampling unit radius, but to distinguish clearly among the spatial scales, we selected five radii: 0.3 m, 0.5 m, 1.0 m, 2.0 m and 5.0 m. Three of these units, the smallest, the middle and largest correspond to the *micro*-scale, the *patch*-scale and the *meso*-scale respectively. The *micro*-scale (0.3 m), which corresponded to the detection range of the antennas, was larger than the *micro*-scale often found in the literature, which typically samples as close as possible as the exact location of the fish (i.e. nose velocity; Degraaf and Bain, 1986; Morantz et al., 1987). However, 0.3 m corresponds more or less to the size of a large boulder or pebble cluster used as a rearing habitat, and to the territory size of a 2+ parr (Keeley and Grant, 1995). Similarly, the 1.0 m radius is herein called the *patch*-scale, as this radius corresponds to the size of relatively homogeneous habitat units (e.g. deep portion of pool, very high velocity habitats, recirculating zone). The largest scale (5.0 m radius) was half of the river width and approximated the size of morphological units in the reach (upstream pool, flat part of the riffle, steep part of the riffle, downstream pool). For larger scales, the subsampling unit included areas outside the river boundaries. In these cases, only the portion of the sampling area located inside the river channel was considered.

Third, for each individual (66), spatial scale (5), and habitat variable (4) the proportion of use associated with each habitat class (8) was estimated. These proportions were obtained by averaging the proportions associated within each habitat radius used by a fish, weighted by its frequency of use for the entire study period. Then, for each habitat class, average fish-habitat associations for all fish (FC) were estimated. Afterwards, *average habitat availability* (HA) corresponding to the average proportion of the specific habitat class in the reach was estimated for the 149 sampling units. Habitat preference or avoidance, for a particular habitat class was estimated as $RC = \log_{10}HA - \log_{10}FC$. Then, the medians of habitat availability (HA) and habitat used (FC) were compared using a Mann-Whitney test with $\alpha=0.01$.

The average range of *micro*-habitat used was estimated over temporal scales ranging from minutes to weeks. For each variable (4), temporal scale (18), and individual fish (66), an average range of values was estimated and plotted in order to examine the average time required for fish to use most of the habitat available in the reach. Ranges of habitat used were compared between day and night and summer (>12°C) and autumn (<12°C) using mixed models. Best models were selected using the lowest AIC approach (Burnham et al., 2011).

6.4. Results

6.4.1. Habitat description

During the study period, water temperature decreased from 19.0°C to 2.8°C (Figure 6.2). From 24 July to 3 September, daily average water temperature was relatively constant, with values fluctuating around 15 ^{o}C. After 3 September, temperature started to decrease linearly. Water temperature reached 12 ^{o}C on 11 September and 8 ^{o}C on 23 September, which corresponds respectively to the upper and lower boundaries of the temperature range at which parr tend to suppress their daytime activity (Valdimarsson et al., 1997). Time periods during which temperature was above and below 12 ^{o}C will be hereafter referred to as "summer" and "autumn", respectively. During the same period, flow stage exhibited substantial variability (Figure 6.2).

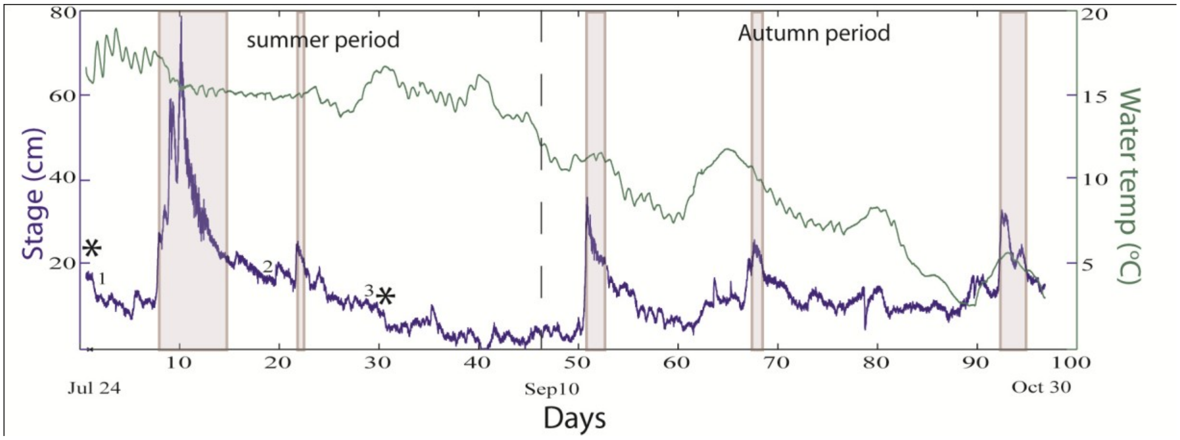

Figure 6.2 Time series of water level and water temperature. Gray shading indicates periods during which river stage was 20 cm over the minimum base level observed during the study period. Vertical dashed line denotes the 12^{o}C diurnal activity suppression threshold defining a warmer summer period and a colder autumn period. Stars indicate the two fish tagging sessions and numbers the flow measurement sessions.

At the beginning of August, a high magnitude flood event occurred, after which the water level decreased until the beginning of September. A prolonged low flow period lasted until mid September, followed by several rainfall events in October. Average flow stage between these rainfall events was roughly 10 cm over minimum flow. During 84 % of the study period, flow stage was lower than 20 cm above the minimum. During this summer low flow period, estimated mean flow stage was 10.2 cm above minimum and the variability around this value followed a normal distribution.

Spatial variations in flow depth were mainly controlled by the presence of a steep pool-riffle sequence. A maximum depth of 1.65 m was observed in the pools and minimum depth in the thalweg was 0.25 m in the riffle (Figure 6.3). The study area was characterized by 50% of the depths lower than 0.5 m and 90% lower than 1.2 m (Figure 6.4). Bed roughness in the reach was highly spatially heterogeneous (Figure 6.3). The downstream pool exhibited the largest coherent region of highly rough bed. However, the remainder of the reach showed apparently random, but clustered spatial patterns of bed roughness values ranged between 0.01 and 0.12 m, with 50% of the bed roughness area being lower than 0.03 m and 90% below 0.07 m (Figure 6.4).

In the thalweg, at approximately median flow stage, mean flow velocity displayed a wide range of values: 0-30 $cm \cdot s^{-1}$ in the pool recirculation zones, 0.4-0.9 $m \cdot s^{-1}$ in the pool tails and 0.75-1.50 $m \cdot s^{-1}$ in the riffle (Figure 6.3). Seventy-five % of the reach area was characterized by flow velocities lower than 80 $cm \cdot s^{-1}$ (Figure 6.4).

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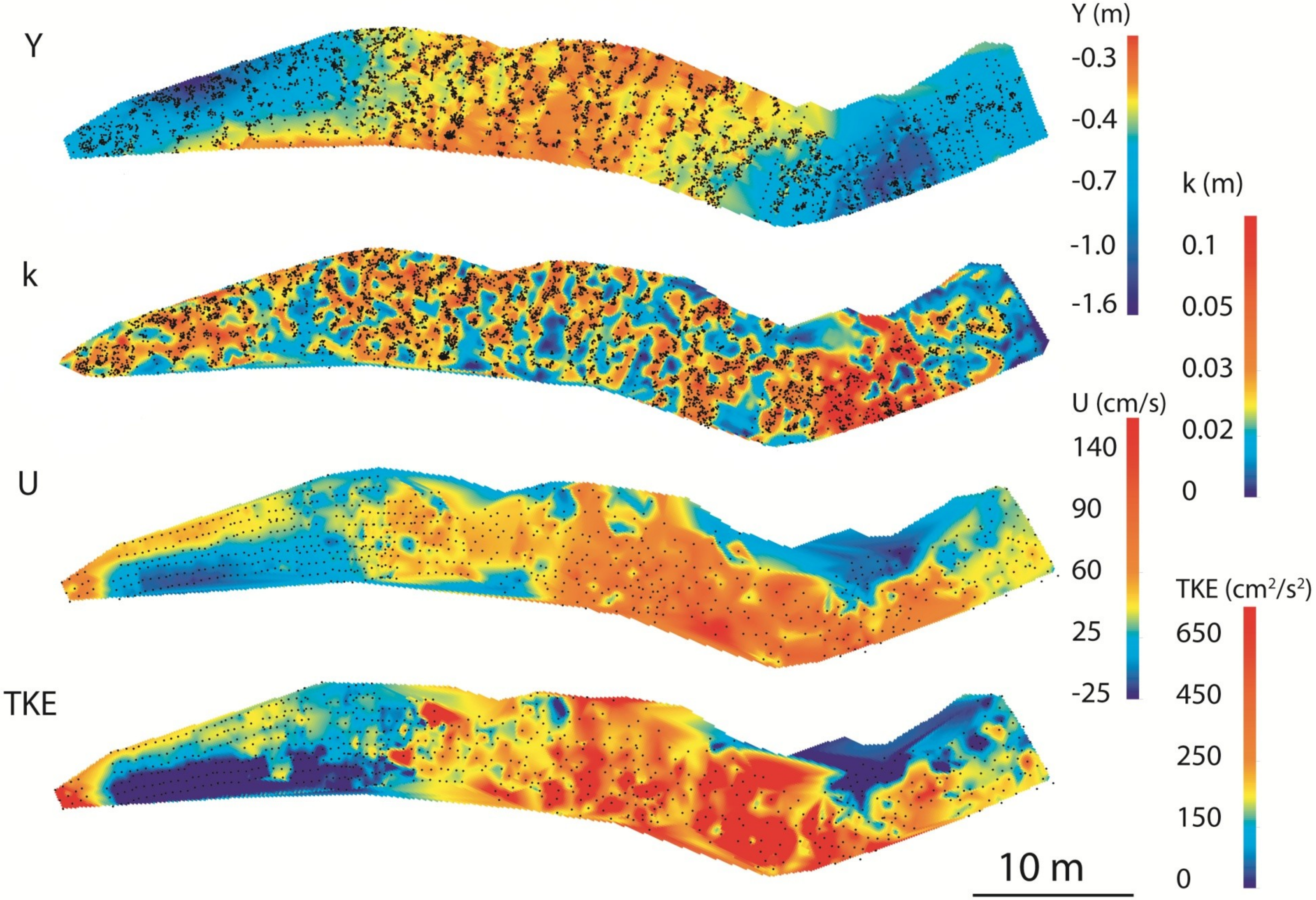

Figure 6.3 Maps of depth (Y), bed roughness (k) (heterogeneity of bed elevations, see text), mean downstream velocity (U) sampled at 10 cm above the bed at base flow and turbulent kinetic energy (TKE). Dots represent the sampling locations.

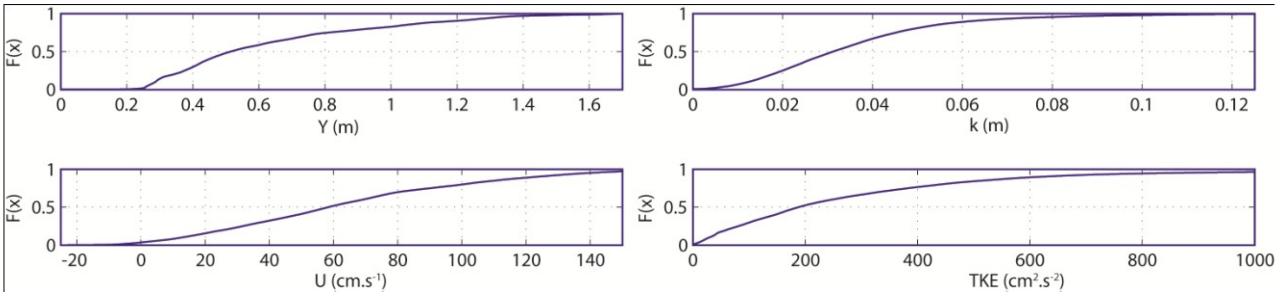

Figure 6.4 Cumulative curve functions of physical habitat availability F(x) in the study reach. Y: flow depth, K: bed roughness, U: flow velocity, TKE: turbulent kinetic energy.

TKE spatial distribution was relatively consistent with mean flow velocity: extremely high *TKE* values were observed on the steep end of the riffle (> 600 $cm^2 \cdot s^{-2}$), medium values were recorded in the constricted part of the pools (400-600$cm^2 \cdot s^{-2}$) and low values were observed in the recirculation zones (0-400 $cm^2 \cdot s^{-2}$, Figure 6.4). Fifty percent of the reach area presented TKE values lower than 200 $cm^2 \cdot s^{-2}$ and 90% were lower than 600 $cm^2 \cdot s^{-2}$.

6.4.2. Fish recordings

A total of 66 fish were PIT-tagged and released in the reach. From the total, 4 individuals (6%) were never detected by the tracking system and 12 individuals (18%) were detected on the study reach for a period of less than 24 hours. These individuals were not taken into account in further analysis. However, 23 individuals (39%) stayed in the reach for a period of 24 hours to 5 days and 27 individuals (37%) settled for a period ranging from 5 days to three months. The 53 individuals that stayed in the reach a minimum of 24 hours were detected on average 80 times per day.

Fish used the entire study reach, as detections were recorded at all antennas during the study period. Each antenna recorded between 2 and 20 different individuals during the study period, with an average of 7.5 individuals (Figure 6.5B).

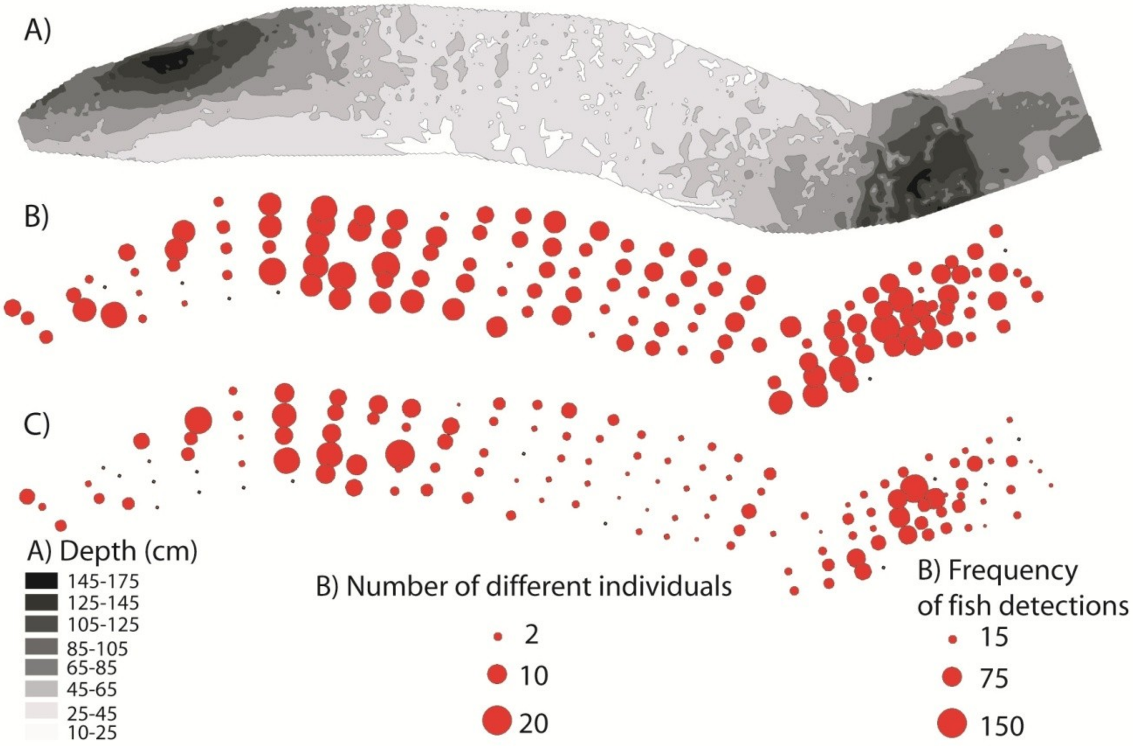

Figure 6.5 Maps of A)Depth (stage:15 cm) B) proportional circles representing the number of different tagged individuals detected at each antenna over the entire study period C) the frequency of fish detections observed. Frequency of fish detections was estimated from time decimated data (i.e. only one location per hour was kept at a single antenna location, see text). Flow is from left to right.

The upstream shallow recirculating zone was used by the fewest individuals, followed by the downstream part of the riffle. The transition between the upstream pool and the riffle, and the entire downstream pool were visited by the highest number of individuals.

The spatial pattern of frequency of fish detections (Figure 6.5C) suggested that although all *micro*-habitats were visited by an individual at a moment in time, some habitats were considerably more attractive than others. The highest frequency of fish detections was recorded in the upstream pool tail, the transition between the upstream pool and the riffle and at the margins of the downstream pool. Relatively few fish were detected in riffle habitats, the upstream recirculation zone and deep pool. Frequency of fish detections presented an aggregated spatial pattern which reflects the spatial variability of habitat variables.

6.4.3. Spatial scales of habitat selection

During the entire study period, habitat preferences exhibited substantial variability between spatial scales (Figure 6.6). The highest statistically significant associations (RC value) were observed at scales varying from the *micro* (0.3 m radius (log0.3=-0.7) and the *patch*-scale (1.0 m radius), depending on the variable examined. The *meso*-scale RC exhibited values close to zero that were often not statistically significant. Furthermore, over the entire study period, fish used a variety of habitats rather than a narrow range of habitat values. This is illustrated by the relatively low RC values, and the substantial variability among the habitat variables observed.

At the *micro-scale* (0.3 m radius), fish were positively associated with intermediate to deep habitats and were negatively associated with shallow habitats (Figure 6.6). A similar habitat selection pattern was observed at the *patch* scale (1.0 m radius), with the exception of a strong positive association with the deepest habitats (classes 7-8), which corresponded to pool habitats. In contrast, at the *meso*-scale, RC was primarily low and not statistically significant for the most part.

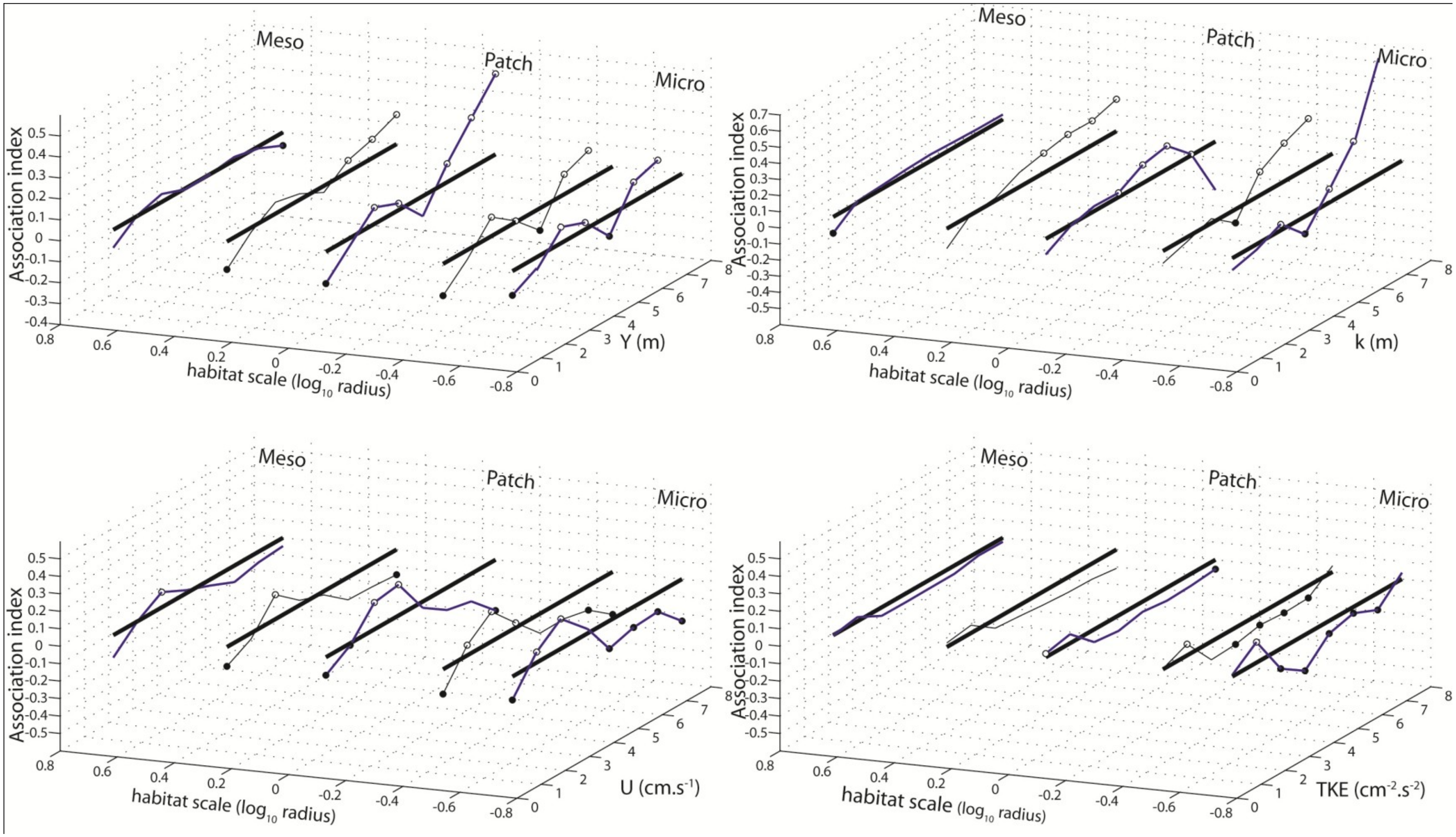

Figure 6.6 Fish-habitat associations of juvenile Atlantic salmon over a range of spatial scales averaged over 98 days for four physical habitat variables Y: depth, k: bed roughness, U: downstream flow velocity and TKE: turbulent kinetic energy. Lines at zero represent null association, closed dots represent a significant negative association whereas open dots represent significant positive associations (M-W test α=0.05). Spatial scales are defined as micro at 0.2 m radius, patch scale at 1.25 m radius and meso scale at 5 m. Unnamed scales show intermediate states.

As opposed to depth, which presented the highest RC values at the *patch*-scale, fish-bed roughness RC values were the highest at the *micro* scale (Figure 6.6). Fish locations were positively associated with the highest bed roughness available in the reach (classes 7-8), which corresponded to areas of large cobbles and bank edges. Similar habitat associations were observed at the *patch*-scale, with the exception of a negative not significant RC value for the highest bed roughness class. At the *meso*scale, none of the RC values were statistically significant, except a negative association with the lowest bed roughness habitats (class 1), which corresponded to a substrate of homogeneous gravel or sand. This negative association was also observed at the other scales but was not statistically significant.

The difference between the spatial scales of fish–habitat associations were not as clear for mean flow velocity as with the two previous topographic variables. At the *micro*-scale, fish were positively associated with intermediate velocity classes (classes 2-3) and generally avoided the fastest flows (4-7), mostly located on the steep part of the riffle (Figure 6.6). Fish locations were also negatively associated with the lowest flow velocity class (1) which represents negative average velocities in recirculating zones.

Similarly, at the *patch*-scale, fish locations were positively associated with habitats of intermediate flow velocity, but also were negatively associated with a higher velocity class (75-100 $cm \cdot s^{-1}$; Table 6.1, Figure 6.6). At the *meso*-scale, values of RC were low and not significant, except for the positive association with intermediate values of flow velocity, which shows that fish were more abundant in *meso*-habitats where intermediate velocities were more frequent. In contrast, significant fish habitat associations with turbulent kinetic energy were restricted to the smallest scales (Figure 6.6). At the *micro*-scale, fish were positively associated with low to intermediate *TKE* (class 2) and negatively associated with higher classes of TKE (3-8). Nevertheless, at larger scales, fish – habitat associations were not significant.

6.4.4. Temporal scales of habitat selection

For all four variables, the average range of habitat values used by fish increased with the temporal scale of observation following an asymptotic curve, as exemplified by the range of depth used in Figure 7. From temporal scales ranging from 5 minutes to 24 days, four broad time periods were identified: 1) 5 min to 60 min scales, during which the range of habitat used increased markedly (Figure 7a); 2) 1h to 6 h scales, during which fish increased their range of used habitat only slightly (Figure 7a); 3) 12h to 3 day scales, during which the range of used habitat increased markedly again, particularly between the 24h to 48 h scale (Figure 7b); 4) 3 day to 24 day scale (Figure 7b), for which habitat range increased only slightly again.

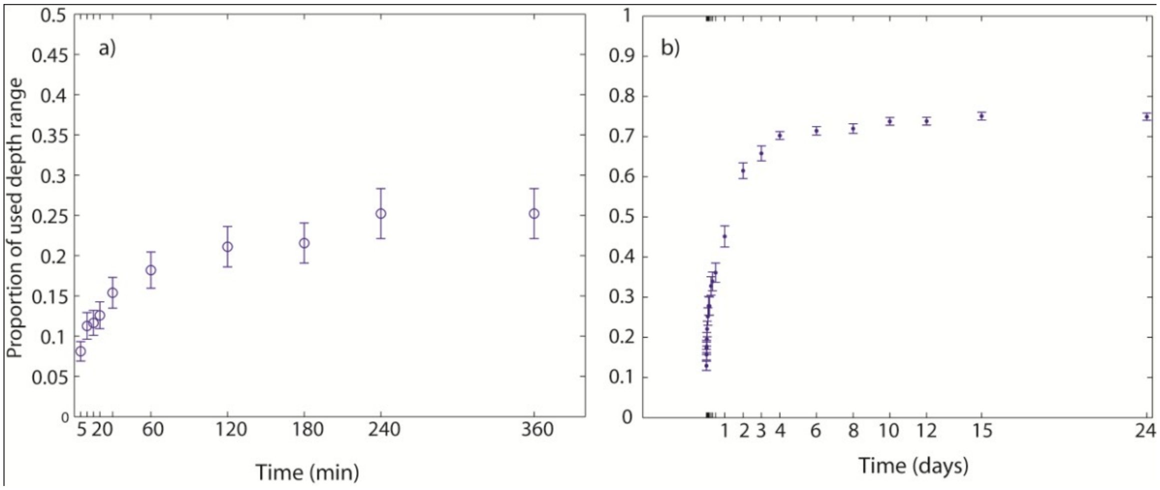

Figure 6.7 Average proportion of total depth (Y), bed roughness (k), mean flow velocity (U) and turbulent kinetic energy (*TKE*) availability used by fish as a function of temporal scales ranging from a) 5 minutes to 24 days and b) 5 minutes to 6h.

For mean flow velocity, depth and bed roughness, ranges of habitat used across temporal scales did not differ between day and night (Table 2). However, fish used a larger range of turbulent kinetic energy values at night than during the day (Table 2).

Table 6.2 Mixed model test for day/night period fixed effects. U: mean flow velocity, TKE: turbulent kinetic energy, Y: flow depth, K, bed roughness.

	df	*F*	*p*
U	1, 574.65	2.674	0.103
TKE	**1, 576.52**	**16.271**	**<0.001**
Y	1, 576.02	1.596	0.207
K	1,575.028	3.397	0.066

For all variables, ranges of habitat used across smaller temporal scales (5 min- 24h) were larger in the summer than autumn (Figure 8, Table 3). However, for larger temporal scales (48h to 24 days), ranges of flow depth, velocity and TKE used were higher during the summer than autumn, but differences in the range of bed roughness used were not significant (Table 3). For all variables, the two distinct asymptotic curves observed in the smaller and larger time scales translated into distinct log-linear relationships separated by a break point between the one day and two days scales (Figure 8). Steeper slopes in the larger scales, particularly for bed roughness and TKE indicated fish doubling their range of used habitat at a faster rate.

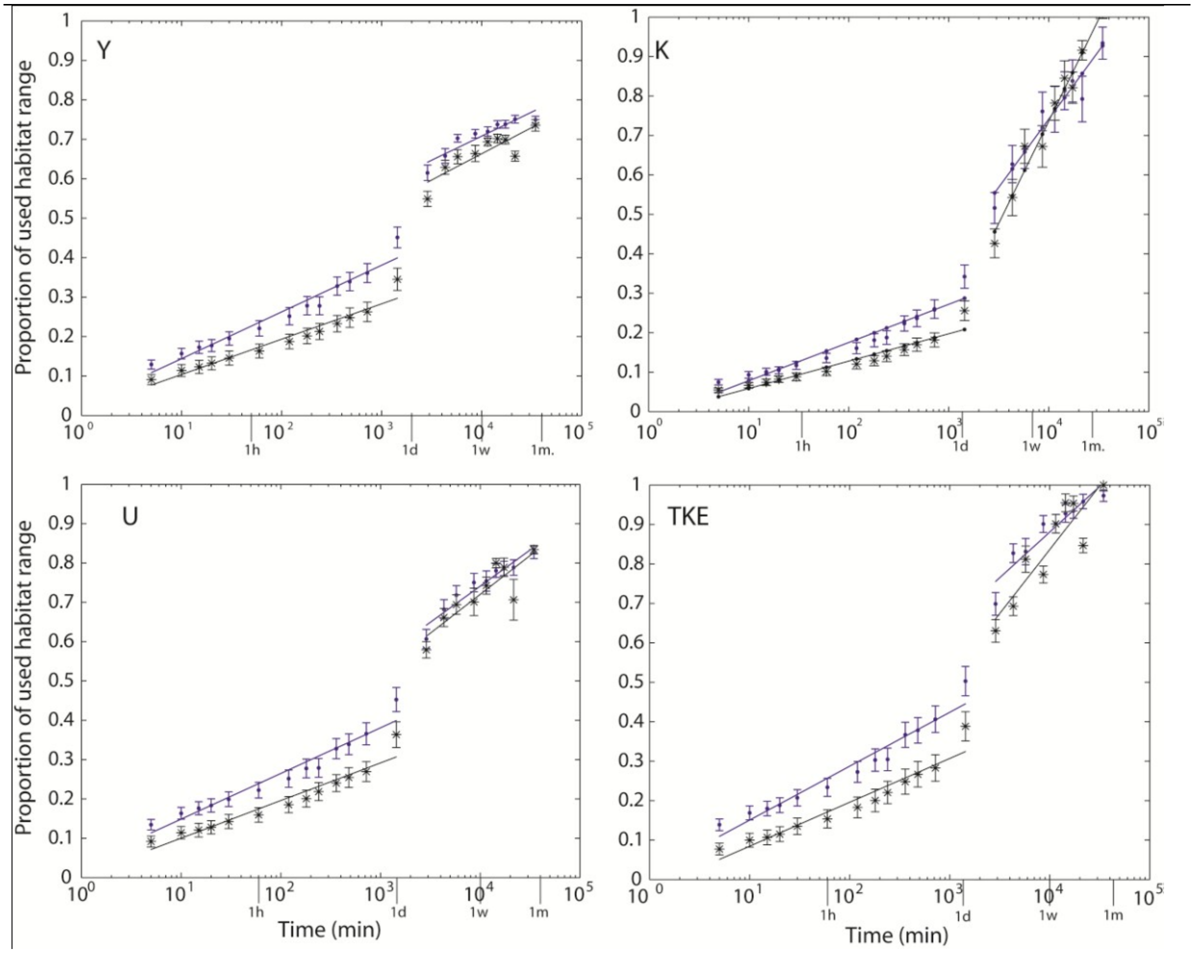

Figure 6.8 Average proportion of total flow depth (*Y*), bed roughness (*k*), mean flow velocity (*U*) and turbulent kinetic energy (*TKE*) availability used by fish as a function of temporal scales ranging from 5 minutes to 24 days represented on a log axis. Dots represent average range used during the summer and stars average proportions of range used during the autumn.

Table 6.3 Mixed model test for summer/autumn fixed effects for smaller scales (5 min to 24 h) and larger scales (2 to 24 days).

	Large scales			Small scales		
	df	*F*	*P*	df	*F*	*p*
U	1, 235.31	10.934	**0.001**	1, 474.3	167.91	**<0.001**
TKE	1, 236.99	23.057	**<0.001**	1, 475.0	240.05	**<0.001**
Y	1, 242.96	62.819	**<0.001**	1. 475.9	130.36	**<0.001**
K	1, 236.94	0.540	0.463	1, 476.7	28.29	**<0.001**

From 5 minutes to 24 h, ranges of habitat used exhibited homogeneous log-linear slopes for all variables, except for bed roughness, which was significantly less steep than *U*, *TKE* and *Y* (Table 4; Figure 9). On average, in 5 minutes, fish used a range of habitats of 8 to 13 % of the habitat range. This range was almost double for the 1h time scale (Figure 9). From 1h to 6h, the average habitat range only increased slightly.

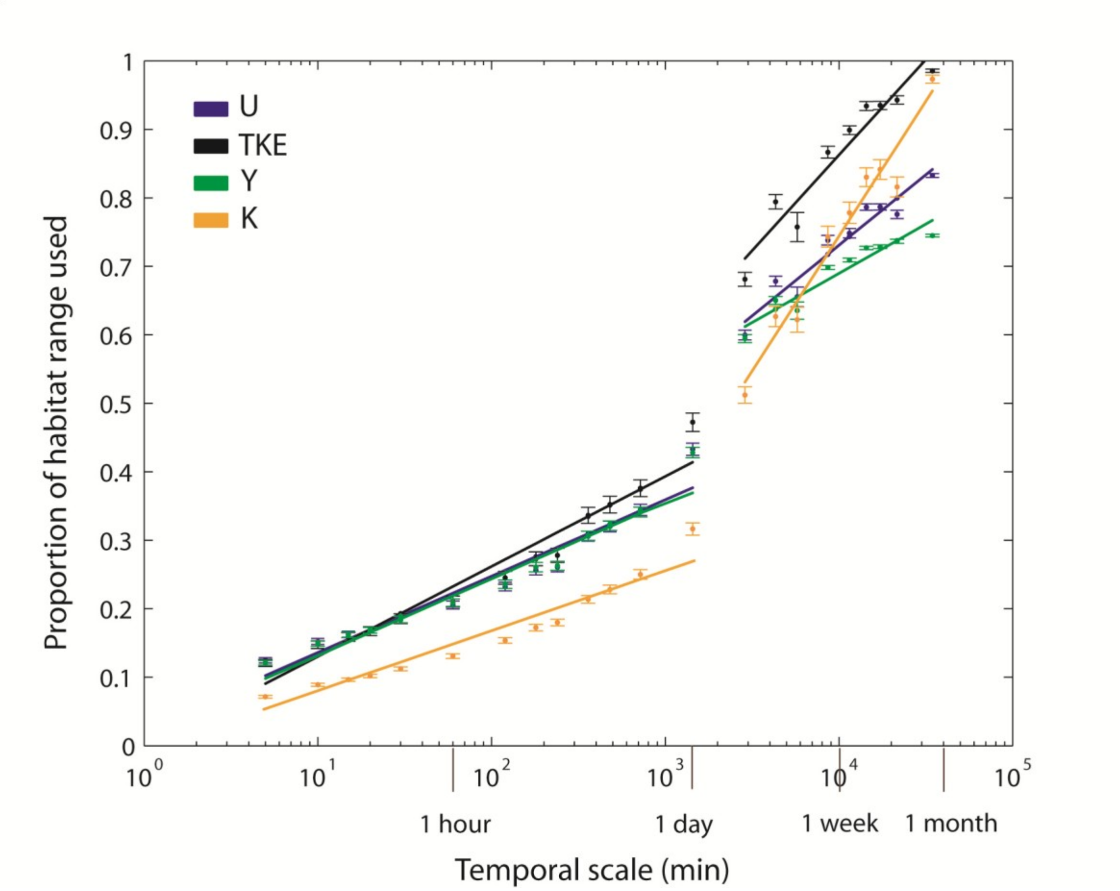

Figure 6.9 Average proportion of the range of used flow depth (*Y*), bed roughness (*k*), mean flow velocity (*U*) and turbulent kinetic energy (*TKE*) availability used by fish as a function of temporal scales ranging from 5 minutes to 24 days represented on a log axis.

The 24 h to 48 h scale was critical, as fish increased their range of used habitat by 30% on average. At larger temporal scales (48h to 24 days), log linear slopes of U, Y and TKE were homogeneous (Table 4; Figure 9). In contrast, the bed roughness slope was significantly steeper, indicating that at larger scales, fish tend to include more systematically very different bed roughness habitats.

Table 6.4 Homogeneity of slopes test (GLM ancova).

	Large scales			Small scales		
	Df	*F*	*P*	*df*	*F*	*p*
U-TKE	7,183	0.310	0.949	12,325	0.951	0.497
U-Y	7,183	0.920	0.492	12,325	0.238	0.996
U-K	7,183	2.518	**0.017**	12,325	4.351	**<0.001**
TKE-Y	7,183	0.724	0.652	12,325	0.898	0.549
TKE-K	7,183	2.589	**0.015**	12,325	2.021	**0.022**
Y-K	7,183	1.873	0.07	12,325	7.752	**<0.001**

On average, over 24 days, fish used close to the entire range of bed roughness variability and turbulence, but only 80% of the depth and mean velocity available.

6.5. Discussion

Our study, designed to provide a quantitative description of habitat selection, revealed a scale-dependant habitat selection, highlighting the relevance of the *patch*-spatial scale and the three day-temporal scale to characterize the range of habitat used by juvenile Atlantic salmon. We focused on examining the behaviour of parr in an unperturbed stream rather than using an experimental approach. Our data set represents one of the highest spatial and temporal resolutions of fish locations for a group of individuals over a period of several months.

We compared fish-habitat associations over a range of spatial scales and observed a considerable degree of variability between the *micro*- to the *meso*-scale habitats. This finding supported the idea that the scale of measurement can determine the perceived importance of a habitat variable in habitat selection behaviour (Bult et al. 1998). Atlantic salmon parr were found in both greater numbers and greater frequency of locations in the transition zone between the upstream pool and the riffle. A *micro*-scale habitat sampling showed a significant positive association with moderate values of depth. These results are consistent with earlier descriptions of suitability curves for juvenile Atlantic salmon, although depth range in this study was slightly higher (See Armstrong et al., 2003 for a review). Yet, increasing the sampling unit size revealed that the fish were associated with deeper habitats at the *patch*-scale than at the *micro*-scale. While parr generally spend most of their active time drift feeding, the proximity to a deep pool habitat might provide refuge from terrestrial and aerial predators (Fausch and White, 1981). Moreover, although tagged parr selected moderate depth habitats, deep pool habitats (>1m) were generally used more than shallow riffle habitats. This apparent preference contrasts with shallow riffles as the typical description of the habitat of Atlantic salmon parr (Degraaf and Bain, 1986; Morantz et al., 1987). However, previous studies have reported that parr are not only found in riffles but can also be abundant in deep pools (Bremset and Berg, 1997).

Linnansaari et al. (2010) hypothesized that the lower parr densities generally observed in pools might be biased by a lower efficiency of capture methods such as electrofishing in these habitats. Furthermore, pools might provide higher energy gain and a larger proportion of energetically profitable habitats than riffles (Rosenfeld and Boss, 2001; Jenkins and Keeley, 2010). The preference of parr for deeper habitats in this study might reflect the positive relationship between fish size and depth use (Mitchell et al., 1998), as only parr larger than 84 mm were tagged.

As opposed to depth, the preference for bed roughness was higher at the *micro*-scale than at the *patch*-scale. These results suggest that the properties of the river bed at the scale of individual boulders or pebble clusters were more important than the bed properties of a *patch*-scale habitat containing multiple foraging stations. Nevertheless, the heterogeneous spatial structure of bed roughness throughout the study reach likely played a role in determining the dominant spatial scales of fish habitat selection. In other words, a lower fish-habitat association at the *patch*-scale might have been partly due to the fact that the spatial variability of bed roughness was generally heterogeneous at the smallest scale and homogeneous at the reach scale (see Figure 6.5). Overall, fish selected the highest bed roughness habitats characterized by either large single protruding individual bed particles or clusters of cobbles, or in some cases, abrupt topography gradients, such as steep banks. The positive association with *micro*-habitats in the cobble-to-boulder class is generally attributed to benefits from hydraulic refuge and cover (e.g. Mitchell et al., 1998).

As reported by previous studies (Armstrong et al., 2003), parr were positively associated with *micro*-habitats of moderate velocity and avoided very high or low velocity *micro*-habitats, as reported by previous studies. However, considering a larger area surrounding the *micro*-habitat, fish in this study showed a positive association with higher-velocity habitats. This observation supports the assumption that parr tend to select habitats to maximize food intake while minimizing energy expenditures (Hughes and Dill, 1990). Moderate velocity *micro*-habitats located close to high velocities provide low swimming energy costs with potential access to abundant drifting prey (Hayes et al., 2007). Because of turbulent mixing such a positive relationship between velocity and drift rate might not be always clear and may sometimes operate at the *meso*-scale rather than at the *micro*-scale (Leung et al., 2009).

In contrast, fish association with classes of turbulent kinetic energy was mainly observed at the *micro*-scale. Consistent with previous studies (Cotel et al., 2006; Smith et al., 2006), fish selected *micro*-habitats where turbulence was low and avoided habitats where turbulence was high, perhaps to minimize swimming energy costs (Enders et al., 2003). In contrast, at the *patch*- to *meso*- spatial scales, fish did not exhibit a significant preference for any turbulence levels. Similarly, Enders et al. (2009) reported a high inter-individual variation in the use of turbulence levels sampled at the *patch* scale. These results suggest that turbulent properties affecting energy costs (Pavlov et al., 2000; Enders et al., 2003) at the *micro*-habitat scale may be a more important driver than turbulence at the *patch*-scale.

Examining the ranges of physical habitat used in a heterogeneous stream revealed an asymptotic increase with the temporal scale of observation. The average fish used habitats with a range of depth of 0.12 m and a range of flow velocities of 16 $cm \cdot s^{-1}$ in 5 minutes. These results indicated that juvenile salmon used a diversity of habitats. This variability in habitat use may have occurred as a result of foraging movements between lower velocity habitats from which fish sit-and-wait and higher velocity habitats in which they forage. However, observing fish for 1h periods resulted in close to double the habitat range of individuals, and only increased slightly between 1h and 6h periods. This suggests that a period of 1h should be considered as a minimum duration to characterize individual habitat use of Atlantic salmon parr. However, during the same period, parr tend to use a wider range of flow velocity and depth than bed roughness. This might reflect the higher flow heterogeneity than bed roughness heterogeneity available in the reach.

The use of multiple adjacent habitats in the course of a single day has been reported for YOY fish (Steingrimsson and Grant, 2008). The present results suggest post-YOY juveniles might behave in a similar way and during the night as much as in the day. The absence of a statistically significant difference between the range of habitat used during the day and night, except for TKE has to be interpreted carefully, as data only consider habitat use of fish while they were active and therefore detected by the system. Otherwise, one could expect the range of habitat use to be higher at night, when fish are more likely to be active (Johnston et al., 2004; Chapter 7).

At the large temporal scale, low among-fish variation was observed, as all fish used a large portion of the range of habitat values. These results support previous work reporting a high within-individual variation indicating a flexible and dynamic habitat use rather than a mosaic of territories fixed in time (Okland et al., 2004; Chapter 8). Despite fish exhibiting preferences for certain types of habitats, individuals use a wide array of different types of habitat in relatively short lapses of time that may be beneficial in providing foraging, resting and shelter habitats.

Between one day and three days time scale, the largest increase in habitat range values was observed. The steep log-linear slope of bed roughness increase in the larger scale might illustrate the uncommon use of some habitats presenting low bed roughness, such as sand patches. We suggest a period of three days as optimal to characterize salmon parr seasonal habitat use, as they use 60-80% of their habitat range within this time scale.

In conclusion, this study underlined the relevance of the *patch*-scale habitat sampling and the temporal variations of Atlantic salmon parr habitat selection and range of habitat use. High resolution tracking systems provided a detailed portrait of fish habitat selection over a range of scales. Individuals used a wide variety of habitats over the study period. We suggest salmonid habitat modelling might benefit from adopting a multiscale approach reflecting the spatial structure and the temporal variations in habitat selection.

6.6. Linking paragraph

The previous chapter showed that juvenile Atlantic salmon use a considerable range of habitats within a few hours. Variation in habitat selection might result from variation in activity patterns, as fish sometimes use different habitats for feeding and sheltering. However, environmental conditions also likely influence fish activity patterns. For instance, juvenile Atlantic salmon tend to become more nocturnal in cold temperatures. In Chapter 7[1], using the same data set as the previous chapter, we examine the effect of variation in flow, temperature and habitat use on the individual variability of activity patterns. To our knowledge, this study is the first to document the effect of temporal variation of flow stage and the interaction between microhabitat use and activity patterns of wild fish. This chapter highlights the importance of crepuscular activity, a period that is often not monitored in studies of activity pattern, which typically compare day and night periods. Furthermore, it shows the plastic behaviour of individuals, who adapt their activity cycle to environmental fluctuations.

[1] Roy, M. L. Roy, A.G., Grant, J. W. and N. Bergeron. Individual variability of wild juvenile Atlantic salmon activity patterns: effect of flow stage, temperature and habitat use. Submitted to the Canadian Journal of Fisheries and Aquatic Sciences.

Chapitre 7: Individual variability of wild juvenile Atlantic salmon: effect of flow stage, temperature and habitat use

7.1. Abstract

The magnitude of variation of diel activity patterns and habitat use of wild Atlantic salmon parr was examined during the summer and autumn through a gradient of declining temperature. Fish were marked with passive integrated transponders and tracked using a large network of flat-bed antennas. High inter-individual variability was observed, as some individuals were predominantly nocturnal whereas others frequently changed their daily activity pattern. Overall activity decreased with temperature and flow stage, but most changes in daily activity occurred during crepuscular periods. Parr used habitats with lower velocity at night than in the day during the summer, but not in the autumn. Furthermore, there was no difference between day and night habitats for fish that were cathemeral (active both day and night during a given day), so differences between day and night habitats were the result of individuals adopting different activity patterns. These results suggest that habitat interacts with activity pattern, as individuals using suboptimal habitats seem to increase daytime foraging to secure sufficient energy. Temporal variability of individual activity patterns among fish illustrate the dynamic nature of foraging decisions resulting from tradeoffs experienced at the microhabitat scale.

7.2. Introduction

Juvenile salmonids exhibit complex and variable diel activity patterns (Reebs, 2002). During the summer, juveniles are active and feed during the day, but as temperature drops to 8-12^{o}C in the autumn and winter, they tend to suppress their diurnal activity, shelter in the interstices of the substrate, and feed only at night (Rimmer et al., 1983; Cunjak, 1988; Bremset, 2000). This switch to nocturnal activity might be explained by reduced metabolic needs and higher predation risk at low temperature. However, nocturnal activity has also been observed in the summer (13-23 ^{o}C), especially for parr (Gries et al., 1997; Johnston et al., 2004), whereas diurnal activity has been observed in the winter (Hiscock et al., 2002). Such variation in activity patterns among studies might be caused by interactions with habitat; Bradford and Higgins (2001) reported important differences in diel activity between two sites of the same river with contrasting flow stages, one site having its flow decreased by a diversion dam. Reduced flow tends to decrease food abundance, which might lead to increased diurnal foraging (Orpwood et al., 2006).

In most studies, diurnal or nocturnal activity tends to be the general pattern rather than a uniform behaviour among all individuals (Bremset, 2000; Bradford and Higgins, 2001). This high degree of variability in activity patterns is presumably the result of individuals reacting differently to environmental fluctuations (Breau et al., 2007). Therefore, in addition to abiotic factors such as temperature and photoperiod, individual variation in diel activity patterns is likely affected by how individuals respond to tradeoffs, based on recent foraging success or exposure to predation risk (Metcalfe et al., 1999). Hence, microhabitat selection might have an important impact on the type of activity pattern adopted by an individual fish. Conversely, activity patterns might induce diel variation in habitat selection, as salmonids tend to use different habitats for feeding and sheltering (Heggenes et al., 1999). For instance, at night young salmon generally select lower velocity habitats with shallower depths and coarser substrates, perhaps to offset a decrease in foraging efficiency (Heggenes et al., 1993; Metcalfe et al., 1997; Mitchell et al., 1998).

The seasonal and diel habitat use of wild juvenile Atlantic salmon has received much attention (Heggenes et al., 1999; Armstrong et al., 2003). Previous studies have described general patterns of typical habitat use and reported differences in habitat use between day and night (e.g. Metcalfe et al., 1997). However, most habitat use studies focus on unmarked individuals, so it is uncertain if these habitat use patterns are performed by most individuals within a given day or if they emerge as an average of individuals with dramatically different daily patterns.

In this study, we monitored the habitat use and activity of 66 Atlantic salmon parr marked with passive integrated transponders (PIT) using a reach scale antenna grid in a natural environment providing both high temporal and spatial resolution. The main goal was to quantify the magnitude of the variation of activity pattern, habitat use and their interaction during the summer and autumn through a gradient of declining temperature ranging from 18 to 3^{o}C. Specifically, we tested the predictions that: 1) parr are predominantly nocturnal during both the summer and the autumn; 2) individual activity patterns (i.e. nocturnal, diurnal, day and night active, or crepuscular) vary on a short term basis, such that individuals are more nocturnal in higher flows and in colder temperatures; 3) parr habitat use interacts with activity patterns – a) activity pattern will influence habitat use: cathemeral individuals will use habitats with higher flow velocity during the day than at night – b) habitat use will influence activity pattern: nocturnal fish will use habitats with lower velocity than diurnal fish

7.3. Materials and methods

7.3.1. Study site

This study was undertaken on Xavier Brook, a tributary of the Ste-Marguerite River in Saguenay, Québec, Canada (48°2591799 N; 69°5394899 W). This stream is 10-15 m wide and flows in a forested watershed. Data were collected in a channel characterized by a steep riffle separated by two pools providing high habitat diversity (Figure 7.1). In the thalweg at low flow (0.4 m^3/s), depth ranged from approximately 0.1 m in the riffle to 1.65 m in the upstream pool. Median substrate size (B-axis, i.e. particle width) varied from cobble-boulders in the riffle to gravel-cobble (classification, after Wolman 1954) in the deep portion of the pools and gravel-sand in the pool recirculation zones.

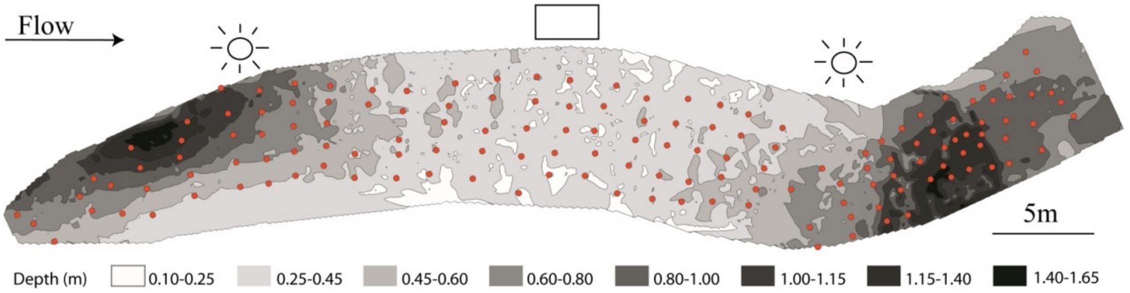

Figure 7.1 Flatbed antenna grid buried in the bed of a reach of Xavier Brook. 144 antennas are displayed in transects (dots), connected to a controller and multiplexer on the bank (rectangle) powered by solar panels (suns). Contours illustrate bathymetry at median flow during the study period.

7.3.2. Fish tracking system

A large flatbed antenna grid was used to monitor fish locations during 97 days, from 24 July to 1 November 2008. The tracking system consisted of an array of 149 circular antennas of 50 cm in diameter. Each antenna, designed to detect the presence of 23 mm PIT tags (Texas Instruments (TIRIS) model RI-TRP-RRHP, 134 2 kHz), was buried in the river bed and covered with substratum. The antennas were distributed systematically along transects of five antennas each. Overall, the detection field of the antenna grid covered 19% of the wetted area of the site at a discharge of 0.4 $m^3 s^{-1}$. Each group of five antennas was linked to a tuning capacitor, which was wired to a CYTEK multiplexer (JX/256 series, mercury wetted 256 single poles relay, www.cytec-ate.com). The multiplexer was connected to an *Aquartis* controller (custom made by Technologie Aquartis; www.aquartis.ca) composed of a TIRIS S-2000 reader, a datalogger and a custom-made controller unit. The system was powered by three solar panels connected to four 6V batteries plugged in series and two 12V batteries plugged in parallel. Each antenna was activated every 34 s successively for the detection of PIT tag presence. When a PIT tagged fish was detected, the date (dd/mm/yy), time (hh/mm/ss), antenna ID (multiplexer card and port number) and fish ID (tag number) were recorded. Detection range varied from 300-400 mm in height and 600-800 mm in diameter. During the study period, all antennas detected at least one individual. For more detailed information on the antenna grid, see Johnston et al. (2009).

7.3.3. Fish tagging

A total of 69 Atlantic salmon parr (1+) were captured in the study reach on two occasions using a backpack electrofishing device: 44 fish were caught on 24 July 2008, and 25 on 28 August 2008. In the first session, fish were captured at the tracking system location and up to 50 m upstream. For the second session, fish were caught up to 200 m upstream from the reach to avoid recapturing tagged fish. Juvenile Atlantic salmon that were smaller than 80 mm in body length were released immediately at the capture location to avoid any possible effect on growth and survival (Sigourney et al., 2005). Juvenile *Salvelinus fontinalis* and

Rhinichthys cataractae were also released upon capture. The retained fish were anesthetised in a clove oil solution (3 ml/10 L) and were surgically implanted with 23 mm PIT tags (*Texas Instruments*) in the abdominal cavity secured with surgical tissue adhesive (Vetbond©). Tagged fish were kept for a maximum recovery period of two hours in fish tanks within the river before being released on the study site. Two and one individual perished during the first and second tagging sessions, respectively. On each occasion, fish were measured (fork length, mean ± SD, L_A: 98 ± 7.4 mm, L_B: 109 ± 8.3 mm) and weighed (M_A= 9.7 ± 1.7 g, 10.7 ± 2.3 g).

7.3.4. Habitat survey

A pressure transducer was used to monitor flow stage and water temperature fluctuations every 15 min. Flow stage was estimated by subtracting atmospheric pressure fluctuations from the signal using data obtained from the closest meteorological station. Then, we subtracted the minimum value recorded during the study period, so flow stage was defined as the water level above minimum summer low flow (Figure 7.2). Considerable precipitation was received during the summer and autumn 2008 (486 mm from July to October). A high magnitude flow event occurred at the beginning of August, followed by a stage decrease in the following month. Then a prolonged low-flow period lasted for 10 days until the end of October. It was interrupted by a few precipitation events and remained about 10 cm above minimum between these events, which corresponded approximately to the median flow stage.

During the study period, water temperature decreased from 19.0°C to 2.8°C (Figure 7.2). In the first part of the study period, water temperature remained relatively stable, with low fluctuations around 15 °C. Around 3 September, water temperature started decreasing, reaching 12 °C on 11 September, which corresponds to the upper boundary of the temperature range at which juvenile suppress daytime activity (Rimmer et al., 1983; Fraser et al., 1993). Therefore, this date was chosen to define the boundary between the summer (12-18 °C) and the autumn (3-12 °C) periods.

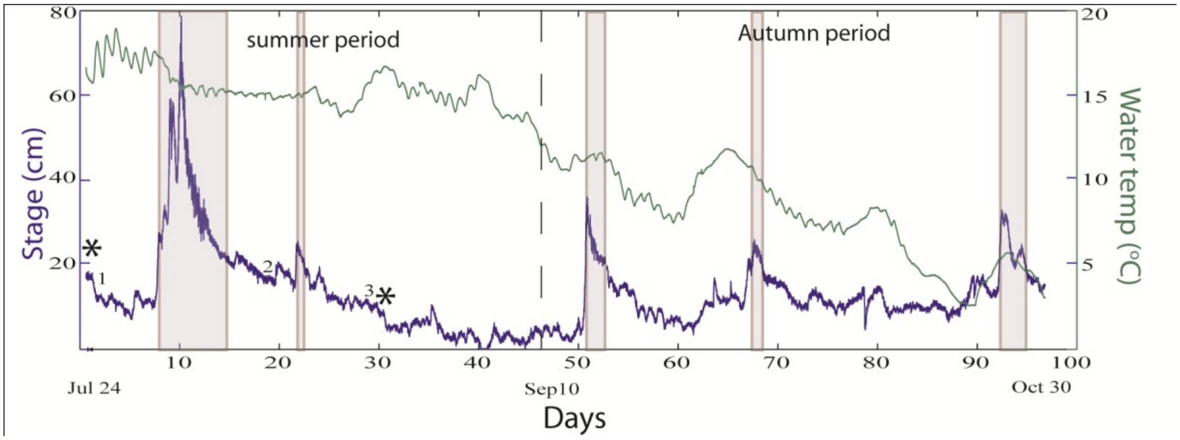

Figure 7.2 Time series of water level and water temperature. Gray shading indicates periods during which river stage was 20 cm over the minimum base level observed during the study period. The vertical dashed line denotes 12°C, defining a warmer summer period and a colder autumn period. Asterisks indicate fish tagging sessions and numbers the days of flow measurement.

The physical characteristics of the study reach were characterized in detail. Micro-topography was surveyed using a robotic total station (Trimble 5600DR) by combining a systematic transect sampling approximately 1m apart with the characterization of individual roughness elements that protruded approximately over 10 cm above the local mean bed elevation. This strategy optimized sampling effort, as sampling point density increased proportionally with bed complexity. From 6250 sample points, we created a digital elevation model (DEM) using a triangular irregular network (TIN) interpolation with pixel size of 10 cm. Depth was obtained by removing the general longitudinal slope of the channel using linear regression, and then by subtracting the water level at average flow (Q = 0.07 $m^3 \cdot s^{-1}$, stage: 10 cm) to all values of the bed elevation DEM. The general slope being removed, the remaining differences in depth within the reach were attributed to the channel shape, particularly to the steep pool riffle sequence. At median flow, maximum depth was recorded in the upstream pool 1.8 m and minimum depth in the thalweg was 0.30 in the riffle (Figure 7.1).

Flow velocity measurements were sampled extensively along the reach on three occasions, close to median flow periods (stages of 13 cm, 14 cm and 16 cm Figure 7.2). Three-dimensional flow velocity measurements were sampled using four acoustic Doppler velocimeters (ADVs, Sontek, San Diego) simultaneously at 10 cm above the bed at a density of three samples$\cdot$m^{-2}. An aluminum frame was used as a support and reference grid for ADV measurements. Each flow measurement was referenced using the total station and mapped. At median flow, mean flow velocity was approximately 0-30 cm$\cdot$s^{-1} in the pool recirculation zones, 0.40-0.60 cm$\cdot$s^{-1} in the pool tails and from 75-125 cm$\cdot$s^{-1} in the riffle. At each antenna location, velocity and depth were averaged within the antenna detection range (0.35 m radius). Although depth and velocity fluctuated during the study period, in this study we focused on habitat use at close to base flow and removed fish detections that were recorded during flood events (flow stage > 20 cm). We assumed that a particular habitat would keep a similar rank in terms of depth and velocity across minor flow stage fluctuations.

7.3.5. Data analysis

7.3.5.1. Diel activity patterns

First, the data set was explored for temporal trends in occurrences of detection of each individual in different periods of the day. For each individual, for each hour, we examined the periods during which fish were continuously detected every 34 s (tracking frequency) without interruptions for more than 30 minutes and removed this hour for this fish from the analysis, as it would be likely indicating that a fish was inactive. For all fish, a total of 175 h were removed this way over the entire study period, including 48 hours for a single fish, and 127 h for 15 other individuals. Afterwards, for each day that a fish was detected for at least 1h, each individual was assigned a "presence/absence" status for each hour. When a fish was not detected during a specific day, no 'presence/absence' status was recorded because we could not assess if the fish had emigrated from the reach or was sheltering. To examine within-individual variability, we first selected the individuals that were detected on the reach a minimum of five days in either the autumn or the summer period or both. We then assumed that presence recordings reflect periods of fish activity, as foraging movements are likely to increase the frequency of fish detection by the system.

To examine the overall temporal patterns of fish activity, we estimated relative frequency of detection for each hour of the day for each individual. For instance, if a fish was detected during 20 days, but only five times between 5h00 and 6h00, its average relative frequency of detection for 5h00 would be 25%. The frequency of detection for each hour were square root transformed and used as datum in the analysis (n = 34 for summer and n = 14 for autumn). To test for the presence of an overall diel activity pattern and for a seasonal interaction, we used a repeated measures general linear model using *hour* as a within-individual factor and *season*, *mass* and *fork length* as between-individual factors or covariates. Only *hour* and *season* remained in the final model, as the other variables did not have significant effects (i.e. $p>0.05$).

To examine activity patterns of each individual, we used logistic regression with *hour* as the explanatory variable and average *relative frequency of fish detection* as a response variable. Quadratic terms were added to the regression, as the variable *hour* was ordered from 1 to 24; the hours of darkness occurred in two non-contiguous portions. Then, based on the circadian cycle and on visualization of activity patterns, periods of 24h were divided into four daily periods: night (0100-0300 and 2100-2400), dawn (0400-0600), day (0700-1800) and dusk (1900-2100). To present the within-individual variation in activity pattern for each individual, for each day, each fish was categorized as 1) nocturnal: active during night and possibly dawn and dusk, 2) diurnal: active during day and possibly dusk and dawn, 3) cathemeral: active both night and day and possibly dusk and dawn 4) crepuscular: active only during dusk and dawn periods.

7.3.5.2. Activity patterns vs. flow and temperature

Next, we investigated the temporal variation and the effect of flow stage and temperature on daily activity (i.e. daily frequency of fish detection), diurnal activity, nocturnal activity and crepuscular activity. Daily averaged temperature and flow stage range of values were divided in nine and seven discrete categories respectively. We estimated the percentage of time an individual was active at a particular daily period at a particular temperature and flow level. We used four distinct mixed-effects models to test the effect of flow and temperature as fixed factors on fish activity (daily, diurnal, nocturnal and crepuscular). Comparison of different fixed effect structures was done using AIC values (Burnham et al., 2011).

7.3.5.3. Habitat use diel patterns

For each hour of each day an individual was considered active, an average depth and velocity values were estimated. To test the presence of an overall habitat use pattern and a seasonal interaction effect, we carried out a general linear model with repeated measures using *daily period* (i.e. night, day, crepuscular) as a within-individual factor and *season* as a covariate. Then, to examine and visualize the individual daily habitat use pattern of each fish, for each individual for each season, quadratic regressions were carried out using *hour* as explanatory variable and *average habitat use* for that hour as the response variable.

7.3.5.4. Diel habitat use vs. diel activity patterns

For each of the habitat variables, four distinct mixed-effects models were performed using fish as subjects, days as repeated measures and diel activity pattern and season as fixed factors. Hence, we compared 1) day and night habitat use within days when individuals were cathemeral, 2) night habitat use when individuals were nocturnal to night habitat use when individuals were cathemeral, 3) day habitat use when individuals were diurnal to when individuals were cathemeral. All analyses were carried out using Matlab R2010a and SPSS 17.0.

7.4. Results

7.4.1. Fish recordings

In this study, a total of 66 fish were captured, PIT-tagged and released in the reach. From the total, four individuals (6%) were never detected by the tracking system and 12 individuals (18%) were detected in the study reach for less than 24 hours, as they most likely left the study site. Ten individuals (15%) were detected on site for a single day, 13 individuals (24%) stayed in the reach between one and four days, and 27 individuals remained in the reach between 5 and 70 days (37%). As we were interested in individual variability, only fish present for five days or more were investigated herein. Of those fish, 13 and two individuals were only detected during the summer and autumn periods, respectively, and 11 were detected during both periods.

Fish used the entire reach, as they were detected at every antenna location during the study period. Each antenna recorded between 2 and 20 different individuals during the study period, with an average of 7.5 individuals. The upstream shallow recirculating zone was used by the fewest individuals, followed by the downstream part of the riffle. The transition between the upstream pool and the riffle, and the entire downstream pool were visited by the highest number of tagged individuals. The highest frequency of fish detections was recorded in the upstream pool tail, the transition between the upstream pool and the riffle and in the margins of the downstream pool. Relatively few fish were detected in riffle habitats, the upstream recirculation zone and the deep pool.

7.4.2. Diel and seasonal activity pattern

In both summer and autumn, the frequency of fish detection exhibited a clear daily pattern, with fish activity peaking at dawn and dusk, and being higher at night than during the day (Two-way repeated measures GLM (hours); $F = 11.854$, df = 23, 851, $p < 0.001$) (Figure 7.3a). During the summer (stars), frequency of fish detection peaked at approximately 0.45 between 0500 and 0600 and between 2000 to 2100, which corresponded with sunrise and sunset. Average frequency of fish detection was 0.25 during the night and decreased to 0.15 to 0.20 during the day. A similar pattern was observed during the autumn period (Figure 7.3a, circles), except the peaks in fish detections at sunrise and sunset occurred one hour earlier (between 0600 and 0700) and later (between 1900 and 2000), respectively.

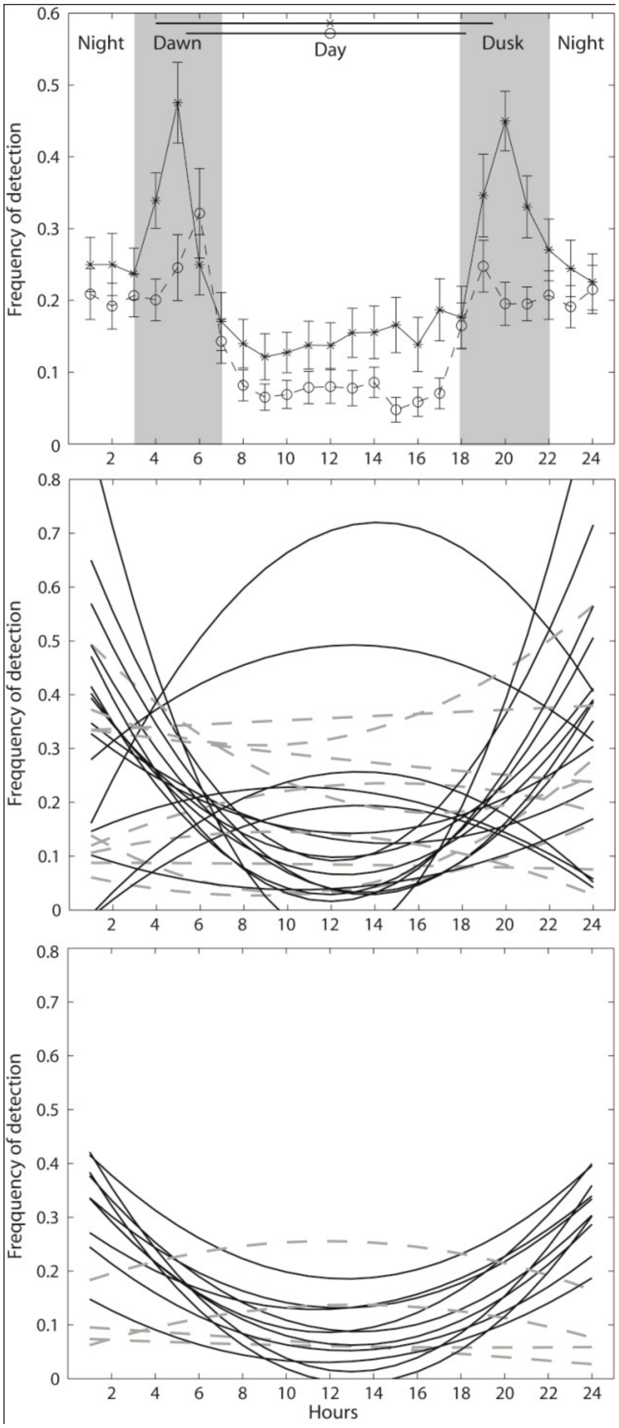

Figure 7.3 Average probability of fish presence per hour during the summer (stars, N=25) and autumn (open circles, N=14). Horizontal line shows average periods of daylight during summer and autumn. Quadratic logistic regression models of probability of fish presence as a function of hours during the (a) summer and (b) autumn. Solid lines indicate significant curves, whereas dashed lines non-significant curves.

Mean frequency of fish detection was lower in autumn than in summer (GLM (season), F = 4.652, df = 1, 37, p = 0.038), particularly during the dawn and dusk peaks of activity.

Although the above results suggested an overall predominance of nocturnal behaviour with activity peaks at twilight, substantial variability among parr was observed. Logistic regressions with added quadratic terms revealed three types of daily patterns: nocturnal, concave quadratic curves; diurnal, convex quadratic curve; or, equally active during day and night, not significant (Figure 7.3b). During the summer, only 11 of 25 individuals exhibited the predominant nocturnal pattern, whereas five individuals (20%) exhibited diurnal behaviour, and nine individuals (36%) showed no significant daily pattern. During the autumn, nocturnal behaviour was adopted by 10 of 14 individuals (71%), with four individuals showing no clear pattern (29%) and no parr exhibiting diurnal behaviour. However, the difference in frequencies of diel patterns between summer and autumn was not significant (χ^2 = 4.20, df = 2, p = 0.12).

Even though some individuals exhibited a predominant diel activity pattern, others exhibited considerable within-individual variability. Fish that did not exhibit a significant nocturnal or diurnal pattern were either active both day and night within the same day or were active only at night on some days and only during the day on other days (Figure 7.4). Juveniles differed in how they adopted different activity patterns over time. Several individuals were only nocturnal or crepuscular, whereas others frequently changed daily patterns between days (Figure 7.4).

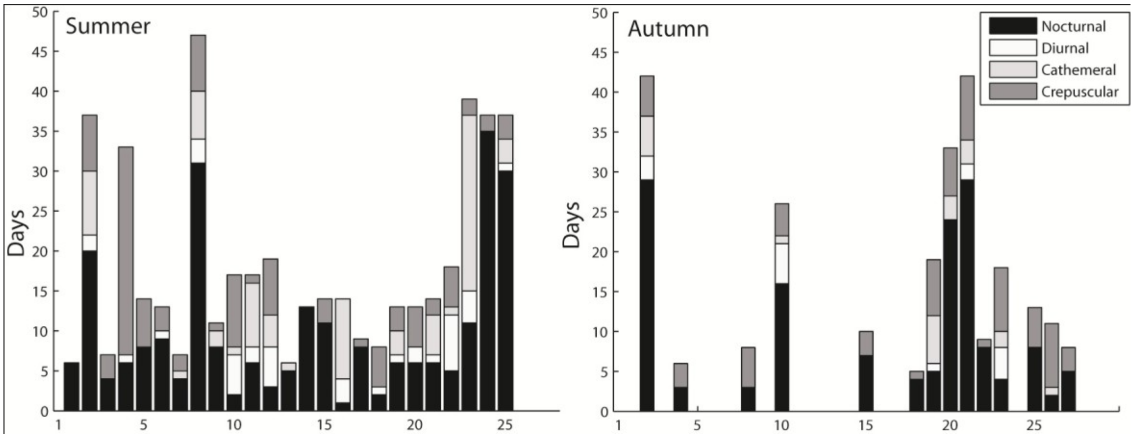

Figure 7.4 Number of days each fish was present in the reach subdivided into diel activity pattern adopted by each individual in the (a) summer and (b) autumn.

During the summer, all fish adopted a nocturnal pattern on at least 10% of the days, but the majority of fish were nocturnal on more than 50% of the days. While seven individuals were never detected during daylight hours, 15 individuals (60%) were active only in the day at least once during the summer. Three individuals (12%) were highly crepuscular and were only detected at twilight periods on more than 50% of the days. Within individual variability of activity pattern decreased during the autumn, as most fish were nocturnal and crepuscular. However, four individuals (30%) still exhibited daytime activity (i.e. either diurnal or both) over 15% of the days.

7.4.3. Daily activity patterns *vs.* flow stage and temperature

Daily patterns of activity varied among fish within days, with all types of activity patterns being observed most days. Daily activity increased significantly with temperature and peaked at 13°C (Figure 7.5a; GLM, F = 2.068, df = 8, 104.50, p = 0.046). This relationship was mainly due to a significant increase in crepuscular activity (GLM, F = 3.812, df = 8, 107.03, p = 0.001), as no significant effect of temperature was observed on diurnal and nocturnal activity (GLM, *F* = 1.626, df = 8, 103.87, *p* = 0.126; *F* = 0.791, df = 8, 106.75, *p* = 0.612).

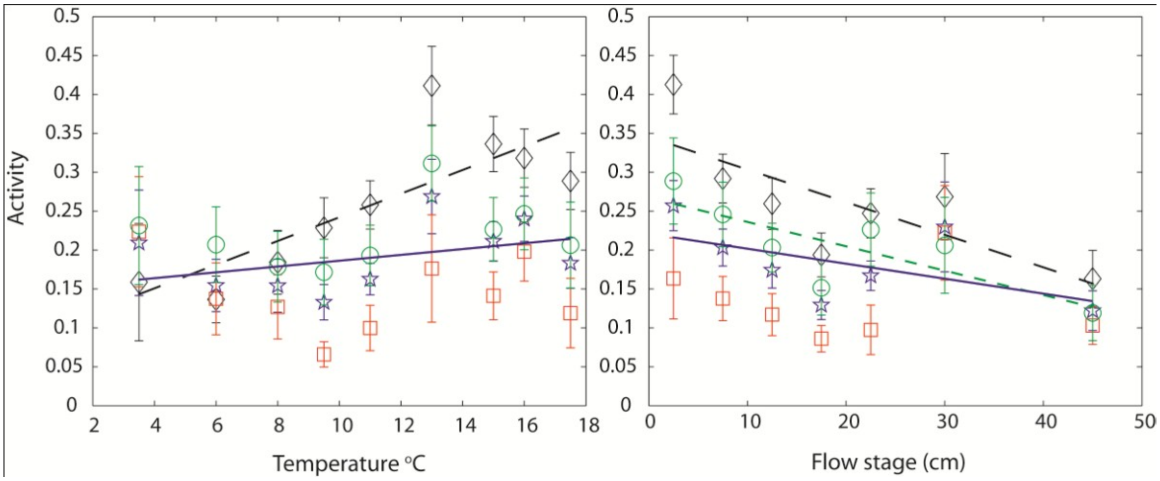

Figure 7.5 Mean + SE activity (i.e. relative frequency of detection) during (stars) the entire day (24 h), (diamonds) crepuscular, (circles) night and (square) day periods of Atlantic salmon parr in relation to a) water temperature and flow stage above minimum recorded for a period of three months in the summer and autumn. Each datum was the mean activity for each marked fish at each temperature and flow stage interval. For each increasing temperature category, n = 3, 6, 14, 14, 16, 18, 22, 26, 17 and for flow category n= 17, 27, 25, 25, 20, 12, 12.

Daily activity also significantly decreased with flow stage (Figure 7.5, GLM, *F* = 3.982, df = 6, 107.10, *p* = 0.001), primarily due to a decrease in nocturnal (GLM, *F* = 2.582, df = 6, 110.39, *p* = 0.022) and crepuscular (GLM, *F* = 5.463, df = 6, 110.274, *p* < 0.001) activity, with no significant effect of flow on diurnal activity (GLM, *F* = 2.14, df = 6, 106.872, *p* < 0.055).

7.4.4. Diel and seasonal habitat use patterns

Average velocity used by parr varied significantly between day, night, and crepuscular periods (Figure 7.6a; GLM within fish repeated measures, *F* = 3.759, df = 3,111 *p*=0.013); parr used lower velocity habitats during the night than during dawn, day and dusk periods.

During the summer, velocity used ranged from 50 to 60 $cm\cdot s^{-1}$ during hours of darkness (2000 to 0500) and from 65 to 86 $cm\cdot s^{-1}$ during the rest of the daily cycle. However, this diel pattern of habitat use was not observed during the autumn period (GLM within fish days x season interaction, $F = 3.775$, df = 3,111 $p = 0.013$), as average velocity used varied irregularly between 64 and 70 $cm\cdot s^{-1}$ for the four daily periods. Nevertheless, overall average velocity used did not differ between the summer and autumn season (between fish GLM, F=0.033, df = 1, 3, $p = 0.857$). Although the use of lower velocity at night was the predominant pattern, substantial variability among individuals was observed. During the summer, 10 individuals (40%) exhibited a convex daily pattern of current velocity used, whereas three individuals (12%) adopted the opposite behaviour and 12 (48%) did not show a clear pattern (Figure 7.6c). During the autumn period, only three fish used lower velocity habitats at night, the remaining 10 individuals did not exhibit significant daily patterns (Figure 7.6e).

Average flow depth used did not differ significantly between day, night and crepuscular periods ($F = 1.457$, df =3, 111 $p = 0.23$) or between summer and autumn (GLM, F=0.845, df = 1, 37, p=0.364), nor was there a significant interaction between daily period and season (Figure 7.6b; GLM season x daily periods interaction, GLM, $F = 0.247$, df = 3,111 $p = 0.863$). However, average patterns obscured interesting variability between fish: six fish (24%) used shallower areas at night than during the day; six others exhibited the opposite pattern; and, half did not exhibit any clear daily flow depth use pattern (Figure 7.6d). During the autumn, six individuals out of 14 (43%) exhibited a different depth use between day and night periods, two using deeper and four using shallower habitats at night than during the day (Figure 7.6f).

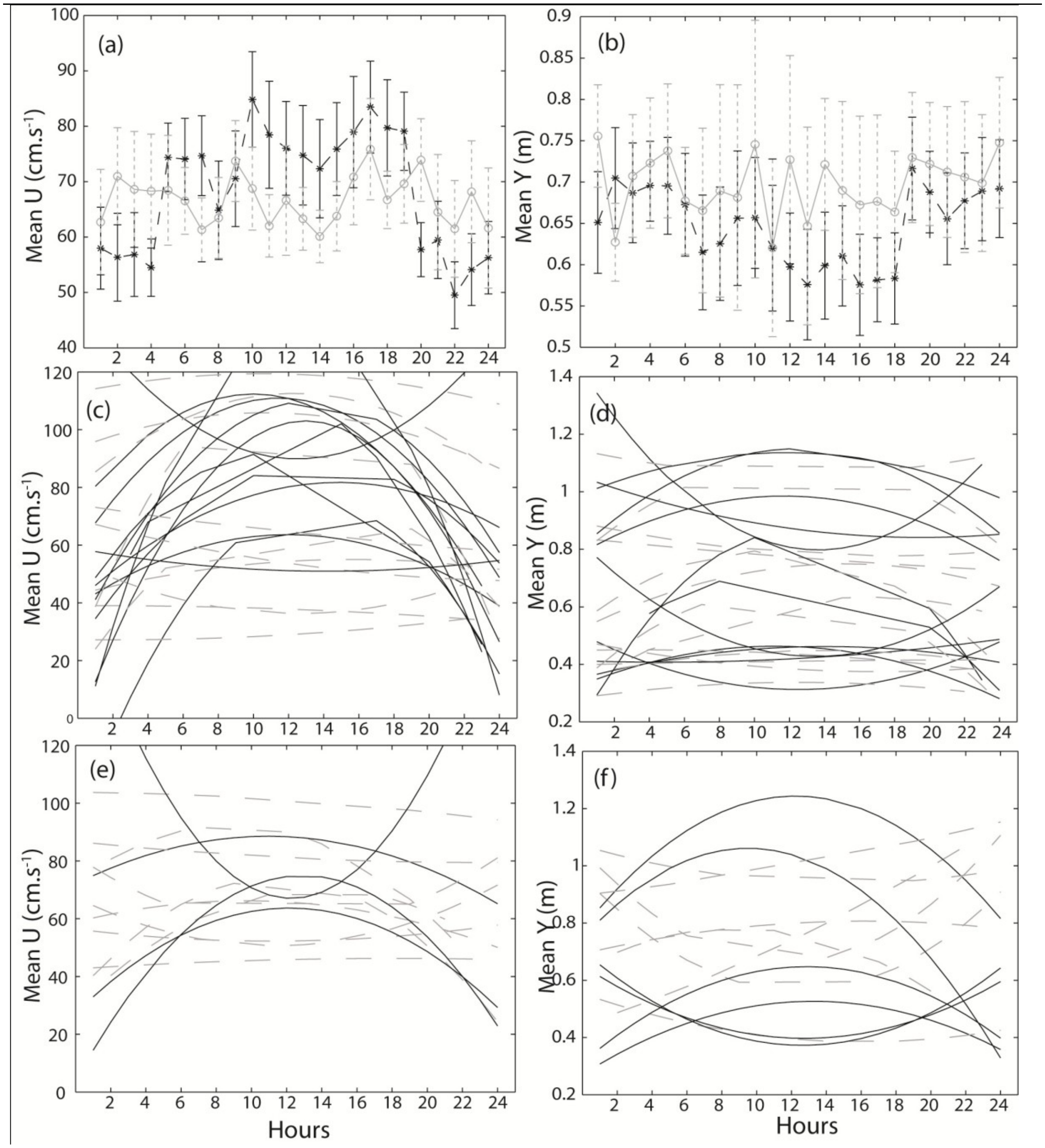

Figure 7.6 Average (a) flow velocity and (b) depth used by Atlantic salmon parr in the summer (stars) and autumn (open circles) per hour. Quadratic regressions of individual average (c) flow velocity and (d) use (c) per hour during the summer (n=25) (significant relationship: solid, non significant: dashed) and (e) and (f) are the same relationships for the autumn period (n=13).

Again, a large proportion of individuals (57%) did not display any particular pattern of depth use.

7.4.5. Diel habitat use vs. activity patterns

Contrary to the average daily patterns of habitat use, when exhibiting a cathemeral daily pattern, individuals did not use lower velocities at night than day (within the same day) in the summer ($F = 2.58$, df = 1, 145, $p = 0.11$) nor autumn ($F = 1.306$, df = 1, 40, $p = 0.26$). Therefore, average differences in daily habitat use were induced by individuals exhibiting different daily patterns (diurnal vs. nocturnal). During the summer, nocturnal individuals used night habitats with significantly lower velocities and lower depths than cathemeral individuals (U: $F = 31.97$, df = 1,271 $p < 0.001$; $F = 15.94$, df = 1,263 $p < 0.001$). However, diurnal individuals did not use different day habitats than cathemeral fish (U $F = 0.95$, df = 1, 84, $p = 0.33$; Y $F = 2.57$, df = 1, 82 $p = 0.113$). In the autumn, fish exhibiting different daily activity patterns did not differ significantly in their habitat use during the day and night (data not shown).

7.5. Discussion

In this study, parr frequently changed their daily activity pattern. Overall activity decreased with temperature and flow stage, but changes in daily activity occurred mostly during crepuscular periods. The results suggest that habitat use interacts with activity pattern, illustrating dynamic foraging decisions resulting from tradeoffs experienced at the microhabitat scale.

7.5.1. Diel and seasonal activity patterns

Our results showed that the probability of detecting a fish, which is assumed to be closely associated with fish activity, peaked during twilight periods, particularly during the summer. Activity was also higher at night than during the day during both summer and autumn. Although parr have been observed switching from a predominantly diurnal to a nocturnal behaviour as temperature drops in the autumn between 8-12^{o}C (Rimmer et al., 1983; Fraser et al., 1993; Bremset, 2000), our results support more recent studies reporting a predominance of nocturnal behaviour during the warmer temperatures in summer (Gries et al. 1997, 13-23^{o}C; Imre and Boisclair 2004, 16-21^{o}C) and in the autumn (Johnston et al. 2004). Nocturnal behaviour might be associated with a size dependant trade-off between growth and predation risk. Post young-of the year parr tend to be more nocturnal to minimize predation risk from diurnal predators, whereas young-of-the-year tend to maximize food intake to increase their growth rate and chances of surviving the winter (Imre and Boisclair, 2004; Johnston et al., 2004). While we observed only post YOY in this study, body size had no significant effect on diel activity pattern, suggesting that small differences in size might be less important than other factors in inducing a particular activity pattern.

Although the crepuscular activity of juvenile salmonids is generally acknowledged (Brittain and Eikeland, 1988), most studies on fish activity and habitat use usually only compare day and night activity. However, our results suggest that dawn and dusk are important, often representing the only periods of activity in a daily cycle for some individuals. Furthermore, the overall low probability of fish detection of 23% suggests low activity levels, even in the summer. Similarly, 1+ Atlantic salmon are active only 37% of the time in the summer (Breau et al., 2007). Low activity in the summer might be explained by individuals gaining enough energy during short periods of activity to survive the next winter without unduly increasing their predation risk (Cunjak et al., 1998). Low activity levels might also have been induced by an abundance of food (Metcalfe et al., 1999;

Orpwood et al., 2006). Nevertheless, in this study, probability of fish detection by the tracking system most likely underestimated fish activity (also see Breau et al., 2007), as sedentary fish might have been active in areas that were not covered by the antenna grid. Hence, probability of detections in this study was primarily a way of comparing activity between periods, rather than as an estimate of absolute mobility.

7.5.2. Individual variability of parr activity

The high within-individual variability in activity pattern confirmed our second hypothesis that parr frequently changed activity patterns. Despite a predominantly nocturnal activity pattern, important variability between individuals was observed, confirming previous studies (Breau et al., 2007). In our study, only 44% of the fish followed the average concave pattern in the summer, which was associated with lower activity in the day than in other periods. These results highlight the importance of examining individual variation in salmonid behaviour, rather than reporting average trends. Our results also suggest that fish behaviour was more homogeneous in the autumn, as the majority of individuals adopted a predominantly nocturnal activity pattern and no fish were predominantly diurnal.

Several individuals exhibited the consistent diel activity pattern of being active only during crepuscular periods and at night. This activity pattern likely provides basic energetic needs while minimizing predation risk: dusk and dawn are typically times of high food abundance (Brittain and Eikeland, 1988), without the high predation risk of daytime (Clark and Levy, 1988). However, many individuals exhibited considerable variability in activity patterns, sometimes being active at night only, during the day only, during both the day and night, and during twilight periods only. This flexibility in behaviour suggests that the choice of an activity pattern is not only driven by fixed life history characteristics, such as body size, but also by how individuals respond to changing biotic or abiotic factors. We suggest that short-term variation in habitat use and an individual's recent foraging success and perceived predation risk (Metcalfe et al., 1999) might be the driving factors.

7.5.3. Activity vs. flow and temperature

Contrary to the prediction, temperature did not significantly affect diurnal and nocturnal activity. However, total activity increased with temperature, mostly due to an increase in crepuscular activity. Our results suggested, therefore, that older parr in the wild are predominantly nocturnal in the summer regardless of temperature (Imre and Boisclair, 2004; Johnston et al., 2004), but also modulate their crepuscular activity levels with temperature, perhaps to benefit from higher food availability at higher temperatures during dusk and dawn. Also contrary to the prediction, nocturnal and crepuscular activity decreased with flow stage. Perhaps the increased food availability in faster flows decreased the time required to fulfill energetic demands while keeping predation risk to a minimum. However, unlike in Bradford and Higgins (2001), daytime activity did not decrease with flow stage.

7.5.4. Seasonal and diel habitat use patterns

On average in the summer, parr used lower flow velocities at night than during the day, perhaps to offset a decrease in their ability to catch prey at night in fast flows (Metcalfe et al., 1997). Interestingly, in the autumn, there was no difference between the flow velocities used during the day and night. Similarly, Riley et al. (2006) reported that young-of-the-year salmon used lower flow velocity at night than during the day, but not for older juveniles. Therefore, differences in day/night habitat use might be related to differences in day and night foraging. Young-of-the-year salmon continue to feed later in the year than older juveniles (Johnston et al., 2004; Breau et al., 2007). If diel patterns in velocity-related habitat use were associated with diel activity patterns, a suppression of activity during daylight would affect the type of habitats used during the day and night. In contrast with previous studies reporting the use of low-velocity habitats at low temperatures (Cunjak, 1988; Metcalfe et al., 1997), we observed no significant differences between summer and autumn. Consistent with previous studies (Riley et al., 2006), parr did not exhibit a significant diel pattern in the use of flow depth. Flow depth may be of less importance than velocity in habitat selection.

Parr exhibited high inter-individual variability, as only 40% of individuals exhibited the predominant pattern of a shift to slower flows at night, with some individuals exhibiting the reverse pattern. Such behaviour might arise as a result of lower velocity habitats being limited by competition. Also, habitat selection might affect short scale foraging success, which indirectly affected activity pattern decisions.

7.5.5. Activity patterns and habitat use patterns

In contrast to the general pattern of lower flow velocity used at night, cathemeral fish did not use different habitats at different times of day. This observation contrasts with previous experiments that showed a preference for lower velocity at night (Metcalfe et al., 1997; Valdimarsson and Metcalfe, 1998). However, these studies were conducted under controlled conditions in the absence of competition, which might prevent some individuals from using already occupied habitats. The overall differences between day and night habitat use observed in this study can therefore be attributed to individuals being nocturnal or diurnal, which supports the hypothesis that habitat use influences the activity pattern adopted by individuals.

When fish were nocturnal, they used habitats with lower flow velocity than when they were cathemeral. Given the relatively high velocities observed on the reach at median flow, we suggest that average velocity selected by nocturnal fish (53 $cm \cdot s^{-1}$) were more profitable than the higher average velocity selected at night by cathemeral fish (68 $cm \cdot s^{-1}$). Perhaps low foraging success at night in fast flows induced a need to forage also during the day. Individuals exhibiting nocturnal activity used lower velocity habitats than other individuals during crepuscular periods, perhaps because low flow velocity habitats were limited in the reach.

7.6. Linking paragraph

The previous chapter revealed a high individual variability of activity patterns and habitat use among juvenile Atlantic salmon. Several fish were mostly nocturnal, but others frequently changed activity and habitat use patterns. Temporal variation in habitat use is one of the likely causes for fish mobility. Therefore, this individual variability in activity and habitat use might translate into high individual variability in mobility. However, previous studies using mark-recapture techniques described stream salmonid populations as composed of fractions of sedentary and mobile individuals. In Chapter 8[1], using the same data set, we revisit the question of juvenile salmon mobility using our high resolution PIT-tag data set. We describe individual variation in movement behaviour in relation to environmental variables over three months in the summer and autumn. Our results reveal high individual variability of movement behaviour on a daily basis, as most individuals exhibited low mobility on most days, but showed occasional bouts of high mobility. Between-individual variability only accounted for a low proportion of the variability in the mobility data. These results challenge the assumption that salmonid populations are composed of fractions of sedentary and mobile individuals. To our knowledge, this study is the first to explicitly address the question of individual variability in mobility on a daily scale. In the context of the thesis, this last results chapter highlights the complexity of fish behaviour and the important amount of information gained from an individual-based approach that would remain mostly obscured using an approach based on average estimates of behaviour.

[1] Roy, M.L., Roy, A.G., Grant, J. W. and N. Bergeron. Individual variability in the movement behaviour of juvenile Atlantic salmon, submitted to the *Canadian Journal of Fisheries and Aquatic Sciences*.

Chapitre 8: Individual variability in the movement behaviour of juvenile Atlantic salmon

8.1. Abstract

Stream-dwelling salmonid populations are generally thought to be composed of both relatively mobile and sedentary individuals, but this conclusion is primarily based on results obtained from recapture methods with low temporal resolution. In this study, the mobility of 66 juvenile Atlantic salmon was monitored using a large array of passive integrated transponder antennas buried in the bed of a natural stream. Fish locations were recorded at a high frequency for a period of three months. Four types of daily behaviour were identified: stationary (detected primarily at one location), sedentary (limited movement between a few locations), floater (frequent movements in a restricted home range) and wanderer (movements across the reach). Most individuals exhibited low mobility on most days, but also showed occasional bouts of high mobility. Between-individual variability accounted for only 12-17% of the variability in the mobility data. These results challenge the assumption of a population composed of a sedentary and mobile fraction. High mobility was more frequent at low flow, but no difference was observed between the summer (12-18°C) and the autumn (4-12°C). Individual variation on a daily basis suggested that movement behaviour is a response to changing environmental conditions rather than an individual behavioural trait.

8.2. Introduction

Early studies depicted juvenile salmonids as sedentary, territorial animals exhibiting high site fidelity (Kalleberg, 1958; Keenleyside, 1962). The development of better tagging technology, which allowed for the tracking of individuals at a higher temporal resolution, revealed that the territorial mosaic of salmon parr was more flexible and dynamic than previously thought (Armstrong et al., 1999; Okland et al., 2004). In particular, Atlantic salmon parr have large, overlapping home ranges, with some individuals moving out of their home ranges to relocate either upstream or downstream (Okland et al., 2004; Ovidio et al., 2007), suggesting little fidelity to a particular microhabitat.

It now seems broadly accepted that both sedentary and mobile individuals occur within a given population (Gowan et al., 1994; Rodriguez, 2002; Morrissey and Ferguson, 2011). While the size of the two fractions varies considerably between sites, species, and life stages, the sedentary fraction tends to be larger than the mobile fraction (Hesthagen, 1988; Heggenes et al., 1991; Steingrimsson and Grant, 2003). Some individuals have been characterized as "movers" (i.e. cruise foragers) whereas others as "stayers" (sit-and-wait foragers), based on the proportion of time spent moving (Grant and Noakes, 1987; McLaughlin et al., 1994). Although spatial behaviour might be a heritable trait (Ferguson and Noakes, 1983), Gowan et al. (1994) suggested that individuals may switch tactics in response to changing environmental conditions. Although some juvenile salmonids can defend the same territory for extended periods (Martel, 1996), a fraction can switch between sedentary and mobile behaviour between two subsequent years (Harcup et al., 1984). However, it remains unclear how common this behaviour is, and at what temporal frequency the switching occurs.

Fish movements have been linked to changes in biotic and abiotic conditions (Gowan et al., 1994), likely due to variation in flow stage, temperature and daily light cycles. However, the effects of these variables on the behaviour of fish seem to be complex, as several studies have provided contrasting results. For instance, salmonids have been reported to decrease their mobility and territory size at high flows (Kemp et al., 2006), whereas others report the opposite trend (Scruton et al., 2003; Riley et al., 2009), or no trend at all (Berland et al., 2004; Heggenes et al., 2007). Similarly, while water temperature affects fish metabolism (Jonsson et al., 2001), its effect on fish activity is less certain (Fraser et al., 1993; Breau et al., 2007). As temperature drops in the autumn, Atlantic salmon parr suppress their daytime activity, presumably as a result of a tradeoff between growth and predation risk (Fraser et al., 1993; Fraser et al., 1995; Johnston et al., 2004). Nevertheless, other proximate factors must also influence fish activity on a seasonal basis (Bremset, 2000), as other studies report either no decrease or an increase in fish mobility (Nykanen et al., 2004; Riley et al., 2006).

The spatial arrangement of microhabitats might also influence mobility because habitat heterogeneity decreases territory size (Venter et al., 2008) and mobility (Heggenes et al., 2007). In less heterogeneous habitats, individuals might have to move farther to encounter complementary microhabitats that provide foraging opportunities and shelter (Venter et al., 2008). However, information on the relationship between habitat structure and fish mobility remains fragmentary. Furthermore, juvenile salmonids are often captured using methods that might be better suited for catching sedentary than mobile fish (Gowan and Fausch, 1996). Therefore, if mobility affects habitat use, the estimation of habitat preference might be biased towards sedentary fish.

The results from movement studies depend on how frequently fish have been located and for what duration (Lucas and Baras, 2000). For instance, fish mobility estimates from radio-telemetry studies are generally greater than those obtained from mark-recapture studies. However, radio-telemetry suffers from the inability to sample small fish and from relatively large sampling units of habitat, making difficult the quantification of small-scale movements. Recent developments in flat-bed passive integrated transponder (PIT) antenna grid provide fish tracking data at both high temporal and spatial resolutions over extended periods of time (Armstrong et al., 1999; Greenberg and Giller, 2000; Riley et al., 2003; Johnston et al., 2009). In this study, we used a large PIT antenna grid to monitor daily movement of a group of individually marked Atlantic salmon parr 1+ in a natural stream. Positions of tagged fish were recorded continually during three months of the summer and autumn. While previous studies have reported a high between-individual variation in parr mobility (Okland et al., 2004; Ovidio et al., 2007), within-individual mobility variation has received little attention. Hence, our primary objective was to document the magnitude of individual variation of parr daily mobility to test the competing predictions that individuals: (1) adopt consistent mobile or sedentary tactics over long periods of time; or (2) modify their mobility based on changing biotic and abiotic conditions. Second, if the data support the second prediction, we tested whether changes in behaviour could be predicted by environmental fluctuations. In particular, we tested the predictions that parr will be more sedentary: (3) when flow stage increases, as both the availability of drifting prey and swimming energy costs increase; (4) in the autumn than in the summer; and, (5) in heterogeneous habitats, which likely provide complementary feeding and sheltering habitats in closer proximity.

8.3. Materials and methods

8.3.1. Study site

This study was carried out on the Xavier Brook, a tributary of the Ste-Marguerite River in Saguenay, Québec, Canada (48°2591799 N; 69°5394899 W). The study reach was approximately 65 x 10 m (lxw), composed of two pools separated by a steep riffle, providing high physical habitat diversity. In the thalweg at low stage (0.4 $m^3 \cdot s^{-1}$), depth ranged from approximately 0.1 m in the riffle to 1.65 m in the upstream pool. Median substrate size (B-axis, i.e particle width) varied from gravel-cobble in the riffle to gravel-cobble in the deep portion of the pools and gravel-sand in the pool recirculation zones (substrate classification according to Wolman, 1954).

8.3.2. Fish tracking system

To monitor fish movements, we used a large flatbed antenna grid covering the entire study reach. The system was used to monitor tagged fish locations in the reach during 97 days (24 July to 1 November 2008). The tracking system consisted of an array of 149 circular antennas (50 cm in diameter), which were buried within the river bed and designed to detect the presence of 23mm PIT tags (Texas Instruments (TIRIS) model RI-TRP-RRHP, 134 2 kHz) and other tags complying with the ISO 11784/11785 international standards. Each antenna was interrogated for fish presence every 34 s (i.e. 0.03 Hz). Antennas were distributed along cross-channel transects each composed of five antennas. Overall, the detection field of the antenna grid covered 19% of the wetted area of the site at a discharge of 0.4 $m^3 \cdot s^{-1}$.

Each group of five antennas was linked to a tuning capacitor, which was wired to a CYTEK multiplexer (JX/256 series, mercury wetted 256 single poles relay, www.cytec-ate.com). The multiplexer was connected to an *Aquartis* controller (custom made by Technologie Aquartis; www.aquartis.ca) composed of a TIRIS S-2000 reader, a datalogger and a custom-made controller unit. The system was powered by three solar panels connected to four 6V batteries plugged in series and two 12V batteries plugged in parallel. Each antenna was activated successively for the detection of PIT tag presence. When a PIT tagged fish was detected, the date (dd/mm/yy), time (hh/mm/ss), antenna ID (multiplexer card and port number) and fish ID (tag number) were recorded. Detection range varied from 300-400 mm above the bed surface and 600-800 mm in diameter. During the study period, all antennas detected at least one fish. For more technical details on the antenna grid, see Johnston et al. (2009).

8.3.3. Fish capture and tagging

We captured 69 Atlantic salmon parr (1+) in the study reach on two occasions using a backpack electrofishing device: 44 fish were caught on 24 July 2008, and 25 on 28 August 2008. During the second electrofishing session, fish were captured immediately upstream of the reach to avoid re-capturing tagged fish. To avoid the potential negative effects of PIT tagging on parr survival and growth (Sigourney et al., 2005), we released juveniles of body length < 80 mm, as well as juvenile *Salvelinus fontinalis* and *Rhinichthys cataractae*. Fish were then anesthetised in a clove oil solution (3 ml/10 L) and implanted with 23-mm PIT tags (*Texas Instruments*) in the abdominal cavity secured with surgical tissue adhesive (Vetbond©). Tagged fish were allowed a recovery period of approximately 2 hours in a fish tank before being released on the study site. A total of three fish died during tagging, two during the first tagging session and one during the second. Average fork length (L ± SD) and average mass (M± SD) of tagged fish were: L_A: 98 ± 7.4 mm; M_A= 9.7 ± 1.7 g; L_B: 109 ± 8.3 mm; M_B: 10.7 ± 2.3 g. The fish captured in August were significantly longer than those captured one month earlier (t = -5.73, df =64, $p < 0.001$), but mass was not statistically different (t = -1.92, df = 64, p=0.06).

8.3.4. Habitat characterization

Flow stage and water temperature fluctuations were recorded every 15 min using a pressure transducer (*Level logger*) installed at the bottom of the upstream pool. Water stage was estimated by correcting the recorded pressure values for changes in atmospheric data obtained from the closest meteorological station, and then subtracting the minimum value observed during the study period. Therefore, stage was defined as the water level above the minimum summer low flow level. The study period was characterized by substantial discharge variability (Figure 8.1). A high magnitude flow event occurred at the beginning of August, followed by a stage decrease in the following month. Then, a prolonged low flow lasted until the end of October when it was interrupted by several precipitation events. Base flow between these events was approximately 10 cm over the minimum flow, which corresponded roughly to the median flow recorded during the study period. Flow stage values were categorized as low (0-10 cm, 35% of days), medium (10-15 cm, 35% of days), high (15-25 cm, 13% of days) and very high (25 cm and higher, 17% of days). Using a field based digital elevation model of the reach, bankful flow was estimated to occur at a stage of 60 cm.

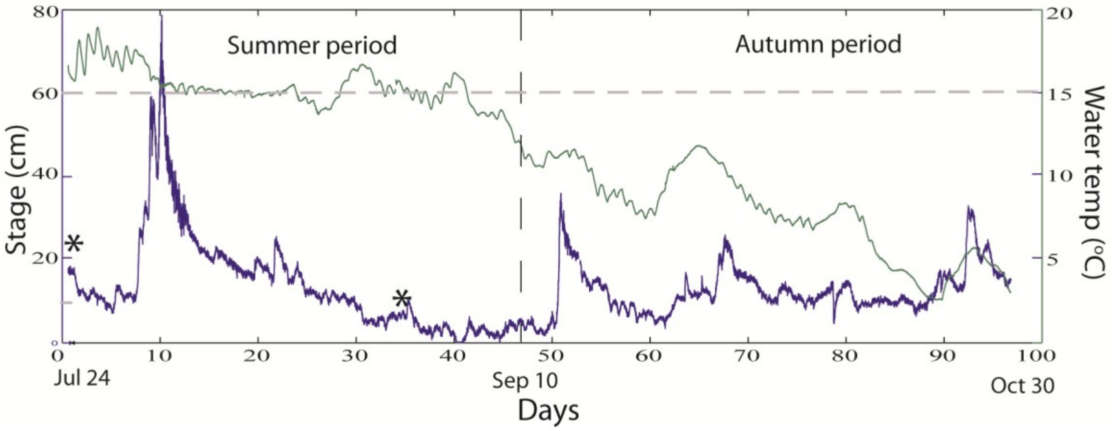

Figure 8.1 Water temperature (upper curve) and stage (lower curve) recorded from 24 July to 30 October 2008. The vertical dashed line divides the study into summer and autumn periods based on a threshold of 12°C. The horizontal dashed line shows the flow stage matching bankfull discharge. *indicates the two fish tagging sessions.

During the same period, water temperature decreased from 19.0°C to 2.8°C (Figure 8.1). From 24 July to 3 September, daily average water temperature fluctuated around 15°C. After 3 September, water temperature decreased linearly. Water temperature reached 12°C on 11 September, which corresponds to the upper boundary of the temperature range at which parr suppress their daytime activity (Valdimarsson et al., 1997). The study period was therefore divided into two periods: summer (12-18 °C) and autumn (4-12 °C).

Depth and bed roughness were also characterized in detail throughout the reach. Topography was surveyed using a robotic total station (Trimble 5600DR) by combining a systematic transect sampling approximately 1 m apart with the characterization of individual roughness elements that protruded approximately 10 cm above the local mean bed elevation. This strategy was adopted to optimize sampling effort, as sampling point density increased proportionally with bed complexity. From the total of 6250 sampled points, a digital elevation model was created using a triangular irregular network interpolation with pixel size of 10 cm. Topography was detrended for mean thalweg slope and water surface at median flow was subtracted to obtain flow depth. Therefore, variability of flow depth mainly reflected height variation induced by the riffle-pool channel morphology. Depth was not temporally adjusted to flow stage to reflect the use of specific habitats rather than specific depth values. This way, across flow stages, high depth use could be interpreted as the use of habitat located in a pool rather than be confused with habitats located in the riffle at a higher flow stage.

Bed roughness, expressed as the spatial standard deviation of bed elevation values of the DEM pixels included in a moving window of 65 cm^2, was characterized by computing an index based on the estimate of local bed elevation variability. The size of the window was determined in order to characterize the roughness of most of the largest particles present on the reach. We focused on protuberance from the bed that might be more important in creating flow refuges and cover than average particle size. For instance, it is common to observe large particles buried in the bed that do not protrude higher above the average bed height than smaller particles (Nikora et al., 1998). The downstream pool exhibited the largest coherent region of high bed roughness, whereas the remainder of the reach showed an apparently random spatial pattern of bed roughness. For every antenna, mean depth at median flow and bed roughness were estimated by averaging all pixel values located in a circle matching the antenna detection range. Fish daily habitat use was then estimated by averaging the mean values associated with all visited locations weighted by the number of detections per antenna.

8.3.5. Data analysis

Fish behaviour was characterized on a daily basis using four variables. The *number of movements* and the *distance travelled* provided estimates of fish mobility, whereas the *number of sites* visited and the *extent* of the reach used by fish gave estimates of home range size. We defined a fish movement as a change of fish location (antenna): i.e. every time a fish was detected at two different locations successively, a movement was recorded. The *number of movements* was an indicator of activity that did not take into account the distance between locations. In contrast, the daily *distance travelled* was defined as the sum of the distance (m) between each antenna successively visited. The *number of sites* represented the number of different antenna locations where a fish was detected in a day. However, despite a high spatial coverage and a high temporal sampling frequency of the tracking system, fish could sometimes travel between two distant locations without being detected by antennas located in between. Hence, the variable *extent* fills this gap by representing a home range length, or the distance between the two most distant locations visited by a fish in a day.

We used a principal component analysis (PCA) on the daily mobility variables to describe the variability of every fish. Prior to the PCA, each variable was normalized ($\log_{10}$+1) and standardized. Then, based on the mobility variables, fish behaviour was classified using a k-means clustering algorithm. The correct number of behavioural types (clusters) was determined by comparing silhouette values between three and five behavioural types (Matlab2010 (c) documentation).

The frequency of occurrence of behavioural types per individual that spent six days or more in the study reach was examined. Then, the components of variance of the four mobility variables were estimated using an additive-variance component model, using individuals as a random factor, in which $y_{ij \text{ (mobility of fish I on day j)}} = \mu+\alpha i+\varepsilon ij$ where μ is the mean of the population, α_i, deviation from the mean of the ith fish (i=1 to 24) ε_{ij}, is the residuals containing the intra-individual variation. To meet the model assumptions, transformed variables were used ($\log_{10}$+1). However, the descriptive statistics shown in the figures and tables are based on non transformed data.

To examine the temporal variability of fish behaviour, the proportion of behavioural types adopted by each individual was plotted on a time series. Then, the frequency of occurrence of behavioural types was examined in relation to flow-stage categories and season. A generalized estimation equation (GEE) approach was used to describe the observed and expected occurrence of a behavioural type as a function of flow stage and season. GEEs are an extension of generalized linear models that accommodate repeated measurement of the same individuals and a categorical response variable (Diggle et al., 2002). Therefore, the variable *days* was used as a repeated measure, *fish* as subjects, flow stage and temperature as fixed factors and behavioural types as a dependent categorical variable. GEEs were performed by SPSS 17 using a Poisson distribution with a log link and repeated measurement covariance structure set to first order autoregressive to account for temporal dependence between successive days. Similarly, to examine differences in habitat use in terms of depth and bed roughness in relation to behavioural types, two distinct mixed-effects models were performed using fish as subjects, days as repeated measures, behavioural types as a fixed factor and depth and roughness as a dependant variable. Again, first order autoregressive covariance of the repeated measurements was chosen. Best suited models were selected based on lowest QIC and AIC values (Burnham et al., 2011).

8.4. Results

8.4.1. Fish tracking

Of the 66 fish that were PIT-tagged and released in the reach, 4 individuals (6%) were never detected by the tracking system and 12 individuals (18%) were detected for either less than 24 hours following release or less than three hours in a single day. These individuals were not included in further analyses. Of the remaining fish, 10 individuals (15%) were detected in the reach during a single day, 16 individuals (24%) were detected for 1 to 5 days and 24 individuals (37%) remained between 6 and 70 days in the reach.

8.4.2. Behavioural types

The daily *distance travelled*, the *number of movements*, the *number of sites* visited and the *extent* of the reach used by fish were positively correlated, which allowed for data reduction. Indeed, 90% of the variability was explained by the two first axes of a PCA (Table 8.1). The primary ordination axis (PCA1), which accounted for 70% of the variability, was positively correlated with all mobility variables, but was least strongly correlated with *extent* (Figure 8.2). Therefore, low values of PCA1 represented lower mobility in smaller home ranges, whereas higher values represented higher mobility in larger home ranges. In contrast, the secondary axis explained 20% of the variability and was negatively correlated to the number of movements and positively correlated to the *extent* of fish movement. Data ordination illustrated the high variability of overall mobility exhibited by fish during the entire study period (Figure 8.2).

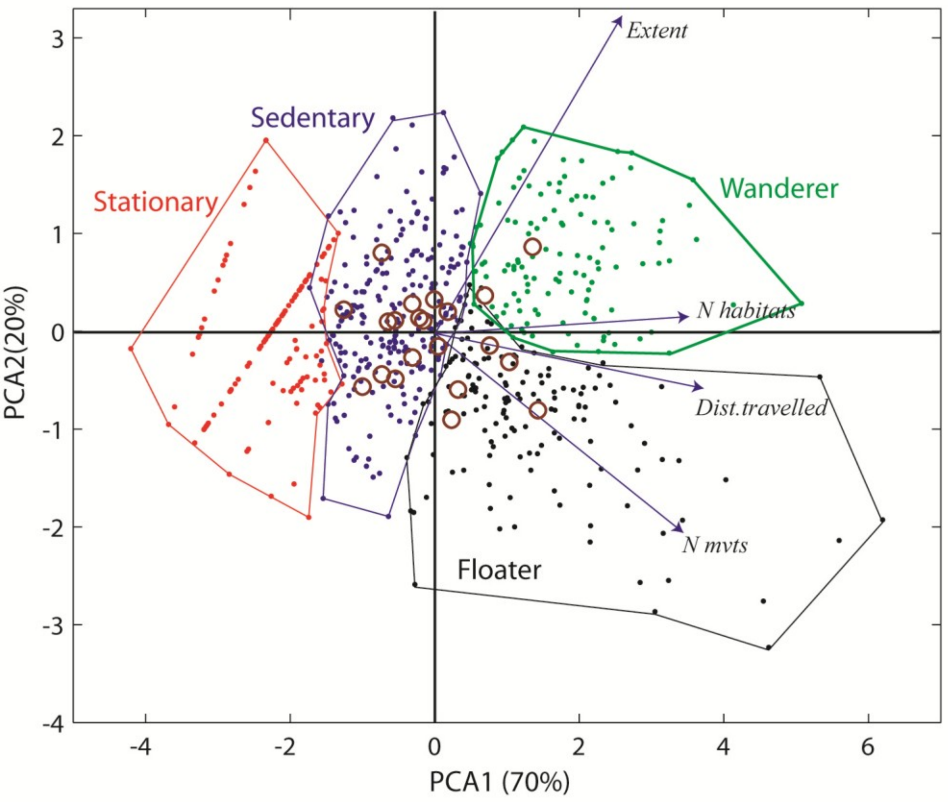

Figure 8.2 Principal component analysis (PCA) on 50 Atlantic salmon parr daily mobility variables (N=681) during 97 days. Each dot represents the mobility of an individual on a particular day. Open circles show individual average values for the 24 fish that remained in the reach for six days or more. Polygons delineate behavioural types (*stationary*, *sedentary*, *floater* and *wanderer)* discriminated by a cluster analysis (K-means) on the daily mobility data: Number of sites, Distance travelled (m), Number of movements and Extent (m).

Based on a cluster analysis, fish spatial behaviour was categorized into four types: *Stationary*, *Sedentary*, *Floater* and *Wanderer (*Figure 8.2*)*. *Stationary* behaviour was characterized by low mobility, being detected most often by a single antenna (Table 8.2). Fish 15 on Day 26 (Aug 18) adopted typical *stationary* behaviour (Figure 8.3). On some occasions, *stationary* behaviour also included the use of more than one location during the day. However, these locations were adjacent to each other and no back and forth movements were observed.

Table 8.1 Pearson correlation coefficients of mobility variables versus axis scores from an ordination of daily fish spatial behaviour in the study reach and proportion of total variance expressed by the two first ordination axes (n=681).

	PCA1	PCA2
Distance travelled	0.56	- 0.52
Number of movements	0.51	- 0.14
Number of sites	0.52	0.04
Extent	0.38	0.83
Proportion of variance	0.70	0.20

When fish were detected at a few locations in a day, their behaviour was characterized as *sedentary* (Table 8.2). Fish exhibiting *sedentary* behaviour travelled on average 10m daily and moved three to four times between locations for an average *extent* of 5.7 m. For example, on Day 61 (22 Sep), Fish 50 exhibited typical sedentary behaviour by using four locations located throughout half the channel length and moved only once between each location (Figure 8.3).

Table 8.2. Frequency of occurrence (n) and mean (range) of the four mobility variables for each behavioural type pooled for all individuals.

	Stationary	Sedentary	Floater	Wanderer
n	161	213	134	111
Distance traveled (m)	2.2(0-12)	10.6(0.7-41)	70(7.6-2454)	115(15-2249)
Number of mvts	1.0(0-4)	3.4(1-11)	36(4-558)	10.9(3-154)
Number of sites	1.8(1-4)	3.3(2-6)	5.7(2-12)	5.8(3-17)
Extent (m)	2.5(0-6)	7.23(1.2-35)	5.7(1.3-15)	28.2(16-43)

Cluster analysis also discriminated two types of higher mobility behaviour (high PCA1 scores) along the *extent-number of movement* gradient (PCA2 axis) (Figure 8.2). When individuals used a relatively restricted home range (average *extent:* 5.7m), but made many movements between locations (mean =36), their behaviour was defined as *floater*

(Table 8.2). For instance, Fish 37 on Day 32 (24 Aug) was detected at only five nearby locations in the downstream pool, but switched 34 times between these locations (Figure 8.3). During the study period, the most extreme floater made 525 *movements*, resulting in a daily *travelled distance* of 2449 m on an *extent* of 5.3 m.

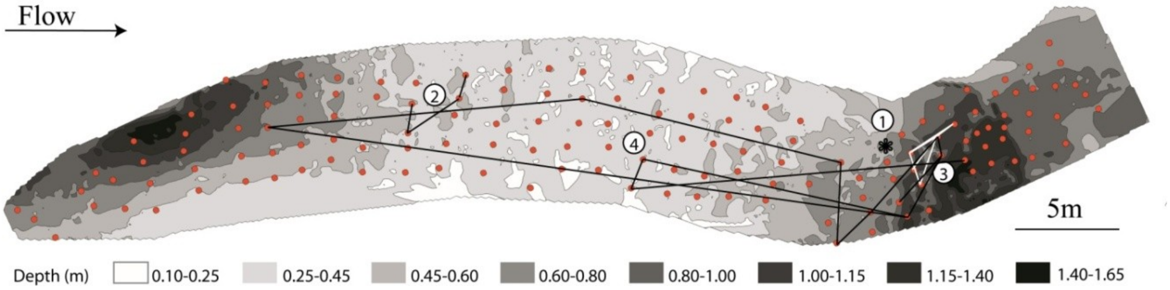

Figure 8.3 Typical daily mobility corresponding to four behavioural types. Examples were selected based on the closest average PCA1 and PCA2 scores for each type: 1- *Stationary*: 0 movement (Day 26, Fish 15); 2- *Sedentary*: 3 movements, 4 sites (Day 61, Fish 50), 3- *Floater*: 37 movements, 5 sites (Day 32, Fish 37), 4) Wanderer 14 movements, 11 sites (Day 61, Fish 66). Contour shows depth at an estimated discharge of 0.4 m^3/s (flow stage: 15 cm).

In contrast, when a fish exhibited a high *distance travelled* (avg: 115 m), but over a larger *extent (avg: 25.3 m)*, their behaviour was defined as *wanderer* (Table 8.2). Typical *wanderer* behaviour involved travelling across the entire reach, from one pool to the other. *Wanderer* behaviour was characterized by a similar *number of sites* visited as the *floater*. However, the *number of movements* between locations was generally lower and the locations visited were farther away. The *number of sites* visited by fish adopting wandering behaviour was not higher than for *floaters*, likely because individuals moving long distances travelled rapidly and were thus difficult to detect. For example, on Day 61 (22 Sep), Fish 66 travelled from the downstream pool almost to the upstream pool, then back again, but was detected at only 11 sites for a total of 16 *movements* (Figure 8.3).

8.4.3. Individual variability in behaviour

Individuals exhibited a variety of types of mobility behaviour rather than 'specializing' on one type over the study period. Among the 26 individuals that were detected on the site for less than six days, their behaviour was sedentary, stationary and wanderer on average for 36%, 30% and 30% of their time, respectively (Figure 8.4a). *Floater* behaviour was only observed in five fish, which represented on average 8% of their time (Figure 8.4a).

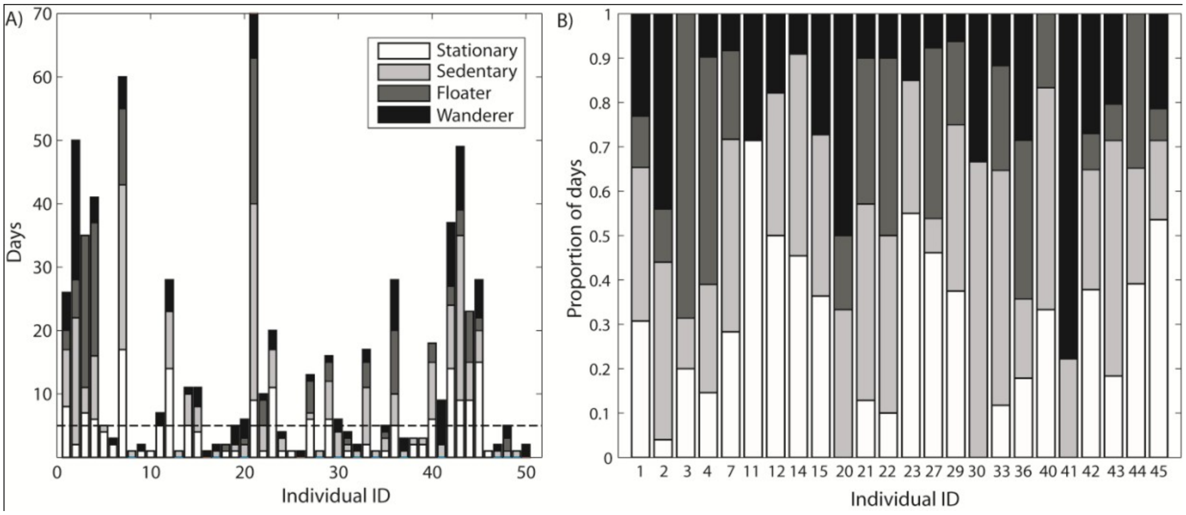

Figure 8.4 A) Number of days Atlantic salmon parr stayed in the reach subdivided by behavioural type. Dashed line indicates the fish that stayed more than 6 days. B) Proportion of days fish showed each of the behavioural types. Most individuals exhibited all types of behaviour during the study period.

Among the individuals that stayed more than six days on the study site, high intra-individual variability of behaviour was observed (Figure 8.4b). Out of 24 individuals, 15 showed all four types of behaviour during the study period. Low-mobility behaviour was most frequently observed, as individuals were sedentary and stationary for 33% and 28% of the days, respectively, during which they were detected in the reach. *Floater* and *wanderer* behaviour were less frequent, with an average of 19% and 20% of the days, respectively. However, six fish were more mobile than the others, exhibiting floater or wanderer behaviour for more than 50% of the days. For fish that stayed more than six days, there was no significant trend between the duration in the reach and the proportion of days each behaviour type was adopted by an individual (df = 22, stationary: r = -0.03, p = 0.89; sedentary r = 0.02, p = 0.92; floater: r = 0.32, p= 0.13; wanderer: r = -0.31, p = 0.14).

All fish were sedentary most of the time, but many individuals exhibited occasional bouts of high mobility. Indeed, all fish that stayed more than 6 days in the reach showed a low median distance travelled, but most moved more than 90 m. The daily *number of movements* displayed a similar pattern, with a relatively low median *number of movements* and numerous extreme values. Although the *number of sites* and the *extent* did not show as many extreme values, there was high intra-individual variability. Decomposing the components of variation of the four mobility variables indicated that intra-individual variation accounted for 83 to 88% of the total variation, compared to 12 to 17% for the inter-individual variation (Table 8.3).

Table 8.3 Geometric mean, total sum of squares, and within- and between-individual variation in four mobility variables and principle component 1 for 24 juvenile Atlantic salmon parr monitored for 6-97 days (619 observations).

	Mean	Total	Intra (%)	Inter (%)
PCA1	-0.1	1655.7	87	13
Distance travelled	0.93	167.7	88	12
Number of mvts	0.68	92.5	87	13
Number of sites	0.69	18.9	85	15
Extent (m)	0.76	57.6	83	17

Similarly, average ordination scores for individuals that stayed more than six days suggested that a considerable number of individuals had relatively similar average mobility

(Figure 8.2). For instance, 17 individuals (70%) had their average ordination scores categorized as sedentary while the remaining fish were categorized as floater or wanderer.

8.4.4. Temporal variability

The frequency of behaviour exhibited over the course of the season suggested that on most days, a mixture of behavioural types was observed (Figure 8.5). Following the tagging of 42 parr on day one, 14 individuals were present on the reach. The number of individuals dropped drastically on day 12 following a major flood event, then fluctuated between 4 and 8 before the second tagging session on Day 36, after which the number peaked at 22 and then constantly decreased until the end of the observation period.

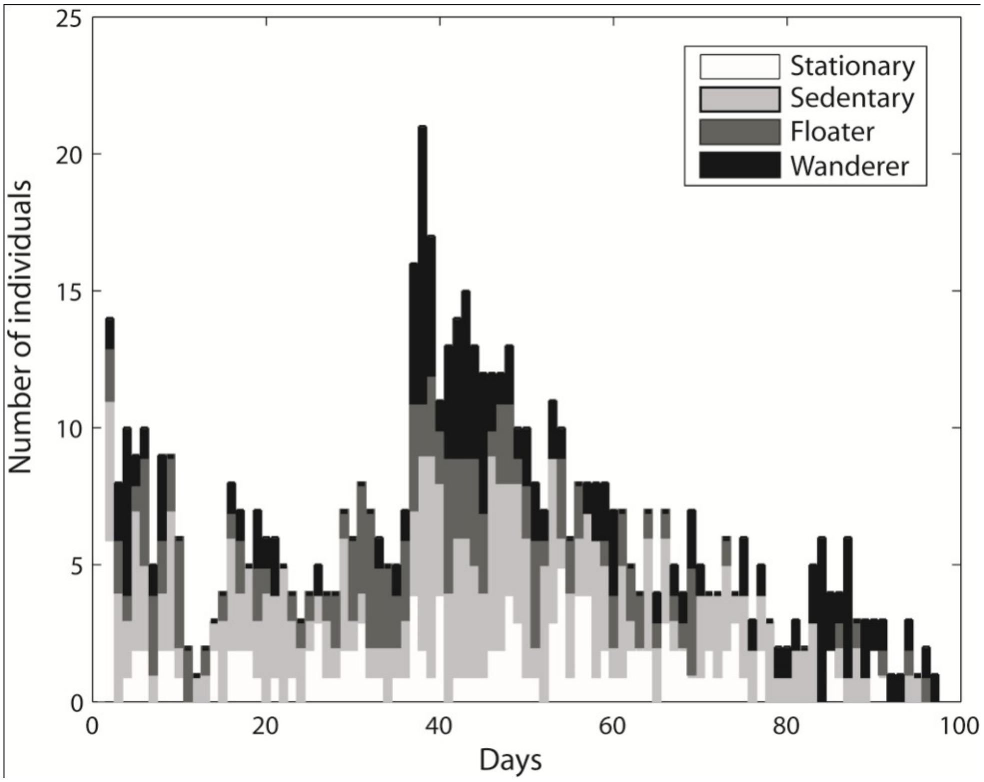

Figure 8.5 Time series of the number of individuals tracked on the study site decomposed by behavioural types, from 24 July to 30 Oct 2008.

Despite the variability of behaviour observed on a daily basis, some periods were dominated by specific behaviour types. For instance, between Day 22 and 36, *wandering* behaviour was observed only four times, whereas most fish exhibited *wandering* behaviour from Day 85 to 89. Similarly, from day 30 to 37, *floater* behaviour was most frequent.

Examining the frequencies of occurrence of behavioural types in relation to flow stage and season using GEE showed a general decrease in mobility with increasing flow stage (Wald χ^2=7.974, df=3, p=0.047). Pooled frequencies of occurrence illustrated an increase in the proportions of sedentary behaviour from 30% to 45% with an increase in flow stage (Figure 8.6).

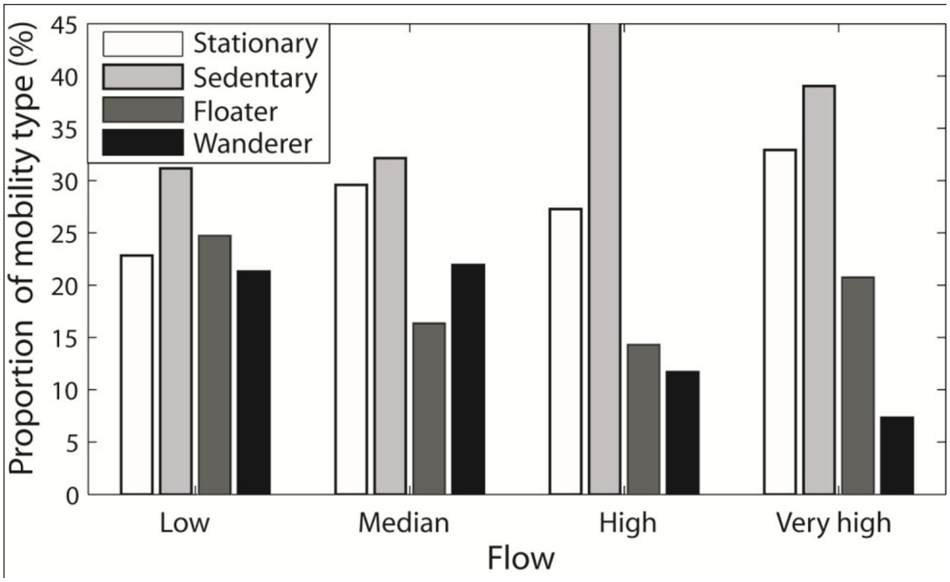

Figure 8.6 Proportion of fish behaviour exhibited on a daily basis by all individuals in relation to flow stage: low (0-10 cm, n= 34days), median (10-15, n=34 days), high (15-20 cm, n=13 days), very high (>20 cm, n=16 days).

Conversely, *wandering* behaviour decreased from 22% of occurrence to 7% from low flow to a very high flow. Over the season, parr used slightly different habitats in terms of depth when adopting different behavioural types (*F* = 5.46, df = 3,514, *p* = 0.001). Daily average depth used was 0.2 m higher for the fish exhibiting floater behaviour than the other behavioural types (Figure 8.7a). However, this trend was observed for only five individuals (Figure 8.7b).

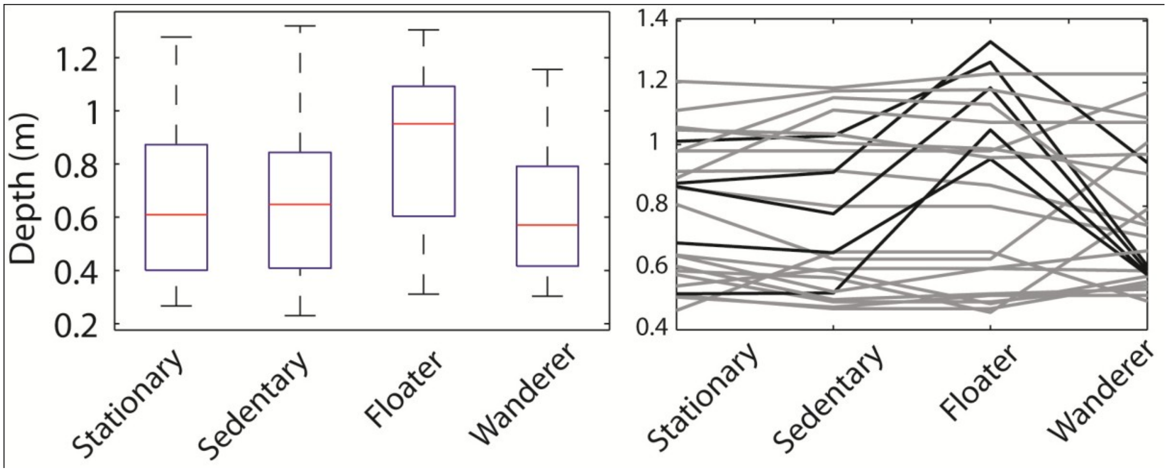

Figure 8.7. A) Daily averaged flow depth used per behaviour types pooled for all fish (unequal number of days per fish). B) Daily averaged depth used, each line representing averages per behaviour types per individual. Five individuals (bold lines) exhibited a relatively higher depth used while adopting floater behaviour.

In fact, a mixed effect model accounting for individual and temporal dependence indicated that wanderer behaviour was associated with lower depths used than the three other behavioural types (confidence interval on depth difference, df = 222-249, $p < 0.03$ for all comparisons, Bonferroni adjustments). In contrast, no difference in bed roughness used was observed for the different behaviour types ($F = 1.235$, df = 3, 549, $p = 0.296$).

8.5. Discussion

In this study, most individuals exhibited low mobility (*stationary* and *sedentary* behaviour) on most days, but most individuals also showed occasional bouts of high mobility, either by carrying out frequent movements in a relatively restricted area (*floater*) or by travelling across the reach, from one pool to the other (*wanderer*). Our data therefore challenge the assumption that populations are composed of two fractions: territorial versus floater (Puckett and Dill, 1985; Armstrong et al., 1999) or sedentary versus mobile (e.g. Morrissey and Ferguson, 2011). Rather, our results suggest that most fish switch behaviour on a daily basis.

Most studies confirming the presence of mobile and sedentary fractions of a population have used recapture techniques with relatively low temporal sampling frequency (e.g. Heggenes et al., 1991; Roghair, 2005). Such techniques require sampling over a long duration to obtain individual variability without underestimating fish mobility. For instance, if an individual moved 40 meters upstream over a short period of time and then back to its original location, the following recapture could lead to the biased conclusion of sedentary behaviour. Harcup et al. (1984) showed that rather than being strictly sedentary or mobile, individual brown trout switched behaviour over the course of a two-year study. Our data support the fluidity of the mobile or sedentary fractions, and furthermore indicated that the switching occurs over shorter time scales.

Because our study reach was only 65m in length, we could not describe the larger-scale movements of parr that have been observed in previous studies in larger rivers (Okland et al., 2004; Ovidio et al., 2007). Therefore, our mobility data might underestimate the mobility of fish exhibiting *wanderering* behaviour. Nevertheless, reach extent likely had a minor effect on the majority of fish, which adopted sedentary behaviour and therefore should not affect our conclusion about intra-individual variability in behaviour.

Salmon parr in our study exhibited a decrease in mobility with an increase in flow stage. Similar results have been observed in previous studies (Kemp et al., 2006), whereas others found no effect of flow stage on mobility (Robertson et al., 2004; Heggenes et al., 2007). Because salmon parr are well adapted to using flow refuges to maintain station on the bed, most of the increased swimming costs that accompany higher flows (Hill and Grossman, 1993) are likely to be associated with foraging movements from or longer range movements from one foraging location to another (Liao, 2007). Moreover, when velocities are higher, parr tend to reduce their foraging territory size in response to the increased swimming costs and prey density (Hughes and Dill, 1990; Piccolo et al., 2008b).

We found no difference in movement behaviour between the summer and autumn, despite the decrease in temperature. A decrease in mobility was expected due to a decrease in metabolic rate (Jonsson et al., 2001) and the expected decrease of diurnal activity (Fraser et al., 1993). However, parr can remain active even when water temperature is close to zero (Bremset, 2000). Indeed, a radio-telemetry study showed that parr home ranges were as large during the autumn as during the summer (Okland et al., 2004). Furthermore, a recent study undertaken under similar temperature ranges reported a higher mobility of parr in the winter (6.6-10.8 ^{o}C) than during the autumn (10.7-14.3^{o}C) (Riley et al., 2006). The authors suggested that this behaviour might be unique to groundwater fed systems. Taken together with previous studies, our results suggest that mobility can remain relatively high even when water temperatures are low. In this study, the effect of lower metabolism on movement might have been offset by several factors including a change from sit and-wait drift foraging to benthic cruise foraging due to a decrease in drift abundance (Nislow et al., 1998). Interestingly, all individuals adopted wandering behaviour on two days in mid-

October close to spawning season when temperature was between 4 and 6^oC. The presence of spawning adults passing through the site may have increased the mobility of tagged fish, particularly the precocious parr.

We hypothesized that individuals would be more sedentary in shallow and heterogeneous habitats because high habitat heterogeneity is more likely to provide complementary feeding and sheltering habitats close together (Johnston et al. 2010) and because territory size tends to decrease with habitat heterogeneity (Kemp et al. 2005; Dolinsek et al. 2007; Venter et al. 2008). Our results did not support this prediction. However, for five individuals that remained over forty days in the reach, deeper habitats were associated with floater behaviour. Finding mobile fish in pools is in agreement with the assumption that foraging fish occupy a larger territory in lower velocity areas (Hughes and Dill 1990). Furthermore, although the term *floater* tends to refer to individuals deprived of a territory, such behaviour could be associated with *multiple central place foraging*, where fish frequently switch from one foraging territory to an adjacent one (Steingrimsson and Grant 2008). Nevertheless, when fish adopted wanderer behaviour, they used slightly shallower habitats than while adopting other behavioural types. These results contrast with our hypothesis and with previous observations on adult grayling (*Thymallus thymallus* (Nykanen et al. 2004). The presence of mobile fish in deeper areas might have implications for the accuracy of abundance surveys. As the capturability of juvenile salmonids decrease with mobility (Crozier and Kennedy, 1994), electrofishing might underestimate abundance in pools, which could be mistakenly considered as low quality or unused habitats (Linnansaari et al. 2010).

In summary, the present study showed that Atlantic salmon parr are sedentary on most days, but also exhibit infrequent bouts of higher mobility. Movement behaviour appears to be plastic, allowing individuals to adapt to changing environmental conditions (Gowan et al. 1994). Even though movement behaviour was linked to variation in flow stage, a high between- and among intra-individual variation was observed, suggesting individuals undertake movements in reaction to other proximate factors operating at shorter time scales. Several studies on fish behaviour, movement and habitat use have reported a high inter-individual variation (Okland et al. 2004; Ovidio et al. 2007). However, studies are often conducted for a shorter duration and at a lower temporal frequency than our study. Furthermore, intra-individual variability is often overlooked by averaging values to estimate home ranges over the entire study period. Therefore, differences in individual behaviour may decrease as study duration increases. Because Atlantic salmon parr exhibit relatively high mobility, maintaining connectivity between different habitats (i.e. pools and riffles) should be considered a priority in salmon conservation practices.

Chapitre 9: Discussion and general conclusion

This thesis has investigated the behaviour of individual juvenile Atlantic salmon in relation to spatial and temporal habitat variability. Habitat influences multiple components of their energy budget and susceptibility to predation, which in turn influence fish behaviour. Using an *in situ* approach and a variety of field sampling and data analysis methods, my thesis has examined three aspects of habitat and juvenile salmon behaviour: 1) the role of turbulence as a habitat variable, 2) the spatial and temporal scales of habitat selection and 3) the variability in individual behaviour. While each chapter has its own specific objectives, together they provide an integrated view of the addressed topics. In this concluding chapter, I will summarize the key findings of the five empirical chapters, highlight the importance of the thesis, and finally briefly discuss the implications associated with the three aspects of habitat and behaviour, underlining topics deserving further study.

9.1. Summary of key findings

In Chapter 4, the spatial structure of fluvial habitat and the relationships between "standard" habitat variables (i.e. depth, velocity and substrate) and flow properties were examined in four morphological units of a gravel-bed river. A variation partitioning analysis was carried out using principal coordinates of neighbour matrices (PCNM) to partition multivariate turbulent flow properties into six significant spatial scales ranging from 0.35 to 3 m. The proportion of variation explained by the larger-scale PCNMs was higher in the most homogeneous units. In general, the spatial dependence of turbulent flow was lower in the riffles than in the pools, where the mean flow velocity was lower. Furthermore, the capacity of 'standard' fish habitat variables to explain turbulent properties was relatively low, especially in the smaller scales, but varied greatly between the units. Most importantly, from a practical point of view, this level of complexity suggested that turbulence should be considered as a 'distinct' ecological variable within this range of spatial scales.

In Chapter 5, we tested the feasibility of using an in situ portable flume to examine the effect of flow properties on juvenile Atlantic salmon prey capture probability and preferential foraging positions. Capture probability was not significantly affected by turbulence, but there was a slight increase of aborted foraging attempts in a more turbulent flow. Fish preferentially selected locations where downstream velocity was moderate and the downward component of velocity was important. Despite the relatively low range of hydraulic variables generated by the portable flume, we consider that the portable flume methodology is a promising way to reconcile experimental control provided by laboratory studies with the biological realism provided by field studies.

In Chapter 6, we observed habitat selection of PIT tagged juvenile salmon using a network of antennas in a natural stream over spatial scales ranging from microscale 0.28m^2 to mesoscale (78 m^2) and over temporal scales ranging from 5 minutes to 24 days during the summer and autumn. Fish exhibited a preference for moderate and high classes of flow depth (0.45-0.90 m) and flow velocity (0-50 cm·s^{-2}), low turbulence (TKE= 0-200 cm^2/s^2) and high bed roughness (>0.05) at the *micro*-scale, but were also positively associated to higher depth and velocity at the *patch*-scale (1.35-1.65 m and 25-75 cm·s^{-1}). These results suggest that fish may select habitat based on micro-scale velocities and depths, but also the depth and velocity in the surrounding area. The range of habitat used increased asymptotically with the temporal scale of observation. On average, individuals used close to 10 % of the range of available habitats in 5 minutes, 20% in one hour and over 60-80% in three days. A period of 1h and was identified as a minimum duration required to characterize the daily habitat range of an individual and a period of three days the minimum duration to characterise the seasonal habitat use range. This high resolution data set illustrates the ecological relevance of the *patch*-scale habitat sampling and the considerable temporal variability of the mean daily habitat used by a group of individuals in a reach.

In Chapter 7, the same data set was used to address the question of individual variability and the relationship between activity and microhabitat use patterns. High inter-individual variability was observed, as some individuals were predominantly nocturnal whereas others frequently changed their daily activity pattern. Overall activity decreased with temperature and flow stage. Interestingly, changes in activity levels were mostly during crepuscular periods. Diurnal fish used higher velocities than nocturnal fish and cathemeral fish (i.e. active both day and night during a given day) did not use lower velocity habitats at night than day. These results suggest that habitat interacts with activity pattern, as individuals using suboptimal habitats seem to increase daytime activity presumably to secure sufficient energy.

In Chapter 8, we examined the variability in the movement behaviour of individual fish. It appeared that most fish exhibited low mobility on most days, but also showed occasional bouts of high mobility. Between-individual variability accounted for only 12-17% of the variability in the mobility data. These results challenge the assumption of a population composed of a sedentary and mobile fraction. Furthermore, mobility was inversely related to flow stage. Individual variation on a daily basis suggested that movement behaviour is a response to changing environmental conditions rather than an individual behavioural trait.

9.2. Originality of the thesis

The results of this thesis emerge from an original approach on several levels. The heterogeneity of topics resulted from a continuously evolving process of reflection. Throughout the thesis, research objectives and their associated methodology were constructed along a gradient of increasing spatial and temporal scales in terms of extent and duration, and complexity in terms of concomitant variables at play. These experiments, individually and combined, have contributed to a better understanding of the role of turbulence as a habitat variable, of the spatial and temporal scales involved in habitat selection and of the individual behavioural variability of juvenile salmon. They also suggested new paths of reflection.

The variety of methods included in the experimental design contributed to the originality of the thesis. A methodology common to several chapters was the flow characterization using multiple ADVs and the associated data analyses. Overall, data sets presented in Chapters 4-8 contained over 3000 velocity time series and reach a combined resolution and extent rarely achieved in natural rivers. Furthermore, the second data set, presented in Chapter 5 was obtained with an innovative methodology, combining underwater video analyses of fish behaviour in a portable flume. The third data set, the basis of the most substantial part of the thesis, provided the largest combined duration, extent and resolution of fish tracking data yet published in the literature.

To analyse such large data sets, we used a wide variety of data analysis methods. We used an array of turbulence analyses methods (e.g. quadrant, U-level, AC functions) well known in fluvial geomorphology (Buffin-Belanger, 1998; Lacey, 2008), but also used innovative spatial analyses of turbulent flow (PCNM) and multivariate statistical techniques to examine individual and general trends in habitat use and variability in behaviour (scaled preferences, GEE, Mixed models, PCA, etc.).

Furthermore, our work is among the rare field studies examining within-individual variability of continuous daily behavioural characteristics. Our results challenged two established assumptions: the sedentary/mobile dichotomy – we suggested that most fish are sedentary, with occasional bouts of high mobility; and the day/night activity dichotomy – our data suggested instead that crepuscular activity was the dominant pattern of activity, and most susceptible to environmental fluctuations.

9.3. Turbulence as an important fish habitat variable

Most of the research on the effect of turbulence on fish has addressed the direct impact of the flow on fish swimming costs (Enders et al., 2003), swimming speed (Pavlov et al., 2000; Nikora et al., 2003), posture and stability (Liao et al., 2003; Tritico and Cotel, 2010). For fish, the selection of a particular habitat is likely based on a tradeoff between the associated energy intake and expenses (Finstad et al., 2011). However, the potential (indirect) effect of turbulence on energy intake is not well known. This thesis was the first to address the question of the effect of turbulence on prey capture probabilities. Chapter 5 highlighted the need to develop effective methods to be able to perform experiments in the field while controlling key variables. This is especially important considering the vast majority of studies on the effect of turbulence on fish were carried out in laboratory conditions and that the turbulence properties in flumes are different from natural rivers (Lacey et al., 2012). Nevertheless, in this thesis, the preference by juvenile salmon for low turbulence intensity was observed in both natural habitat (Chapter 6) and in the portable flume (Chapter 5), confirming previous results from laboratory studies (Enders et al., 2003; Smith et al., 2005). Furthermore, the correlations between flow depths, bed roughness, flow velocity and turbulence properties were relatively low, supporting the potential of turbulence as an important habitat variable predicting fish abundance.

Several questions remain to be investigated regarding the effect of turbulence on fish. First, the question of the effect of turbulence on prey capture probability and prey distribution is of great interest. In Chapter 5, the flume experiment could be considered as preliminary, as we had difficulty distinguishing fish inactivity from fish ability at detecting prey. This experiment could be repeated with smaller fish, more likely to feed constantly during daylight periods. The scale at which turbulence affects the distribution of drift also deserves further study. In Chapter 5 we noted a slight increase in the rate of aborted foraging attempts associated with the addition of a flow obstacle. However, it was not related to turbulence intensity variables (i.e. TKE, τ). We hypothesized that the predictability of prey trajectories might not be strongly related to turbulence intensity, but could instead be associated with other properties such as periodicity, orientation or scale of the macroturbulent flow structures (Roy et al., 2004). Systematically quantifying the relative importance of these turbulence properties on prey capture probability and on fish energetics is a crucial preliminary step to the addition of turbulence in habitat models

(Lacey et al., 2012). Furthermore, more field studies carried out in real flow conditions are needed to understand the effect of river turbulence on fish. For instance, replicating the work of Liao et al. (2003) in the field using muscle activity sensors and *in situ* PIV (Tritico et al., 2007), which are in development (Lacey et al., 2012), might provide valuable information on fish locomotion in natural river flows.

9.4. Scales of habitat selection

The influence of scale on ecological studies has long been recognized. This thesis reiterates the importance that the scale of measurement will determine the perceived relative role of a particular variable in habitat selection. Our experiments covering a range of scales of flow variability from turbulence to mean velocity to daily flow stage variations, have revealed scale-dependant fish-habitat associations. We also showed that the relationship between habitat variables and turbulent properties are scale-dependant and that these patterns are complex and can vary within types of morphological units . Together, these findings suggest that a multiscale approach to habitat selection models might improve our capacity to predict fish density and assess fish requirements. More generally, with the increasing availability of spatial high resolution data at the scale of fluvial systems (Marcus and Fonstad, 2008), multiscale and spatially explicit approaches might be highly beneficial to improve the predictive power of habitat models. The relatively infrequent, but high extent movements exhibited by juvenile Atlantic salmon in Xavier Brook, suggested that microhabitat and habitat structure at larger spatial scales may influence fish behaviour and mobility. If certain reach-scale or fluvial river system spatial configurations affect fish mobility, it might have important repercussions on individual fitness and potentially on relative fish abundance. Clearly, the identification of the relevant scales at which habitat heterogeneity influence fish mobility, fitness and survival needs further investigation.

While performing more detailed spatially explicit models might improve our knowledge of fish ecology, their complexity might represent an obstacle to their utility as a management tool. In this regard, a new habitat classification including spatially explicit and scale-dependant characterization might be useful. Based on simple field measurements, such classification could include intermediate (i.e. patch) scale characterization and metrics of distance or contiguity/connectivity (e.g. distance from typical foraging and sheltering habitats). Furthermore, given the high heterogeneity of within-type morphological units observed in this study, classification of habitats based on subtypes might be useful (e.g. types of pools, types of riffles).

9.5. Individual variability of fish behaviour

This thesis has highlighted the complexity of juvenile salmon behaviour. Tagged fish were neither inherently nocturnal, diurnal or crepuscular, nor entirely sedentary or mobile. They rather exhibited flexible behaviour, adapting to biotic and abiotic fluctuations. For specific individuals, the predominance of certain behavioural characteristics may depend on condition and life history status. Previous studies examining the behaviour of individually marked fish reported a high variability among individuals (Armstrong et al., 1999; Okland et al., 2004; Breau et al., 2007). However, within-individual variation of fish behaviour is rarely quantified. Extracting average trends of behaviour characteristics provides important knowledge, but individual variation represents another layer of information, which value is getting increasingly recognized (Steingrimsson, 2004; Breau et al., 2007). The interest in individual-based bioenergetics models as management tools is currently increasing (Hayes et al., 2007). Individual-based models generally incorporate functions of prey capture success in relation to velocity, food abundance and temperature to predict fish distribution. However, individual-based field studies examining activity patterns and habitat use using marked fish are relatively rare (Breau et al., 2007). The results from this study have shown that individual activity patterns, habitat use and the extent of mobility can change on a daily basis. While the average variation was linked to flow stage and temperature variations, the variation in the individual response to these environmental fluctuations was also high. Further studies are needed to understand the causes and consequences of this individual variation in several types of fluvial environments.

In parallel, further technological advances in PIT tag technology are currently being made, as new networks of antennas are being developed, which will be able to scan every antenna simultaneously, thus improving significantly the temporal resolution of measurements (Bergeron, N., personal communication). This improvement could allow the examination of new aspects of fish behaviour, such as the link between fish social interactions and activity patterns. Further study should attempt to relate fitness estimates to different behavioural strategies, which we were unable to do because most fish had left the study site at the end of the study period. Furthermore, few studies have been carried out in large rivers and the implications for fish living in these environments remain unclear (Linnansaari et al., 2010).

9.6. Concluding remarks

Finally, my thesis was based solely on field measurements, leading to a quantitative description of habitat and fish behaviour. It provided few empirical functions of behaviour-environment relationships such as would be provided by a laboratory setting allowing to control for environmental covariates. Instead, our work gives a portrait of fish behaviour in a complex ecosystem. The thesis reiterated the relevance of turbulence as a variable predicting fish distribution, but highlights the need for further studies identifying what characteristics of turbulence have the most effect on different aspects of a fish's energy balance. Most importantly, the impact of turbulence on prey capture probability needs further examination in a wider range of turbulence levels and in relation to prey capture trajectories. The conjunction of 3D videography and *in situ* PIV might offer the most appropriate resolution to examine these questions. The thesis also highlighted the relevance of intermediate *patch* scale and the variety of habitats used by fish in relatively short periods of time.

Recent technological progress might soon allow to remotely characterize complex fluvial habitat using optical imagery, including flow velocity and turbulence (Plant et al., 2009; Jung et al., 2010; Chickadel et al., 2011). Ultimately, these data could become spatially and temporally continuous, thus allowing examination at multiple scale to better describe the dynamics over entire fluvial systems. However, multidimensional high resolution data often represents a challenge to handle and analyse. Therefore, for river habitat management purposes, simple spatial metrics could also be used to characterize habitat heterogeneity. My thesis has showed a high temporal variability in behaviour of juvenile salmon, which might explain the often contrasting results from previous field studies using telemetry. Several days are needed to properly describe the behaviour of an individual. Perhaps, such dynamic habitat selection of a small group of fish over a long period would provide preference curves that would be similar to the population. Furthermore, in Xavier Brook, behavioural movement strategies differed with flow depth, floater behaviour being more frequent in deeper habitats. It would be interesting in the future to determine to what extent movement strategies are stream or reach-specific and related to which hydromorphological habitat variables.

Today, individual-based models (IBM) are presented as a very promising avenue for both research and management (Finstad et al., 2011). By integrating multiple mechanistic functions, they could allow future studies to integrate the three themes addressed in this thesis. The general idea of these models is to assess the net rate of energy intake (NEI) by subtracting the energy expenditures related to the swimming cost to the gross energy intake for each particular microhabitat velocity.

1) Turbulence: Prey capture and swimming energy costs functions could be implemented in order to improve the accuracy of the energy budget associated to particular microhabitats. However, prior to this, laboratory studies are needed to build these functions across the full range of turbulence levels encountered in natural rivers. Laboratory methods to create turbulence that is similar to river turbulence need to be developed.

2) Spatial scale: Foraging models generally define the boundary of a fish microhabitat as the maximum capture area, the size of which depends on flow velocity. Bioenergetic functions related to the capture area, but also to adjacent microhabitats could be incorporated to model the impact of patch scale habitat on NEI. The temporal variability of NEI could be adjusted.

3) Individual variability of behaviour: Using our empirical data as a basis, IBMs might permit linking individual variability in behavioural strategies to associated levels of NEI. To model temporal variations of NEI at the individual level, 2D hydraulic modelling could be useful to predict microhabitat mean flow velocity across flow stage. This would provide valuable insights on the impact of adopting various behavioural strategies on fitness and survival.

Finally, the temperature functions of IBMs make them especially relevant to understand and assess the effect of climate change on fish (Jenkins and Keeley, 2010). Altogether, we hope our results will contribute to the development of improved management plans considering the diversity of individual behaviour, and ultimately to the conservation of Atlantic salmon.

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