SPATIAL ECOLOGY AND LIFE-HISTORY DIVERSITY OF SNAKE RIVER FINESPOTTED CUTTHROAT TROUT *ONCORHYNCHUS CLARKII BEHNKEI* IN THE UPPER SNAKE RIVER, WY

by

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APPROVAL

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This dissertation has been read by each member of the dissertation committee and has been found to be satisfactory regarding content, English usage, format, citation, bibliographic style, and consistency and is ready for submission to The Graduate School.

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DEDICATION

I dedicate this dissertation to my parents, Steven and Terry, and my siblings, Jen, Mike, and Lisa, who have supported and encouraged me in all my endeavors, and to Benny, my dearest friend.

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ABSTRACT

Life-history diversity, movement patterns, and habitat associations of cutthroat trout *Oncorhynchus clarkii* have been widely studied in smaller river systems and are critical components of conservation planning. However, much less is known about how the patterns observed in smaller systems may “scale up” in larger, complex river systems. In my dissertation, I evaluated the life-history variation and spatial ecology of Snake River finespotted cutthroat trout *O. c. behnkei* in the upper Snake River, WY and collaborated on a statistical method to characterize habitat occupancy from radio-telemetry data. For my first chapter, I identified the life-history diversity and movement patterns of cutthroat trout in a large river network using radio-telemetry. Spawning occurred from May through July throughout the upper Snake River in spring creeks, tributaries, and side channels over a spatial extent > 100 km. Postspawning movement patterns varied among spawning areas and life-history forms. Results indicated that life-history diversity in large river networks is substantially more complex than may be observed in headwater systems, reflecting increased habitat complexity and availability in larger systems. For my second chapter, I collaborated on a method to address three biases in radio-telemetry datasets: (1) data may be collected at sparse, unequal sampling intervals, (2) encountering an individual in a location does not imply occupancy, and (3) all locations between where individuals are encountered are occupied to some extent, despite the lack of observations. The resulting adaptive kernel density interpolation method treated location as a utilization distribution for each tracking interval (e.g., a week) and estimated time spent per location as a function of individual movement speed and time since last relocation. For my third chapter, I evaluated habitat occupancy and movement patterns at multiple spatiotemporal scales. Spatial variation and hierarchical structure in the physical template interacted to produce contextual variation in the availability and function of habitat attributes (e.g., wood functioning as cover or as a velocity break). Collectively, these studies provide a more complete understanding of life-history diversity in a large river network and the way in which variation in the physical template shapes habitat occupancy, and movement patterns.

INTRODUCTION TO DISSERTATION

Introduction

Over the last century, native trout have experienced dramatic declines in distribution and abundance as a result of habitat degradation, fragmentation, invasive species, and hybridization (Gresswell et al. 1988; Miller et al. 1989; Hudy et al. 2007). Many rivers have been dammed, channelized, or simplified, and access to habitat associated with different life stages or life-history strategies has been lost (Thurow et al. 1997; Fausch et al. 2002). Declines have been particularly pronounced for riverine migratory fish that rely on intact corridors to access seasonal habitat and encounter more degraded habitat in the course of migration (Thurow et al. 1997). In response to these declines, conservation of native trout has focused on factors that promote population resiliency, including life-history diversity (Gresswell et al. 1994; Rieman and Dunham 2000) and habitat patch size (Hilderbrand and Kershner 2000a). Each of these factors is closely associated with characteristics of the physical template (Southwood 1977; Poff and Ward 1990). However, the template is dynamic, patchy, and hierarchical (Frissell et al. 1986; Poole 2002; Thorp et al. 2006), which hinders predictions of a population-level response over time or across systems.

Life-history variation describes traits associated with survival and reproduction and relates directly to variation in the physical template; where a greater diversity of habitat types are available, a greater diversity of life histories may be expressed to connect those habitat types with movement (Cole 1954; Stearns 1977). Life-history variation is linked to population resilience (Hilborn et al. 2003) through spreading of extirpation risk through space and time (Den Boer 1968; Stearns 1989; Greene et al. 2010). For example, spawning behaviors are often associated with temporary occupation of spatially discrete seasonal habitats (e.g., lake or tributary spawning areas; Gresswell et al. 1994). When multiple spawning behaviors are present in a population, disturbance at the local scale might only cause extirpation of the portion of the population currently associated with the affected habitat (Den Boer 1968). Subsequently, recolonization may occur by other individuals from the same population over time (Rieman et al. 1997; Gresswell 1999). Life-history sets the context for understanding the specific habitats required by trout, but the physical template determines the availability, quality, and spatiotemporal occupancy of those habitats.

Efforts to understand how trout respond to the physical template have advanced in both spatially implicit and spatially explicit directions, and the characteristics of each differ in important ways. In spatially implicit models, habitat use is described in terms of the habitat patches that individuals connect with movement through corridors (Schlosser and Angermeier 1995; Northcote 1997); the specific habitat occupied may differ seasonally (Fretwell 1972), by life stage, by life-history form, and by species (Schlosser 1991; Northcote 1997). Moreover, the physical template of a stream network influences fish distribution patterns at hierarchical spatial scales (Levin 1992; Rabeni and Sowa 1996; Lowe et al. 2006). At broad scales (e.g., watershed), physical attributes, such as watershed connectivity (MacArthur and Wilson 1967; Hitt and Angermeier 2006; Muneepeerakul et al. 2008), stream network topology and complexity (Cuddington and

Yodzis 2002; Benda et al. 2004; Grant et al. 2007), and temperature (Torgersen et al. 2006) or gradient (Kruse et al. 1997) are directly related to habitat suitability and access. Conversely, at local scales (e.g., reach), fish distribution may be influenced by physical structure (e.g., large woody debris; Abbe and Montgomery 1996), and thermal or velocity refugia (Torgersen et al. 1999; Ebersole et al. 2003). Although these spatially implicit models may be useful for identifying habitat relationships, they tend to do an inadequate job of predicting fish-habitat relationships in different locations within a stream or different streams.

Recently, there has been a greater emphasis on the importance of spatially explicit processes in stream systems (Fausch et al. 2002; Weins 2002; Carbonneau et al. 2011). In spatially explicit models, habitat use incorporates both position within the stream network (resulting from major downstream changes in the biophysical characteristics of streams; Vannote et al. 1980) and heterogeneity (because local physical heterogeneity may be greater than longitudinal variation in the stream at smaller spatial scales; Poole 2002; Ganio et al. 2005; Thorp et al. 2006). The location within the stream network sets the context of how different types of habitat or habitat forming processes may occur in different portions of the watershed and structure fish distribution or abundance. Consequently, a riverscapes perspective allows integration of how life cycles are linked to habitat characteristics in specific locations within a watershed (Fausch et al. 2002).

Much of the work on life-history diversity or habitat occupancy of trout has been conducted in headwater systems or lake-stream systems (Hilderbrand and Kershner 2000b; Brown and Mackay 1995; Gresswell 2011), partly because there are few large river systems where migration is still possible throughout a complex network of streams. This bias toward studies in smaller streams has resulted in generalizations about habitat use or movement patterns that may be true of smaller systems but may not apply in larger systems. For example, it appears that trout connect seasonal habitat with shorter movements in smaller streams than in larger rivers (Colyer et al. 2005; Gresswell and Hendricks 2007), suggesting that attributes of the physical template associated with that movement differ. However, it is not enough to identify that individuals move longer distances in larger streams without considering how those movements, and subsequent habitat occupation, are products of stream-size specific habitat availability, quality, and spatial arrangement.

Large river networks differ physically from small streams in several ways that could potentially influence fish distribution and habitat use patterns. Large rivers display a greater range of network topologies than small streams, and the spatial pattern of tributary confluences of varying size could affect the spatial availability of habitat (Benda et al. 2004; Torgersen et al. 2008). Irrespective of the topology, fewer tributary confluences are large enough relative to the main stem to impart a geomorphic effect that could form seasonal or annual habitat at the confluence (Benda et al. 2004). Hence segments tend to be much longer downstream than in headwaters and contribute to longitudinal variation in the physical template. Thus, the specific fish-habitat relationships that exist in small streams (e.g., the importance of overhanging vegetation) may have no clear analog in larger rivers (where habitat along banks is a small portion of the total available habitat), and predicting large river fish habitat may not be a simple matter of scaling up small stream habitat relationships.

In the upper Snake River, Snake River finespotted cutthroat trout *Oncorhynchus clarkii behnkei* provide a unique opportunity to evaluate the life-history diversity and habitat occupancy of a native cutthroat trout in a large connected river network. Snake River finespotted cutthroat trout are the primary subspecies of cutthroat trout found in the main stem of the Snake River between Jackson Lake Dam and Palisades Reservoir (which comprises the majority of the native range of the subspecies) and express multiple life-histories. Although two large dams and many small impoundments exist in the upper Snake River watershed, a substantial amount of connected habitat remains in the stream network, providing the potential for a diverse array of life-history expression. Much of this portion of the Snake River is federally owned, and in 2009, the Craig Thomas Snake River Headwaters Legacy Act was passed and designated an extensive portion of the upper Snake River and tributaries as “wild and scenic.”

Background

Research was conducted on the Snake River below Jackson Lake Dam, Grand Teton National Park, WY. Jackson Lake Dam was constructed at the outflow to Jackson Lake on the Snake River in 1905 and initially managed to provide irrigation water for agriculture interests in Idaho. From 1916-1957, the peak of the spring flood was elevated (mean = 255 m^3/s; Nelson 2007) and was generally delayed by 2 months; little to no water (mean = 0.3 m^3/s; Nelson 2007) was released October 1 – March 30 (Figure 1).

Following the construction of Palisades Dam in 1958, management of Jackson Lake Dam changed, and minimum winter flows were obtained (≥ 7.9 CMS; Nelson 2007). In addition, the peak of spring discharge was modified to mimic unregulated run-off patterns discharge (mean = 182 CMS; Nelson 2007); however, elevated discharge (relative to estimates for an unregulated Snake River; Nelson 2007) was released throughout the summer until October 1 in order to support summer recreational activities on the main stem of the Snake River (Figure 1).

Despite this shift in management, discharge patterns differ substantially from estimates for an unregulated system (Figures 2 and 3). For example, during the last 8 years, flow regulation has produced attenuated, delayed peak discharge releases in the spring, and variable but unnaturally high discharge releases in the fall (Figure 2), relative to what would occur in an unregulated system (Figure 3). Many of the effects of discharge regulation on channel change appear to be mitigated by large tributary influences 8 km below Jackson Lake Dam (Marston et al. 2005, Nelson 2007), but there has been a 45% decrease in the magnitude of floods with a 2-year recurrence interval, significant aggradation at tributary junctions, and an alteration of the late summer discharge regime (Nelson 2007). All of these perturbations could affect the spatiotemporal availability of trout habitat.

Both Snake River finespotted cutthroat trout and Yellowstone cutthroat trout *O. clarkii bouvieri* co-occur in the upper Snake River system below Jackson Lake Dam, although Yellowstone cutthroat trout predominantly occupy the upstream positions of tributaries in the river system (Loudenslager and Kitchin 1979; Novak et al. 2005). The two subspecies typically do not overlap in their distribution, but where they co-occur, intermediate phenotypes are found (Novak et al. 2005). Other native species include: mountain whitefish *Prosopium williamsoni* , Utah sucker *Catostomus ardens*, mountain sucker *C. platyrhynchus*, bluehead sucker *C. discobolus*, speckled dace *Rhinichthys osculus*, longnose dace *R. cataractae*, redside shiner *Richardsonius balteatus*, and mottled sculpin *Cottus bairdi*. Rainbow trout *O. mykiss*, brown trout *Salmo trutta*, lake trout *Salvelinus namaycush*, and brook trout *S. fontinalis* have been introduced to the system but currently occur at a low relative abundance in the Snake River between Jackson Lake Dam and Palisades Reservoir.

Snake River finespotted cutthroat trout express several potamodromous life-history strategies. Cutthroat trout may spawn in streams (fluvial) or tributaries (fluvial-adfluvial), or migrate from lakes into tributaries (lacustrine-adfluvial) or the lake outflow (allacustrine) to spawn (Gresswell et al. 1994). The lacustrine-adfluvial and allacustrine forms have only been documented in the Gros Ventre and Salt River systems (Gregory and Yates 2009, Sanderson and Hubert 2009). These iteroparous spring spawners return to natal streams from March to July as peak discharge subsides (Kiefling 1978). The timing of spawning migrations appears to be associated with water temperature, photoperiod, and stream discharge (Varley and Gresswell 1988, Gresswell 2009). In the upper Snake River, spawning has been observed in side channels, tributaries, and spring creeks (Sanderson and Hubert 2009). Behavioral variation may exist within and among individuals using different types of spawning habitat, including variation in the timing and frequency of spawning, the length of time that immature life stages reside in the natal stream, and the migration patterns that link seasonal habitat (Kiefling 1978; Gresswell et al. 1997).

Seasonal movement patterns of Snake River finespotted cutthroat trout are similar to those observed for other subspecies of cutthroat trout (Brown and Mackay 1995, Young 1996, Hilderbrand and Kershner 2000b); small movements within seasons are linked with large movements between seasons (e.g., seeking spawning or overwintering habitat; Novak et al. 2004, Harper and Farag 2004, Sanderson and Hubert 2009). For example, Snake River finespotted cutthroat trout are found in areas with substantial structure (e.g., large woody debris or undercut banks) in the summer, and deep or off-channel habitat in the winter (Harper and Farag 2004). The majority of movement between discrete spawning, overwintering, and feeding habitats is thought to be linked by a repetitive annual cycle of movement. However, use of additional post-spawning habitat has been observed (Sanderson and Hubert 2009).

Threats to Persistence

Several potential threats to Snake River finespotted cutthroat trout persistence exist in the upper Snake River watershed. For example, nonnative species have been implicated in the decline of cutthroat trout populations (Gresswell 1988; Gresswell 2011), and brook trout, brown trout, and rainbow trout are all present in the upper Snake River. Brook trout and brown trout may out-compete, displace, or prey upon cutthroat trout (Shepard 2004, McGrath and Lewis 2007). For the Yellowstone cutthroat trout, hybridization resulting from introductions of rainbow trout and nonnative cutthroat trout subspecies is a major cause of the decline and extirpation of the subspecies (Varley and Gresswell 1988; Kruse et al. 2000; Gresswell 2011). Recent evidence suggests that some hybridization between rainbow trout and Snake River finespotted cutthroat trout has occurred in the upper Snake River (Novak et al. 2005; Gregory and Yates 2009; Kovach et al. 2011). Although, hybridization appears to be restricted to a few tributary drainages (e.g., Gros Ventre River, Hoback River, and Greys River; Novak et al. 2005), rapid increases of hybrid swarms of rainbow trout and cutthroat trout have occurred in other spawning streams (Henderson et al. 2000; Muhlfeld et al. 2009).

Other potential threats to cutthroat trout persistence include whirling disease, habitat destruction, and climate change. Larval cutthroat trout are highly susceptible to whirling disease (Wagner et al. 2002), and in the upper Snake River watershed, fish infected with whirling disease have been detected in spring creek complexes of the Salt River (Hubert et al. 2001). However, neither infected fish nor the parasite that causes whirling disease (*Myxobolus cerebralis*) has been detected in the Snake River. Habitat destruction, such as channelization of the Snake River from flood control structures, or unnatural timing and magnitude of discharge releases from Jackson Lake Dam, may also negatively affect population persistence. Finally, changes in temperature and discharge resulting from climate change may exacerbate current threats to persistence and fragment or degrade existing habitat (Williams et al. 2009; Gresswell 2011).

Overview of Chapters

In my dissertation research I explored how life-history diversity and habitat occupancy of Snake River finespotted cutthroat trout are associated with the complexity of the physical template in a large river network, and identified an analytical approach for processing movement data. Radio telemetry was used to identify movement patterns and habitat occupancy, and identify which individuals were spawners over the course of the study. In chapter two, I describe life-history diversity related to spawning and post-spawning movement patterns. Next, I wanted to describe habitat occupancy. However, in preparing to analyze the radio-telemetry data, I was confronted with several common problems in stream telemetry studies: (1) data were analytically sparse (one observation per week), (2) data were sometimes collected with an uneven sampling interval (due to missed detections), and (3) observation of an individual in a location could mean the individual was occupying the habitat or moving through it, and (4) analysis of only locations where fish were encountered ignored the occupation or movement through habitat between locations where fish were encountered. Therefore, in chapter three I collaborated on a new analytical method to interpolate utilization distributions (a histogram of the amount of time spent in a set of locations) that could be arrayed temporally to capture the probable amount of time spent in all locations in a linear (river) system over the duration of radio-tracking. In chapter four, I explored how spatial variation and hierarchical structure in the physical template corresponded with differential availability and function of habitat. Finally, in chapter five, I summarized the overall conclusions of this research and discussed future considerations. Collectively, these data will provide a more complete understanding of potamodromous trout life history in a large connected river network, and the influence of habitat in shaping the way that trout use a watershed through time. Furthermore, the behavioral complexity demonstrated by this native trout in a relatively intact large watershed may serve as an analog or restoration goal for the types of behaviors that could be demonstrated by other subspecies of trout, were their habitat intact.

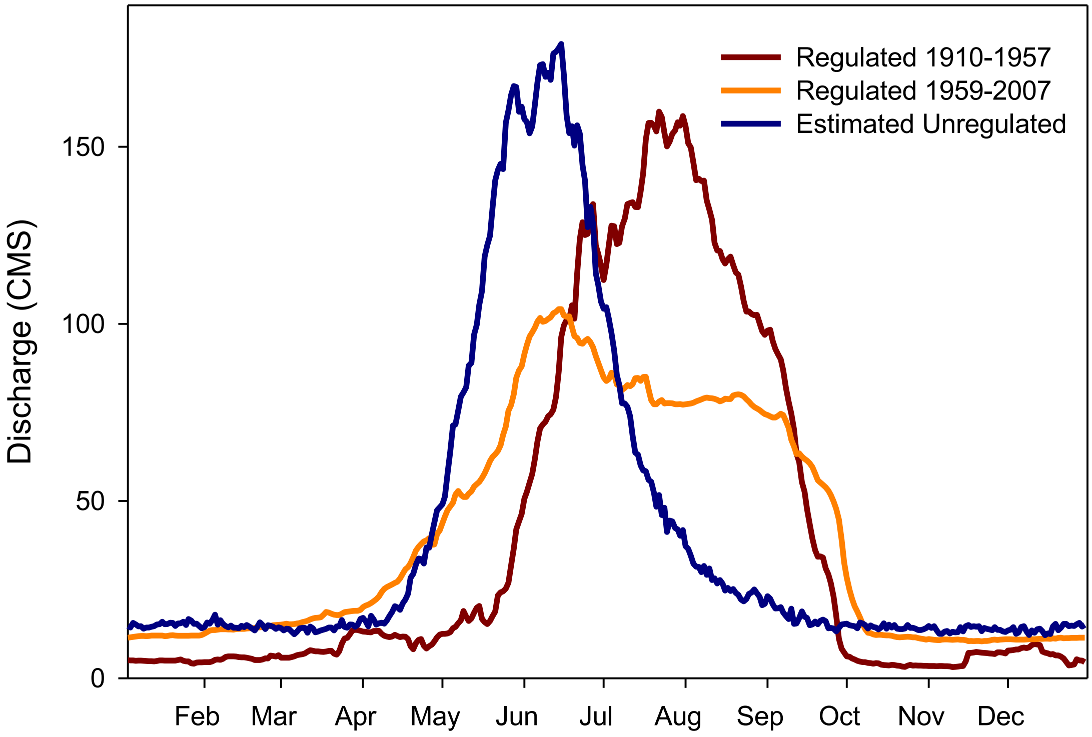

Figure 1.1—Mean daily discharge (cubic meters per second; CMS) recorded at the USGS gage (Moran, WY) immediately below Jackson Lake Dam for the periods of time 1910-1957 (prior to construction of Palisades Dam) and 1959-2007 (beginning after full pool was reached in Palisades Reservoir) and the estimated unregulated mean daily discharge that would be released from Jackson Lake in the absence of Jackson Lake Dam.

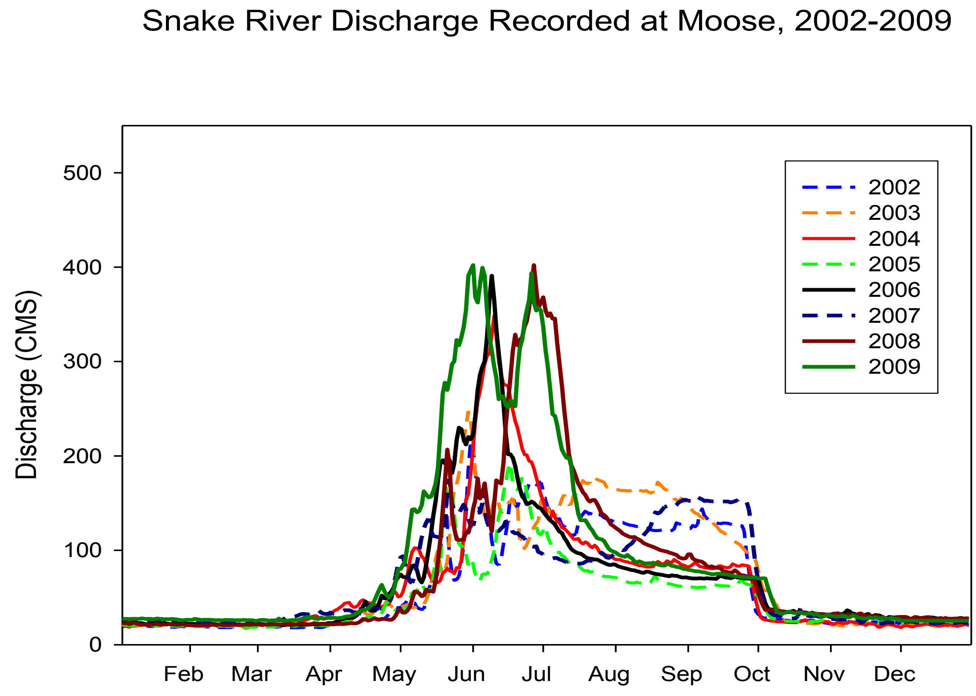

Figure 1.2—Discharge (cubic meters per second; CMS) recorded at Moose Junction on

CMS

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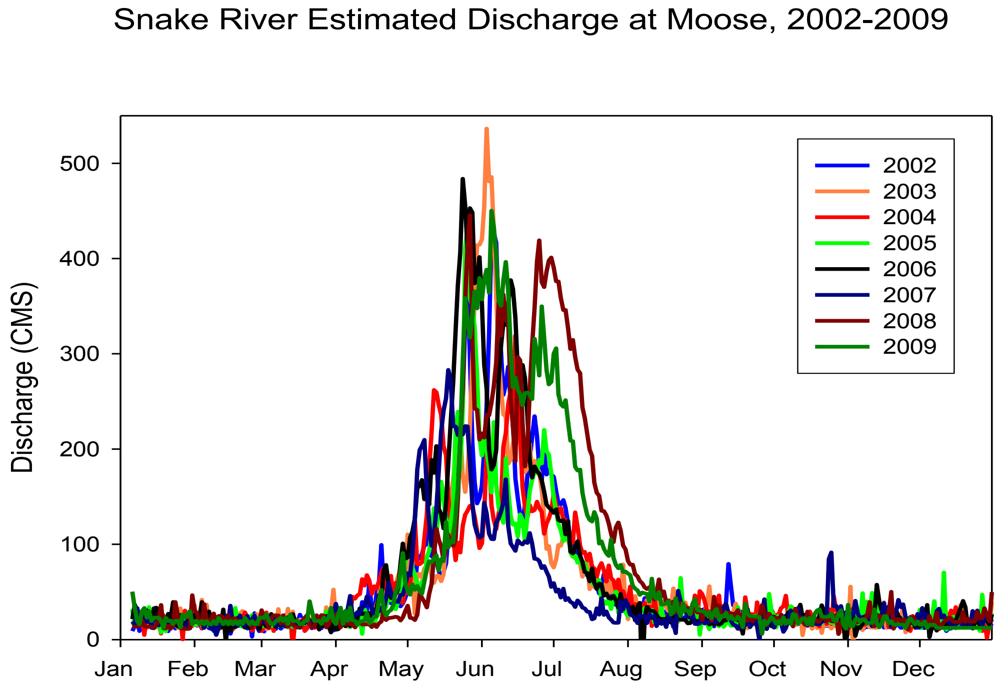

Figure 1.3—Estimated discharge (cubic meters per second; CMS) at Moose Junction on the Snake River that would occur in the absence of Jackson Lake Dam, 2002-2009. Estimated discharge is sum of (1) the estimated discharge at Jackson Lake Dam produced by the Bureau of Reclamation, (2) the discharge recorded at Pacific Creek, and (3) the discharge recorded at Buffalo Fork. Solid lines are years when peak discharge is > 283 CMS (corresponding to 10,000 CFS) dashed lines are years when peak discharge is < 283 CMS.

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CHAPTER TWO

LIFE-HISTORY DIVERSITY OF SNAKE RIVER FINESPOTTED CUTTHROAT TROUT IN THE UPPER SNAKE RIVER: IMPLICATIONS FOR THE CONSERVATION OF NATIVE TROUT IN A LARGE RIVER NETWORK

Abstract

Over the last century, native trout in western North America have experienced dramatic declines in distribution, abundance, and life-history diversity resulting from anthropogenic alterations to habitat. In response to these declines, conservation of native trout has focused on factors that promote population resiliency including life-history diversity. The majority of research on life-history diversity has occurred in smaller systems, and it is unclear whether the patterns observed in those systems are an analog for diversity expressed in larger river systems. In this study, radio telemetry was used to identify the spawning, distribution, and movement patterns expressed by Snake River finespotted cutthroat trout *Oncorhynchus clarkii behnkei* in the upper Snake River. Individuals were implanted with radio tags in October, 2007 (n = 49) and 2008 (n = 199), and monitored through October, 2009. In 2008 and 2009, cutthroat trout spawned in runoff-dominated tributaries (hereafter, tributaries), groundwater tributaries (hereafter, spring creeks), and side channels of the Snake River, altering a perception held for over 40 years that most spawning occurred in spring creeks. Spawning habitat was located throughout the upper Snake River watershed, and migration distances extended up to 100

km between tagging and spawning locations. Postspawning, side-channel spawners exhibited diverse movement patterns; however, spring-creek spawners often remained in the spring creek spawning area, and tributary spawners tended to migrate rapidly from the tributary. In the 12 months following spawning, approximately 33% of tributary spawners died, compared to 17% each of spring creek and side channel spawners. In the upper Snake River, expression of life-history diversity reflects a dynamic behavioral response to a complex and dynamic physical template. Ultimately, managing for diversity, rather than the most common behavior, may provide the most opportunities for persistence in an environment that is likely to experience increased variation from climate change and invasive species.

Introduction

Over the last century, native trout in western North America have experienced dramatic declines in abundance and distribution as a result of habitat degradation, fragmentation, invasive species, and hybridization (Miller et al. 1989; Rieman et al. 2003; Hudy et al. 2007). Many rivers have been dammed, channelized, or simplified, and access to habitat associated with a variety of life stages or life-history strategies has been lost (Thurow et al. 1997; Fausch et al. 2002). In response to these declines, conservation of native trout has focused on factors that promote population resiliency, including life-history diversity (Gresswell et al. 1994; Rieman and Dunham 2000) and habitat patch size (Hilderbrand and Kershner 2000a). Each of these factors is closely associated with characteristics of the physical template (Southwood 1977; Poff and Ward 1990).

However, the template is dynamic, patchy, and hierarchical (Frissell et al. 1986; Poole 2002; Thorp et al. 2006), which hinders predictions of a population-level response over time or across systems.

Life-history variation describes traits associated with survival and reproduction (both of which are under strong natural selection; Cole 1954; Stearns 1977) and is linked to population resilience (Hilborn et al. 2003) through risk spreading and bet hedging (Den Boer 1968; Stearns 1989; Greene et al. 2010). Life-history forms (related to spawning) are often associated with temporary occupation of spatially discrete seasonal habitats (e.g., lake or tributary spawning areas; Gresswell et al. 1994). When multiple forms are present in a population, disturbance at the local scale might only cause extirpation of the portion of the population currently associated with the affected habitat (Den Boer 1968). Subsequently, recolonization may occur by other individuals from the same population over time (Rieman et al. 1997; Gresswell 1999).

Occupation of discrete habitats spreads extinction risk, and it may also be associated with spatiotemporal differences in fitness among individuals expressing different life-history forms (Gross 1991; Sibly 1991; Northcote 1992) or using different spawning locations. In dynamic or heterogeneous stream networks, particular locations (e.g., stream) or types of habitat (e.g., spring creeks) may be differentially productive over time, and the life-history forms associated with that habitat may be differentially successful. Conceptually, expression of multiple life-history forms or use of multiple spawning locations increases the probability that some component of a population will successfully reproduce in a given year (Northcote 1992; Schindler et al. 2010). Over time, this population-scale bet hedging reinforces selection for multiple life-history forms (Kaitala et al. 1993) and provides a greater range of opportunities for population persistence in a spatially and temporally variable environment (Greene et al. 2010).

Life-history variation related to spawning patterns may occur at three hierarchical scales: the type of spawning habitat (life-history form), the locations of spawning habitat, and the behaviors of individuals from a particular spawning location. Where the physical template is diverse, a greater range of life history forms may be expressed (Southwood 1988; Gresswell et al. 1994; Saiget et al. 2007). For example, in the Elwha River, anadromous migrations by bull trout *Salvelinus confluentus* and steelhead trout *Oncorhynchus mykiss* have been blocked by two dams since the early 1900s; dam removal is predicted to allow rapid reexpression of anadromous behavior (Brenkman et al. 2008). Diversity of the physical template may also result in unique life-history traits (e.g., body size or run timing) as a response to unique conditions in particular spawning areas (Gresswell et al. 1997). Likewise, the spatial arrangement of spawning habitat relative to other seasonal habitat represents a unique set of conditions (Wiens 2002) that could be associated with differential growth and survival by individuals from different spawning areas (Rieman and McIntyre 1993). If multiple habitat types or locations are available, a greater diversity of distribution and movement patterns may result (Gresswell et al. 1994; Saiget et al. 2007; Meka et al. 2010).

Currently, the majority of streams and rivers in the historical range of cutthroat trout are no longer in the same condition that permitted the evolution of diverse life-histories (Gresswell 1988; Behnke 1992; Hudy et al. 2007). For larger systems in particular, fragmentation and simplification of the physical template have led to a reduction in the diversity of migratory forms, and in some systems, a loss of larger, more fecund, migratory fish (Rieman and McIntyre 1993; Nelson et al. 2002). However, the majority of research on life-history diversity has occurred in smaller systems (Young 1996; Hilderbrand and Kershner 2000b; Starcevich 2005), and it is unclear whether the patterns observed in those systems may be an analog for the diversity that might be expressed in a larger river system. Given the importance of life-history diversity to population persistence, there is a need to better understand life-history diversity in a large river network.

The Snake River finespotted cutthroat trout *Oncorhynchus clarkii behnkei* is a model subspecies for describing life-history variation in a relatively intact, complex, large river network. This subspecies occurs throughout its historic range in the upper Snake River between Jackson Lake Dam and Palisades Reservoir. Snake River finespotted cutthroat trout express multiple spawning strategies (Novak et al. 2004; Sanderson and Hubert 2009) including fluvial (migration within a river for the purpose of spawning), fluvial-adfluvial (migration from a river into a tributary for spawning), lacustrine-adfluvial (migration from a lake into a tributary for spawning), and allacustrine (migration from a lake into an outflow for spawning; Varley and Gresswell 1988). Historical data from the upper Snake River (below Jackson Lake Dam) suggested that spring creeks were the primary spawning habitat (Kiefling 1978), because high flows and sediment transport in the main stem may impede egg survival (Kiefling 1978). Research on the Salt River, a tributary to the Snake River, also documented use of spring creeks for spawning (Joyce and Hubert 2004; Sanderson and Hubert 2009). Both studies reported that Snake River finespotted cutthroat trout spawned during April and May in spring creek complexes (Kiefling 1978; Sanderson and Hubert 2009), which is earlier than in runoff-dominated habitats where spawning occurs during the descending limb of the hydrograph (usually June or July; Novak et al. 2004; Gregory and Yates 2009). This subspecies has also been observed to migrate long distances to spawn (Harper and Farag 2004; Novak et al. 2004; Sanderson and Hubert 2009), supporting the hypothesis that life-history diversity may correspond with the complexity or spatial extent of accessible habitat.

In this study, radio telemetry was used to identify the life-history diversity of Snake River finespotted cutthroat trout during the year spawning occurred. Specifically, the following research questions were addressed: (1) What spawning patterns are expressed by native Snake River finespotted cutthroat trout in the upper Snake River, and (2) How do life history and location of spawning habitats affect the distribution and movement patterns of adult cutthroat trout before and after spawning. Ultimately, this study provided an opportunity to characterize aspects of life-history diversity of migratory Snake River finespotted cutthroat trout in a large river network as a template for conservation and recovery planning of native trout in other large, degraded river systems.

Methods

Research on Snake River finespotted cutthroat trout spawning patterns was conducted in the Snake River between Jackson Lake Dam and Palisades Reservoir (Figure 1). Jackson Lake Dam was constructed at the outflow to Jackson Lake on the Snake River in 1905 and initially managed to provide irrigation water for agriculture interests in Idaho. From 1916-1957, discharge regulation resulted in elevated peak discharge (mean = 255 m^3/s; Nelson 2007) that was generally delayed by 2 months. Additionally, dam releases between October 1 and March 30 were low (mean = 0.3 m^3/s; Nelson 2007). Following the construction of Palisades Dam in 1958, management of Jackson Lake Dam changed. The peak of spring discharge (mean = 182 m^3/s; Nelson 2007) was modified to mimic unregulated run-off patterns; however, discharge after the spring peak remained elevated (above the estimated unregulated discharge; Nelson 2007) until October 1 (Figure 2), when minimum winter discharge ($\geq$ 7.9 m^3/s; Nelson 2007) was released. For 8 km below Jackson Lake Dam, the hydrograph of the Snake River is entirely regulated by releases from the dam, and below this point, two major tributaries enter the Snake River and mitigate the effects of discharge regulation (Nelson 2007).

Geomorphic segments and reaches were designated in the Snake River between Jackson Lake Dam and Palisades Reservoir (Figure 1). River segments were bounded by tributary junctions or major geomorphic features (e.g., alluvial fans). Reaches within each segment were classified according to channel constraint, channel morphology, and bank structure (Frissell et al. 1986). Constraint (i.e., entrenchment ratio) was determined as the ratio of bankfull width to flood-prone area width (Rosgen 1994; Knighton 1998). This ratio was calculated by digitizing polygons for each reach in the Snake River using Arc GIS (ArcMap version 9.2). Where geomorphic features delineating the floodplain width were absent and the floodplain had a low gradient, a maximum distance of 1 km from the bankfull channel edge was used as the boundary of the floodplain polygon. Bank structure was calculated as the percent of the total main stem channel bank that was levied (based on 2009 orthoimagery in Arc GIS). Using these criteria, seven reach types were identified for the Snake River: (1) constrained single channel with natural banks, (2) constrained multi-channel with natural banks, (3) constrained single channel with levied banks, (4) constrained multi-channel with levied banks, (5) unconstrained single-channel, (6) unconstrained multi- channel, and (7) unconstrained braided channel.

A total of 248 cutthroat trout were implanted with radio tags in 2007 (n = 49) and 2008 (n = 199; Figure 1). Cutthroat trout were captured in September and October of each sample year by angling, raft electrofishing, and backpack electrofishing (Figure 2). Three sizes of tags were used (Lotek Wireless MCFT series: 3EM, 3FM, and 3A; MHz frequencies: 164.000, 164.100, 164.200, 164.280, 164.400, 164.500, 164.560, 165.000, 165.100, 165.300, 165.600, 165.700, and 165.900) so that a tag did not exceed 3 % of the body weight of the individual. Individual cutthroat trout were held in a container, which was oxygenated with bubblers, and anesthetized with clove oil (1 ml/20 L stream water) one at a time. Once anesthetized, total length (nearest mm) and weight (nearest 0.1 g) were recorded, and the individual was placed on a v-shaped padded board for surgery. A maintenance dosage of anesthetic (0.5 ml clove oil/ 20 L stream water) was pumped over the gills during surgery. Tags were implanted using a modified shielded-needle technique (Ross and Kleiner 1982). Incisions were closed with 3-4 interrupted sutures. Following surgery, the individual was immediately transferred to an insulated cooler filled with oxygenated river water until equilibrium was restored (approximately 20 minutes). Subsequently, the individual was placed in a flow-through recovery tank for approximately 30 minutes and then returned to slow-water habitat within 1 km of the capture location.

Initial relocation of cutthroat trout occurred two weeks after radio-tagging. For fish tagged in 2007, relocation events occurred bimonthly in November and January, when it was thought that little movement would occur (Sanderson and Hubert 2009), and then weekly April-November. For fish tagged in 2008, relocations occurred bimonthly in November and January, weekly May-July, and biweekly August-October. During the spawning period (April through July), approximately 500 km of the stream network between Jackson Lake Dam and Palisades Reservoir (including tributaries) were surveyed weekly to detect fish. Relocation surveys were conducted by foot, raft, automobile, and fixed-wing aircraft. All fish relocations were georeferenced, but locations obtained from fixed-wing aircrafts were sometimes less accurate than ground relocations (up to 500 m offset). Therefore, locations were described at the reach scale because it was accurate for both ground and aerial tracking.

Spawning locations of radio-tagged Snake River finespotted cutthroat trout in 2008 and 2009 were defined as the most upstream extent of any tributary in which an individual was relocated, or any location where an individual was observed on a redd. It was not possible to observe spawning activity (redd construction or pairing of fish) at every site because of turbidity or access to spawning streams on private property. Therefore, it was assumed that fish making distinct, rapid, and directed migrations to tributaries, spring creeks, or side channels between April and July were moving to a spawning area (Henderson et al. 2000). These criteria have been used routinely in other cutthroat trout spawning studies (Schmetterling 2001; Sanderson and Hubert 2009; Carlson and Rahel 2010).

Spawn timing was defined as the day(s) when active spawning was observed, the day corresponding with the most upstream location in a tributary, or the last day an individual was detected in a side channel area before moving to another location. Spawners were grouped according to the specific spawning tributary, spring creek or Snake River reach, hereafter referred to as a spawning group. For Snake River spawners, the abundance of spawners per reach type was summarized. All relocations of spawning fish were georeferenced, and fish status (i.e., alive, spawning, dead) was determined when possible.

Life-histories were described for Snake River finespotted cutthroat trout that spawned in 2008, 2009, or both years based on the habitat used for spawning and rearing (Gresswell et al. 1994). Given that fish were all tagged in the Snake River, two potential life-history forms could exist: fluvial (spawning and rearing in the main stem of the Snake River), or fluvial-adfluvial (migrating between the Snake River and a tributary for the purpose of spawning; Gresswell et al. 1994). The fluvial life-history form was further divided into individuals that migrate for the purpose of spawning to tail waters below a dam, lake outflows, and side channel or main stem habitat. Likewise, the fluvial-adfluvial life-history form was subdivided into those spawning in tributary habitat characterized by snowmelt runoff (hereafter, tributary spawners) and those spawning in tributaries characterized by a groundwater-dominated hydrograph (hereafter, spring-creek spawners).

For each life-history strategy, distribution patterns were described for three time periods: tagging, spawning, and postspawning (a single location per individual during September). Displacement distance from tagging to spawning location was calculated for each individual and summarized by life-history form. Subsequently, three patterns were described to categorize migration between tagging and spawning locations: (1) limited movement (the individual spawns and remains in the same segment in which it was tagged for the duration of the study), (2) homing to prespawning habitat (the individual migrates from the tagging location to the spawning location and returns to the tagging location, postspawning), and (3) alternate postspawning habitat (the individual migrates from the tagging location to the spawning location and then to a different postspawning location). In addition to these three migration patterns, postspawning mortality was quantified for each life-history form based on recovery of radio-tags.

Results

A total of 12 segments (length = 4.2 – 34.6 km, mean = 9.8 km) and 80 reaches (length = 0.2 – 15.7 km, mean = 1.4 km) were delineated in the Snake River between Jackson Lake Dam and Palisades Reservoir (Figure 1). In segment 1 (below Jackson Lake Dam), the channel is constrained with deep bedrock pools and a hydrograph dominated by releases from the Jackson Lake Dam. Below segment 1, the regulated discharge regime is mitigated by two major tributaries (Pacific Creek and Buffalo Fork) and sediment delivery and large woody debris inputs result in more complex channel patterns (Marcus et al. 2002; Marston et al. 2005; Nelson 2007). Segments 8-10 are levied with active, braided channels, and segments 11 and 12 are constrained by the Snake River canyon with primarily single channel morphologies (Figure 3).

Radio tags were allocated spatially in proportion to the relative abundance of cutthroat trout captured in each segment from Jackson Lake Dam to Moose Junction during continuous raft-electrofishing surveys in October of 2007 and October of 2008. Few individuals were captured and tagged in segments 1 and 5, and most individuals (52%) were captured and tagged in segment 6 (Table 1). No cutthroat trout were captured in segment 4 during raft-electrofishing surveys or angling, and hence no tagging occurred there. All cutthroat trout (n = 248) recovered from tagging, and no tag-related mortality was detected (e.g., death from post-tagging infection). Individuals were relocated an average of 15 times (range 1-43) during the study.

A total of 140 radio-tagged cutthroat trout spawned in 2008 (n = 23) and 2009 (n = 124), including 7 cutthroat trout that spawned in both 2008 and 2009. Spawning occurred in tributaries, spring creeks, and side channels of the Snake River (between Jackson Lake Dam and Palisades Reservoir; Figure 4). Radio-tagged cutthroat trout migrated to 15 areas for spawning in 2008 and 24 areas in 2009 (12 of those areas from 2008 and 12 new areas). Cottonwood Creek, Blacktail Ponds, and two side channels of the Snake River were major spawning areas in both 2008 and 2009 (Table 2). Spawning in side channels was observed in only unconstrained, braided reaches between Jackson Lake Dam and Moose Junction.

Cutthroat trout began migrating to spawning areas in April and May, and spawning activity peaked in June and July (Table 2) for spawners in all types of habitat. Although there were no pronounced differences in spawn timing among tributaries, spring creeks, and side channels, spawn timing varied substantially among individual areas. For example, spawning in two spring creeks, Cowboy Cabin and Fish Creek, started a month sooner than spawning in other upstream spring creeks (e.g., Blacktail Ponds or 3 Channel). Spawning duration also varied among areas, with prolonged spawning in Cottonwood Creek and side channel areas, and abbreviated spawning in lower Bar BC spring creek and Buffalo Fork (tributary). Finally, there was some evidence that spawn timing was earlier in 2009 than 2008, corresponding with earlier runoff in 2009; because of the smaller sample size in 2008, this pattern could not be evaluated statistically.

Radio-tagged Snake River finespotted cutthroat trout exhibited two life-history forms: fluvial (spawning in side channel and main stem habitat) and fluvial-adfluvial (spawning in spring creek and tributary habitat). The proportion of spawners expressing each life-history differed between 2008 and 2009 (Table 2); however, fluvial-adfluvial spring creek spawners were common in both years (39 % and 55 %, for 2008 and 2009, respectively). Of the seven cutthroat trout that spawned in both 2008 and 2009, five (71 %) used the same spawning location as the prior year, spawning within 500 m of the previous spawn site. However, two of those seven not only spawned in a different location, but they spawned in a different type of location (e.g., tributary or side channel).

Distribution patterns prior to, and during spawning were characterized by movement from tagging locations to overwinter refugia and rapid migration to spawning areas (Figure 4). After spawning, most tagged fish returned to segments 2 – 7 (Figure 5). Migration distance between tagging and spawning locations differed among life-history forms: fluvial fish migrated 0 – 29 km (median 4 km), fluvial-adfluvial-spring creek spawners migrated 0 – 70 km (median 24 km), and fluvial-adfluvial tributary spawners migrated 0 – 101 km (median 10 km). Although tributary spawners migrated the longest distances, they were more likely to migrate into tributaries within the spatial extent of the Snake River where tagging occurred. The frequency distribution of migration distances was right-skewed; median migration distance between tagging and spawning location was 13.8 km for all of the life-history types combined and few individuals migrated > 45 km.

Movement patterns varied among individuals expressing different spawning life histories. For example, fluvial individuals spawned in the segment in which they were tagged more often than did fluvial-adfluvial spawners (Figure 5). Furthermore, fluvial individuals that migrated out of a tagging segment to spawn returned to tagging segments (particularly segments 2 and 6) more often than those displaying other migration patterns (Figure 5). In contrast, fluvial-adfluvial spawners using spring creeks tended to remain in the spring creeks following spawning, and few returned to the segment in which they were tagged (Figure 5). Finally, fluvial-adfluvial spawners using tributaries rapidly outmigrated from the spawning tributary either returning to the tagging segment (50%) or remaining in the vicinity of the confluence of the main stem and spawning tributary

(50%; Figures 4 and 5). Movement patterns of tributary spawners were only based on data from Cottonwood Creek and Lake Creek because they were the only tributaries with more than one spawner that lived through the season.

Movement patterns also varied among spawning areas in the same type of habitat (e.g., among spring creeks). For example, postspawners remained in some spring creeks for months following spawning (e.g., Blacktail Ponds and Three Channel Spring Creek), but spawners from others (e.g., Upper Bar BC spring creek) dispersed rapidly from the area. Limited data from 2008 spawner migrations suggests that if individuals had not returned to the tagging locations by October, they did not return for the duration of the study.

Approximately 10% of spawners in 2008 (n = 2) and 2009 (n = 14) died within 2 weeks of spawning. In addition, 13 other spawners (for which movement patterns were identified) died between August and October, 2009. Mortality sources included: avian predation (great blue heron *Ardea herodias* n = 14, bald eagles *Haliaeetus leucocephalus* n = 3, and pelican *Pelecanus erythrorhynchos* n =1) and angler harvest (n = 2). A specific mortality source could not be identified for the remaining 11 known mortalities. Overall, tributary spawners had the highest mortality rates (33%), followed by spring-creek spawners (17%) and side-channel spawners (17%).

Discussion

This study provided new and detailed information on the life-history diversity of Snake River finespotted cutthroat trout in a large river network. Spawning and movement patterns reflected the connectivity and habitat diversity of the Snake River study area and provided insight into the range of life-histories that can be expressed in a spatiotemporally dynamic system. These patterns did not support existing generalizations regarding spawn timing or habitat type (Kiefling 1978); migrations occurred approximately two months later in the year and to a greater range of locations and habitat types than were previously observed. Postspawning movement patterns also varied among spawning locations and spawning habitat type. Consequently, it appears that descriptions of spawning life histories in complex river networks may be improved by considering how spawning and movement patterns vary spatially.

In 2008 and 2009, radio-tagged cutthroat trout migrated to spring creek, side channel, and tributary spawning areas, but the relative proportion of each spawning pattern differed between years. Although spring creeks were an important component of spawning habitat, particularly in 2009, almost half of all spawning occurred in side channels and tributaries, similar to observations in the Snake River below Palisades Dam (Henderson et al. 2000). This observation contrasted with a perspective accepted for almost 40 years that Snake River finespotted cutthroat trout in the Snake River above Palisades Dam predominantly spawn in spring creeks (Kiefling 1978).

Considering the environmental variability in the upper Snake River, particular locations or types of spawning habitat may be associated with differential production of offspring in different years. For example, Kiefling (1978) suggested that between 1906 and 1957, increased variation and increased magnitude of discharge releases in the Snake River (Marston et al. 2005; and Nelson 2007) may have limited spawning success in side-channel habitat. Since 1957, interannual variation in the timing of peak discharge has varied by several months, and multiple flood events may be released from Jackson Lake Dam in a single year (Nelson 2007), suggesting that the production from main stem habitats may still be variable.

In addition to variation in the hydrograph related to releases from Jackson Lake Dam, there is substantial natural interannual variation in runoff pattern. Therefore, the production of offspring from tributary habitats may be naturally variable, as well. Although spring creek systems are more hydrologically stable, the total area of this type of spawning habitat is limited. Potentially, a relatively consistent contribution of offspring from spring creek habitats might be supplemented annually by a varying level of production out of tributary or side-channel habitats, depending on prevailing environmental conditions. Future research on the relative production of offspring from different habitat types would clarify the relationship of behavioral diversity to spatial and temporal variation in the environment.

In this study, fluvial and fluvial-adfluvial spawners migrated to most of the accessible spawning areas in the upper Snake River watershed, but most spawning was concentrated between Pacific Creek and Moose Junction (corresponding to where most tagging occurred). Distribution of spawners differed from historical reports that suggested spawning, or potential spawning activity, was limited to 15 of 36 tributaries between Jackson Lake Dam and Palisades Dam (Hayden 1967). To access these spawning locations, half of all spawners moved less than 14 km between tagging and spawning locations. This pattern is typical of cutthroat trout movement patterns where some cutthroat trout migrate long distances to access spawning areas and most migrate much shorter distances (Colyer et al. 2005; Muhlfeld et al. 2009; Sanderson and Hubert 2009).

Based on distribution and movement patterns, it appears that suitable habitat exists as a mosaic throughout the river in locations with a range of physical attributes that may be connected with a variety of movement patterns. This stands in stark contrast to distribution patterns in more degraded systems, which often reflect an aggregation of individuals in the few remaining suitable locations and potentially long migrations through unsuitable locations (Colyer et al. 2005). Because of this aggregation, populations are highly susceptible to extirpation resulting from stochastic events or mortality occurring in what little habitat exists (Den Boer 1968). For cutthroat trout in this study, the availability of multiple spawning and postspawning locations minimized avian predation that was concentrated near some spawning locations. Avian predation on cutthroat trout is commonly reported (Carlson and Rahel 2010; Gresswell 2011), but when habitat is limited, that predation may be more concentrated into fewer locations and result in negative effects to the population (Teuscher and Schill 2010).

Collectively, variation in spawning, distribution, and movement patterns allows a complex response to a dynamic template and is often linked to increased population persistence through spreading extirpation risk due to natural causes (Den Boer 1968). However, when threats to persistence are a result of introduced species (e.g., hybridization with rainbow trout *Oncorhynchus mykiss*), life-history variation alone may be insufficient to maintain viable populations. For example, hybridization between cutthroat trout and rainbow trout has been observed in complex river systems despite some differences in spawning patterns (DeRito et al. 2010). Early studies on spawning patterns of Snake River finespotted cutthroat trout suggested that peak spawning in spring creeks occurred in April and May (Kiefling 1978), which could suggest complete overlap in spawn timing between rainbow trout and cutthroat trout (Henderson et al. 2000; DeRito et al. 2010). However, temporal patterns of spawning from the current study did not support that generalization; some spawning in May was observed in side channel, tributary, and spring creek habitat, but peak spawning occurred in June and July.

At this time, little hybridization between rainbow trout and cutthroat trout exists in the Snake River above Palisades Dam (Novak et al. 2005; Kovach et al. 2011), indicating that some degree of separation in spawning patterns between the two species still exists. However, hybridization has been detected in tributaries to the Snake River, including the Gros Ventre River (Novak et al. 2005; Kovach et al. 2011), the Hoback River (Novak et al. 2005), the Grays River (Novak et al. 2005), and tributaries to the Salt River (Joyce and Hubert 2004). Hybridization has also been detected in the main stem Snake River and tributaries below Palisades Dam (Henderson et al. 2000). As climate change produces earlier snowmelt and warmer water temperatures, mechanisms that currently limit rainbow trout distribution may break down (Williams et al. 2009). Subsequently, hybridization might be expected to progress upstream into cutthroat trout strongholds, as has been documented in the Snake River below Palisades Dam (Henderson et al. 2000), the Flathead River (Muhlfeld et al. 2009), and the Yellowstone River (DeRito 2010; Gresswell 2011).

The upper Snake River is a complex and environmentally variable system, both currently and historically (Nelson 2007). Cutthroat trout in this study inhabited and migrated through substantial portions of the watershed and expressed a complex array of behavioral strategies, although potential behaviors and accessible habitat were somewhat constrained because of Jackson Lake Dam. Diversity in spawning, distribution, and movement patterns may be critical for survival and reproduction in a variable environment as the climate changes and invasive species become more prevalent. As such, maintaining diversity in the physical template (Poff et al. 1997; Ebersole et al. 1997) and preserving the connectivity that permits life-history diversity (Den Boer 1968; Warren and Liss 1980) may be more important for population resiliency (Hilborn et al. 2003) than management for a specific spatial extent of the stream network (a minimum area required for persistence; Cowley 2008). Although diversity may be a critical component of population resilience in a changing climate, it may be insufficient to prevent the spread of rainbow trout hybridization in the system. Consequently, management of Snake River finespotted cutthroat trout may also need to focus on preserving strongholds of genetically-pure cutthroat trout by isolating or removing hybrid populations or rainbow trout sources (e.g., Gros Ventre River or Cottonwood Creek) when opportunities exist (Bennett and Kershner 2009).

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Figures

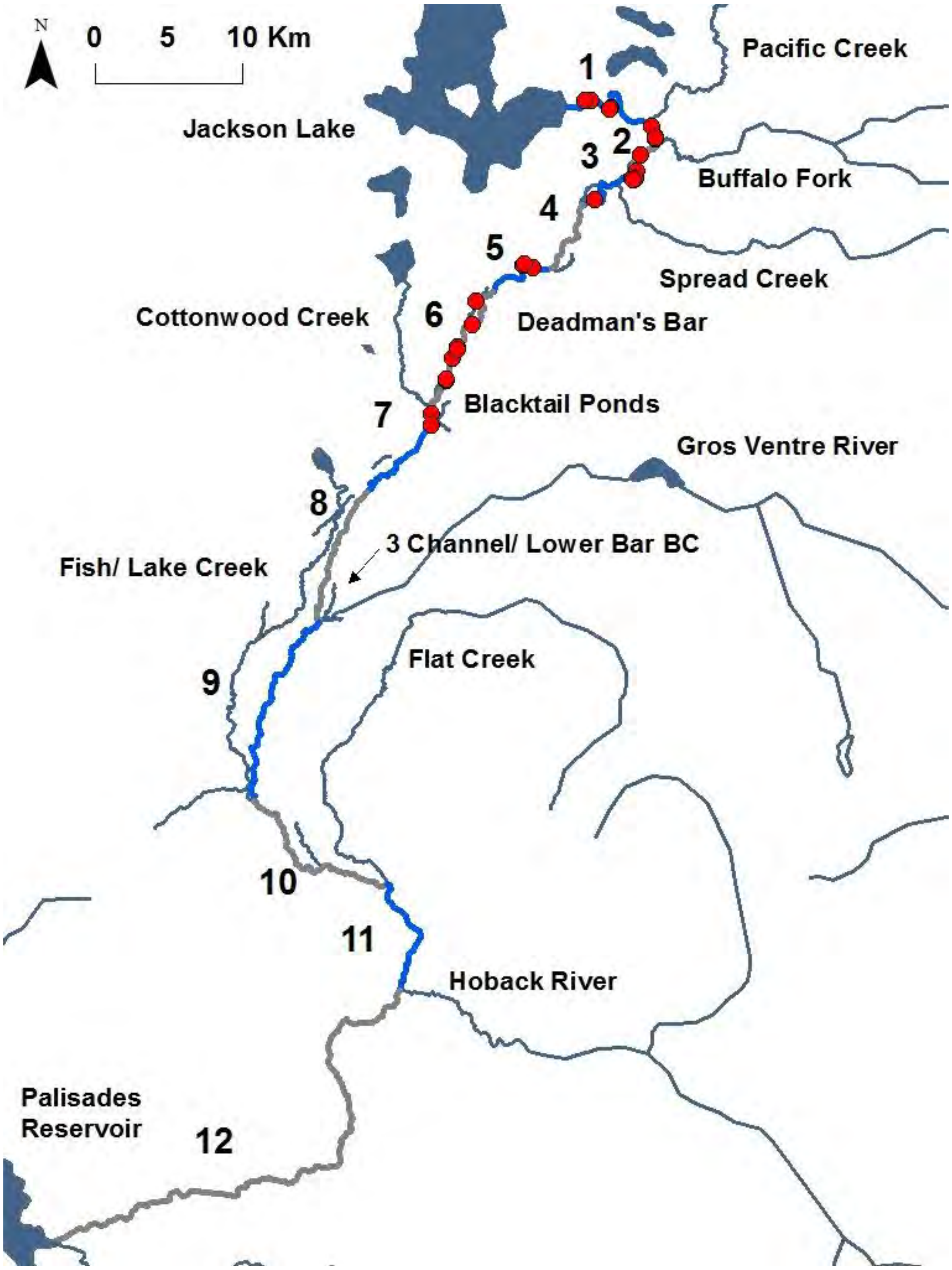

Figure 1—Snake River study area from Jackson Lake Dam to Palisades Reservoir, Wyominh. Major tributaries are labeled, and sample segments classified for habitat surveys are labeled and delineated with unique colors. Tagging locations of Snake River finespotted cutthroat trout *Oncorhynchus clarkii behnkei* are shown as red dots.

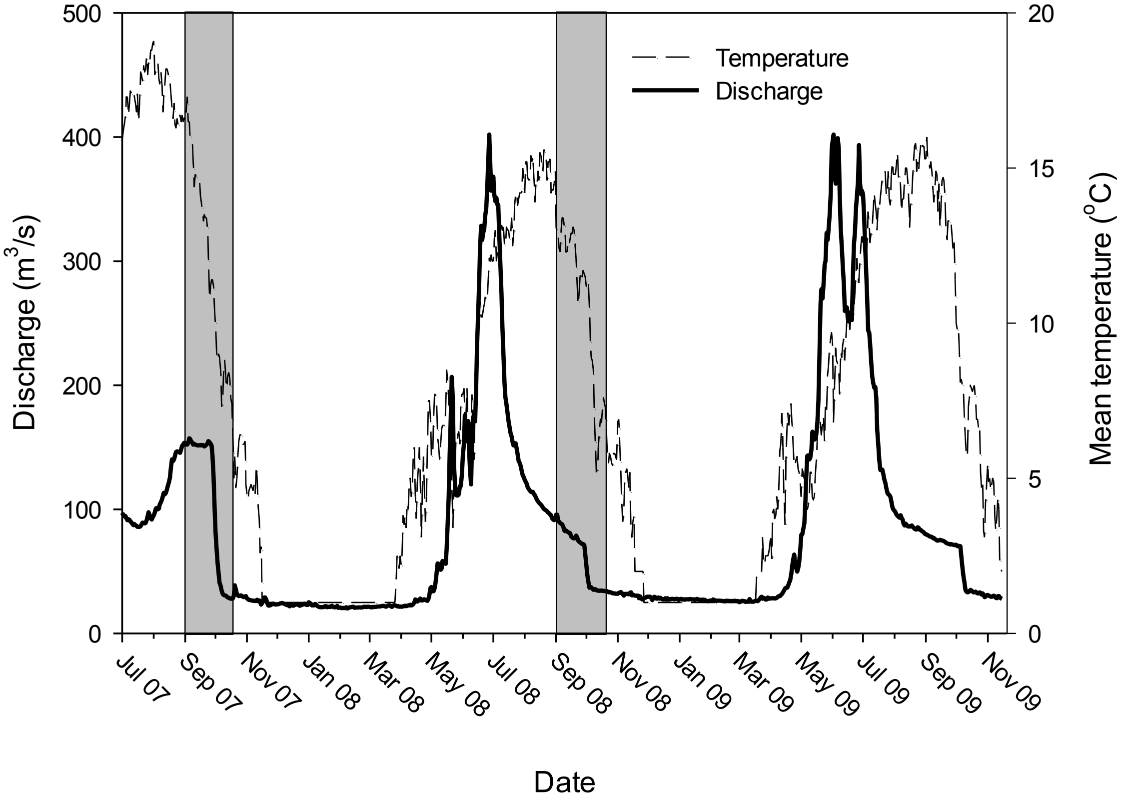

Figure 2—Discharge (cubic meters per second; m^3/s) and mean temperature (Celsius; C) recorded at the USGS Moose Junction gauging station on the Snake River from July 1, 2007 to November 15, 2009. Snake River finespotted cutthroat trout *Oncorhynchus clarkii behnkei* were radio-tagged during September and October of 2007 and 2008 (grey bars) and relocated until November of 2009.

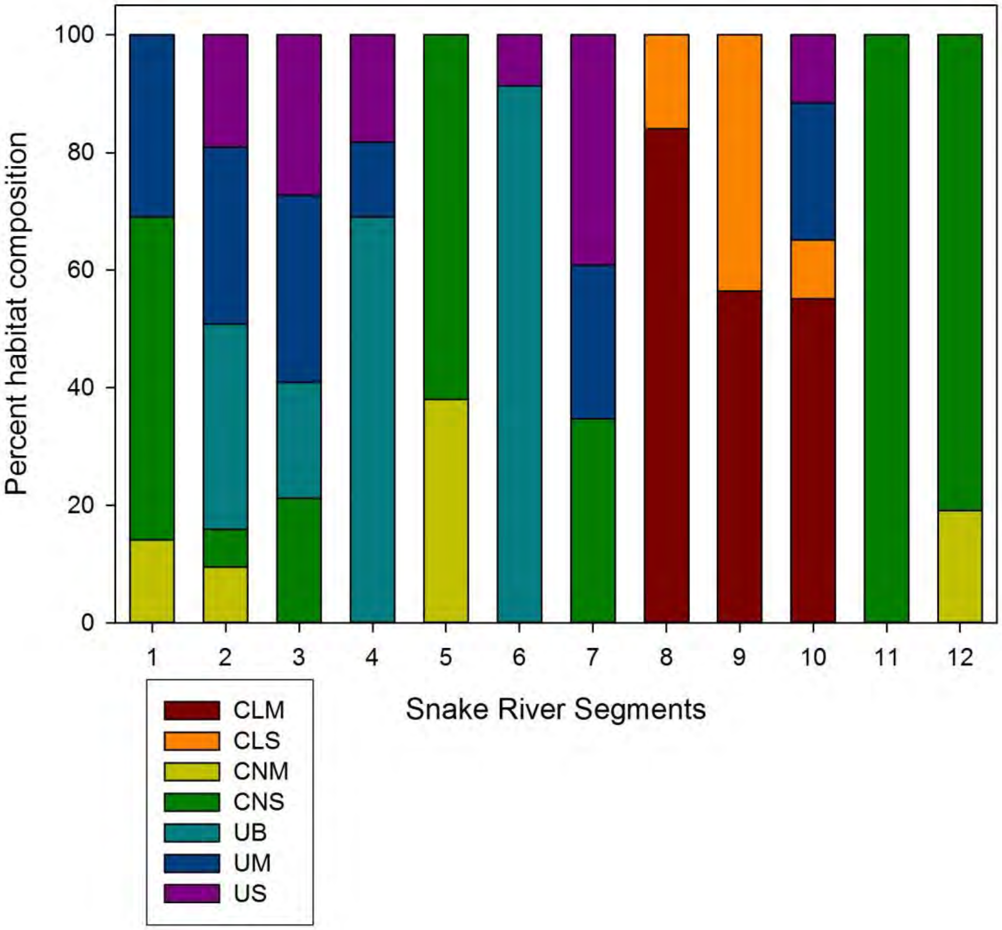

Figure 3—Percent composition of habitat types within each segment (n = 12) of the Snake River from Jackson Lake Dam (the top of segment A) to Palisades Reservoir (the bottom of segment L). Habitat can be Constrained (C) with Levied (L) or Natural (N) banks, Unconstrained (U), and with a channel geometry of Single (S), Multiple (M), or Braided (B) channels.

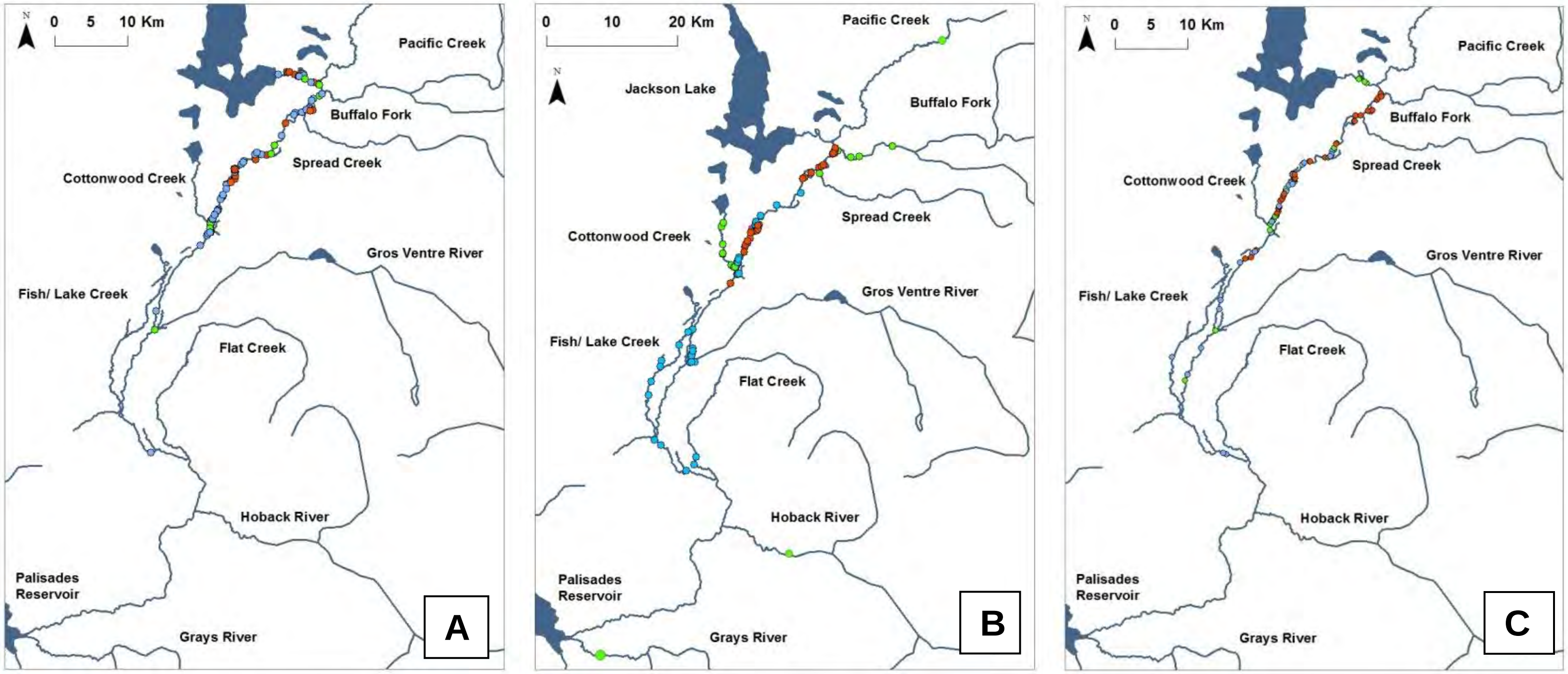

Figure 4—Location of radio-tagged Snake River finespotted cutthroat trout *Oncorhynchus clarkii behnkei* in the Snake River and tributaries during the prespawning (October; panel A), spawning (panel B), and postspawning (September; panel C) periods. Individual spawners are color-coded by life-history strategy (fluvial = orange, fluvial-adfluvial spring = pale blue, and fluvial-adfluvial tributary = green).

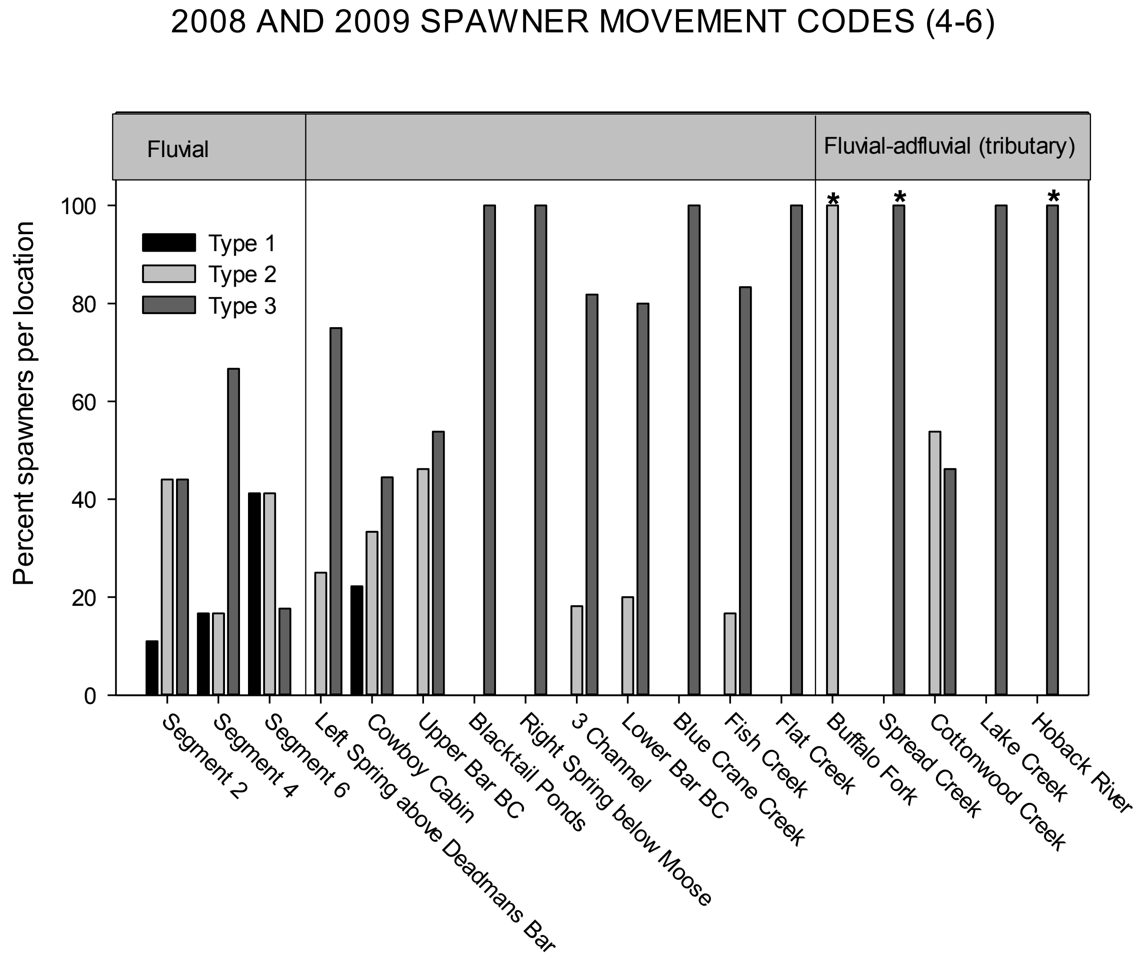

Figure 5—Percent of each movement pattern expressed by radio-tagged Snake River finespotted cutthroat trout *Oncorhynchus clarkii behnkei* in the upper Snake River in each spawn location. Movement type 1 are individuals that spawned in the segment in which they were tagged, type 2 returned to the tag segment postspawning, and type 3 did not return to the tag segment postspawning. Only locations where individuals survived postspawning are included and locations marked with "*" indicate a single observation.

Table 1—Total number of Snake River finespotted cutthroat trout *Oncorhynchus clarkii behnkei* captured and radio-tagged in segments of the Snake River between Jackson Lake Dam and Moose Junction in 2007 and 2008. Average and range of total length is summarized by river segment.

Segment	Number (percent) radio-tagged	Mean total length (range)
1	23 (9.3%)	367 (325-472)
2	33 (13.3%)	395 (325-493)
3	38 (15.4%)	404 (383-467)
4	0	NA
5	25 (10%)	390 (325-448)
6	129 (52%)	401 (332-505)

Table 2—Spawning date, location, and habitat type (tributary, spring creek, or side channel) for 140 Snake River finespotted cutthroat trout *Oncorhynchus clarki behnkei* that made distinct spawning migrations in 2008 and/or 2009 in the upper Snake River watershed below Jackson Lake Dam. Springs designated as "left" or "right" are on river left or right.

	Spawners		Spawning Dates	
Spawning Location	2008	2009	2008	2009
Spring Creeks	9	68	26 June – 21 July	14 May – 23 July
3 Channel	1	11	15 July	18 June - 8 July
Blacktail Ponds	3	9	2 July - 9 July	16 June - 6 July
Blue Crane Creek		4		5 June - 18 June
Cowboy Cabin	1	8	26 June	14 May - 10 July
Fish Creek	2	7	16 July - 21 July	18 May - 23 June
Flat Creek	1	2	8 July	23 June
Left Spring above Deadman's Bar		3		4 June - 24 June
Lower Bar BC	1	6	7 July	17 June - 9 July
Right Spring below Moose		4		5 June - 12 July
Upper Bar BC		14		17 June - 8 July
Tributaries	9	19	14 June – 16 July	26 May – 28 July
Buffalo Fork		4		26 May - 15 June
Cottonwood Creek	3	11	17 June - 16 July	2 June - 28 July
Ditch Creek		1		16 June
Greys River	1		4 July	
Gros Ventre River	1		7 July	
Hoback River	1		14 July	
Lake Creek		2		5 June
Pacific Creek	1		14-June	
Spread Creek	2	1	17 June – 14 July	24 June
Snake River Side Channels	5	37	19 June – 17 July	27 May – 23 July
Segment 2		10		28 May - 14 July
Segment 4	1	5	17 July	4 June – 11 June
Segment 6	4	22	19 June – 15 July	27 May – 23 July

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CHAPTER THREE

INTERPOLATING PROBABILISTIC MOVEMENT PATHS FROM SPARSE TELEMETRY DATA IN A LINEAR SYSTEM

Abstract

Movement paths elucidate underlying processes and scales associated with patterns of space-use (the continuous use of locations in the spatial dimension). In river systems, technology and logistics limit collection of continuous fish movement data, and resulting discrete data are often sparse. Sparse data may miss important ecological features of fish movement and be biased toward over-representing use of locations where fish are detected. Here, we address this issue with a new method for interpolating movement paths from sparse relocation data collected at uneven sampling intervals. In this adaptive kernel density interpolation (AKDI) method, a probabilistic distribution for each time step is computed as a function of (1) the elapsed time to the temporally-nearest relocation point, (2) the average velocity between consecutive relocations, and (3) the degree of randomness in the movement. The AKDI method is compared with three existing methods (sample data, fixed kernel density, and linear interpolation) in their capacity to estimate a known utilization distribution. The AKDI method error rates are significantly lower than the other three methods across a range of sample sizes. Consequently, for real datasets, the AKDI method effectively generates movement paths from sparse data as a precursor to better understanding space-use in river systems.

Introduction

Movement paths describe the continuous sequence of locations occupied by an individual in the spatial domain during a defined temporal domain (Turchin 1998). The spatial component of this path describes the pattern of space-use (i.e., the frequency of use per location), whereas the temporal component describes the timing, direction, and rate of movement between locations (Lucas and Baras 2000; Patterson et al. 2008). Both components of the movement path are fundamental to describe the ecological link between organisms and their environment and to investigations of how ecological interactions and processes operate in space and time (Addicott et al. 1987; Turner et al.1995; Keating and Cherry 2009). Moreover, movement paths are uniquely valuable for elucidating the scales associated with hierarchical patterns of space-use (Johnson 1980; Wiens 1989; Pace 2001).

In stream systems, the capacity to identify movement paths is limited by technology and logistics. As continuous GPS tracking signals do not travel through water, movement paths must be determined from discrete tracking technology such as radio telemetry (for multidirectional movement and assessments of habitat use), or fixed antennae (for unidirectional movement past antennae when data on habitat use between antennae is not needed). With radio telemetry, the frequency of relocations must be balanced with spatial accuracy and sample size constraints (Garton et al. 2001; Hodder et al. 2007). Consequently, data associated with discrete tracking are often sparse and may produce misleading patterns of space-use. For example, discrete relocations of an individual in a stream system may suggest areas of use and avoidance. However, given that an individual is constrained to a continuous path, there should be no zero-probability of space-use between locations where an individual was detected. Additionally, uneven sampling intervals violate the implicit assumption that increased observations in a location correspond to increased time spent in a location (Rogers and White 2007). Finally, utilization distributions calculated from the density of relocation points (and not temporally ordered points) may misrepresent the underlying movement path as the same set of relocation points could be connected with different paths that each have unique utilization distributions (Figure 1a and 1b). Given the potential biases of using discrete sample data to understand space-use in stream systems, it may be preferable to interpolate between sequential sample points to estimate a continuous movement path.

Numerous methods exist to interpolate movement paths, but each has specific data requirements that are rarely met in telemetry datasets from stream systems. Moreover, there are conceptual limitations that make existing methods unsuitable for interpolating biologically meaningful movement paths. For example, if relocations are represented as points in a space-time domain (X-t space), a linear interpolation between these points will produce continuous movement paths even when data are sparse (Wentz et al. 2003). However, interpolated values may be arbitrary because (1) the individual is implicitly assumed to move at a constant velocity between relocations, and (2) the sample frequency determines the perceived movement rate between locations. Time geography (Downs 2010), Brownian bridges (Bullard 1999; Horne et al. 2007), and biased random bridges (Benhamou 2011) estimate the probability that an individual will occur at a specific distance from the last sample point as a function of a diffusion (or advection-diffusion) rate, but these techniques have not been adapted for sparse data in one-dimensional systems. Alternatively, kernel density techniques estimate a discontinuous probability of use around sample points (Worton 1989; Manly et al. 2002; Vokoun 2003) and account for error in telemetry relocations (Nams 1989). However, this approach is sensitive to sample size and does not include the temporal component of space-use (Rogers and White 2007).

In this paper, we describe a new method to generate a continuous probability field of use across a spatiotemporal domain from sparse relocation data collected at variable sampling intervals or during rapid migrations. Conceptually, this adaptive kernel density interpolation method (AKDI) expands the concept of linear X-t interpolation by placing an adaptive kernel over each point on the interpolation path to represent the probability of time spent (and not density of relocation points) in the surrounding spatial domain. The model takes the form of a piecewise advection-diffusion equation that captures both the random (diffusive) and directed (advective) components of the movement path between sample points, similar to the biased random bridge approach by Benhamou (2011). However, the biased random bridge approach estimates three-dimensional space-use and requires frequent relocation data and user-defined truncation of points that are too distant from the interpolated path. In contrast, the AKDI approach applies the concept to a one-dimensional physical space, for which a continuous probability field can be constructed from sparse data with no arbitrary user inputs. The AKDI method is directly applicable to stream systems where continuous data collection is precluded, but it could also be applied to other one-dimensional systems such as wildlife corridors. Here we illustrate the improved performance of the AKDI method relative to existing methods in estimating a known movement path using sparse data.

Methods

The AKDI interpolation method was compared against raw data (naïve distribution), linear interpolation, and fixed kernel density in their accuracy at representing a "true" movement path with a utilization distribution. Simulated movement paths were generated using a random walk algorithm and then randomly sampled to provide a relocation dataset. Each method was applied to the relocation data without knowledge of the "true" path or any user-defined input parameters, and the interpolated paths were converted to utilization distributions. For each method, the difference between the interpolated utilization distribution and the true utilization distribution were calculated using root mean squared error (RMSE) for a uniform binning of the statistical results. The process was repeated until the average error for a given number of relocations converged for each method. (Supplement 1).

Adaptive Kernel Density Interpolation (AKDI) Method

The AKDI method estimates the probability that an individual was at a given distance from a known relocation point after some elapsed time. Consider two relocations whose coordinates are given by (x_1, t_1) and (x_2, t_2). In a logically one-dimensional (1-D) system, there exists a non-zero probability that the individual will pass through all points internal to the observed locations during the time interval $t_1 < t < t_2$.

The *average* velocity over that time interval can be defined as $\bar{V} = (x_{n+1} - x_n)/(t_{n+1} - t_n)$, which represents a linear path in xt space connecting the relocations. The true behavior will deviate from this linear path, with the probable true location becoming more uncertain with increasing time to the temporally-nearest relocation point. Based on the probability of a 1-D biased random walk, we define a continuously adaptive kernel density function, centered around the linear path, where the probability at each point in the spatiotemporal domain is a function of the time (τ) and distance (δ) to the temporally nearest relocation point, and characterized by a parameter ($\hbar$) that represents degree of randomness in the motion:

$$P(\delta, \tau) = \frac{1}{\sqrt{4\pi\hbar\tau}} e^{-(\frac{\delta - \bar{V}\tau}{4\hbar\tau})}$$

This distribution is of the same form as the 1-D advection-diffusion equation, where $\hbar$ is analogous to the diffusion coefficient of the system. However, $\hbar$ *can be determined solely from relocation data with no knowledge of the true motion and without relying on user-specified parameters*. For a given data set, the parameter $\hbar$ can be estimated by first defining a piecewise-linear interpolation path from the relocation data. At a given point in time, the probability distribution around the linear path is a function only of the two temporally-bounding relocation points. Therefore, at each relocation point, the probability distribution can be computed based on a linear path directly connecting the surrounding points to determine the value of $\hbar$that maximizes the probability at the interior point. This is done for each point in the data set (except the first and last), and the results are averaged to determine a value of $\hbar$ that best represents the system in an overall sense.

In practice the AKDI analysis is computed with the spatiotemporal domain discretized into finite regions (bins) with modifications to avoid a singularity near the relocation points as $\tau \rightarrow 0$. The probability distribution is normalized at each point in time allowing for finite spatial domains that may exist due to a physical barrier in the system. Each time increment is equally weighted, and the results are averaged to determine spatial distribution over a prescribed temporal domain; this provides an intrinsic tolerance to uneven sampling frequencies.

Linear Interpolation

The linear interpolation method is a special case of AKDI with a zero-width kernel, equivalent to estimating the distribution as that of a fish moving at a constant velocity between relocation points. This method also has an intrinsic tolerance to sampling frequency bias, and will converge as the number of samples increases, but it does not account for the uncertainty inherent in a sparse dataset (Supplement 1).

Fixed Kernel Density

In the fixed kernel density method, a Gaussian probability field (kernel) was calculated around each sample point (Supplement 1), and each sample point was evenly weighted. As the choice of the kernel bandwidth may influence the resulting utilization distribution (Silverman 1986), we used Silverman’s rule of thumb (SROT) to select the optimal bandwidth and used the reduced factor of 0.9 to increase the probability that the kernel would capture bimodality (Silverman 1986). This created a highly smoothed and continuous probability of space-use that would be most comparable to the utilization distributions calculated from the linear interpolation and AKDI methods.

Comparing Interpolation Methods

Simulated movement paths were created using a spatially 1-D random walk algorithm in which the velocity and step size were randomly selected. (Supplement 1). A single set of sample points was randomly selected from each random walk and used to compute a utilization distribution with each of the interpolation methods (Appendix A). This methodology avoided the biasing results based on the character (degree of randomness) in a given dataset and provided a “true” path as a basis for quantitative error analysis. (Appendix B). The utilization distribution of each interpolation method was compared to the “true” utilization distribution by calculating root mean squared error (RMSE; the difference in the frequency of use for each spatial bin in the domain). Test runs were repeated until the RMSE for an approach at a given sample size converged.

Results

Interpolation methods were tested across sample sizes ranging from 5- 100 points drawn from a random walk. With lower sampling efficiency, the domain of achievable states around the interpolation path expands resulting in a more uniformly-distributed space-use prediction, whereas high sampling efficiency leads to a narrow distributed probability (Appendix B). The probability that an individual was at a given point in space and time can be visualized as a 3-D surface across the spatiotemporal domain (Figure 2). We note that while spatial extrapolation is allowed (either unbounded or with some physical constraint such as a dam or waterfall) the temporal domain is limited to the extents of the measured data.

The AKDI method was significantly better at estimating the space-use distribution of the “true” movement path across sample sizes than the other three approaches (Figures 1 and 3). It is important to note that the “raw data” error is a function of the bin size and should only be qualitatively compared to the other methods, which each generate a continuous distribution. For example, at a sample size of 15, average RMSE was 8%, 11%, 16%, and 25% for AKDI, fixed kernel density, linear interpolation, and raw data, respectively (Figure 3).

Discussion

In this paper, we described a new interpolation method that calculated a continuous probability of time spent across the spatial domain of the data based on sparse sample data. The AKDI method performed significantly better across sample sizes in representing the “true” movement path than sample data, fixed kernel density, or linear interpolation, while providing an intrinsic tolerance to uneven sampling frequency. Irrespective of the interpolation method used, modeling results suggest that interpolated movement paths better describe the underlying movement path than does raw sample data. Only in the strict case where an individual migrates rapidly among discrete habitat units would it be expected that sample point data would accurately represent space-use. Thus, it appears that interpolation methods may represent a significant improvement over existing techniques in describing patterns of space-use in a one dimensional system.

The AKDI method provided a better assessment of space-use because use was calculated in terms of time spent in a location and accurately described positive values for time spent across the spatiotemporal domain of the data. When the sample data were sparse and unequally distributed across the spatial domain of the random walk, there were areas of high and low densities of data collection (not necessarily corresponding to differential densities in time spent; Rogers and White 2007). With sample data or fixed kernel density, the areas of high sample point density were over emphasized, and little to no probability of use was determined for areas of low density. In contrast, both the AKDI and linear interpolation calculated space-use as a sample of time such that multiple relocations in close temporal proximity counted for less time spent in that location than if the same relocations had occurred further apart in time (Johnson et al. 2008a). Conceptually, calculating use as the amount of time spent in a location improved assessments of space-use when the sampling interval was uneven and was directly analogous to point density estimates when the sampling interval was even.

The AKDI method was less sensitive to sample size than the other three methods because it accounted for data sparseness by decreasing the probability of space-use for interpolated points that were further from sample points. Both sample data and linear interpolation did not capture the variability in space-use when based on small sample sizes. However, if the true movement path were less random than the path tested here, it is possible that linear interpolation would be sufficient to characterize the path (Wentz et al. 2003). The performance of the kernel density estimator was also influenced by sample size; at smaller sample sizes, the fixed kernel method performed slightly less well than the AKDI method, particularly under conditions when the samples drawn from the random walk were highly clustered. At larger sample sizes, the performance of the fixed kernel method was more similar to the linear interpolation method due to the effect of uneven sampling intervals. When using the SROT estimate for an optimal bandwidth smoother, there is a balance between selecting a small enough factor value to capture multimodality and selecting a large enough factor value to produce non-zero values across the spatial domain of the data (Silverman 1986). The selection of this factor value may be data-driven, but there is no clear "best" method for determining the bandwidth value. Thus, although the RMSE of the kernel method may approximate the AKDI method at small sample sizes, it is inherently based on arbitrary selection of a bandwidth. More importantly, however, datasets based on actual movement patterns may not conform to the random movements parameterized here. If the underlying utilization distributions is more multimodal (e.g., for individuals that exhibit seasonal shifts in habitat use), the fixed kernel method may perform more poorly, whereas the performance of the AKDI method would be unaffected by the data distribution.

The AKDI method relies on the principle that information associated with observed locations could inform estimates of use at intermediate locations because data points within movement paths are serially autocorrelated (Manly et al. 2002). Other researchers have used subsampling or aggregation techniques to create independence in autocorrelated data (Johnson et al. 2008a). However, independence comes at the cost of decreasing sample size and precision and of losing the context of the movement path or behaviors that connect locations through time (de Solla et al. 1999; Nations and

Anderson-Sprecher 2006; Fieberg 2007; Johnson et al. 2008b). In contrast, space-time movement paths retain the full sample size and the context of the movement path, and thus represent an improvement in our understanding of space-use.

As presented, the AKDI method used equal-sized spatial bins for interpolation, but unequal-sized bins could be used without modification to the method (complete code for data processing provided in Supplement 2). This could be particularly useful if the bin size were selected to correspond to hierarchical habitat features, which are generally variable in length (Frissell et al. 1986). When combined with a spatial classification system that is geomorphically-derived, the interpolated movement paths are even more likely to capture those features of the physical template that influence movement rate through a heterogeneous stream network (Johnson et al. 1992; Schippers et al. 1996). The choice of spatial bin size in the interpolated path is limited to the smallest spatial scale at which relocations are accurate because different movement patterns occur at different spatiotemporal scales (Johnson 1980; Wiens 1989; Rettie and McLoughlin 1999). Likewise, interpolation only describes the time period (e.g., daylight hours) that was sampled (Rettie and McLoughlin 1999).

This study highlighted the importance of using interpolated utilization distribution data rather than raw sample point data to characterize space-use. Currently, most telemetry studies in stream systems quantify relocation points in spatial units (e.g., reaches) to describe patterns of space-use, rather than analyze interpolated path data. However, our modeling results suggest that under certain conditions (e.g., rapid, random, or frequent movement), this approach may be significantly biased, perhaps to the point of producing erroneous results. For example, in a 10-week telemetry study of fish movement with weekly relocations, the average RMSE ≈ 30% for raw sample point data, whereas the average RMSE would be < 10% for the AKDI method. In this case, the sample point data may mischaracterize use of important habitat or corridors that would be otherwise captured by the AKDI method.

In conclusion, the AKDI method can be used to identify a continuous probability of space-use intermediate to sample points as a precursor to better understanding space-use patterns in stream systems. Although data collection should not be reduced (as important behavioral patterns may be missed), this method is quite useful for improving our understanding of space-use when continuous data collection is precluded. It also presents an array of opportunities to integrate sparse telemetry data sets into emerging analytical frameworks (e.g., resource selection functions that use utilization distributions, Millspaugh et al. 2006; or analyzing movement paths with state-space models, Jonsen et al. 2003; Patterson et al. 2008) that require continuous data (Fieberg et al. 2010).

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Figures

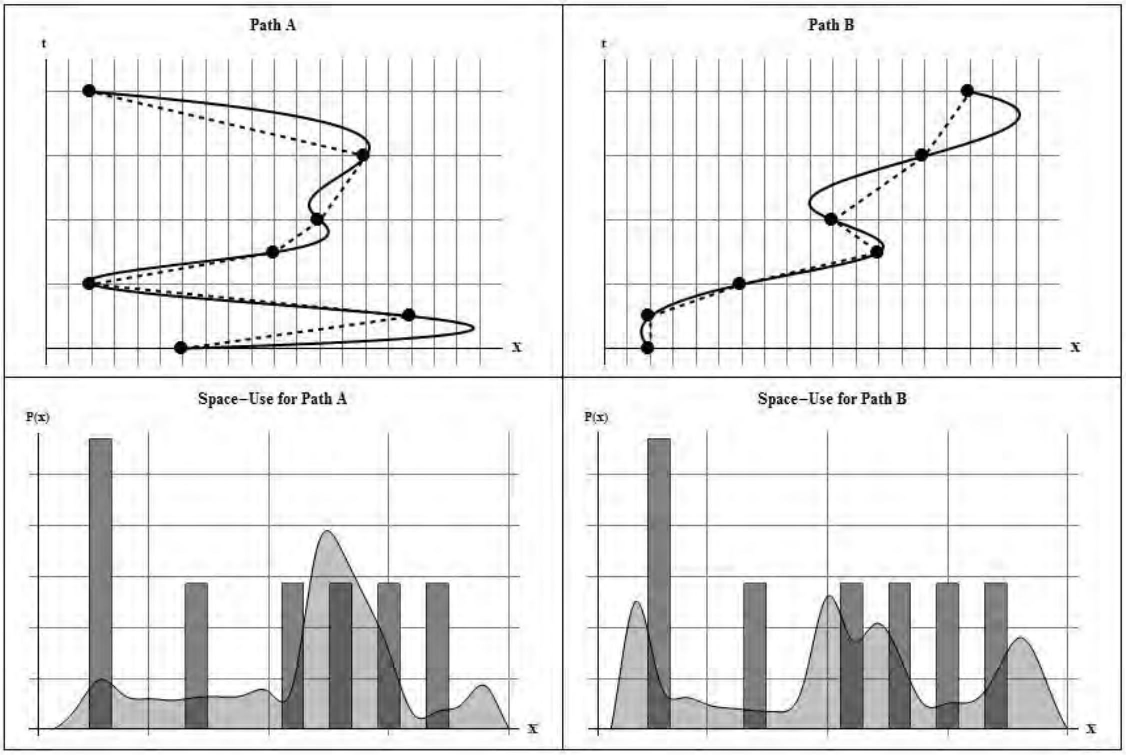

Figure 1.—Two potential movement paths (A and B) connecting identical relocation points (panel A) with the corresponding patterns of space-use frequency generated from sample points contrasted against the actual utilization distribution of each movement path (panel B).

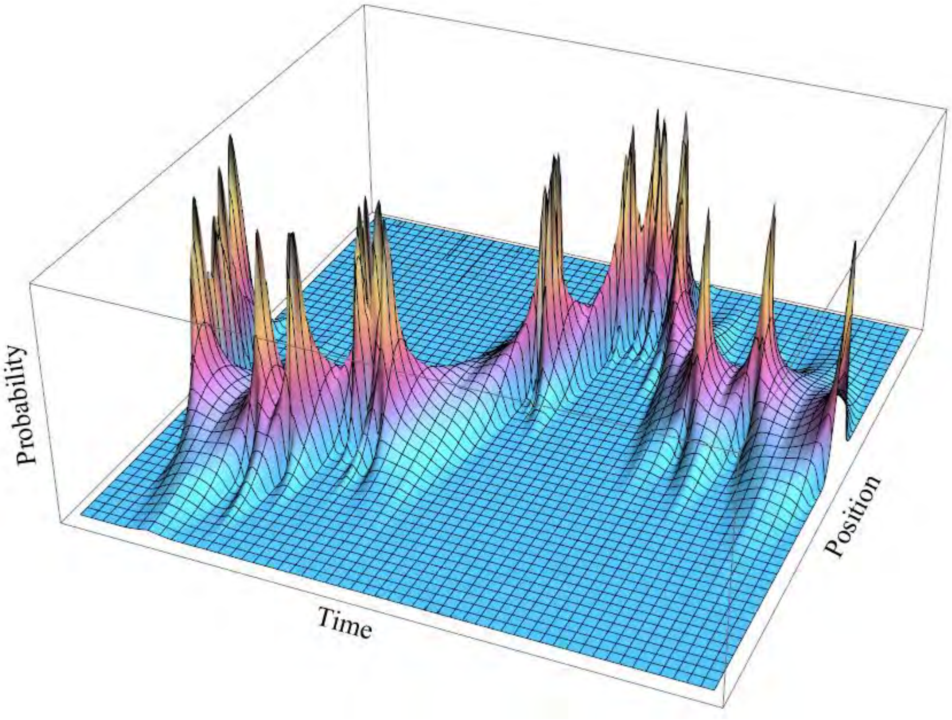

Figure 2.—Interpolated probability of time spent along a continuous path through X (location)-t (time) space generated using the adaptive kernel density interpolation method (AKDI). The height of the plot corresponds to the probability of time spent in a particular location at a particular time.

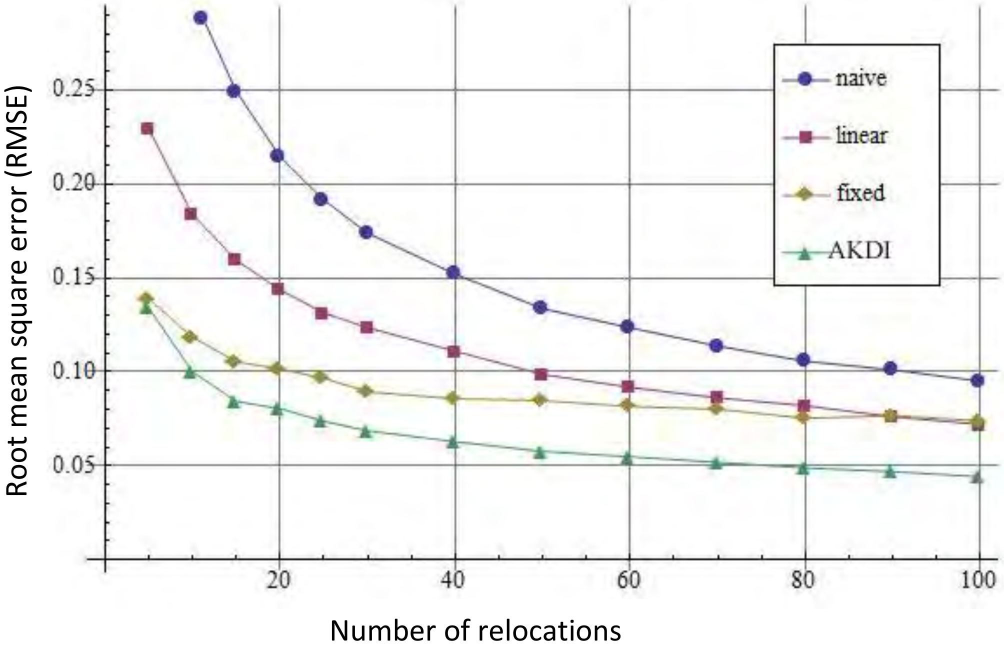

Figure 3.—Root mean square error of the adaptive kernel density interpolation method (AKDI), naive sample data, linear interpolation, and fixed kernel density across sample sizes ranging from 5 to 100.

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CHAPTER FOUR

SCALING UP: SPATIAL AND HIERARCHICAL VARIATION IN MOVEMENT AND HABITAT OCCUPANCY PATTERNS OF CUTTHROAT TROUT IN THE UPPER SNAKE RIVER, WY

Abstract

Numerous salmonid habitat studies have described how habitat is hierarchically structured, with physical characteristics at coarser spatiotemporal scales constraining the expression of characteristics at finer scales. However, over longer spatial extents, longitudinal and patchy variation in the physical template also affect habitat availability. In particular, physical characteristics differ substantially among segments of stream bounded by tributary junctions or pronounced changes in underlying geology, and it is difficult to investigate habitat relationships that extend across multiple segments. To date, most habitat and movement studies have focused on smaller streams and finer spatial scales, and it is unclear whether relationships observed in smaller systems can "scale up" in 4^{th}-6^{th} order river systems. In this study, radio-telemetry was used to evaluate nonreproductive movement patterns and spatial variation in habitat occupancy of Snake River finespotted cutthroat trout *Oncorhynchus clarkii behnkei* (n = 94) at two spatial scales in the upper Snake River. Habitat availability and occupancy differed substantially throughout the study area; one sample reach was associated with 24% of occupancy, whereas several others were rarely occupied. In general, more time was spent

in reaches with a greater abundance of large woody debris and a greater maximum depth. However, in the reaches immediately below Jackson Lake Dam, a stronger relationship existed with submerged macrophytes. Habitat relationships were consistent throughout the year because individuals exhibited little movement (primarily among adjacent reaches). These data suggest that longitudinal and patchy variation in the physical template, along with hierarchical habitat structure, produced variation in the spatial availability of habitat attributes and occupancy. By evaluating habitat occupancy and movement over a large spatial extent (45 km), with a large sample size of radio-tagged cutthroat trout, and with data collected in great detail over multiple years, this study addressed a data gap in our understanding of how cutthroat trout respond to habitat in larger rivers.

Introduction

Salmonids connect seasonal (Fretwell 1972; Schlosser and Angermeier 1995; Northcote 1997) or life-stage specific (Schlosser 1991) habitats with movement to complete the life cycle (Schlosser 1991). Movement distance is a function of the differential availability (Albanese et al. 2004), quality (Albanese et al. 2004), and spatial arrangement (Kocik and Ferreri 1998; Bahr and Shrimpton 2004) of habitat (Carlson and Rahel 2010). However, unique physical processes structure habitat across spatiotemporal scales (Wiens 1989; Bult et al. 1998; Lowe et al. 2006), and it may be difficult to identify important habitat relationships and associated movement scales across streams or stream sizes.

Hierarchical structure in the physical template produces scale-specific habitat relationships (Bozek and Rahel 1991; Rabeni and Sowa 1996; Bult et al. 1998). Geomorphic features of the physical template are delineated according to a set of criteria related to channel form and the frequency of channel reorganization (Frissell et al. 1986). These features are nested hierarchically such that coarse-scale physical attributes constrain the expression of fine-scale physical attributes (Frissell et al. 1986; Townsend 1996; Poole 2002). As a result, different habitat relationships may be associated with particular scales in the hierarchy. For example, bull trout have been shown to select redd sites in complex habitat characterized by upwelling groundwater at the reach scale, yet downwelling flow at the microhabitat (redd-site) scale (Baxter and Hauer 2000). Although habitat relationships are associated with different scales (Rabeni and Sowa 1996), spatial variation in the physical template affects the specific habitat availability or relationships that can exist throughout a river network.

Habitat availability, occupancy, and movement patterns vary spatially in response to habitat patchiness (Pringle et al. 1988) and longitudinal change (Vannote et al. 1980) in the physical template. First, spatial variation among habitat at a given scale (e.g., variation among reaches) produces a *patchy riverscape* (Pringle et al. 1988; Poole 2002; Thorp et al. 2006). For example, sediment erosion, transport, and deposition vary spatially (Montgomery and Buffington 1997) and affect channel form (Montgomery and Buffington 1997) and habitat availability. Thus, spatial variation in habitat availability may result from underlying geology. This patchiness (or discontinuum; Poole 2002) may be more pronounced at the segment scale, where segment breaks are defined by tributary junctions or pronounced changes in geomorphology or geology that persist at intervals greater than 100 years (Frissell et al. 1986; Ward and Stanford 1983).

In longer sections of streams, *longitudinal changes* to the physical template result from increasing drainage area, spatial variability of the hydrograph (Vannote et al. 1980; Gomi et al. 2002), disturbance regime (Montgomery 1999; Gomi et al. 2002), decreasing elevation, and increasing temperature (Isaak and Hubert 2001). As such, the physical attributes of reaches in a headwater stream may be dissimilar from attributes of reaches lower down in the river (Gomi et al 2002). Moreover, in larger systems, fewer tributary confluences are large enough relative to the main stem to impart a geomorphic effect (Benda et al. 2004) or act as a segment boundary, and therefore, downstream segments are often much longer than upstream segments. Thus, coarse, longitudinal change in habitat-forming processes (e.g., temperature associated with elevation) influences the attributes of individual reaches or segments spatially (Poff and Ward 1990; Montgomery and Buffington 1997; Torgersen et al. 2006).

Collectively, hierarchical habitat structure, habitat patchiness, and longitudinal changes to the physical template interact to define the set of habitat attributes available in a particular location (Poole 2002; Benda et al. 2004). For example, different locations are associated with different underlying geology, land use, discharge regime (Gomi et al. 2002), temperature regime, drainage pattern (Benda et al. 2004), or substrate size (Schlosser 1991). Consequently, different habitat forming processes (e.g., sediment transport) and habitat attributes (e.g., undercut banks) are distributed spatially throughout the riverscape (Montgomery and Buffington 1997), and location within the riverscape sets the context of how individuals use a system (Fausch et al. 2002; Weins 2002; Carlson and Rahel 2010).

Recently, there has been a greater emphasis on riverscape-scale studies in stream systems (Carbonneau et al. 2011; Brenkman et al. 2012; Thorp et al. 2013) as a way to relate spatiotemporal variability in the physical template to salmonid habitat occupancy or movement. However, most of the data on habitat occupancy or movement patterns comes from smaller streams or finer spatial scales. Considering the substantial variation in disturbance regimes and physical characteristics associated with stream size and habitat scale, it is unlikely that patterns observed in smaller systems or finer scales can "scale up" to describe patterns in larger systems or coarser scales. Consequently, there is a need to explicitly evaluate spatial patterns of habitat occupancy and movement in 4th – 6th order rivers at the segment scale at which many trout complete their life cycle (Fausch et al. 2002).

In this study, we evaluated spatial variation in habitat relationships and movement patterns at the reach and segment scales, with emphasis on identifying spatial variation in habitat relationships. Snake River finespotted cutthroat trout *Oncorhynchus clarkii behnkei* in the upper Snake River provided a model system to explore habitat occupancy and movement patterns. This subspecies persists throughout the native range in the upper Snake River between Jackson Lake Dam and Palisades Reservoir. Much of the range in the headwaters of Pacific Creek and Buffalo Fork was declared wild and scenic in the Craig Thomas Snake River Headwaters Legacy Act of 2008. Because of the size of the river system, cutthroat trout have the potential to make long-distance movements to access seasonal habitat in a complex physical template (Sanderson and Hubert 2009; Homel et al. *in prep-a*).

To better understand spatial habitat relationships, radio telemetry was used to identify movement and habitat use by Snake River finespotted cutthroat trout in the upper Snake River. Our specific objectives were (1) to identify the spatiotemporal scales associated with nonreproductive movement patterns of cutthroat trout in the Snake River, and (2) to evaluate spatial and hierarchical habitat relationships of adult cutthroat trout in the Snake River. Previous research had identified complex movement patterns by adult cutthroat trout throughout the year spawning occurs (Homel et al. *in prep*-a). To remove potential bias in habitat occupancy that could result from a spawning migration, analysis was restricted to adult cutthroat trout for which a spawning migration was not detected during the study.

Methods

Research on the movement patterns and habitat occupancy of cutthroat trout occurred in the upper Snake River in Grand Teton National Park between Jackson Lake Dam and Moose Junction (45 km downstream of the dam; Figure 1). Jackson Lake Dam was constructed at the outflow to Jackson Lake in 1906 to provide flood control and irrigation water, which resulted in a modified discharge regime (Nelson 2007). Following the construction of Palisades Dam (110 km below Jackson Lake Dam) in 1958, peak discharge released from Jackson Lake Dam has been more consistently timed with natural runoff (mean = 182 m^3/s at Jackson Lake Dam and 352 m^3/s at Moose

Junction; Nelson 2007), and minimum winter discharge has been released (≥ 7.9 m^3/s; Nelson 2007). However, above average discharge is released from the dam during July, August, and September for recreation activities on the Snake River and to maintain sufficient irrigation water in Palisades Reservoir. At the confluence with Pacific Creek and Buffalo Fork, 8 km below Jackson Lake Dam, the effects of discharge regulation (sediment deficit, limited large woody debris, and altered hydrology; Marcus et al. 2002; Marston et al. 2005; Nelson 2007) are mitigated by these two major tributaries.

Within the study area, sample segments and reaches were delineated according to geomorphic characteristics (Frissell et al 1986). Segment breaks were established at tributary junctions or where major geologic features (e.g., alluvial fan) exerted a geomorphic control over a large section of river. Reaches were classified based on channel constraint and channel morphology (i.e., single, multiple, or braided channels).

Cutthroat trout were implanted with radio tags in 2007 (n = 49) and 2008 (n = 199). Radio tagging effort was allocated spatially in proportion to the density of fish observed during raft-electrofishing surveys conducted with Wyoming Game and Fish in October (see Homel et al. *in prep-a* for a detailed description of radio-tagging methods). All adult cutthroat trout > 325 mm (total length; TL) were implanted with a Lotek Wireless radio-tag using a modified shielded needle technique (Ross and Kleiner 1982). A total of 13 radio frequencies were used with approximately 19 fish per frequency. At each frequency, unique burst patterns differentiated individual fish. Four tag sizes were used (Lotek Wireless MCFT series: 3EM, 3FM, 3A, and 3L) to maximize the size range of cutthroat trout that could be tagged without the tag weight exceeding 3% of the body weight. Burst rates were programmed at 3-5 seconds to decrease the amount of signal collision that could happen in a small study area with a large number of tagged fish. Estimated tag battery life ranged from 334 days for the smallest tags (3EM) to 1,100 days for the largest tags (3L).

From the initial sample size of 248 cutthroat trout, only those cutthroat trout that were not detecting making distinct spawning migrations and were relocated at least two times were considered non-spawning cutthroat trout with sufficient data for analysis. Spawning migrations were defined in Homel et al. (in prep(a)) as rapid, directed migrations between April and July. Cutthroat trout tagged in 2007 were relocated bimonthly November-January and weekly April- November. Cutthroat trout tagged in 2008 were relocated bimonthly November- January, weekly May-July, and biweekly August- October. Relocations were obtained by hiking, rafting, driving, and biking with an antenna through the study area. Additional relocation data were obtained from telemetry flights using a fixed wing aircraft with 4-element Yagi antennae, and attempts were made to obtain a second ground relocation for these cutthroat trout within a week of the telemetry flight.

Relocation data for each individual provided an observed location at a point in time. However, some individuals were not encountered every week, and observed locations did not necessarily indicate an individual was “using” the habitat where it was encountered. Moreover, locations between where fish were observed were known to have been occupied for some amount of time, but there was uncertainty in the estimate of time spent in those locations. Therefore, it was necessary to interpolate between observed relocation points and represent location uncertainty with utilization distributions (an estimate of time spent per week in each reach). The adaptive kernel density interpolation method (AKDI; Homel et al. *in prep-b*) was used to estimate utilization distributions for each individual for the duration that the individual was alive and actively tracked. These utilization distributions encompassed the probable range of reaches that could be occupied by an individual during each week, given an observed movement rate before and after that week. Practically, these utilization distributions represented an estimate of reach occupancy for each time step; the term 'reach occupancy' will be used hereafter to describe the probable time spent in each reach, for each week.

Spatiotemporal Movement Patterns

Movement paths were assembled from the dataset of weekly reach occupancy. For each week, the description of reach occupancy was reduced to the single reach in which the majority of time was spent. Each of these weekly maximum values was aggregated into a set of consecutive locations through time that comprised a movement path.

Spatiotemporal movement patterns (movement distance and percent of individuals moving) were identified at the reach and segment scales from October 2007 through September 2009 for each month, season, and year of the study. Seasons were defined by the hydrograph as base flow (October 1-April 14), runoff (April 15-July 31), and elevated summer flow (August 1-September 30; Figure 2). Movement distance was calculated as the difference (in reaches or segments) between the most upstream and downstream reach or segment occupied by an individual during each month. Monthly movement distance was aggregated at seasonal and annual scales. The percent of individuals moving was calculated based on the total number of living fish during a time step. Individuals were considered to be moving if a single change in location at the reach or segment scale occurred during the time interval (e.g., month). To facilitate comparisons across time intervals, distance moved per time interval and percent fish moving per time interval were standardized by the number of days in the time interval (e.g., season length).

Habitat Relationships

Prior to evaluating habitat relationships, reach occupancy data were transformed to the appropriate temporal scale for analysis. First, weekly estimates of reach occupancy were aggregated to create monthly estimates of reach occupancy, which were then standardized by the duration of each month. Because the focus of this study was to evaluate habitat patterns and not to predict individual relationships, monthly estimates of reach occupancy were summed across individuals to produce a single monthly estimate of reach occupancy for all fish, combined. Next, many of the monthly estimates of reach occupancy were expected to be similar due to limited movement at certain times of the year. Therefore, principle components analysis (PCA) was used to reduce the number of months in the dataset (rows = reaches, columns = monthly occupancy) by identifying clusters of months with similar estimates of reach occupancy (R, package labdsv, version 1.5-0; Roberts 2012). Similar clusters were subsequently aggregated to reduce the total number of monthly reach occupancy analyses that were performed.

For each reach, habitat attributes were delineated according to the channel form in 2009 (corresponding to the time frame when radio-tagged cutthroat trout were tracked, habitat attributes were measured, and current aerial photographs were available to derive GIS habitat attributes for the habitat analysis; Table 1). Habitat attributes were selected that were frequently cited as important habitat for cutthroat trout either individually (e.g., large woody debris, Young 1996; Kershner et al. 1997; and pools, Harper and Farag 2004; Sanderson and Hubert 2009) or as components of habitat complexity (braid index and channel form; Horan et al. 2000). In addition, macrophytes and bank structure were selected because they were common in different portions of the upper Snake River and could be important sources of habitat complexity (Table 1).

The relationship between spatial patterns of reach occupancy and habitat attributes was evaluated using multiple regression (R, package nlme, version 3.1-106; Pinheiro et al. 2012). Specifically, regression was used to (1) identify the relationship between reach occupancy and physical attributes throughout the study area, (2) determine whether differences in the physical characteristics between segment 1 (the upper most, regulated segment below Jackson Lake Dam) and the remaining five segments (downstream of large tributary inputs), resulted in different reach-scale habitat relationships, and (3) determine whether segment-scale attributes produced different reach-scale attributes throughout the study area.

To address the first two objectives, regression models were fit to three datasets: a full dataset of all reaches, a dataset of only the reaches in segment 1, and a dataset of all reaches from segments 2 - 6. To address the third objective, mixed effects models were constructed for the full dataset and the segments 2-6 dataset with segments modeled as a random grouping variable to test whether relationships between reach occupancy and habitat attributes varied systematically due to segment-level characteristics. Models were constructed using the following formula:

$$Y_{ij} = \gamma_{00} + u_{0i} + \beta_1(X_{1ij}) + \beta_2(X_{2ij}) \ldots + r_{ij} \quad i = 1, \ldots, n$$

where Y_{ij} is the total amount of time spent per location across all individuals, γ_{00} is the common intercept, u_{0i} is the between-group error term, β_1 is the slope of the first predictor (X_{1ij}), and r_{ij} is the within-group error term. Fixed effects models were constructed for the segment 1 dataset (because there was no grouping variable) using the following formula:

$$Y_{ij} = \beta_1(X_{1ij}) + \beta_2(X_{2ij}) \ldots + \varepsilon_{ij} \quad i = 1, \ldots, n$$

where Y_{ij} is the total amount of time spent per location across all individuals, β_1 is the slope of the first predictor (X_{1ij}), and ε_{ij} is the error term.

For the full and segment 2-6 datasets, the same *a priori* candidate models were constructed. For the segment 1 dataset, attributes used in the candidate models were evaluated individually because the sample size precluded more complex model constructions. In order to minimize the potential for multicollinearity in the model, a correlation matrix (Table 2) was constructed for all predictor variables (Table 1). For pairs of variables that were strongly correlated ($r > 0.7$), only the variable that was more strongly correlated with reach occupancy was retained in the dataset. From that reduced dataset, variables that were moderately correlated ($r = 0.5 - 0.7$) were not combined in candidate models, but were used in independent models.

Models in the full and segment 2-6 datasets were contrasted using AIC scores to show relative difference from the global model; scores differing by two or more points (for models containing only significant variables) were considered to be significantly different (Burnham and Anderson 1998). The variance explained by the random intercept in each model (group level differences among segments) was calculated as intercept variance/ (intercept + residual variance). Models in the segment 1 dataset were not nested, so comparisons among significant models were ranked by the r^2 value.

Results

A total of 6 segments (length = 4.9 – 11.7 km, mean = 7.2 km) and 32 reaches (length = 0.3 – 4.9 km, mean = 1.4 km) were delineated in the Snake River between Jackson Lake Dam and Moose Junction (Figure 1; Table 2). In segment 1 (below Jackson Lake Dam), the channel is constrained with deep bedrock pools, and the hydrograph is dominated entirely by releases from Jackson Lake dam. In contrast, segments 2-6 have more complex habitat and substantially more gravel and large woody debris, due to inputs from Pacific Creek and Buffalo Fork (Marcus et al. 2002; Marston et al. 2005; Nelson 2007; Table 2). However, segment 4 is constrained by alluvial deposits and has simpler habitat than upstream and downstream segments (Table 2).

A total of 94 cutthroat trout (mean length = 394 mm TL, range = 325 - 505) were considered to be nonspawners based on a lack of directed movement to known spawning areas between April and July when spawners were moving (Homel et al. *in prep- a*). Of these 94 cutthroat trout, 19 were tagged in 2007 and relocated an average of 16.4 times (range =2 - 42 relocations) from October 2007 to September 2009. The 75 cutthroat trout tagged in 2008 were relocated an average of 12.6 times (range = 2 - 30 relocations) from October 2008 to September 2009.

Spatiotemporal Movement Patterns

During all months, approximately 10% of individuals were moving at the reach scale, but up to 45% moved during November, February, and May in 2007 and 2008 (Figure 3). At the segment scale, approximately 10 - 30% of individuals were moving during all months except June-August in 2007, when only 5% of individuals were moving; most segment-scale movement occurred during October, February, April, and May (Figure 3). Likewise, most seasonal movement occurred during base flow and runoff in 2007 and 2008, and substantially fewer individuals moved during the post-runoff season (< 40% at the reach scale and < 20% at the segment scale; Figure 4).

Although the majority of individuals moved among reaches or segments at least once during the year, monthly movement distances were very short (of those individuals that moved, median = 2 reaches and 1 segment) in 2007 and 2008. Seasonal reach-scale movement distances were also very short in 2007 (median = 2 reaches and 2 segments in all seasons), and 2008 (base flow median =3 reaches and 1 segment, runoff median = 5 reaches and 2 segments, and post-runoff median =4 reaches and 1 segment). Annual reach-scale movement distances (sum of monthly movement distances in 2007 and 2008) were more pronounced; 62 individuals (66%) moved > 5 reaches (median = 8; Figure 5) and 52 individuals (55%) moved > 1 segment (median = 3; Figure 6).

Habitat Relationships

Physical attributes of reaches and reach occupancy differed within and among segments throughout the study area (Table 2). Large woody debris was extremely abundant in segment 6, whereas macrophytes were abundant in segment 1 (Table 2). Deep water was found throughout the study area, but the deepest channels were in segment 1 (Table 2). Vertical or undercut banks were common in segment 2, 4, and 6 (Table 2). Overall, different types of complex habitat were available spatially, and most reaches contained multiple types of complex habitat (e.g., braided channels and undercut banks both common in the reaches of segments 2 and 6). Following the pattern of where complex habitat was located, reach occupancy was highest in segments 1, 2, and 6, with 41% of occupancy in reaches 29, 31, and 32 of segment 6 (Figure 1, Table 2).

Although limited movement was detected among reaches during all time steps, movement did not result in a change in reach occupancy (Figure 7). Variation in occupancy among reaches was greater than variation in reach occupancy among months (Figure 8); the first component of the PCA explained 99% of the variation, and all reaches were loaded equally onto that component (Figure 8). Equal loading of reaches suggests that the component was associated with variation in reach occupancy among reaches, but not variation in occupancy among months. Accordingly, all monthly estimates of reach occupancy were summed into a single, annual estimate of reach occupancy, which was used as the response variable in the habitat analysis.

Many of the environmental predictor variables were correlated (Table 3), and from an initial dataset of 11 variables (Table 1), 8 were retained in candidate models. For the full dataset and the segment 1 dataset, a square root transformation was required for reach occupancy and two of the predictor variables (thalweg length and large woody debris) in order to normalize the residuals and achieve homoscedasticity. For the segment 2-6 dataset, a log transformation was required for those same variables. Accordingly, 10 mixed-effects models were constructed for each dataset (Table 4) with a random intercept for each segment.

Top models varied among analyzed datasets. For the full dataset, the top model predicted reach occupancy as a function of large woody debris and maximum depth (Table 5), with segment modeled as a random intercept. No other models were within two AIC points (Table 5). For the segments 2 - 6 dataset, the top model predicted reach occupancy as a function of large woody debris and maximum depth (Table 5), identical to the top model for the full dataset. For the segment 1 dataset, only single variable, fixed effects models were fit because of the decreased sample size (n = 7 reaches; Table 4). For this dataset, the best predictor of reach occupancy was the length of the channel dominated by submerged macrophytes (Table 5).

Discussion

This study provided new information on habitat relationships and movement scales by cutthroat trout in an intermediate-sized river. By collecting detailed habitat and movement data over a large spatial extent (45 km), for multiple years, and with a large sample size of radio-tagged cutthroat trout (n = 94), movement and reach occupancy patterns could be detected at a level of detail not previously described. Nonspawning adults exhibited limited movement among reaches, but movements were still longer than those typically observed in headwater streams because reach length increases with stream size. Thus, movement distance appeared to increase from headwater streams to larger rivers, but movement scale (movement at the reach scale) did not. Analysis of occupancy data demonstrated that spatial variation in habitat availability and habitat forming processes among segments produced unique reach-scale habitat relationships throughout the study area. These patterns were not analogous to those seen in headwater streams, where salmonids occupy shorter extents of the stream (Heggenes et al. 1991; Petty et al. 2012) and encounter less longitudinal variation in habitat. As conservation efforts increase in larger river networks, it will be important to consider contextual habitat relationships that span stream sizes associated with different disturbance regimes (Gomi et al. 2002) and habitat attributes.

In the upper Snake River, movements among reaches and segments were more frequent during times of rapidly changing discharge (October), base flow, or spring runoff, but distances were typically short (< 5 reaches or 1 segment). This seasonal movement is similar to what has been seen in smaller systems, where short, channel unit-scale movements are more common throughout the year, and longer reach and segment-scale movements occur during periods of elevated discharge (Young 1996; Gresswell and Hendricks 2007). With such limited movement by nonspawners, movement patterns did not support the generalization that trout in larger systems move much longer distances (Schrank and Rahel 2004; Zurstadt and Stephan 2004; Colyer et al. 2005) and have much larger home ranges (Colyer et al. 2005; Schoby and Keeley 2011) than in headwater systems. Although long spawning migrations were observed in this system (Homel et al. *in prep-a*), it appears that nonspawners occupying a high-quality stream have little need to move. Overall, movement among reaches indicated that habitat availability or quality differed among reaches, and infrequent movement among segments implied that segments contained the seasonal diversity of habitat required by nonspawning adult cutthroat trout.

Reach occupancy was positively associated with complex habitat, however different attributes comprised that complexity. In the Full and Segment 2-6 models, reach occupancy was positively associated with large woody debris and maximum depth of the reach. Large woody debris (Young 1996; Kershner et al. 1997) and pools (Dare and Hubert 2003; Harper and Farag 2004; Sanderson and Hubert 2009) are frequently identified as habitat for cutthroat trout, yet in the Snake River, these features were much larger than may be seen in smaller systems. For example, in a small stream, pieces of wood 1 m long and 10 cm in diameter may function as large woody debris (Kershner et al. 2004). In the upper Snake River, whole trees or log jams functioned as large woody debris, resulting in gravel deposition and formation of complex channels (Abbe and Montgomery 1999). Likewise, pools in this system ranged from 10s of meters to over a kilometer in length, consistent with the pattern that pool depth increases with increasing stream size (Carlson and Rahel 2010). However, deep water was more often associated with runs or glides, than actual pools. Finally, in the Segment 1 model, macrophytes were positively associated with occupancy. Macrophytes have been shown to function as complex habitat in the Henry’s Fork of the Snake River (Van Kirk and Martin 2000) and were encountered in quasi-lentic reaches in the upper Snake River. Overall, although habitat relationships appeared to be a scaled-up version of what is seen in smaller streams based on the increased size of habitat attributes, spatial analysis of occupancy revealed strong contextual variation within and among stream segments.

Spatial variation in habitat relationships was produced by longitudinal increases in stream size. Longitudinal changes from major tributary inputs were pronounced between segments 1 and 2. Above the tributaries, cutthroat trout were associated with complex habitat in low gradient habitat. Below the tributaries, the geomorphic characteristics of the Snake River changed substantially because of increased discharge and increased delivery of sediment and large woody debris (Marcus et al. 2002; Marston et al. 2005; Nelson 2007). Here, cutthroat trout were associated with large woody debris and reaches with a greater maximum depth.

Segment-scale constraints on reach habitat also produced habitat patchiness and contextual variation in occupancy. In segment 5, for example, the channel was constrained by alluvial deposits and the gradient and water velocity increased dramatically relative to upstream and downstream segments. Despite the availability of velocity refugia (boulders and large woody debris), individuals spent very little time in this segment. Likewise, the channel form in segment 4 was very complex, but with little wood in the reach, occupancy was low. Thus, the combination of longitudinal, patchy, and hierarchical variation in the physical template produced spatial variation in habitat availability and habitat relationships.

Because particular reaches were occupied substantially more often than others, perceived habitat relationships in the Full model were driven by the relationships found in high occupancy reaches. In particular, reaches 29, 31, and 32 were associated with 40% of occupancy and 71% of the large woody debris. In contrast, reaches 6 and 7 had 17% of occupancy in rare macrophyte habitat, which provided the majority of complex habitat in those two reaches. Relationships to abundant habitat types are more easily detected, but rare habitat types have the potential to increase the area of stream that can provide habitat. A common example of this is the occupancy of relatively rare thermal refugia in temperature limiting reaches of a river network (Torgersen et al. 1999; Ebersole et al. 2003). Although important locally (Ebersole et al. 2001), in a basin-scale analysis, the relative abundance of individuals in thermal refugia may be minimal, and the importance of thermal refugia may not be detected.

The movement patterns and habitat relationships observed in this study were distinct, but there were two potential limitations. First, this study was conducted with 94 radio-tagged nonspawners, over a period of 2 years, in a 45 km section of the Snake River. Considering the dynamic temperature, precipitation, and discharge regimes in this system, it is possible that other habitat relationships or movement patterns could be detected at other times or with a larger sample size. A second potential, albeit minor, limitation was that our definition of "nonspawning" cutthroat trout was based on a lack of directed migration to spawning areas during runoff. This definition was similar to the implicit assumptions of other trout movement studies (Schmetterling 2001; Sanderson and Hubert 2009; Carlson and Rahel 2010), and was validated by Henderson et al. (2000). For tributary spawners, migrations were distinct (Homel et al. *in prep* a), but for cutthroat trout that spawned in side channels, migrations were less distinct. Therefore, it is possible that some of the nonspawners in this study could have made short spawning migrations into a side channel. However, the removal of spawners from the habitat analysis was only done to minimize potential bias in habitat relationships resulting from long migrations; thus, it is not thought that the inclusion of potential spawners that made short migrations would bias the results of this study. Despite these potential limitations, this study was able to identify movement patterns and spatial variation in habitat relationships in an intermediate-sized river system.

Variation in physical characteristics of segments was particularly important when considering cutthroat trout movements that crossed segment boundaries or encompassed large extents of the stream network. For example, despite limited movement by nonspawners, 77% of radio-tagged cutthroat trout occupied more than one segment over the study period. These movements were described in terms of the number of segments moved as a way to relate movement to variation in the physical template (Gresswell and Hendricks 2007). However, over larger spatial extents, the progressive increase in size of segments in a downstream direction would likely result in an underestimation of physiological movement costs for a given number of segments moved. Effectively, moving five segments in a headwater stream is very different than moving five segments in a larger river in terms of absolute distance moved and encountered habitat conditions. Likewise, movement between segments bounded only by a tributary junction differs from movement between segments with physical characteristics that differ dramatically due to variation in underlying geology, constraint, or gradient (Pringle et al. 1988; Poole 2002, Thorp et al. 2006).

Variation in habitat relationships among segments suggested that reaches should not be treated as experimental replicates, even if reaches are defined by consistent geomorphic features and disturbance intervals (Frissell et al. 1986). Rather, it may be more appropriate to conceptualize rivers as a series of unique segments with characteristics that vary due to hierarchical structure, longitudinal changes, and patchiness (Poole 2002). Within each segment, different habitat attributes can function as the same kind of habitat (e.g., undercut banks or large woody debris providing cover), or different kinds of habitat may be required (e.g., temperature refugia required lower down in a river) in different segments. Thus, a riverscape-scale analysis could be paired with analysis of individual segments to identify any rare reach-scale habitat relationships that are important in particular segments, while also identifying broad patterns in occupancy within the riverscape.

This study demonstrated that although movement distances increase with stream size, habitat relationships in small streams are not analogous to those seen in larger rivers. Just as movement patterns or reach occupancy are evaluated independently at hierarchical habitat scales (because each is associated with different disturbance frequencies and habitat forming processes), it may be necessary to explicitly consider the effects of stream size or spatial variation in the analysis of movement or habitat occupancy patterns. However, unlike comparisons among reaches and segments, stream size may increase rapidly (from punctuated increases at large tributary confluences) or gradually, and it is not always clear at what point stream sizes and associated habitat are different enough to not be comparable. Considering the contextual variation in habitat relationships observed here, conservation of cutthroat trout in larger river systems may benefit from managing for a diverse range of habitats and preserving habitat patch sizes that are appropriate for larger rivers, where movement distances are longer.

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Figures

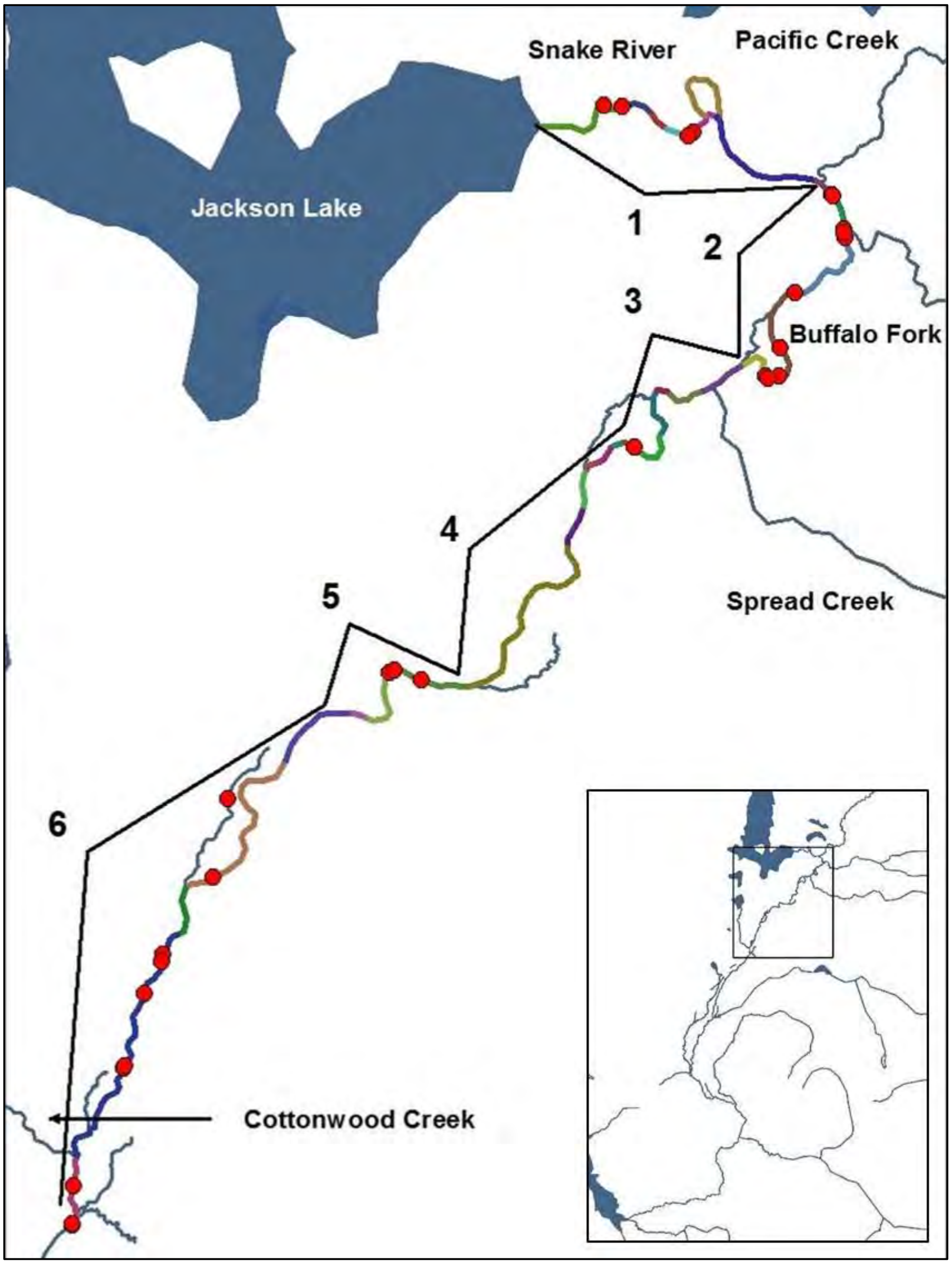

Figure 1. —Snake River study area from Jackson Lake Dam to Moose Junction, WY. Major tributaries are labeled, and sample segments classified for habitat surveys are

labeled and reaches are delineated with unique colors. Tagging locations of Snake River finespotted cutthroat trout *Oncorhynchus clarkii behnkei* are shown as red dots.

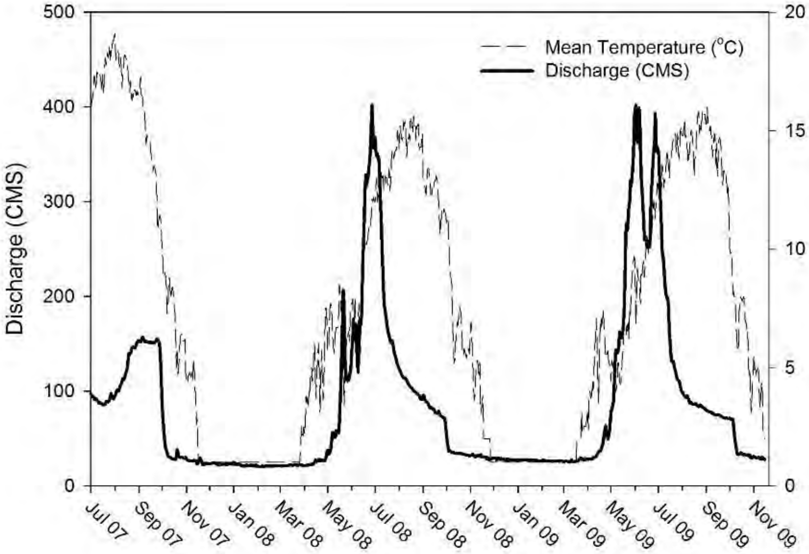

Figure 2.—Discharge (cubic meters per second; m^3/s) and mean temperature (Celsius; C) recorded at the USGS Moose Junction gauging station on the Snake River from July 1, 2007 to November 15, 2009. Snake River finespotted cutthroat trout *Oncorhynchus clarkii behnkei* were radio-tagged during September and October of 2007 and 2008 (grey bars) and relocated through October, 2009.

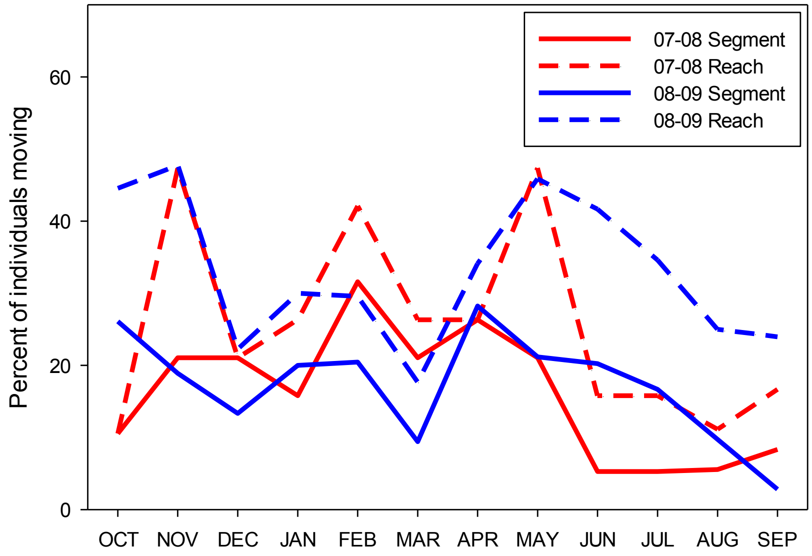

Figure 3.—Percent of radio-tagged Snake River finespotted cutthroat trout *Oncorhynchus clarkii behnkei* moving each month at the reach (dashed line) and segment scales (solid line) in 2007 (red line) and 2008 (blue line) in the upper Snake River ,WY.

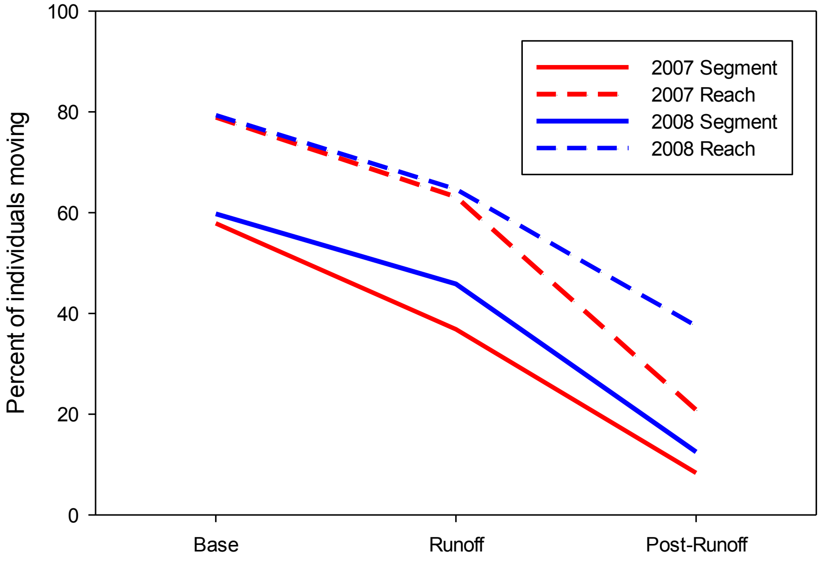

Figure 4.—Percent of radio-tagged Snake River finespotted cutthroat trout *Oncorhynchus clarkii behnkei* moving during base flow (October 1 – April 14), runoff (April 15 – July 31), and post-runoff (August 1 – September 30) at the reach (dashed line) and segment scales (solid line) in 2007 (red line) and 2008 (blue line) in the upper Snake River ,WY.

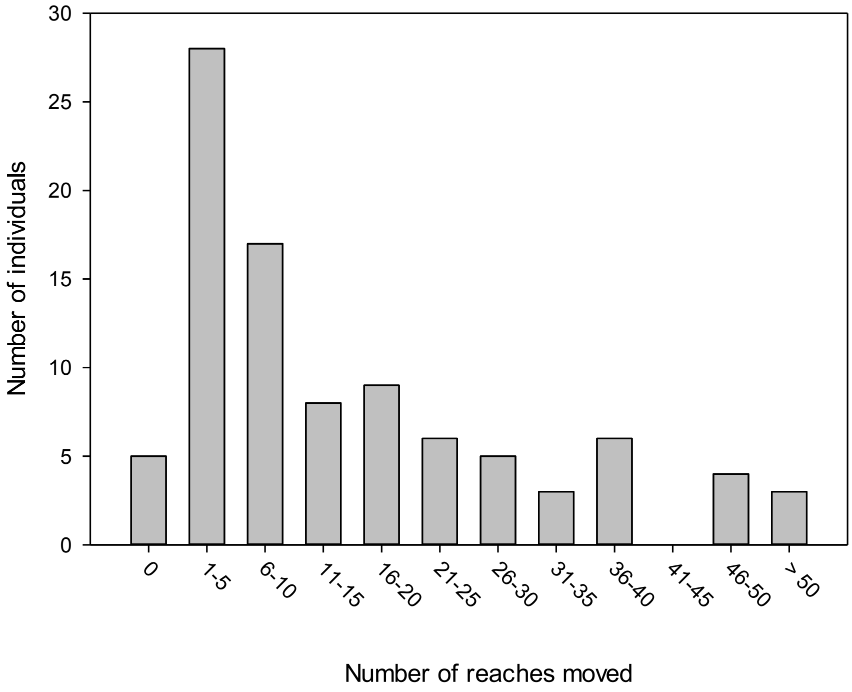

Figure 5.—Annual sum of monthly movement distances (in reaches) by radio-tagged Snake River finespotted cutthroat trout *Oncorhynchus clarkii behnkei* (n = 94) in the Snake Rive

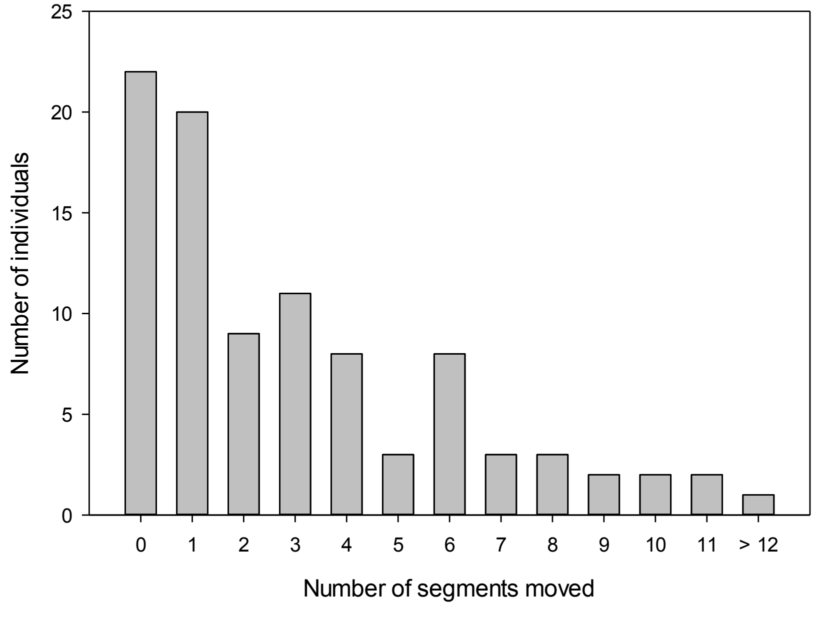

Figure 6.—Annual sum of monthly movement distances (in segments) by radio-tagged Snake River finespotted cutthroat trout *Oncorhynchus clarkii behnkei* (n = 94) in the Snake River, WY October 2007 – September 2009.

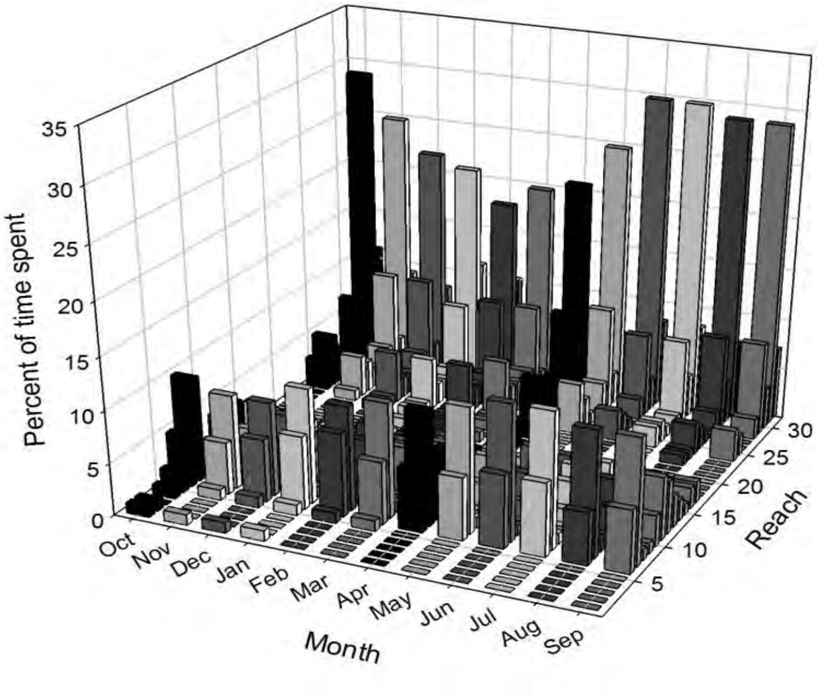

Figure 7.—Monthly reach occupancy of radio-tagged cutthroat trout *Oncorhynchus clarkii behnkei* (n = 94) in the upper Snake River, WY October 2008 – September 2009. Monthly reach occupancy represents the total amount of time spent in each reach during each month by all individuals, collectively.

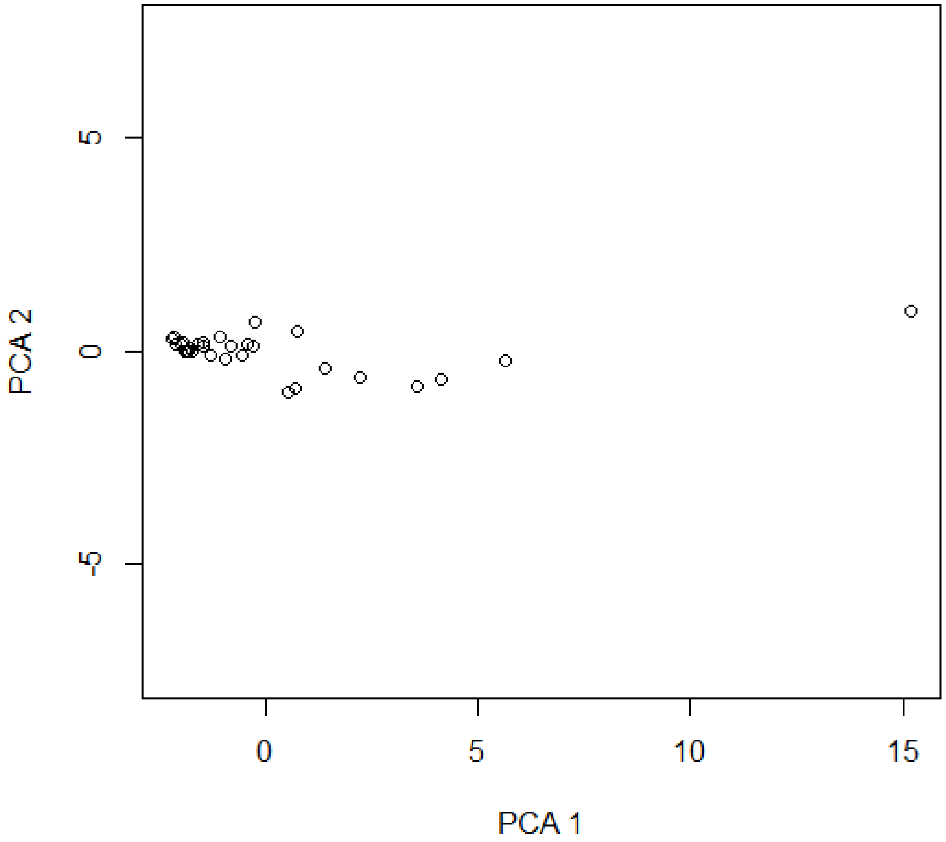

Figure 8.—Principle coordinates analysis of monthly utilization distributions for all radio-tagged Snake River finespotted cutthroat trout *Oncorhynchus clarkii behnkei* combined. The first component explained 99% of the variation among monthly utilization distributions and described differences in spatial patterns of time spent. The second component explained 1% of the variation and described differences between winter and summer utilization distributions.

Tables

Table 1.—Physical habitat attributes (with methods and references) recorded in the upper Snake River during 2009 or derived using GIS based on 2009 LIDAR data.

Attribute	**Technique (reference)**
Bank structure	Total length of thalweg banks that are vertical (with vegetation) or undercut
Braid Index	Total channel thalweg length of main channel and side channels divided by thalweg length of main channel (Knighton 1998)
Channel Form	Number of side channels within each reach determined from 2009 NAIP imagery in GIS.
Confluences with Spring Creeks and Tributaries	Number of confluences with spring creeks or tributaries within a reach (including downstream and upstream at reach breaks)
Constraint	Ratio of bankfull width to flood-prone area width (Rosgen, 1994; Knighton 1998). Bankfull and flood-prone area polygons digitized in GIS based on identifiable geomorphic features. Where features were insufficient to delineate the edge of the floodplain, the polygon border was digitized at a maximum of 1 km from the edge of the bankfull channel.
Depth	Data on maximum depth of each reach provided by Carl Legleitter.
Number of Fast Water Patches	Number of slow and fast water patches per unit length of reach (Hawkins et al. 1993). Patch must span > 50% of channel width to be counted.
Large Woody Debris (LWD)	To reflect the relationship between channel size and the size of woody debris that contributes to structure channels (Piegay 2003), LWD is defined as individual wood pieces or aggregates that are partially imbedded within a channel feature or that cause scour immediately downstream of the wood deposition site. Tally of single or aggregate pieces of LWD within each reach.
Macrophytes	Thalweg length of channel where macrophytes extend across > 50% of the wetted width of the channel
Reach Thalweg Length	Thalweg length from reach top to bottom obtained using GIS with reach locations overlayed on 2009 NAIP imagery
Sinuosity	Straight-line reach length/ thalweg length calculated using GIS in main stem (Knighton 1998)

Table 2.—Reach occupancy by radio-tagged Snake River finespotted cutthroat trout *Oncorhynchus clarkii behnkei* and physical characteristics of each stream reach in the upper Snake River from Jackson Lake Dam to Moose Junction, 2009.

Reach	Segment	Reach occupancy	Thalweg length (m)	Braid index	Channel form	Confluences	Number fast water patches	Constraint	Sinuosity	Large woody debris	Max depth (m)	Macrophytes	Bank structure (m)
1	1	74	1843	1.00	0	3	0	2	1.21	3	4.0	0	562
2	1	48	742	2.35	2	0	6	2	1.15	22	2.0	0	75
3	1	34	408	1.52	0	0	0	1	1.00	66	2.0	0	232
4	1	54	506	2.87	2	0	1	1	1.01	100	3.0	0	157
5	1	152	767	1.00	0	0	0	1	1.18	8	6.9	0	396
6	1	1149	2047	1.49	3	1	0	2	7.01	204	6.0	2047	331
7	1	2037	2699	1.00	0	1	0	1	1.14	95	7.5	2699	525
8	2	145	414	1.00	0	1	1	2	1.01	26	1.5	0	256
9	2	197	609	1.35	4	0	0	1	0.98	65	1.7	0	452
10	2	699	2238	1.42	6	2	15	2	1.30	312	3.0	0	2404
11	2	919	1928	2.64	3	0	10	3	1.19	306	2.5	0	1246
12	2	794	1221	1.85	2	0	0	3	1.45	22	3.2	0	790
13	3	489	1054	1.00	0	2	0	1	1.00	6	2.4	0	284
14	3	302	729	2.56	1	0	5	3	1.22	41	1.6	0	609
15	3	111	323	1.00	0	0	0	3	1.22	7	2.3	0	346
16	3	345	978	3.32	4	0	16	3	1.17	148	2.4	0	511
17	3	224	818	1.00	0	0	1	5	1.62	19	2.9	0	329
18	3	98	435	1.84	1	0	1	5	1.15	22	2.2	0	306
19	3	43	209	1.00	0	0	0	8	1.05	3	1.7	0	0
20	3	79	419	1.62	1	0	4	4	1.02	14	1.7	0	348

Table 2.—Continued

Reach	Segment	Reach occupancy	Thalweg length (m)	Braid index	Channel form	Confluences	Number fast water patches	Constraint	Sinuosity	Large woody debris	Max depth (m)	Macrophytes	Bank structure (m)
21	4	52	304	2.84	1	0	0	5	1.09	1	1.9	0	0
22	4	118	765	2.62	1	0	4	3	1.02	34	1.2	0	273
23	4	122	789	1.00	0	0	0	15	1.01	14	1.6	0	0
24	4	769	4143	3.26	9	2	26	5	1.23	330	3.1	0	1135
25	5	468	1591	1.76	1	1	3	2	1.05	15	2.4	0	924
26	5	323	1447	1.00	0	0	3	2	1.41	16	2.3	0	0
27	5	70	357	1.77	1	0	1	2	1.02	13	1.5	0	0
28	5	433	1735	1.00	0	0	3	3	1.10	12	1.9	0	425
29	6	1677	3945	2.56	5	1	28	3	1.28	392	2.3	0	2665
30	6	525	1022	2.38	3	1	3	4	1.10	91	2.6	0	423
31	6	4549	5393	6.42	23	3	94	3	1.11	3899	3.3	0	2927
32	6	1503	1380	4.02	6	4	7	3	1.06	663	2.4	0	1173

Table 3.—Correlation matrix of environmental attributes in the upper Snake River below Jackson Lake Dam, 2009. Only variables with a correlation less than 0.7 were retained and combined in regression models.

Attributes	Thalweg length	Braid index	Channel form	Confluences	Number fast water patches	Constraint	Sinuosity	Large woody debris	Max depth	Macrophytes
Braid index	0.53									
Channel form	0.77	0.84								
Confluences	0.58	0.41	0.55							
Number fast patches	0.79	0.79	0.95	0.45						
Constraint	-0.09	-0.04	-0.05	-0.15	-0.01					
Sinuosity	0.13	-0.09	0.02	0.04	-0.07	-0.09				
Large woody debris	0.69	0.77	0.93	0.50	0.95	-0.03	-0.01			
Max depth	0.34	-0.11	0.06	0.22	0.03	-0.30	0.43	0.09		
Macrophytes	0.23	-0.17	-0.07	0.07	-0.11	-0.18	0.58	-0.03	0.72	
Bank Structure	0.81	0.56	0.76	0.56	0.77	-0.14	-0.04	0.67	0.11	-0.06

Table 4.—Candidate regression models to evaluate the relationship between habitat occupancy and reach-scale habitat attributes for Snake River finespotted cutthroat trout *Oncorhynchus clarkii behnkei* in the upper Snake River, WY 2009. The full dataset and Segments 2-6 datasets were evaluated with mixed effects models where segments were modeled as a random intercept. The Segment 1 dataset was evaluated with fixed effects models. Akaike's information criterion (AIC) are presented for all models. The Δ AIC (difference from top model) and r^2 value (for the linear regression models with the Segment 1 dataset) are presented for models where all variables were significant. Segment 1 models were not nested, so AIC values were not presented. LWD = large woody debris, Depth = maximum depth, Banks = bank structure, and Mac = macrophytes.

Model	AIC	ΔAIC	DF	Variance explained by random intercept	r^2 of fixed effects
<u>Full dataset</u>					
Banks + Thalweg + LWD + Constraint + Sinuosity + Confluences + Depth + Mac	221.8	-	18	0.69	-
LWD + Constraint +Sinuosity + Confluences + Depth	215.9	-	21	0.46	-
LWD + Constraint +Sinuosity + Confluences + Mac	223.3	-	21	0.37	-
LWD + Depth	215.6	0	24	0.49	-
Thalweg + Constraint +Sinuosity + Confluences + Depth	218.4	-	21	0.52	-
Thalweg + Constraint +Sinuosity + Confluences + Mac	223.3	-	21	0.64	-
Thalweg + Depth	218	2	24	0.54	-
Banks + Constraint +Sinuosity + Confluences + Depth	233.6	-	21	0.20	-
Banks + Constraint +Sinuosity + Confluences + Mac	236.4	-	21	0.25	-
Banks + Depth	236.4	20	24	0.28	-
<u>Segments 2-6 dataset</u>					
Banks + Thalweg + LWD + Constraint + Sinuosity + Confluences + Depth	160.6	-	13	0.22	-
LWD + Constraint +Sinuosity + Confluences + Depth	151.5	-	15	0.11	-
LWD + Depth	155.8	0	18	0.26	-
Thalweg + Constraint +Sinuosity + Confluences + Depth	156.4	-	15	0.47	-
Thalweg + Depth	162.4	-	18	0.61	-
Banks + Constraint +Sinuosity + Confluences + Depth	168.7	-	15	0.07	-
Banks + Depth	176	20.2	18	0.31	-

Table 4. —Continued

Model	AIC	ΔAIC	DF	Variance explained by random intercept	Adjusted R^2 of fixed effects
Segment 1 dataset					
Banks	NA	NA	5	NA	-
Thalweg	NA	NA	5	NA	0.63
LWD	NA	NA	5	NA	-
Constraint	NA	NA	5	NA	-
Sinuosity	NA	NA	5	NA	-
Confluences	NA	NA	5	NA	-
Depth	NA	NA	5	NA	0.53
Macrophytes	NA	NA	5	NA	0.97

Table 5.—Top regression models to evaluate the relationship between habitat occupancy and reach-scale habitat attributes for Snake River finespotted cutthroat trout *Oncorhynchus clarkii behnkei* in the upper Snake River, WY 2009. Parameter estimates, parameter transformations, standard error (SE), and significance (*p*-value) are presented for the top regression model(s) for each dataset (Full dataset = segments 1-6). LWD = large woody debris.

Model	Variable (transformation)	Estimate	SE	*p*-value
	Full dataset			
Mixed	Intercept	0.7	3.37	0.83
Mixed	LWD	0.8	0.11	0
Mixed	Maximum depth	4.56	0.86	0
	Segments 2 - 6 dataset			
Mixed	Intercept	0.22	4.12	0.95
Mixed	LWD (square root)	0.74	0.09	0
Mixed	Maximum depth	5.95	1.9	0.01
	Segment 1 dataset			
Fixed	Intercept	8.13	1.06	0
Fixed	Macrophytes	0.013	< 0.001	0

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CONCLUSION TO DISSERTATION

Native trout have experienced declines throughout their range as a result of multiple anthropogenic factors (Gresswell 1988; Miller et al. 1989; Hudy et al. 2007). Declines have been particularly pronounced for migratory trout that move through degraded corridors or encounter downstream portions of the river network where all upstream impacts are integrated (Thurow et al. 1997). In response to declines, conservation and management of trout has focused on attributes associated with population resiliency, including life-history diversity (Gresswell et al. 1994; Rieman and Dunham 2000), and sufficient stream area to encompass the habitat needs throughout the life-cycle (Hilderbrand and Kershner 2000a). For cutthroat trout in particular, most of the existing research has occurred either in small streams at fine spatial scales (Hilderbrand and Kershner 2000b; Brown and Mackay 1995; Gresswell 2009), or in larger streams at coarser spatial scales (Colyer et al. 2005; Torgersen et al. 2012). Given the need to understand life-history diversity and habitat occupancy in larger river systems, it is not clear whether the patterns and variability in smaller streams can scale up or serve as an analog for patterns in larger rivers.

In my dissertation, I studied the spatial ecology and life-history diversity of Snake River finespotted cutthroat trout in the upper Snake River. The connectivity and high-quality habitat in the river network, combined with the size of the river system and the spatial variability, allowed me to assess specific relationships to habitat, life-history diversity, and movement patterns. To do so, radio-telemetry was used to monitor the movements of 248 cutthroat trout. In the course of analyzing these radio-telemetry data, I encountered a set of common problems with this type of data, namely that data are sparse and collected at an uneven sampling interval (Rogers and White 2007). Thus, I collaborated on a statistical method that addressed these data problems and presented an improved assessment of space use (that could feed into multiple types of analysis). Collectively, the three papers in this dissertation provide an improved understanding of life-history diversity, habitat occupancy, and movement patterns by native trout in a large river network.

Principle Findings

In chapter 2, I explored the life-history diversity of Snake River finespotted cutthroat trout in a large river network. Spawning and movement patterns reflected the connectivity and habitat diversity of the Snake River study area and provided insight into the range of life-history strategies that can be expressed in a spatiotemporally dynamic system. Specifically, fluvial and fluvial-adfluvial spawners migrated to most of the accessible spawning areas in the upper Snake River watershed, with the majority of spawning between Buffalo Fork and Moose Junction. Post-spawning movement patterns varied among individuals spawning in different streams or expressing different life-history strategies.

In summary, cutthroat trout in this study inhabited and migrated through substantial portions of the watershed and expressed a complex array of behavioral strategies, although potential behaviors and accessible habitat were somewhat constrained because of Jackson Lake Dam. The patterns observed here were substantially more complex than what may be observed in a smaller system, suggesting that behavioral diversity relates to the complexity of the physical template, and more so, that patterns observed in smaller systems are not an analog for potential diversity in larger systems. Ultimately, diversity in spawning, distribution, and movement patterns may be critical for persistence in a variable environment (Den Boer 1968), particularly given the uncertainties of climate change (Williams et al. 2009).

In chapter 3, I collaborated on a new interpolation method to address sparseness and unevenness in the relocation data associated with radio-telemetry studies. This adaptive kernel density interpolation method (AKDI) calculated a continuous probability of time spent across the spatial domain of the data based on sparse sample data. Overall, the AKDI method performed significantly better across sample sizes or sampling frequencies in representing the “true” movement path than sample data, fixed kernel density, or linear interpolation.

Irrespective of the interpolation method used, modeling results suggest that interpolated utilization distributions were significantly better at describing the underlying pattern of space-use than raw sample data. Currently, most telemetry studies in stream systems quantify the number of relocations in spatial units (e.g., reaches) to describe patterns of space-use, rather than analyze continuous, interpolated path data inclusive of interior locations where individuals were never encountered. However, our modeling results suggest that when movements are rapid, random, or frequent, use of raw point data may produce significantly biased or potentially erroneous results. Thus, it appears that interpolation methods may represent a significant improvement over existing techniques in describing patterns of space-use in a linear system.

In chapter 4, I identified spatiotemporal movement patterns and spatial variation in habitat occupancy by radio-tagged cutthroat trout in the upper Snake River. Movements of adult nonspawning cutthroat trout predominantly occurred at the reach scale during base flow and runoff conditions. However, these movements were typically short (< 5 reaches or 1 segment) and did not result in substantial changes to the monthly utilization distribution of time spent by all individuals in each reach. Reach-scale habitat occupancy varied within and among segments. Where channels were complex with increased gradient, velocity, and sediment or wood delivery, reach occupancy was associated with large woody debris and the maximum depth of a reach. However, where the channel was simple and quasi-lentic, reach occupancy was associated with the length of the reach dominated by submerged macrophytes. Consequently, it appeared that the availability of habitat varied spatially and the function of habitat varied in response to the constraining effects of segment-scale attributes.

Given the spatial and hierarchical variation in habitat availability and function observed in this study, it was apparent that throughout the physical template, reaches or segments were not experimental replicates; rather, contextual variation in the physical template resulted in contextual habitat relationships. Consequently, the following recommendations could improve assessment of habitat occupation and movement patterns in river networks. First, a focus on functional habitat relationships (Schlosser 1991; Northcote 1997) may be more transferable across systems than one based on attributes. Second, spatial processes should be explicitly incorporated in analysis as they set the context for observed behaviors (Fausch et al. 2002, Poole 2002; Brenkman et al 2012). Third, in evaluating spatial data, utilization distributions (e.g., as created by AKDI) may provide a useful method to incorporate uncertainty into observed habitat occupancy or movement patterns. Finally, hierarchical and spatial variation in disturbance regimes (Frissell et al. 1986; Gomi et al. 2002) suggests that small streams are not comparable to large streams just as fine spatial scales are not comparable to coarse spatial scales.

Summary

In synthesizing these chapters, several common themes emerged. First, there was consistent evidence that the upper Snake River is a very complex system that may be representative of other intermediate sized river networks that are in a relatively pristine condition. Against this backdrop of complexity, spatiotemporal variation in the physical template created a range of habitat attributes and functions. In response to the spatial availability of habitat, cutthroat trout expressed complex life-history strategies and variation in habitat occupancy and movement patterns. However, this diversity illustrated the importance of conceiving life-history diversity more broadly than the categorical descriptions (based on spawning and rearing habitat) that are commonly used. Moreover, movement patterns expressed by spawners and nonspawners differed considerably during both spawning and nonspawning time periods, suggesting that it is important to consider these stages independently when evaluating habitat occupation and movement.

Collectively, variation in spawning, habitat occupancy, and movement patterns allows a complex response to a dynamic template and is often linked to increased population persistence through spreading extirpation risk from natural causes (Den Boer 1968). Certainly, the spatial range of habitats occupied in this study would suggest that local disturbances (e.g., debris torrent in a tributary) would not have a population-level consequence. However, other threats to persistence, such as introduced species or climate change, may operate at a larger spatial scale. Consequently, there is a need to balance management for diversity and spatial variation to minimize extirpation risk from spatially discrete, local disturbances, with consideration of specific actions that could minimize risk from regional disturbances (e.g., climate change or invasive species). The challenge is that the same actions that may prevent hybridization (e.g., barriers), may reduce the capacity to respond to a changing climate where complex habitats (particularly thermal refugia) and large habitat patches (Cowley 2008) may be required. As such, management for maintaining diversity in the physical template (Poff et al. 1997; Ebersole et al. 1997) and preservation of the connectivity that permits life-history diversity (Den Boer 1968; Warren and Liss 1980) may be effective at achieving population resiliency (Hilborn et al. 2003). However, targeted removal of invasive species (Bennett and Kershner 2009) or targeted isolation of portions of river networks may be required as well (Muhlfeld et al. 2012).

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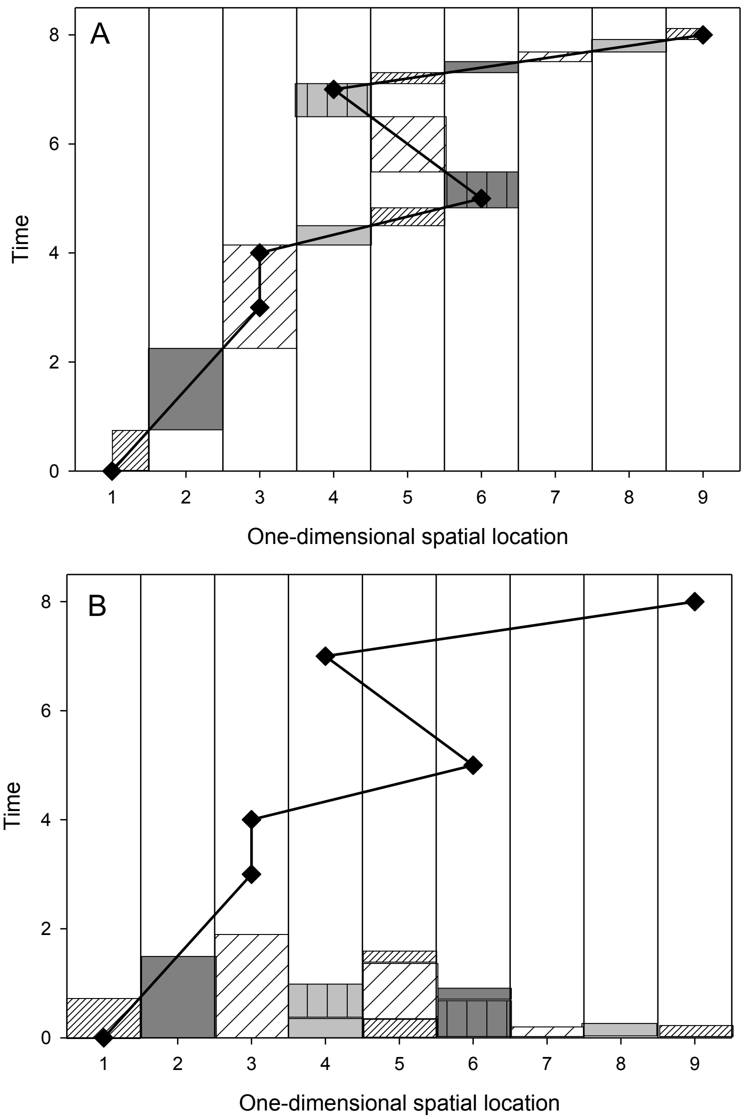
APPENDICES

APPENDIX A

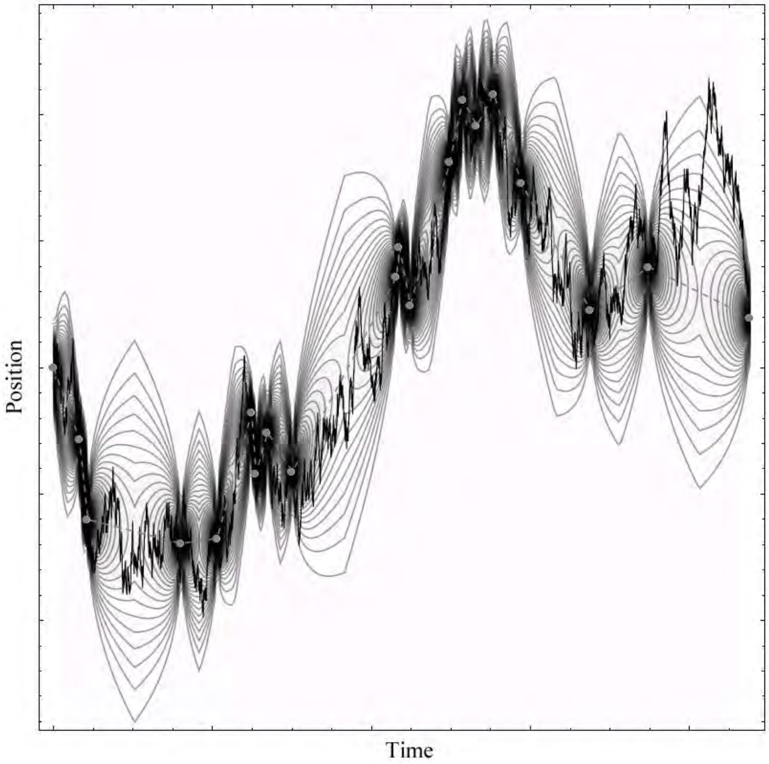
CALCULATING UTILIZATION DISTRIBUTIONS



Appendix A.—Method to calculate discrete utilization distributions from continuous movement paths. Utilization distributions were calculated for each random walk ("true" path) and interpolated path. The true and interpolated paths were divided into spatial bins corresponding to the spatial scale at which sample data were collected. Time spent in each spatial bin was calculated by defining a box around the section of the movement path encompassed by that spatial bin (panel A). The height of the box described the total amount of time spent in each spatial bin and where a path passed through the same location multiple times, all boxes for the same spatial bin were summed to produce the total time spent in each spatial bin. Boxes were accumulated on the X-axis to produce a histogram of the utilization distribution (panel B). For the AKDI method, time spent in each spatial bin was the sum of the height of each kernel that occurred in the same spatial bin at all time periods where the movement path intersected the spatial bin. This approach abstracted the temporal component of the path; however, it provided a simple way to compare discontinuous data methods and continuous interpolation methods to the true path.

APPENDIX B

PROBABILITY FIELD UNDERLYING AKDI KERNEL



Appendix B.—Random walk (solid line) with sample points (grey dots), linear interpolation path (dashed line), and probability field contours (generated from adaptive kernel density method). The probability field surrounding the interpolated path was derived based on an advection-diffusion equation (see Supplement 1) that described the probability of an individual moving to each location in a given amount of time. Where the time between relocation points is greater, the potential distance that an individual could move away from the linear interpolation path between sample points was greater and hence the probability field around the path was more widely distributed. In contrast, where sample points were closer together, the potential locations accessed by an individual were decreased, corresponding to a narrow probability distribution around that section of the path. Because the advection-diffusion parameter *h* was calculated from the sample points, it was not biased by arbitrary investigator inputs and is transferable across systems and species. This figure and underlying modeling was created by Michael Homel.

APPENDIX C

ANNOTATED CODE (CREATED BY MICHAEL HOMEL USING THE PROGRAM MATHEMATICA) FOR EACH INTERPOLATION METHOD, RANDOM-WALK SIMULATIONS, AND METHOD COMPARISON

Input

Generates "random swim" data sets, and computes space-use distribution from simulated relocation data using AKDI Method. Results are compared to raw data histograms, linear interpolation, and fixed kernel methods.

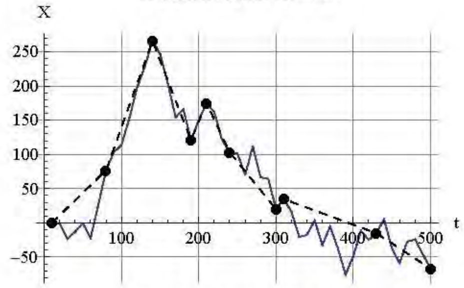
- **Initialize**

```
Quiet[Remove["Global`*"]]
```

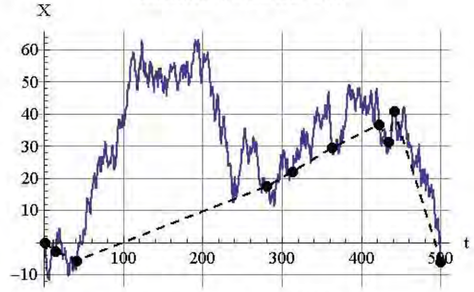
- **Random Swim Data Set:**

Number of Divisions in the Generated "True" Data. This is not just a resolution parameter, it affects the nature of the random swim and the probability distribution that best describes the movement. It is not sufficient to simply described the mean velocity of the fish, rather a behavioral parameter, analogous to diffusivity must be taken into account.

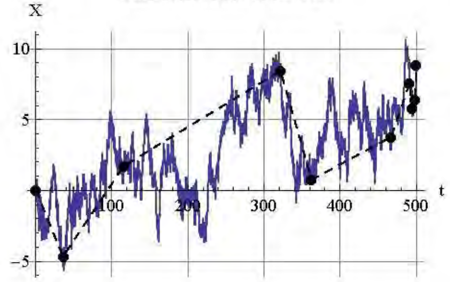
To understand this, consider the following three random swim datasets. In each case the velocity is 5 km/h, and the total time is 500 h, but the number of steps varies from 50 to 5000 in the three simulations. The total distance traveled is the same in each case $\left(5\,\frac{\text{km}}{h}\right)(500\,h)$, but the distance from the initial position is much greater when the step size is larger.



Random Swim: nT=50



Random Swim: nT=500



Random Swim: nT=5000

Einstein showed that for molecular diffusion, the diffusion coefficient was $D = \frac{L^2}{2\,\Delta t}$, where L and Δt are the length and duration of the 'step' in a random walk analysis. In diffusion, the diffusion coefficient has SI units of $\left[m^2/s\right]$. To interpret this physically for fish migration, we can express the diffusion coefficient for fish movement as $\mathcal{D} = \frac{\bar{v}^2}{2}\,\Delta t$, where $\bar{v}$ is the characteristic velocity of the fish motion, and Δt is the characteristic time between changes in direction (where the change could be a zero change). Thus 'diffusion coefficient' becomes a parameter to describe the nature of movement that would vary based on species, and could also vary based on behavioral mode.

Random Swim Parameters

Nominal magnitude of the streamwise component of the fish velocity used to generate the "true" data (km/h).

```
vT = 3;
```

Duration of the data set (hr)

```
Time = (365) 24;
```

Number of divisions in the data set (for determining the step duration)

```
nT = (365) 24;
```

Time of each step (hr)

```
Δt = Time / nT;
```

Effective "diffusion coefficient" to match the random swim data $\left(\mathrm{km}^2/h\right)$ (For Reference, **not** used in the model)

$$\mathcal{D} = \frac{\Delta t\ vT^2}{2}\ \text{// N;}$$

- **Analysis Parameters**

While the random walk can be described as pure diffusion from some starting position, we seek a method to compute the probable utilization density between known relocation points. For this analysis, we use an advection-diffusion equation where the mean velocity between the relocation points is the advection velocity in the interior domain. The diffusion from this path is described by a coefficient h, which is **not equal to the diffusion coefficient for the random swim dataset.** The reason for this is that while the random swim is pure diffusion, the local motion from a sampling of the "true" data has a large bias, which becomes the advection component of the motion. The diffusion effects remaining after the advection is removed are much less significant than those governing the random swim set, so the values of h and $\mathcal{D}$ may differ by orders of magnitude.

Expressed in terms of this local advection diffusion coefficient, h, the probability distribution becomes:

$$P(\delta, \boldsymbol{\tau}, h) = \frac{1}{\sqrt{4\pi h \tau}}\, e^{-\left(\frac{\delta-\overline{V}\tau}{4h\tau}\right)},$$

where δ and $\boldsymbol{\tau}$ are the distance and time, respectively, from the temporally nearest relocation, and $\overline{V}$ is the average velocity between the bounding relocation points, which is the slope of the linear interpolation path in X-t space. We note that this is identical in form to the advection-diffusion equation for the concentration at point x after time t from some initial injection of material into a flowing 1D stream.
The first term in the equation normalized the distribution such that the summed probability is unity over the real spatial domain, i.e. $\int_{-\infty}^{\infty} \overbrace{\frac{1}{\sqrt{4\pi h\tau}}}^{\text{Normalization Factor}} e^{-\left(\frac{\delta-\overline{V}\tau}{4h\tau}\right)} dx = 1$. In analysis of a home range, there may exist physical barriers to fish motion such that the achievable domain is bounded. To accommodate this, we eliminate the normalization term, and numerically normalize the results for each time increment such that the summed probability over the finite home range is unity at any time.

Analysis Parameters

Number of Random Samples

```
nS = 20;
```

Number of Bins for Plotting:

```
nBins = 50;
```

Fixed Kernel Density (For comparison only, not part of the method)

```
hkmax = 50;
hkmin = 1;
nhk = 25;
```

Numerical Parameters

x-Domain Scaling (How far beyond the limits of measured x-values should the X domain span)

```
xScale = 1.25;
```

Time Domain Divisions:

```
nJ = 250;
```

Spatial Domain Divisions:

```
nI = 250;
```

Minimum h for point-wise optimization (numerical parameter to avoid singularities, just needs to be $0 < h_{\min} < h$)

```
hmin = .001;
```

Calculations

■ Random Swim Data Set

To generate our "well characterized system" we begin with by computing a random swim by accumulating the specified number of random steps, where the length and time of each step are determined by the specified dataset duration and characteristic velocity:

```
                                                     Time       Time
randomSwim = Join[{0.}, Accumulate[RandomReal[{-vT ─────, vT ─────}, {nT - 1}]]];
                                                      nT         nT
```

Create a 2-column array containing the time and position data for the random swim

```
                      Time
randomSwim = Table[{i ─────, randomSwim[[i]]}, {i, nT}];
                       nT
```

Determine the limits of the spatiotemporal domain. The time is the specified range, the spatial limits are set as a multiple the furthest distance traveled in the random swim, to minimize the effects of boundary truncation:

```
tmin = 0;
tmax = Time;
Xmax = (xScale) Max[Abs[randomSwim[[All, 2]]]];
Xmin = -Xmax;
```

Compute the spatial and temporal increment, based on the desired grid resolution and the calculated domain extents:

```
     tmax - tmin
dt = ─────────── // N;
       nJ - 1

     Xmax - Xmin
dX = ─────────── // N;
       nI - 1
```

We then "randomly" sample the data at nS points, But here we force the first and last points to be the temporal end points of the domain, to make more consistent plots and facilitate direct comparisons between different simulated data sets and also to increase computational efficiency (i.e not compute "true data" that are outside of the domain of analysis):

```
data = Sort[RandomSample[randomSwim[[1 ;; nT]], nS - 2]];
data = Prepend[data, randomSwim[[1, All]]];
data = Append[data, randomSwim[[nT, All]]];
```

The linear fit generally captures the overall trends but may misrepresent key features of the true data.

- **Analysis**

- **Diffusion Parameter**

It is necessary to determine the diffusion parameter that characterizes the model, only from the available relocation points, with no knowledge of the "true" dataset. To do this we look at each interior point and compute the probability for that point based on the distribution around the linear path connecting the adjacent two points. We then sum the probability for all the interior points, constructed in this manner, and select *h* to maximize this probability.

We note that the calculated value will generally be such that $h << \mathcal{D}$, because $\mathcal{D}$ is the pure diffusion coefficient describing the random swim from an initial condition, whereas *h* is the local diffusion coefficient that maximizes the probability for the advection-diffusion equation. In the latter case, much of the total motion is due to advection (at the mean velocity between adjacent relocations) and thus the diffusivity is likely to be much less. This is desirable, as it prevents widely spaced points from weighting the result over the entire home range.

```
h1 = Table[0, {i, nS - 2}];
h2 = Table[0, {i, nS - 2}];

For[i = 2, i ≤ (nS - 1), i ++,
     data[[i + 1, 2]] - data[[i - 1, 2]]
 v = ───────────────────────────────────
     data[[i + 1, 1]] - data[[i - 1, 1]]
 (*average velocity between adjacent data points*);
 τ1 = data[[i, 1]] - data[[i - 1, 1]] (*time to upwind data point*);
 δ1 = data[[i, 2]] - data[[i - 1, 2]] (*distance to upwind data point*);
                                     ((δ1-v τ1)^2   )
                                   - (───────────── )
                       1             (4 h Abs[τ1]   )
 p1 = If[τ1 == 0, 1, ───────────────── e                ] (*upwind probability field*);
                     √(4 π h Abs[τ1])
 h1[[i - 1]] = h /. Maximize[{p1, h > hmin}, h] [[2]]
 (*diffusivity parameter from upwind optimization*);
 τ2 = data[[i, 1]] - data[[i + 1, 1]] (*time to downwind data point*);
 δ2 = data[[i, 2]] - data[[i + 1, 2]] (*distance to downwind data point*);
                                     ((δ2-v τ2)^2   )
                                   - (───────────── )
                       1             (4 h Abs[τ2]   )
 p2 = If[τ2 == 0, 1, ───────────────── e                ] (*downwind probability field*);
                     √(4 π h Abs[τ2])
 h2[[i - 1]] = h /. Maximize[{p2, h > hmin}, h] [[2]]
 (*diffusivity parameter from downwind optimization*);
]
```

Average upwind and downwind values to determine diffusivity parameter for the dataset.

```
h = Mean[{Mean[h1], Mean[h2]}];
```

We note that more elaborate methods of computing *h* are possible. Here we have, for simplicity, normalized the probability function for an infinite domain, neglecting a potentially bounded homerange. Additionally we could use every possible path to compute the probability at each point rather than using only the probability for the path of the two adjacent points as reference. The method could also be adjusted to avoid sampling bias by weighting the probability for each point by the spacing, but this may not actually minimize error.

Linear Interpolation Path

Compute a piece-wise linear interpolation function between he sampled data points:

```
f = Interpolation[data, InterpolationOrder → 1];
```

Create a $[n_J \times 2]$ table of t-X data points using the linear interpolation function:

```
Quiet[Data = Table[{t, f[t]}, {t, tmin, tmax, dt}]];
```

Extract columns of Data as individual $[n_J \times 1]$ arrays:

```
t = Table[Data[[j, 1]], {j, nJ}] // N;
x = Table[Data[[j, 2]], {j, nJ}] // N;
```

Create an array containing the index of the temporally nearest sample point to each of the points in the interpolated data array.

```
near = Table[{Nearest[data[[All, 1]] → Automatic, Data[[j, 1]]][[1]]}, {j, nJ}];
```

Create an array of the x-value of the temporally nearest point to each point in the interpolated data set:

```
X = Table[data[[near[[j, 1]], 2]], {j, nJ}];
```

Create an array of the t-value of the temporally nearest point to each point in the interpolated data set:

```
T = Table[data[[near[[j, 1]], 1]], {j, nJ}];
```

Create an array containing the local slope of the linear x-t curve, which is the average velocity between two measured sample points.

```
Quiet[V = f'[t]];
```

▪ Mesh Grid

X-coordinate of each point in the X-t Domain:

```
xGrid = Table[Xmin + (i - 1) dX, {i, nI}, {j, nJ}];
```

Time coordinate of each point in the X-t Domain

```
tGrid = Table[tmin + (j - 1) dt, {i, nI}, {j, nJ}];
```

Time coordinate of the temporally nearest point:

```
TGrid = Table[T[[j]], {i, nI}, {j, nJ}];
```

X-coordinate of the temporally nearest point:

```
XGrid = Table[X[[j]], {i, nI}, {j, nJ}];
```

Average velocity (of the linear path) for each point in time.

```
VGrid = Table[V[[j]], {i, nI}, {j, nJ}];
```

X-distance to the temporally-nearest sample point:

```
δGrid = xGrid - XGrid // N;
```

t-distance to the temporally-nearest sample point:

```
τGrid = tGrid - TGrid // N;
```

The continuous function for the probability distribution is undefined when $\tau = 0$. However, since our numerical analysis only resolves the temporal domain to within $\pm\frac{\mathrm{dt}}{2}$, we can replace any values of $t < \frac{\mathrm{dt}}{2}$ with this value with no loss of precision. The data is normalized after this modification, so there is no introduction of error.

```
For[i = 1, i ≤ nI, i++,
 For[j = 1, j ≤ nJ, j++,
  τGrid[[i, j]] =
                              dt                            dt
   If[Abs[τGrid[[i, j]]] < ——, Sign[τGrid[[i, j]]] ——, τGrid[[i, j]]];
                              2                             2
                                                      dt
  τGrid[[i, j]] = If[Abs[τGrid[[i, j]]] == 0, ——, τGrid[[i, j]]]
                                                      2
 ]
]
```

- **Statistical Analysis**

Expressed in terms of this movement parameter, the probability distribution becomes: $P(\delta, \boldsymbol{\tau}) = \frac{1}{\sqrt{4\pi\hbar\tau}}\, e^{-\left(\frac{\delta-\overline{V}\tau}{4\hbar\tau}\right)}$, where δ and $\boldsymbol{\tau}$ are the distance and time, respectively, from the temporally nearest relocation, and $\overline{V}$ is the average velocity between the bounding relocation points, which is the slope of the linear interpolation path in X-t space:

$$\texttt{wGrid} = e^{-\left(\frac{(\delta\texttt{Grid}-\texttt{VGrid}\ \tau\texttt{Grid})^2}{4\hbar\,\texttt{Abs}[\tau\texttt{Grid}]}\right)};$$

The first term in the equation normalized the distribution such that the summed probability is unity over the real spatial domain, i.e. $\int_{-\infty}^{\infty} \overbrace{\frac{1}{\sqrt{4\pi\hbar\tau}}}^{\text{Normalization Factor}} e^{-\left(\frac{\delta-\overline{V}\tau}{4\hbar\tau}\right)} dx = 1$. In analysis of a home range, there may exist physical barriers to fish motion such that the achievable domain is bounded. To accommodate this, we eliminate the normalization term, and numerically normalize the results for each time increment such that the summed probability over the finite home range is unity at any time:

```
For[j = 1, j ≤ nJ, j++,
                          wGrid[[All, j]]
  wGrid[[All, j]] = ──────────────────────── ];
                     Total[wGrid[[All, j]]]
```

Output

Plotting Arrays for X-t Method

Rearrange the $\left[n_I \times n_j\right]$ grid into 1D arrays for plotting:

```
wArray = tArray = xArray = Table[0, {q, 1, (nI ) (nJ)}];
```

```
c = 0;
For[i = 1, i ≤ nI, i ++,
 For[j = 1, j ≤ nJ, j ++,
  c = c + 1;
  wArray[[c]] = wGrid[[i, j]];
  xArray[[c]] = xGrid[[i, j]];
  tArray[[c]] = tGrid[[i, j]];
 ]
]
```

Create Uniform Bins from probabilities across X-t Domain for plotting and error analysis

```
X = xGrid[[All, 1]];
```

```
             Table[Total[wGrid[[i, All]]], {i, nI}]
akdi = ─────────────────────────────────────────────── ;
       Total[Table[Total[wGrid[[i, All]]], {i, nI}]]
```

```
                                         Table[Total[wGrid[[i, All]]], {i, nI}]
sb = Interpolation[Transpose[{X, ───────────────────────────────────────────────}],
                                 Total[Table[Total[wGrid[[i, All]]], {i, nI}]]

   InterpolationOrder → 1];
```

```
      Xmax - Xmin
δX = ───────────── ;
        nBins
```

```
                                     δX          δX
akdiBins = Table[sb[ξ], {ξ, Xmin + ──── , Xmax - ──── , δX}];
                                     2           2
```

■ Error Analysis

```
trueBins = BinCounts[randomSwim[[All, 2]], {Xmin, Xmax, (Xmax - Xmin)/nBins}];
linBins = BinCounts[x, {Xmin, Xmax, (Xmax - Xmin)/nBins}];
rawBins = BinCounts[data[[All, 2]], {Xmin, Xmax, (Xmax - Xmin)/nBins}];
rawBins = rawBins/Total[rawBins] // N;
linBins = linBins/Total[linBins] // N;
akdiBins = akdiBins/Total[akdiBins] // N;

trueBins = trueBins/Total[trueBins] // N;
rawL2 = Sqrt[Total[(rawBins - trueBins)^2]];

linL2 = Sqrt[Total[(linBins - trueBins)^2]];
akdiL2 = Sqrt[Total[(akdiBins - trueBins)^2]];
```

- **Simple Kernel Method with True Optimal Bandwidth, requiring knowledge of true data (For comparison only, not part of the LKDI method)**

  We determine the kernel density that minimizes the RMSE over the data set, as a reference for the accuracy of the method. We note that the fixed kernel method optimization requires knowledge of the true data, so the results are more accurate than could realistically be obtained. Thus this is a conservative comparison. A more balanced comparison would be to use a method similar to what was used to find *h*, in order to obtain a value for the kernel density using only sample relocation data.

  Optimize the fixed point kernel method:

$$\texttt{K[u\_] := Evaluate}\left[\frac{1}{\sqrt{\texttt{2 Pi}}}\, e^{-\frac{1}{2}\texttt{u}^2}\right]$$

$$\texttt{fK[x\_, h\_] := Evaluate}\left[\frac{1}{\texttt{nS h}}\sum_{\texttt{c}=1}^{\texttt{nS}}\texttt{K}\left[\frac{\texttt{x - data[[c, 2]]}}{\texttt{h}}\right]\right]$$

$$\texttt{kernelBins = Table}\left[\texttt{fK}[\xi,\ \eta],\ \left\{\xi,\ \texttt{Xmin} + \frac{\delta\texttt{X}}{2},\ \texttt{Xmax} - \frac{\delta\texttt{X}}{2},\ \delta\texttt{X}\right\}\right];$$

$$\texttt{kernelBins} = \frac{\texttt{kernelBins}}{\texttt{Total[kernelBins]}}\ \texttt{// N;}$$

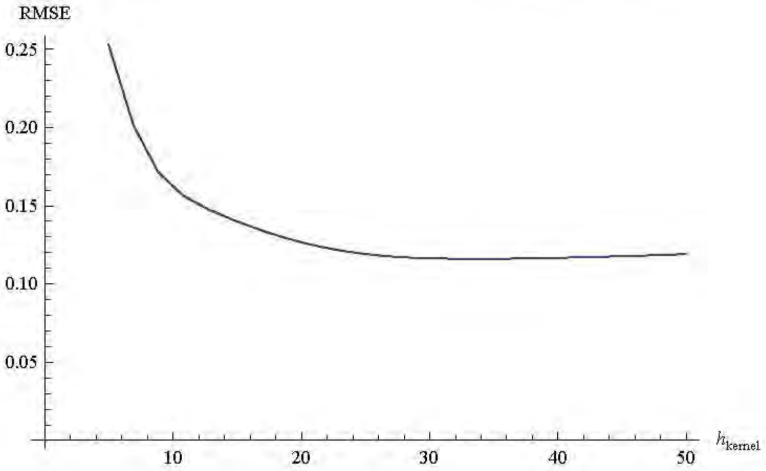
$$\texttt{kernelL2} = \sqrt{\texttt{Total}\left[\texttt{(kernelBins - trueBins)}^2\right]}\ ;$$

$$\texttt{hks = Table}\left[\texttt{i},\ \left\{\texttt{i, hkmin, hkmax},\ \frac{\texttt{hkmax - hkmin}}{\texttt{nhk}}\right\}\right]\ \texttt{// N;}$$

$$\texttt{kernalError = (kernelL2 /. }\{\eta \to \texttt{hks}\}\texttt{) // N;}$$

$$\texttt{kernelData = Transpose[\{hks, kernalError\}];}$$

```
ListLinePlot[kernelData, AxesLabel → {"hkernel", "RMSE"}]
```



Create interpolation function to find minimum:

```
f = Interpolation[kernelData, InterpolationOrder → 2];

hk = h /. Minimize[{f[h], h > hkmin, h < hkmax}, h][[2]];
```

Compute histogram, kernels, and RMSE based on the optimal value.

```
kernelOptBins = Table[fK[ξ, hk], {ξ, Xmin + δX/2, Xmax - δX/2, δX}];

kernelOptBins = kernelOptBins/Total[kernelOptBins] // N;

kernelOptL2 = √(Total[(kernelOptBins - trueBins)^2]);
```

■ Simple Kernel Method with Silverman Optimal Bandwidth (For comparison only, not part of the LKDI method)

Using Silverman's rule for determining optimal bandwidth for a Gaussian kernel:

Standard Deviation of Spatial Data:

```
sx = StandardDeviation[data[[All, 2]]];
```

Interquartile range of the data

```
IQRx = InterquartileRange[data[[All, 2]]] // N;
```

Estimate of Scale:

$$\texttt{σhat} = \texttt{Min}\left[\left\{\texttt{sx}, \frac{\texttt{IQRx}}{\texttt{1.349}}\right\}\right];$$

Silverman's optimal bandwidth for a Gaussian kernel:

$$\texttt{hS}\phi = \texttt{0.9 σhat nS}^{\frac{-1}{5}};$$

Compute histogram, kernels, and RMSE based on the Silver man optimal bandwidth.

$$\texttt{kernelSilvermanBins} = \texttt{Table}\left[\texttt{fK}[\xi, \texttt{hS}\phi], \left\{\xi, \texttt{Xmin} + \frac{\delta\texttt{X}}{2}, \texttt{Xmax} - \frac{\delta\texttt{X}}{2}, \delta\texttt{X}\right\}\right];$$

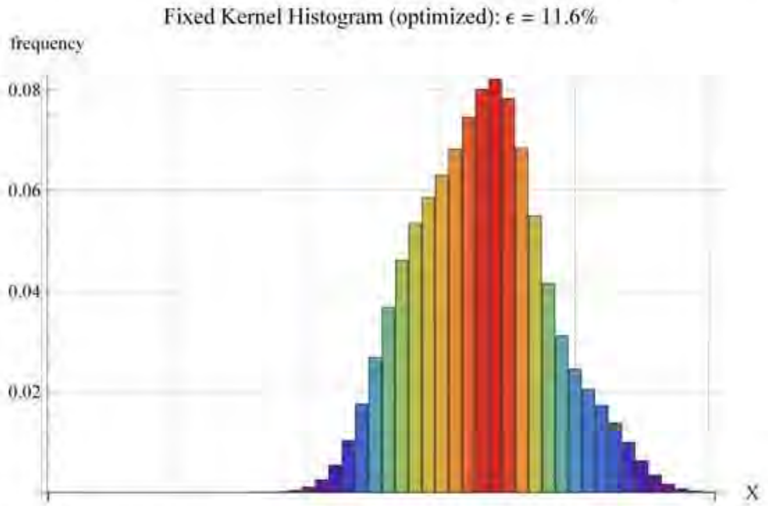
$$\texttt{kernelSilvermanBins} = \frac{\texttt{kernelSilvermanBins}}{\texttt{Total[kernelSilvermanBins]}} \texttt{ // N};$$

$$\texttt{kernelSilvermanL2} = \sqrt{\texttt{Total}\left[(\texttt{kernelSilvermanBins} - \texttt{trueBins})^{2}\right]};$$

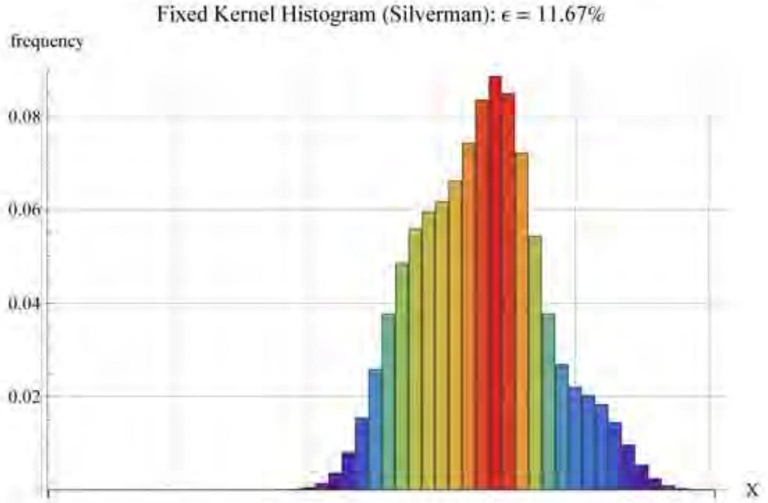
Output

■ Histogram Data

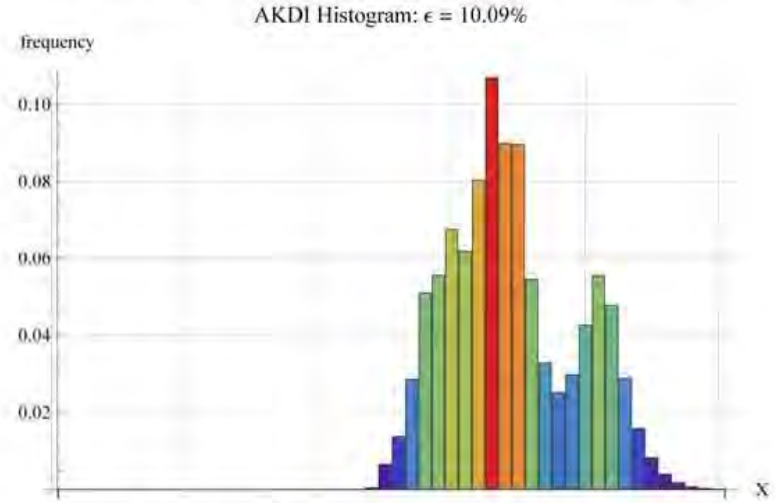
```
kernelOptHist =
 BarChart[kernelOptBins, PlotLabel → "Fixed Kernel Histogram (optimized): ϵ = " <>
    ToString[Round[100 kernelOptL2, .01]] <> "%"
  , ColorFunction → Function[{height}, ColorData["Rainbow"][height]],
  AxesLabel → {"X", "frequency"}, GridLines → Automatic]
```



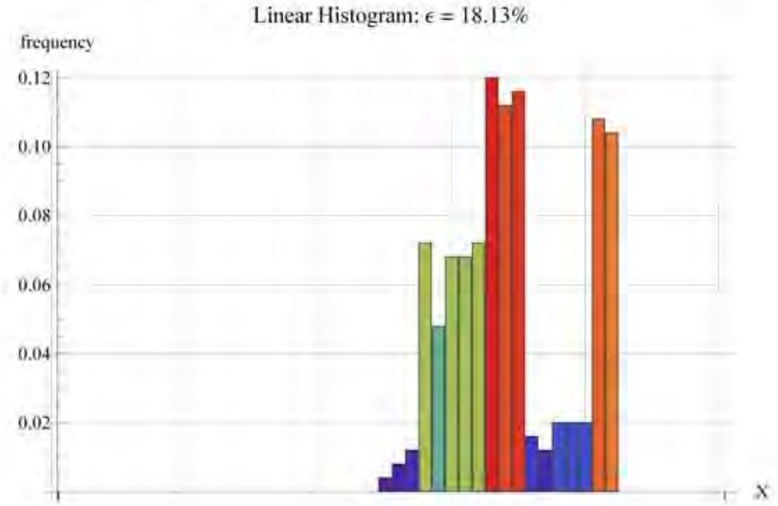
```
kernelSilvermanHist = BarChart[kernelSilvermanBins,
  PlotLabel → "Fixed Kernel Histogram (Silverman): ϵ = " <>
    ToString[Round[100 kernelSilvermanL2, .01]] <> "%"
  , ColorFunction → Function[{height}, ColorData["Rainbow"][height]],
  AxesLabel → {"X", "frequency"}, GridLines → Automatic]
```



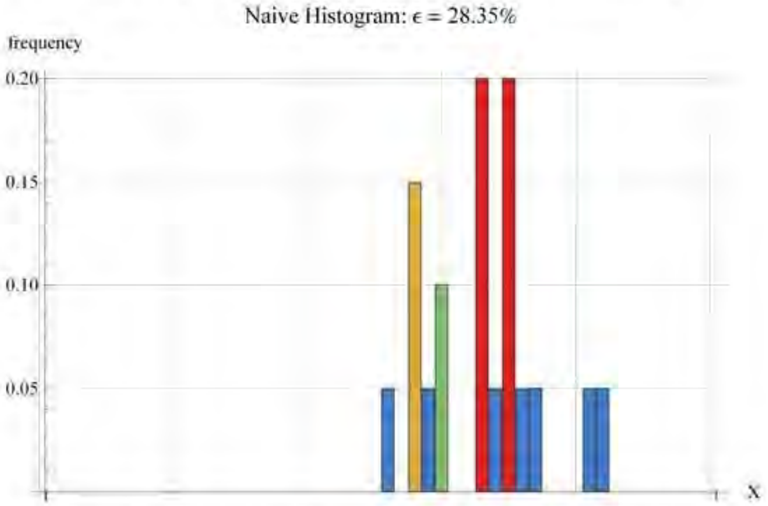
```
akdiHist = BarChart[akdiBins,
  PlotLabel → "AKDI Histogram: ϵ = " <> ToString[Round[100 akdiL2, .01]] <> "%"
  , ColorFunction → Function[{height}, ColorData["Rainbow"][height]],
  AxesLabel → {"X", "frequency"}, GridLines → Automatic]
```



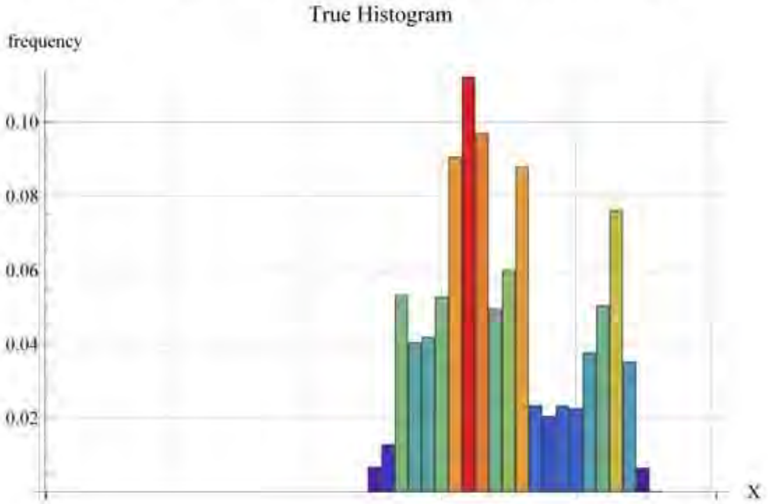
```
linHist = BarChart[linBins,
  PlotLabel → "Linear Histogram: ϵ = " <> ToString[Round[100 linL2, .01]] <> "%"
  , ColorFunction → Function[{height}, ColorData["Rainbow"][height]],
  AxesLabel → {"X", "frequency"}, GridLines → Automatic]
```



```
rawHist = BarChart[rawBins,
  PlotLabel → "Naive Histogram: ϵ = " <> ToString[Round[100 rawL2, .01]] <> "%"
  , ColorFunction → Function[{height}, ColorData["Rainbow"][height]],
  AxesLabel → {"X", "frequency"}, GridLines → Automatic]
```



```
trueHist = BarChart[trueBins, PlotLabel → "True Histogram"
  , ColorFunction → Function[{height}, ColorData["Rainbow"][height]],
  AxesLabel → {"X", "frequency"}, GridLines → Automatic]
```

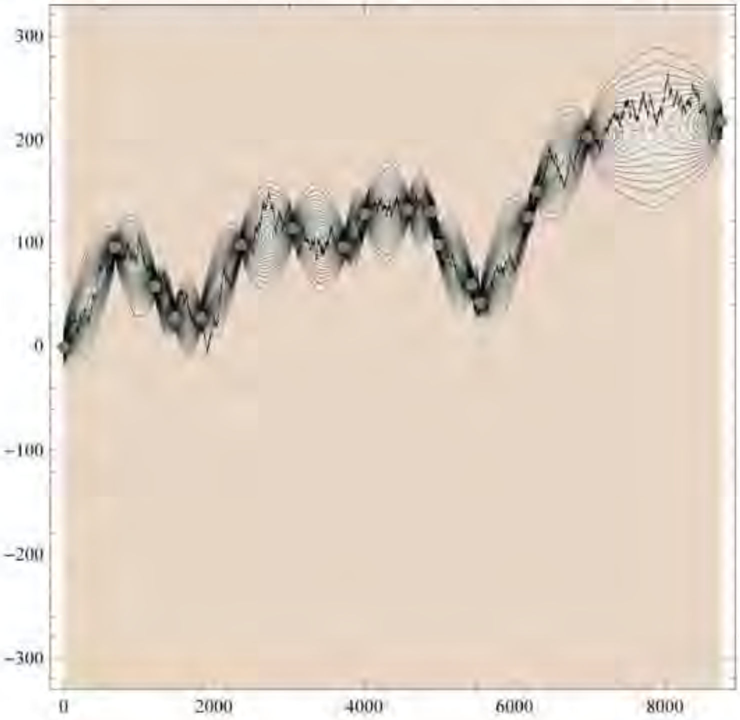


■ Visualization Plots

We now plot the "true" data (blue), along with the sampled data points (black) and the linearly interpolated path (dashed black):

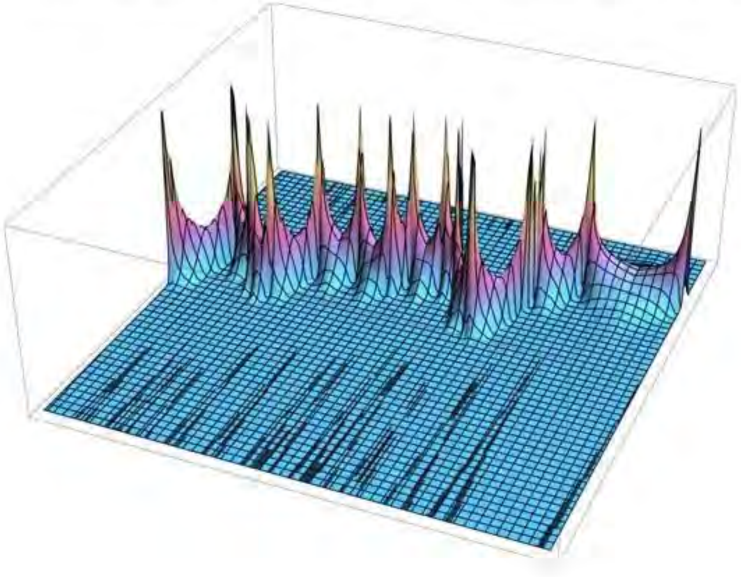
<u>Contour Plot (Needs Swim Plot)</u>

```
dataPlot = ListLinePlot[randomSwim, PlotRange → {All, {Xmin, Xmax}},
    AxesOrigin -> {0, 0}, AxesLabel -> {"t", "X"}, GridLines → Automatic,
    PlotStyle → {Thin, Black}, ImageSize → 500];
samplePlot = ListLinePlot[data,
    PlotRange -> {{Min[data[[All, 1]]], Max[data[[All, 1]]]}, All},
    AxesOrigin -> {0, 0}, AxesLabel -> {"time (hours)", "position (km)"},
    PlotStyle → {Gray, Dashed}, PlotMarkers → Automatic,
    ImageSize → 500, PlotRange → {All, {Xmin, Xmax}}];
swimPlot = Show[dataPlot, samplePlot, PlotRange → {All, {Xmin, Xmax}}];
contourPlot = ListContourPlot[Transpose[{tArray, xArray, wArray}],
    AxesLabel → {"t", "X", "Probability"}, PlotRange → {All, {Xmin, Xmax}, All},
    ColorFunction → "PearlColors", Contours → 50, ImageSize → 500];
lkdiContours = Show[contourPlot, swimPlot, ImageSize → 350]
```



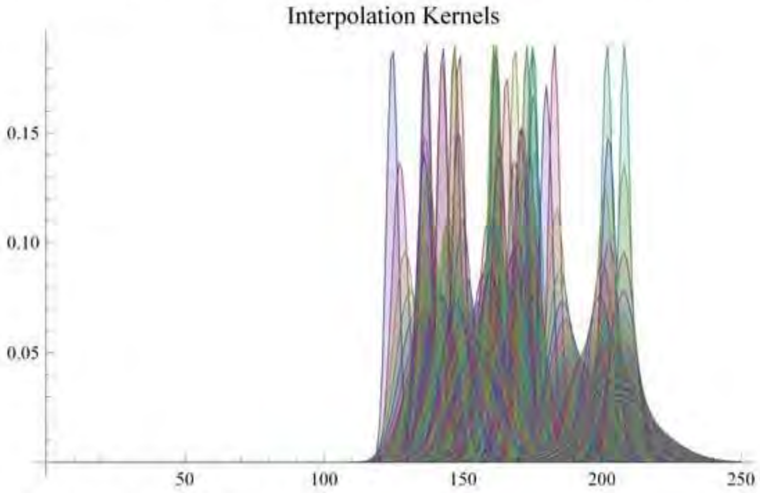
3D Probability Map

```
wX3D = ListPlot3D[Transpose[{tArray, xArray, wArray}],
   InterpolationOrder -> 1, Axes → False, Mesh → 50,
   ColorFunction → "CMYKColors", PlotRange → All, ImageSize → 350]
```



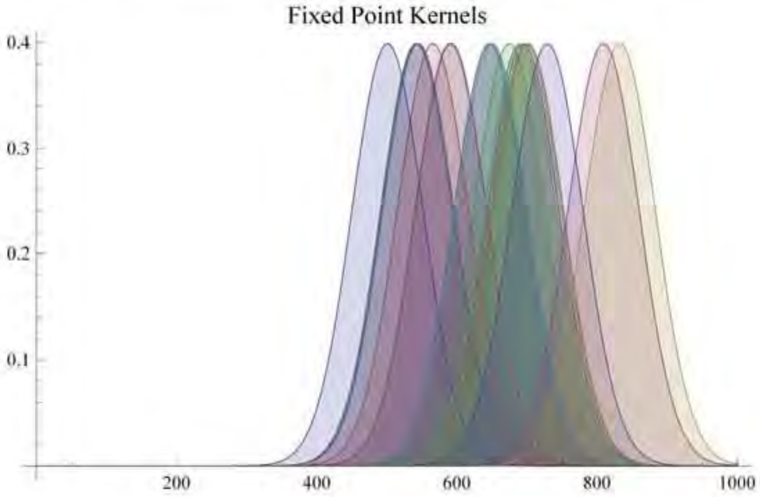
AKDI Kernal Slices

```
akdiKernels = ListLinePlot[Transpose[wGrid],
  PlotRange -> All, Filling -> Axis, PlotLabel → "Interpolation Kernels"]
```



Fixed (optimized) Kernel Slices

```
fixedKernels = ListLinePlot[
            Table[i, {i, Xmin, Xmax, (Xmax - Xmin) / 1000}] - data[[i, 2]]
  Table[K[―――――――――――――――――――――――――――――――――――――――――――――――――――――――――――――――――]], {i, 1, nS}],
                                   hk
  PlotRange -> All, Filling -> Axis, PlotLabel → "Fixed Point Kernels"]
```

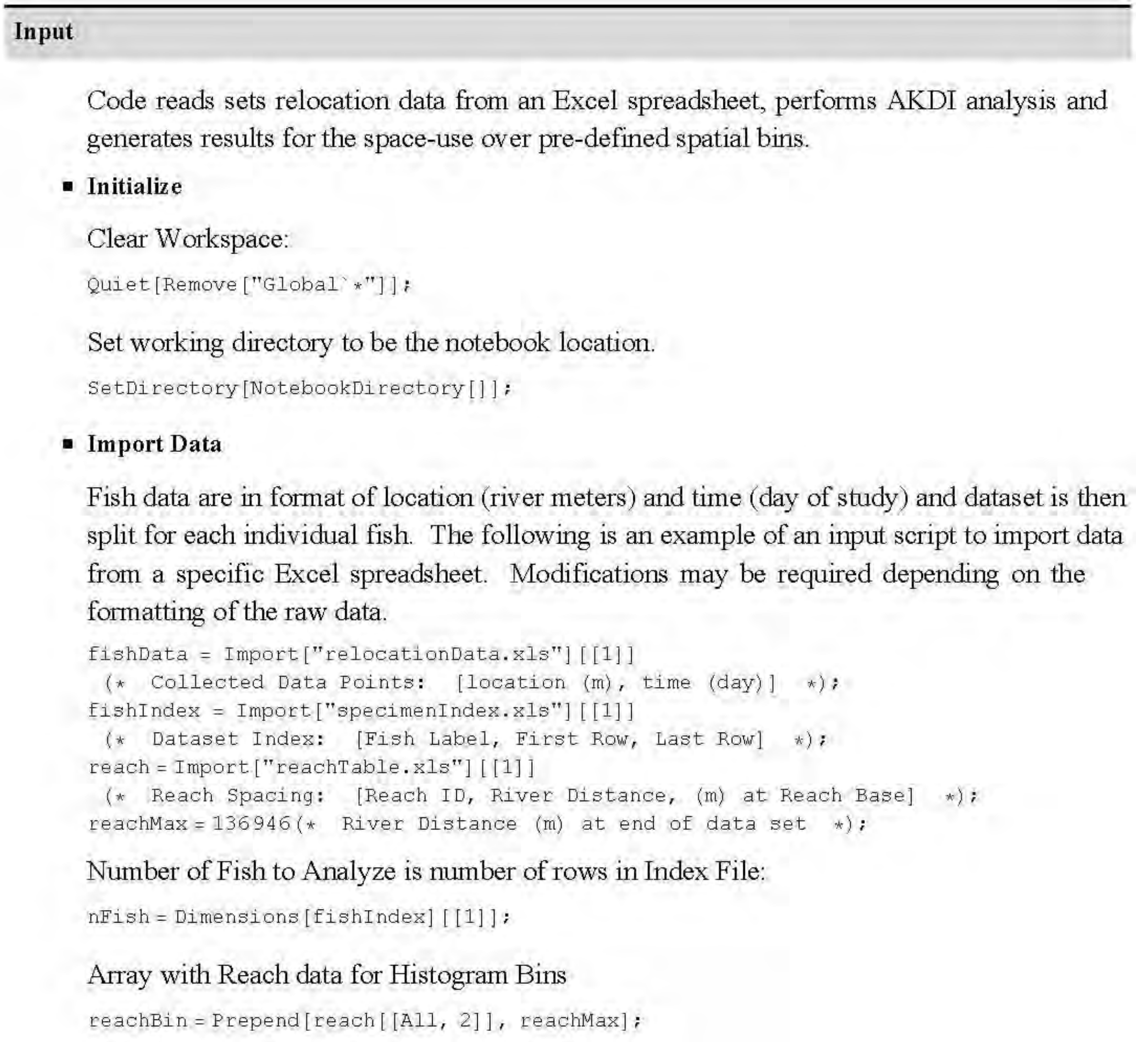


\

APPENDIX D

ANNOTATED MODEL CODE (CREATED BY MICHAEL HOMEL USING PROGRAM MATHEMATICA) FOR APPLYING THE ADAPTIVE KERNEL DENSITY INTERPOLATION METHOD TO AN ACTUAL DATASET

Input relocation data need to take the form of column 1 = individual location (e.g., in river meters) and column 2 = time (e.g., in day of study, not calendar date) without any headings. Data must be sorted by individuals and ordered temporally. Once data are imported into Mathematica, the dataset needs to be split into smaller sets corresponding to the line numbers that encompass the relocations of a single individual. The spatial scale of the data should correspond to a reasonable temporal scale (e.g., meters and hours or kilometers and days) and the code is currently programmed to convert data in meters into kilometers. Spatial binning into geomorphic reaches can be easily accomplished by creating a spreadsheet with the reach identifier in column1 and the river meter location at the bottom of each reach in column 2.



Input

Code reads sets relocation data from an Excel spreadsheet, performs AKDI analysis and generates results for the space-use over pre-defined spatial bins.

- **Initialize**

Clear Workspace:

```
Quiet[Remove["Global`*"]];
```

Set working directory to be the notebook location.

```
SetDirectory[NotebookDirectory[]];
```

- **Import Data**

Fish data are in format of location (river meters) and time (day of study) and dataset is then split for each individual fish. The following is an example of an input script to import data from a specific Excel spreadsheet. Modifications may be required depending on the formatting of the raw data.

```
fishData = Import["relocationData.xls"][[1]]
 (*  Collected Data Points:  [location (m), time (day)]  *);
fishIndex = Import["specimenIndex.xls"][[1]]
 (*  Dataset Index:  [Fish Label, First Row, Last Row]  *);
reach = Import["reachTable.xls"][[1]]
 (*  Reach Spacing:  [Reach ID, River Distance, (m) at Reach Base]  *);
reachMax = 136946 (*  River Distance (m) at end of data set  *);
```

Number of Fish to Analyze is number of rows in Index File:

```
nFish = Dimensions[fishIndex][[1]];
```

Array with Reach data for Histogram Bins

```
reachBin = Prepend[reach[[All, 2]], reachMax];
```

- **Analysis Parameters**

Spatal Domain Divisions:

```
nI = 150;
```

Define the desired ouput temporal bin width, with in the units of the time column of the imported data. (i.e. for 1wk spacings, with user input in days, the bin width is 7)

```
tBW = 7;
```

Roundoff limit for output table.

```
wmin = .001;
```

Select a single data set and specify ouput filename:

```
index = 4
```

```
4
```

```
label = "fish " <> ToString[index]
data = fishData[[Round[fishIndex[[index, 2]]] ;; Round[fishIndex[[index, 3]]]]]
```

```
fish 4
```

```
⎛395.  93765.⎞
⎜408.  93428.⎟
⎜502.  70107.⎟
⎜610.  91438.⎟
⎜628.  87945.⎟
⎜641.  92387.⎟
⎜646.  87684.⎟
⎜665.  90461.⎟
⎜674.  91140.⎟
⎜717.  90600.⎟
⎝734.  90466.⎠
```

The following command will tell you where the output is being saved:

```
Directory[]
```

```
C:\Users\User\Personal\AKDI
```

Analysis

Data Scaling and Domain Specification

Convert to kilometers. **This is important.** The probability function computes $w(x, t) = \frac{1}{\sqrt{4 \pi h |\tau|}} e^{-\frac{(\delta - \overline{V} \tau)^2}{4 h |\tau|}}$, so units should be selected such that $\left| \frac{\delta^2}{\tau} \right|$ is as close to unity as possible to avoid roundoff error or overflow/underflow in the calculation.

```
reachBin = reachBin / 1000;
data[[All, 2]] = data[[All, 2]] / 1000;
```

Number of Samples in data set

```
{nS, temp} = Dimensions[data];
```

This should be the physical domain, not data extents. Note that if the probability field extends well beyond the domain of the relocations there is likely large error.

```
xMin = Min[reachBin];
xMax = Max[reachBin];
```

x-Doman Scaling ratio, allowing for spatial extrapolation beyond the extents of the data

```
xScale = 1;
```

Temporal Domain: NOTE the code does not support temporal extrapolation.

```
tMax = Max[data[[All, 1]]];
tMin = Min[data[[All, 1]]];
```

Compute the minimum integer time step to avoid having multiple relocations in one time step. THIS SHOULD BE GREATER THAN 1 or the units need to change (i.e. use hours instead of days). The data are then checked for duplicate data at a single point:

```
dataSpacing = Min[data[[2 ;; All, 1]] - data[[1 ;; nS - 1, 1]]] / 2;
tS = If[dataSpacing < 1, Ceiling[1/dataSpacing], 1];
If[dataSpacing == 0,
 Print[Style["Data set contains duplicate entries for a single point in time",
   18, Red]], Print[Style["Data Are All Good", 18, Green]]]
```

```
Data Are All Good
```

The previous computation was just a data check. To allow for binning, set the actual spacing to the greatest common denominator of dataSpacing, temporal bin width and temporal domain.

```
dataSpacing = 1/tS GCD[tBW, Round[tMax - tMin + 1], Floor[tS dataSpacing]];
```

Numerical Parameters

Time Domain Divisions (this is ideally finer scale than the number of days):

```
nJ = Ceiling[(tMax - tMin) / dataSpacing] + 1;
```

Determine the limits of the spatiotemporal domain. The time is the specified range, the spatial limits are set as a multiple the furthest distance travelled in the random swim, to minimize the effects of boundary truncation:

Compute the spatial and temporal increment, based on the desired grid resolution and the calculated domain extents:

```
      tMax - tMin
dT = ------------- // N;
        nJ - 1
      xMax - xMin
dX = ------------- // N;
        nI - 1
```

- **Calculations**

- **Diffusion Parameter**

Minimum ***h*** for point-wise optimization (numerical parameter to avoid singularities, just needs to be $0 < h_{\min} < h$)

```
hmin = .00001;
```

It is necessary to determine the diffusion paramter that characterizes the model, only from the available relocation points, with no knowledge of the "true" dataset. To do this we look at each interior point and compute the probablity for that point based on the distribution around the linear path connecting the adjacent two points. We then sum the probability for all the interior points, constructed in this manner, and select ***h*** to maximize this probability.

We note that the calculated value will generally be such that $h << \mathcal{D}$, because $\mathcal{D}$ is the pure diffusion coefficient describing the random swim from an initial condition, whereas ***h*** is the local diffusion coefficient that maximizes the probabiltiy for the advection-diffusion equation. In the latter case, much of the total motion is due to advection (at the mean velocity between adjacent relocations) and thus the diffusivity is likely to be much less. This is desirable, as it prevents widely spaced points from weighting the result over the entire home range.

```
h1 = Table[0, {i, nS - 2}];
h2 = Table[0, {i, nS - 2}];

For[i = 2, i ≤ (nS - 1), i ++(*iterate over internal data points*),
```

$$\texttt{v} = \frac{\texttt{data[[i + 1, 2]] - data[[i - 1, 2]]}}{\texttt{data[[i + 1, 1]] - data[[i - 1, 1]]}}$$

```
 (*average velocity between bounding data points*);
 τ1 = data[[i, 1]] - data[[i - 1, 1]] (*elapsed time to upwind datapoint*);
 δ1 = data[[i, 2]] - data[[i - 1, 2]] (*distance to upwind datapoint*);
```

$$\texttt{p1 = If}\left[\texttt{τ1 == 0, 1, } \frac{1}{\sqrt{4\,\pi\,h\,\texttt{Abs[τ1]}}}\;e^{-\left(\frac{(\delta 1 - v\,\tau 1)^2}{4\,h\,\texttt{Abs[τ1]}}\right)}\right]$$

```
 (*probability field from upwind direction*);

 h1[[i - 1]] = h /. Maximize[{p1, h > hmin}, h] [[2]]
 (*optimal diffusion coefficient from upwind field*);

 τ2 = data[[i, 1]] - data[[i + 1, 1]] (*elapsed time to downwind datapoint*);
 δ2 = data[[i, 2]] - data[[i + 1, 2]] (*distance to downwind datapoint*);
```

$$\texttt{p2 = If}\left[\texttt{τ2 == 0, 1, } \frac{1}{\sqrt{4\,\pi\,h\,\texttt{Abs[τ2]}}}\;e^{-\left(\frac{(\delta 2 - v\,\tau 2)^2}{4\,h\,\texttt{Abs[τ2]}}\right)}\right]$$

```
 (*probability field from downwind direction*);
 h2[[i - 1]] = h /. Maximize[{p2, h > hmin}, h] [[2]]
 (*optimal diffusion coefficient from downwind field*);

]
```

Average the upwind and downwind values:

```
h = Mean[{Mean[h1], Mean[h2]}];
```

■ Linear Interpolation Path

Compute a piece-wise linear interpolation function between the sampled datapoints:

```
f = Interpolation[data, InterpolationOrder → 1];
```

Create a $[n_J \times 2]$ table of t-X data points using the linear interpolation function:

```
Quiet[Data = Table[{t, f[t]}, {t, tMin, tMax, dT}]];
```

Extract columns of Data as individual $[n_J \times 1]$ arrays:

```
t = Table[Data[[j, 1]], {j, nJ}] // N;
x = Table[Data[[j, 2]], {j, nJ}] // N;
```

Create an array containing the index of the temporally nearest sample point to each of the points in the interpolated data array.

```
near = Table[{Nearest[data[[All, 1]] → Automatic, Data[[j, 1]]][[1]]}, {j, nJ}];
```

Create an array of the x-value of the temporally nearest point to each point in the interpolated data set:

```
X = Table[data[[near[[j, 1]], 2]], {j, nJ}];
```

Create an array of the t-value of the temporally nearest point to each point in the interpolated data set:

```
T = Table[data[[near[[j, 1]], 1]], {j, nJ}];
```

Create an array containing the local slope of the linear x-t curve, which is the average velocity between two measured sample points.

```
Quiet[V = f'[t]];
```

▪ Mesh Grid

X-coordinate of each point in the X-t Domain:

```
xGrid = Table[xMin + (i - 1) dX, {i, nI}, {j, nJ}];
```

Time coordinate of each point in the X-t Domain

```
tGrid = Table[tMin + (j - 1) dT, {i, nI}, {j, nJ}];
```

Time coordinate of the temporally nearest point:

```
TGrid = Table[T[[j]], {i, nI}, {j, nJ}];
```

X-coordinate of the temporally nearest point:

```
XGrid = Table[X[[j]], {i, nI}, {j, nJ}];
```

Average velocity (of the linear path) for each point in time.

```
VGrid = Table[V[[j]], {i, nI}, {j, nJ}];
```

X-distance to the temporally-nearest sample point:

```
δGrid = xGrid - XGrid // N;
```

t-distance to the termporall-nearest sample point:

```
τGrid = tGrid - TGrid // N;
```

The continuous function for the probabiltiy distribution is undefined when $\tau = 0$. However, since our numerical analysis only resolves the temporal domain to within $\pm\frac{\mathrm{dt}}{2}$, we can replace any values of $t < \frac{\mathrm{dt}}{2}$ with this value with no loss of precision. The data is normalized after this modification, so there is no introduction of error.

```
For[i = 1, i ≤ nI, i++,
 For[j = 1, j ≤ nJ, j++,
  τGrid[[i, j]] =
                           dT                           dT
   If[Abs[τGrid[[i, j]]] < ——, Sign[τGrid[[i, j]]] ——, τGrid[[i, j]]];
                           2                            2
                                                 dT
  τGrid[[i, j]] = If[Abs[τGrid[[i, j]]] == 0, ——, τGrid[[i, j]]]
                                                 2
 ]
]
```

▪ Statistical Analysis

```
                 (δGrid-VGrid τGrid)²
              -( ———————————————————— )
                   4 κ Abs[τGrid]
wGrid = ⅇ                              ;
```

Normalize data so the probability sums to unity at each point in time.

```
For[j = 1, j ≤ nJ, j++,
                        wGrid[[All, j]]
  wGrid[[All, j]] = —————————————————————— ];
                     Total[wGrid[[All, j]]]
```

Output

Create Table of Binned output Data

Bin Interpolation

Number of temporal and spatial bins

```
nTbins = Ceiling[(nJ/tS)/tBW];
nXbins = (Dimensions[reachBin] - 1)[[1]];
```

Reach Bin (spatial) domain midpoints (for plotting).

```
reachBins =
  reachBin[[1 ;; nXbins]] + (reachBin[[2 ;; All]] - reachBin[[1 ;; nXbins]]) / 2;
```

Initialize the [nXbins × nTbins] Ooutput Table and the x-value array for interpolation:

```
outputTable = Table[0, {i, nXbins}, {j, nTbins}];
𝕏time = xGrid[[All, 1]];
err = Table[0, {i, nTbins}];
```

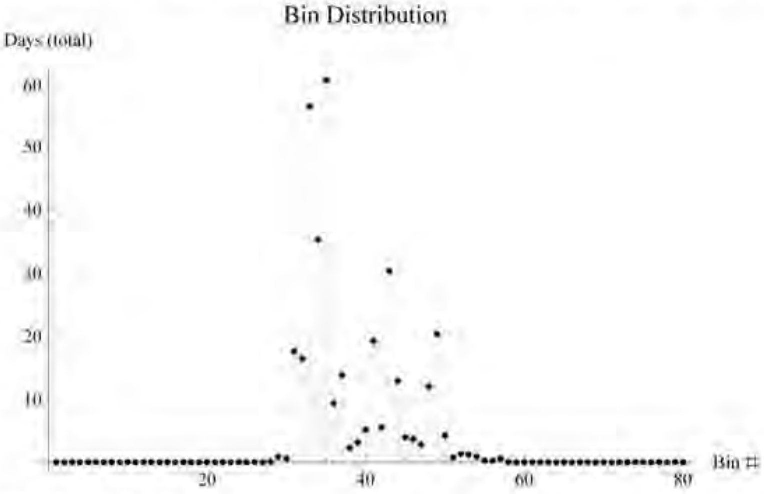
Compute all but the last temporal bin:

```
For[jj = 1, jj ≤ nTbins - 1, jj ++,
 wGridtime = wGrid[[All, (tS tBW) jj - ((tS tBW) - 1) ;; (tS tBW) jj]];
 err[[jj]] = Mean[Abs[τGrid[[1, (tS tBW) jj - ((tS tBW) - 1) ;; (tS tBW) jj]]]];
 akdiTime = Table[Total[wGridtime[[ι, All]]], {ι, nI}] /
   Total[Table[Total[wGridtime[[ι, All]]], {ι, nI}]];
 ab = Interpolation[Transpose[{𝕏time, akdiTime}], InterpolationOrder → 1];
 For[ii = 1, ii ≤ nXbins, ii ++,
  outputTable[[ii, jj]] =
   Round[(tBW) Integrate[ab[ξ], {ξ, reachBin[[ii]], reachBin[[ii + 1]]}] /
      Integrate[ab[ξ], {ξ, reachBin[[1]], reachBin[[nXbins + 1]]}], wmin]
 ]]
```

Compute the last temporal bin

```
jj = nTbins;
wGridtime = wGrid[[All, (tS tBW) jj - ((tS tBW) - 1) ;; nJ]];
err[[jj]] = Mean[Abs[rGrid[[1, (tS tBW) jj - ((tS tBW) - 1) ;; nJ]]]];
akdiTime = Table[Total[wGridtime[[ι, All]]], {ι, nI}] /
   Total[Table[Total[wGridtime[[ι, All]]], {ι, nI}]];
ab = Interpolation[Transpose[{Xtime, akdiTime}], InterpolationOrder → 1];
For[ii = 1, ii ≤ nXbins, ii++,
 outputTable[[ii, jj]] =
   Round[(tBW) Integrate[ab[ξ], {ξ, reachBin[[ii]], reachBin[[ii + 1]]}] /
      Integrate[ab[ξ], {ξ, reachBin[[1]], reachBin[[nXbins + 1]]}], wmin];
]
```

```
ListPlot[Total[Transpose[outputTable]],
 Filling → Axis, PlotRange → All, PlotStyle → {Thick, Black},
 PlotLabel → "Bin Distribution", AxesLabel → {"Bin #", "Days (total)"}]
```



Weeks for table labels:

```
week = Table[Round[d/tBW], {d, tMin, tMax, tBW}];
```

Reach ID for table labels:

```
reach = Table[r, {r, 1, nXbins}];
```

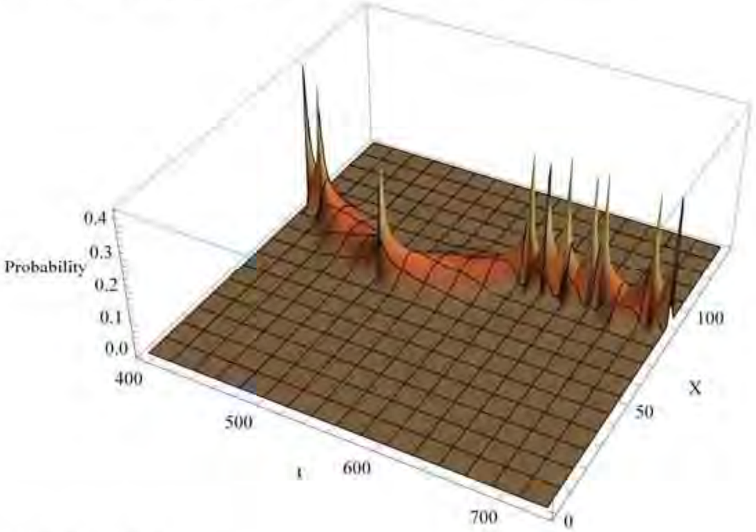
Export table of AKDI results across the computational domain to Excel:

```
export = Table[0, {i, nXbins + 2}, {j, nTbins + 1}];
export[[3 ;; All, 2 ;; All]] = outputTable;
export[[3 ;; All, 1]] = reach;
export[[1, 2 ;; All]] = week;
export[[2, 2 ;; All]] = Round[err, .1];
export[[1, 1]] = "reach.week";
export[[2, 1]] = h;
```

■ Create a 3D Plot of the X-t Distribution

Rearrange the $[n_I \times n_j]$ grid into 1D arrays for plotting, and generate a contour plot of the probability field.

```
wArray = tArray = xArray = Table[0, {q, 1, (nI) (nJ)}];
c = 0;
For[i = 1, i ≤ nI, i++,
  For[j = 1, j ≤ nJ, j++,
    c = c + 1;
    wArray[[c]] = Max[{wGrid[[i, j]], 1 × 10^-10}];
    xArray[[c]] = xGrid[[i, j]];
    tArray[[c]] = tGrid[[i, j]];
   ];
 ];
wX3D = ListPlot3D[Transpose[{tArray, xArray, wArray}],
  AxesLabel → {"t", "X", "Probability"}, InterpolationOrder -> 1,
  ColorFunction → "SouthwestColors", PlotRange → All]
Export[label <> "_3Dplot" <> ".jpg", wX3D]
```



```
fish 4_3Dplot.jpg
```

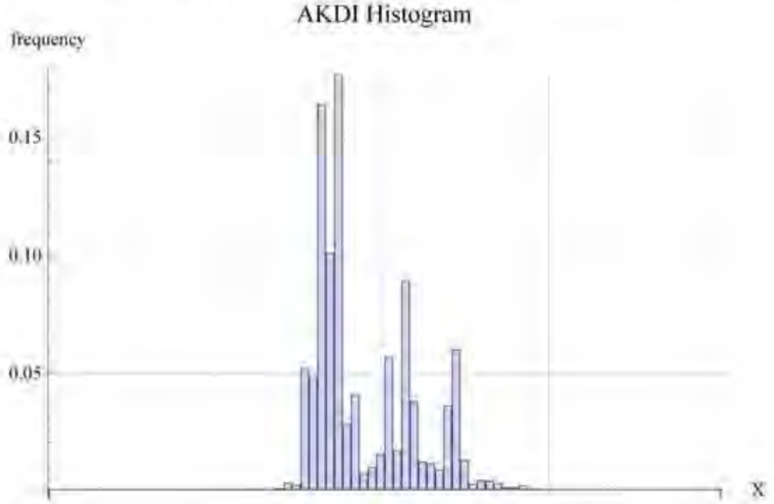
Output to Excel Format

```
Export[label <> "_output" <> ".xls", export]
```

```
fish 4_output.xls
```

▪ Create a Histogram of the Spatial Distribution

```
X = xGrid[[All, 1]];
              Table[Total[wGrid[[i, All]]], {i, nI}]
akdi = ─────────────────────────────────────────────────────;
          Total[Table[Total[wGrid[[i, All]]], {i, nI}]]
ab = Interpolation[Transpose[{X, akdi}], InterpolationOrder → 1];
akdiBins = 0 reachBins;
For[ii = 1, ii ≤ nXbins, ii++,
   akdiBins[[ii]] = Integrate[ab[ξ], {ξ, reachBin[[ii]], reachBin[[ii + 1]]}] /
       Integrate[ab[ξ], {ξ, reachBin[[1]], reachBin[[nXbins + 1]]}];
  ];
reachHist = BarChart[akdiBins, PlotLabel → "AKDI Histogram",
   AxesLabel → {"X", "frequency"}, GridLines → Automatic]
```



Export Histogram Plot to .jpg image

```
Export[label <> "_ReachHist" <> ".jpg", reachHist]
```

```
fish 4_ReachHist.jpg
```