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Estimation of brook trout movement in a beaver pond complex using multi-state capture-recapture models: examination of restricted movement

Ryan L. Benson
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ESTIMATION OF BROOK TROUT MOVEMENT IN A BEAVER POND COMPLEX USING MULTI-STATE CAPTURE-RECAPTURE MODELS: EXAMINATION OF RESTRICTED MOVEMENT

by
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B.Sc. University of Lethbridge, 1997

presented in partial fulfillment of the requirements for the degree of Master of Science in Wildlife Biology The University of Montana 2002

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5-22-02 Date
Estimation of Brook Trout Movement in a Beaver Pond Complex Using Multi-State Capture-Recapture Models: Examination of Restricted Movement

Abstract:

Past research involving movement of resident stream fishes concludes that most fish move little throughout their lifetime, from which developed the restricted movement paradigm, but many of these studies were biased against detecting movement. More recent studies have demonstrated significant movement in stream fishes. I estimated movement of brook trout \textit{(Salvelinus fontinalis)} in a beaver pond complex in Waterton Lakes National Park, Canada, using multi-state capture-recapture methods. Individual trout were tagged with passive integrated transponder (PIT) tags. The monthly probability of a fish moving a mean distance of 74 m was 0.165 over 12 months. I observed long distance movement of up to 2.1 km between recaptures. Movement and frequency analysis indicate a leptokurtic distribution and evidence of static and mobile components of the population. Results of this study do not support the restricted movement paradigm. The methods used here can be replicated to further address issues concerning fish movement.
PREFACE

This project would not have been successful without the help of many people and organizations, whom I wish to acknowledge. First, I thank my mentor Dr. Andrew Sheldon, who provided inspiration and insight during all stages of the project. My graduate committee, Dr. L. Scott Mills and Dr. Michael Young provided valuable editorial comments on versions of this thesis. Dr. Mark Lindberg, John Citta, and Dr. Chris Frissell helped with the study design and analysis. The staff and wardens at Waterton Lakes National Park provided logistic support, particularly Kevin Van Tighem and Rob Watt. Ron Beck provided technical advice and field assistance. I also wish to thank Elliot, Gifford, and Jason Fox, Dave and Myrna Pankhurst, Brent Pruden, and Arnell, Garret, Rick, Shaun, and Tim Tailfeathers for field assistance. This material is based on work supported under a National Science Foundation Graduate Research Fellowship. The Blood Tribe and the Fields Memorial Scholarship provided additional funding.

Any opinions, findings, conclusions or recommendations are those of the author and do not necessarily reflect the views of the National Science Foundation.
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Chapter 1. Introduction

Animals typically have complex life histories that require various resources throughout the life span of the individual. In a heterogeneous environment, resources may be irregularly distributed throughout the landscape, and individuals must move to obtain all necessary resources. Significant movement is a critical behavior required by most animal species in a complex landscape. Improvements in technology and theory have allowed researchers to reliably quantify animal movement.

The Restricted Movement of Stream Fishes

Much early research of resident stream fishes supported a paradigm of restricted movement. Resident populations of stream fishes were considered to be non-mobile. Studies have indicated a tendency for stream fish to remain in a small stretch, usually between 30 and 60 m of stream (Gerking 1950, 1953). Movement studies conducted since Gerking’s research have reached similar conclusions. Shetter (1968) found that the majority of brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) remained within 150 m of their original tagging location. Miller (1957) concluded that most resident cutthroat trout (*Oncorhynchus clarki*) moved little. Individuals that did move were captured within 180 m. Movement patterns of coastal cutthroat trout were generally restricted to less than 3 m and occasionally up to 50 m (Heggenes et al. 1991). LeClerc and Power (1980) suggested that all resources required to sustain life for brook trout and land-locked Atlantic salmon (*Salmo salar*) can be obtained within small stream reaches. Similar results were observed in salmonids (Jenkins 1969; Nakano et al. 1990), centrarchids and percids (Freeman 1995), and cyprinids (Aparicio and DeSostoa 1999).
The typical capture-recapture methods employed in support of the restricted movement paradigm are biased against the detection of movement (Gowan et al. 1994). In a computer simulation, individuals with high movement rates quickly moved out of the study reach boundaries and became unavailable for recapture. Slow movers and sedentary individuals remained in the home reach. This gives the appearance of restricted movement in the population because the majority or recaptured fish did not move (Gowan and Fausch 1996a). In addition, these types of studies have low statistical power to detect movement (Gowan and Fausch 1996a).

Evidence of homing and territoriality supports the idea of restricted movement in stream fishes. Experiments conducted by Miller (1954, 1957) demonstrate the ability of cutthroat trout to home after either upstream or downstream displacement. Sixty-seven percent of recaptured fish occupied a home territory. Comparable homing abilities were observed in brown trout. Mean distance moved by displaced fish was 75 m upstream and 111 m downstream (Harcup et al. 1984). Other researchers support territoriality in stream fishes (Kalleberg 1958; Berra and Gunning 1972; Kennedy 1981).

Restricted movement and territoriality may benefit stream fish in four ways (Jenkins 1969). Residents are better able to defend themselves in dominance hierarchies. Residents have a better ability to escape predation. An individual expends less energy by remaining static than by moving. Finally, a moving individual is in danger of losing energetically profitable territories and ending up with unprofitable ones.

Alternatively, Bachman (1984) suggested that the concept of territoriality did not apply to stream salmonids. Brown trout were observed using multiple foraging sites throughout any given day, and none of the sites was occupied exclusively by one.
individual. Foraging sites are energetically efficient with low probability of predation. Agonistic behavior results in the formation of linear dominance hierarchies, which gives the appearance of territoriality when observed over a short period. Agonistic behavior is less energetically costly than scramble contests for drift items (Bachman 1984).

Evidence suggests that some fish populations are composed of a larger sedentary component, and a smaller mobile component (Funk 1955; Stott 1961, 1967; Soloman and Templeton 1976; Harcup et al. 1984; Smithson and Johnston 1999). Observations of static and mobile groups do not contradict Gerking (1950, 1953), but are a supplement to his findings, assuming he only studied the sedentary component of the population (Funk 1955). Furthermore, fish moving less than 1.6 km were classified as sedentary. Sedentary fish may move significantly, depending on the observer’s definition of movement (Funk 1955). The small mobile component of a brown trout population traveled up to 17 km (Shetter 1968). Gerking (1953) recognized mobile fish, which he called “stray fish”, that exhibited significant movement.

Fish populations with mobile members may have an advantage. Mobile fish may represent natural biological variability within the population (Berra and Gunning 1972). The mobile component may be a source to repopulate areas eradicated by environmental disturbance (Gerking 1953).

On the other hand, the static versus mobile dichotomy of fish movement may be inappropriate. Kennedy (1981) observed a spectrum of movement patterns of European minnows (*Phoxinus phoxinus*) ranging from sedentary to completely mobile. Cyprinid communities may be totally mobile. Movement may be influenced by environmental characteristics and changes in behavior in response to environmental changes (Linfield
1985). Fish movement may be plastic rather than dichotomous. Cyprinid and centrarchid populations had members of the population that traveled outside of their home pool at any given time. That proportion turned over constantly (Smithson and Johnston 1999). Movement plasticity allows individuals to adapt to environmental variation (Gowan et al. 1994). For example, fishes in a warm-water stream had to crowd in stagnant pools due to regular periods of low water and discontinuous flow. When flow was re-established, fishes rapidly dispersed (Larimore et al. 1959).

Moreover, radio-telemetry studies have indicated that movement in resident stream salmonids may be common and significant (Gowan et al. 1994). The mean displacement between telemetry observations for brown trout ranged between 46 and 480 m. The maximum displacement between observations was 16,800 m (Clapp et al. 1990). Brown trout implanted with radio-transmitters had larger ranges than previously recorded (Young 1994, 1996). The average distance moved by brown trout over a diel cycle ranged between 110 and 152 m (Young 1999). Meyers et al. (1992) observed brown trout movement up to 8 km during the summer. The median distance moved by brown trout and rainbow trout (Oncorhynchus mykiss) was 208 m and 1109 m, respectively (Young et al. 1997a). Cutthroat trout moved more over a diel cycle than previously reported over a whole year. The discrepancies in movement may be due to differences in technique (Young et al. 1997b).

Other methods have been employed to document fish movement. Riley et al. (1992) used 2-way weir traps and repeat electrofishing to evaluate movement of brook trout. Following habitat manipulation and improvement, treatment areas increased in brook trout abundance. The increase was attributed to immigration by mobile fish. The
migrants originated from beyond the study site boundary rather than adjacent regions (Gowan and Fausch 1996b). Studies using turnover rates of marked and unmarked individuals, assuming the majority of the population was marked, may be a better indicator of movement (Gowan et al. 1994; Fallau 1995). However, turnover rates may be misleading if there is high turnover but low displacement (Rodriquez 2002). Hughes (1998) was able to infer interannual movement from whole-stream patterns of age segregation. In order to maintain the age class segregation evident in a population of arctic grayling (Thymallus arcticus), substantial movement must occur.

Maximum likelihood estimators are an alternative and practical method of modeling fish movement. Several properties make MLEs efficient. Estimators are asymptotically unbiased and provide maximum efficiency (Burnham et al. 1987). In addition, they are normally distributed, and have minimal variance (Lebreton et al. 1992). The normal distribution and lack of bias indicate the estimators are reliable when the sample size is large. Furthermore, the minimal variance property indicates the estimators have optimal precision (Lebreton et al. 1992). These methods have been the backbone of capture-recapture studies for over 50 years (Burnham et al. 1987). Hilborn (1990) estimated oceanic movement of skipjack tuna (Euthymus pelamis) using tag recovery data and maximum likelihood estimators (MLEs).

The basic model for studying open populations is the Cormack-Jolly-Seber (CJS) model (Pollock et al. 1990; Lebreton et al. 1992). Apparent survival may be estimated, and is symbolized by the letter phi “\( \phi \)”. This parameter is the probability of survival for all individuals, given they are available for recapture, or in other words, have not permanently emigrated. The parameter “\( p \)” estimates the encounter probability (capture
or re-sight) for all individuals (Pollock et al. 1990). Moreover, given the following parameter estimates:

\[ \phi_{ijk} = \text{the probability an individual alive and present in region } j \text{ during the time period } i \text{ survives and is present in region } k \text{ during time } i+1, \text{ and} \]

\[ p_{ij} = \text{probability an individual in region } j \text{ during time } i \text{ is observed or encountered} \]

it is possible to break apparent survival into a movement and a true survival component. We can write movement probabilities as:

\[ \phi_{ijk} = S_{ij} \Psi_{ijk} \]

where \( S_{ij} \) is the probability an individual alive in time \( i \), region \( j \) survives until \( i+1 \), and \( \Psi_{ijk} \) is the probability an individual in region \( j \) (time \( i \)) moves to region \( k \) at \( i+1 \). The parameter \( \Psi \) is conditional on survival (Hestbeck et al. 1991; Brownie et al. 1993; Nichols and Kendall 1995).

Multi-state models are able to estimate true survival and movement between strata or states, as well as encounter probability. A state or stratum may be a geographic location or a physiological state, such as juvenile or adult (Brownie et al. 1993). Multi-state models have been employed for a variety of species including brook trout (Gowan and Fausch 1996b), Canada geese (\textit{Branta canadensis}) (Hestbeck et al. 1991; Brownie et al. 1993), roseate tern (\textit{Sterna dougallii}) (Spendelow et al. 1995) and black brant (\textit{Branta bernicla nigricans}) (Lindberg and Sedinger 1998).

**Landscape Dynamics and Fish Movement**

Landscape dynamics are important processes that affect the structure of a community. Diverse ranges of habitat patches within the landscape contain different qualities and quantities of resources. Animal communities inhabiting the landscape need
to be highly mobile to obtain resources. Movement within the complex array of habitat patches may be an important component in the life history of these organisms.

Stream fishes often have a complex life history that requires habitat heterogeneity. The fish life history extends over long temporal and large spatial scales. Different life stages require distinct habitats that are spatially heterogeneous (Schlosser 1995b). Habitat heterogeneity directly regulates fish populations. Population dynamics are a function of immigration, emigration, natality, and mortality (Werner and Gilliam 1984; Schlosser 1995b). Stream fish require spatial heterogeneity and connectivity of habitat patches to survive and reproduce (Schlosser 1991). The scale of spatial heterogeneity depends on the life history of the particular species (Schlosser and Angermeier 1995).

A landscape has been defined as a mosaic of habitat patches with imbedded focal patches. The appropriate configuration of the landscape is species specific. The landscape is intermediate in size between the species' home range and regional distribution (Dunning et al. 1992). Several processes affect populations using the landscape.

Habitat complementation occurs when an individual must travel between habitat patches to obtain different but equally important resources. A landscape in which complementation occurs is able to support a larger population than when patches are isolated (Dunning et al. 1992). Complementation can increase fish populations by reducing the energetic cost of migrating between two patches and travel-related exposure to predation (Schlosser 1995b).

Habitat supplementation occurs when individuals augment their resource use from nearby patches of the same habitat. The resources may be substitutable. Thus, a
population may be sustained on a relatively small patch, when ordinarily the patch would be too small or resource poor to support such a population (Dunning et al. 1992). Landscape supplementation allows for increased food consumption or an increased range of foraging habitats. This will also increase growth, survival, and fecundity rates (Schlosser 1998).

Source and sink relations refer to high and low quality habitat patches. The sink area has low reproductive output that is insufficient to balance mortality. The source area has higher reproduction than the sink, and is able to maintain the population by emigration (Pulliam 1988). A hybrid model combines characteristics of a patchy population and source/sink model (Harrison 1991). The patchy population model is similar to the concept of a metapopulation, where local populations become extinct and are re-colonized by neighboring populations in the region (Hanski and Gilpin 1991). However, the patchy population model has high movement rates between local populations that exceed extinction rates, resulting in individuals in different patches that behave as one population (Harrison 1991). The hybrid model is an appropriate representation of the spatial variation of demographic processes that affect stream fish populations (Schlosser and Angermeier 1995; Adams 1999).

Neighborhood effects refer to the greater importance and effects of adjacent patches versus distant patches. The significance of neighborhood effects on individuals depends on the placement of habitat patches within the landscape (Dunning et al. 1992). Furthermore, the ability of individuals to disperse between neighboring patches depends on the permeability of patch boundaries (Schlosser 1995b).
Finally, the spatial distribution of refugia is a functional factor that controls population dynamics. The distribution and location of refugia from extreme environmental conditions may influence survival and dispersal rates between feeding and other habitat patches (Schlosser 1995b).

A beaver pond complex is an example of a heterogeneous landscape. Beaver (*Castor canadensis*) can significantly alter their habitat. Some of these alterations involve temperature, nutrient loads, production, and morphology. Alterations affect the distribution and dynamics of the aquatic community.

Beaver ponds with stabilized temperatures are not greatly influenced by changes in air temperature (Gard 1961). Temperature stratification in ponds results in cooler lower strata, which may be used as a retreat for trout species (Gard 1961; Call 1970). However, vertical changes in beaver ponds were minimal in New Mexico (Huey and Wolfrum 1956). Large ponds may act to buffer thermal extremes (McRae and Edwards 1994). Downstream temperatures may rise slightly, however daily fluctuations are minimized. Maximum temperatures may be variable. Due to local differences in shading, ground water inflow, and volume, it is difficult to generalize the effects of beaver ponds on stream temperatures (McRae and Edwards 1994). The age of the pond affects the downstream temperature (Call 1970). In old ponds, stream water comes from the surface, which is likely to be warmed. In contrast, newer ponds have increased percolation through the dam, thus, water enters the stream from the lower strata. The water is further cooled as it percolates because the surface area is increased and loses heat due to evaporative cooling resulting in cooler water downstream.
Beaver ponds tend to have higher production than adjacent streams. There is increased nitrogen fixation primarily in the sediments (Naiman and Melillo 1984; Francis et al. 1985), and storage of organic nutrients (McDowell and Naiman 1986; Naiman et al. 1986). Ponds contain a greater number and biomass of organisms and invertebrates compared with adjacent streams (Huey and Wolfrum 1956; Gard 1961; McDowell and Naiman 1986). Ponds may have poor per area production of benthic invertebrates, but since the bottom area of impounded streams is greatly increased, the total production in the pond is increased (Rupp 1954). Higher water temperatures increase the length of the growing season and production (Huey and Wolfrum 1956).

Impoundments may alter invertebrate community structure. Sprules (1941) documented a change in insect fauna from a lotic community to predominantly lentic after the creation of a beaver impoundment. Diptera were important fish foods in warm-water beaver impoundments (Pullen 1971). These ponds had poor benthic community development and retarded planktonic growth.

Beaver impoundments also alter the fish community. Larger trout were found in ponds, while more fry were found in the stream (Gard 1961). Older ponds silt over, eventually losing spawning substrate over time. As a result, older ponds produce larger trout because of reduced competition (Call 1970). Rabe (1970) observed high standing crops of small brook trout in spawning areas and lower numbers of fish in seep ponds with inferior spawning substrate. Pond size and recruitment are major influences on standing stock and densities (Winkle et al. 1990). Variables include surface area, mean depth, volume, discharge, elevation, and morphoedaphic index. There is generally a negative correlation between fish recruitment and mean fish size (Winkle et al. 1990).
High species diversity and standing crop are associated with beaver activity (Pullen 1971). Snodgrass and Meffe (1998) observed high fish species richness in beaver-impounded streams and shift from a lotic to a lentic community. Keast and Fox (1990) observed lower species richness when barriers limited fish migration.

Gard (1961) observed minimal movement into and out of ponds in the summer. Data were limited to a three-week period. Seasonal spawning movements were observed. Beaver dams were significant obstacles to brook trout movements, but were not complete barriers (Rupp 1954). Dams are not barriers to migration because small trout are able to penetrate the interstitial spaces (Gard 1961). Schlosser (1995a) suggested that dams pose a semi-permeable barrier to downstream movement. Probability of movement is greater upstream of the pond into the adjacent stream. Seasonal movement of brook trout was not affected by the formation of an artificial pond in Price Edward Island (Smith and Saunders 1967).

Downstream processes and factors have the potential to affect upstream community dynamics (Ruhr 1956; Erman 1973; Winston et al. 1991; Osborne and Wiley 1992; Pringle 1997; Schlosser 1998). For example, after a stream impoundment, populations of brown trout in upstream tributaries were maintained by immigration from downstream reaches (Ruhr 1956). Bullhead [sculpin] (*Cottus gobio*) extended upstream distribution and established breeding populations after impoundment (Crisp et al. 1984). Downstream habitat patches may potentially be of great importance to upstream communities, especially if non-permeable or semi-permeable boundaries are a factor in the landscape.
**Summary and Objective**

Early studies implied that resident stream fishes restrict their movements to a small reach and do not move throughout life. Many species protect a territory and will return when physically relocated. Populations may consist of a large sedentary segment and a small mobile segment. More recent work indicated that movement may be an essential part of the life history of stream fishes. In a complex landscape, fish need to travel substantially to obtain different but essential resources. Previous movement studies were biased against detecting movement. Alternative techniques have demonstrated that stream fish movement is important and more prevalent than previously recognized.

I will attempt to demonstrate the significance of movement in a brook trout population residing in a headwater beaver pond complex. This type of fish habitat is a heterogeneous landscape that is temporally dynamic. I submit that trout in this type of system need to move substantially during the non-breeding summer periods to obtain resources and take refuge from environmental extremes. I will quantify movement using maximum likelihood estimators and multi-state models. By modeling movement as a likelihood rather than as a population proportion, I hope to avoid the pitfalls of previous capture-recapture studies.

**Literature Cited**


Pullen, T.M. Jr. 1971. Some effects of beaver (Castor canadensis) and beaver pond management on the ecology and utilization of fish populations along warm-water streams in Georgia and South Carolina. Doctoral Dissertation. University of Georgia. Athens, Georgia.


Chapter 2. Estimation of Brook Trout Movement in a Beaver Pond Complex using Multi-State Capture-Recapture Models: Examination of Restricted Movement

Introduction

Movement is an important attribute in the life history of many fishes, and affects dispersal and recolonization (Andrewartha and Birch 1954; Sheldon and Meffe 1995; Adams 1999), gene flow (Fausch and Young 1995), and metapopulation and landscape dynamics (Rieman and McIntyre 1993, Schlosser 1995b, Gilliam and Fraser 2001).

Gerking (1950, 1953) concluded that individuals of certain species occupy small ranges throughout their lifetime. This conclusion was apparently supported for various salmonid species (Miller 1954, 1957; Shetter 1968; Jenkins 1969; LeClerc and Power 1980; Bachman 1984; Nakano et al. 1990; Heggenes et al. 1991; Rodriguez 2002), centrarchids (Freeman 1995; Smithson and Johnston 1999), and cyprinids (Aparicio and DeSostoa 1999; Smithson and Johnston 1999).

Some have hypothesised that populations of stream fish are composed of a large sedentary segment and a smaller mobile segment (Funk 1955; Stott 1967; Solomon and Templeton 1976; Harcup et al. 1984; Smithson and Johnston 1999). Gerking (1953) recognised that mobile fish, which he called “stray” fish, may be a potential source to re-establish depopulated areas. The presence of static and mobile components does not contradict Gerking’s observations, but supplements them, assuming Gerking studied only the sedentary component of the population (Funk 1955). Funk (1955) considered fish sedentary if they moved less than 1.6 km. Therefore, “sedentary” fish may move substantially, depending on one’s definition of movement.
Contrary to this paradigm of restricted movement, movement of resident stream salmonids may be widespread and significant (Gowan et al. 1994). Telemetry-implanted brown trout (Salmo trutta) and cutthroat trout (Oncorhynchus clarki) exhibited extensive movement that was greater than previously reported (Young 1994, 1996). Telemetry-implanted brown trout and rainbow trout (Oncorhynchus mykiss) had relatively large summer home ranges (medians, 131 m and 606 m, respectively; Young et al. 1997). The mean displacement of telemetry-marked brown trout during spring and summer in a Michigan river ranged from 48 to 480 m and maximum individual displacement ranged from 270 to 16,800 m (Clapp et al. 1990). Mark-recapture experiments with two-way traps revealed that large proportions of marked brook trout (Salvelinus confluentus) in headwater mountain streams were mobile (Riley et al. 1992). Moreover, increases in brook trout abundance in reaches containing improved habitat were attributed to immigration of mobile fish (Gowan and Fausch 1996b). The typical method of marking and recapturing fish to study movement by repeated sampling in the same reaches to recapture marked fish is strongly biased against detecting movement because conclusions are based on recaptures of marked fish in the original release area (Gowan et al. 1994; Gowan and Fausch 1996a). Recapture efficiencies are often low or undocumented and mortality rates are inferred and may not be a reflection of true mortality in the system (Gowan et al. 1994). Furthermore, typical studies have low power to detect movement (Gowan and Fausch 1996a). Gowan and Fausch (1996a) proposed that mobile fish move outside of the study site boundaries, while sedentary fish remain within the original marking site, giving the appearance of restricted movement.

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Alternative, unbiased methods should be employed to document fish movement. Radio-telemetry movement studies tend to demonstrate considerable mobility in fish, but inferences are based on low sample sizes and severely handled fish. Population turnover studies, where inferences are based on the presence of unmarked individuals after the majority of the population has been marked, may be a suitable indicator of movement (Gowan et al. 1994; Fallau 1995). Spatial patterns of age segregation (Hughes 1998a) and analysis of tag recovery data with maximum likelihood estimators (Hilborn 1990) have also been used to assess movement.

My objective was to evaluate movement of brook trout in a headwater beaver pond complex, a heterogeneous landscape that is temporally and spatially dynamic. I hypothesised that trout in this system move substantially during the non-breeding summer periods to obtain resources and take refuge from environmental extremes. I quantified movement using maximum likelihood estimators and multi-state models. This method permitted the estimation of movement probabilities rather than measuring a proportion of the population that was recaptured outside of the original capture location.

Materials and Methods

Study Area

Crooked Creek is a second-order tributary to the Waterton River (confluence at 1,300 m elevation), part of the South Saskatchewan River drainage (Fig. 1). The headwaters (1,900 m elevation) are located in Waterton Lakes National Park, Alberta, Canada. Crooked Creek originates in a glacial cirque and flows over a set of falls impassable to fish. Snowmelt feeds the headwaters of this system, and the stream often dries up at higher elevations during the summer. The study site is at 1,550 m elevation in
a low-gradient beaver pond complex. The stream-pond complex meanders for 4-5 km before crossing the park boundary into private land. At this point the creek enters Bird's Eye Lake, a reservoir. The levels of the lake are controlled for cattle production. The creek re-enters the park 3-4 km upstream from the confluence with the Waterton River (Fig. 1).

For the purposes of modelling, I divided the study area into a lower (L) and upper reach (U) (Fig. 1). The upper reach is mostly unaffected by beaver activity. The substrate is predominantly cobble and gravel. This habitat consists of a sequence of riffles and pools with numerous undercut banks and coarse woody debris. Mean width was 2.8 m and mean depth was 0.3 m, based on 11 transects. Beaver activity was prevalent in the lower reach, which made this habitat difficult to quantify. The stream channel is much wider and deeper (mean width 4.6 m, mean depth 0.7 m, 10 transects), with mostly silt and sand substrate. Throughout the summer 2000, beaver activity caused some sections in this reach to change from lotic to mostly lentic habitat. Summer discharge (June-September) ranged from 0.022 to 0.459 m³ s⁻¹ over a 2-year period.

Temperature fluctuations within the beaver pond reach are substantial. Temperatures ranged between 8.3° C-18.9° C in August 1999 (daily minimum median = 11.5° C, daily maximum median = 16.6° C) in one representative location. Fall temperatures (23 September-11 October 1999) ranged between 2.0° C and 12.8° C. In addition, there is evidence of partial temperature stratification in deep ponds. In one 1.5-m deep transect, the temperature difference was 6.3° C (14.8° C-21.1° C).

The predominant fish species present is introduced brook trout. Cutthroat trout are native to the stream but are now uncommon. Other species present include longnose
sucker (Catostomus catostomus), longnose dace (Rhinichthys cataractae), and hybrid northern redbelly/finescale dace (Phoxinus spp.)

Field Methods

For the first year, I conducted preliminary research to determine large-scale movement patterns and to test various field methods. During the second and third years I employed a different procedure that provided better resolution on specific patterns of movements.

Live fish were captured and treated under a protocol approved by the University of Montana Institutional Animal Care and Use Committee (ACC 028-00). Trapping and electro-fishing was conducted under the authority of Parks Canada Research Collection Permits (Research Permit #WL-99-11, #WL-2000-05, and #WL-2001-02).

Beginning 12 June 1999, I installed four V-shaped directional weir traps in various locations throughout the drainage (Fig. 1). Traps 1, 3, 4, and 2b were located in sections 1, 14, 15 (L/U boundary), and 27, respectively (Fig. 1). Traps measured 90 cm x 180 cm x 120 cm and were framed with wood and lined with 127-mm mesh hardware cloth. At the apex of the “V,” a mesh cone (25.4 cm wide, tapering to 7.6 cm) directed fish into an appropriate upstream or downstream compartment. Trap 1 was 60 m upstream from a culvert. I chose this boundary to avoid bias in case the culvert affected fish movement. Trap 2b was situated 50 m below a large, old dam and pond. Trap 4 was installed on a small dam at the inlet of the largest set of ponds in the study reach. This area was a transition zone between reaches L and U. On 3 July I moved trap 2a (henceforth trap 2b), which had caught very few fish in a secondary channel, to a new
location. Trap 3 and 2b were breached several times during the course of the study because of high discharge.

I checked traps every 1-3 days until 26 August, when the traps were removed. Traps were not checked 13-24 August. I anaesthetised fish with sodium bicarbonate tablets as described by Peake (1998) until fish lost equilibrium. Induction time was 5-8 minutes. I measured mass in grams and fork length to the nearest millimetre. I individually marked fish by cutting specific fin rays (Welch and Mills 1981). I cut different combinations of rays in the anal and dorsal fins so that each fish had an individual mark. I batch-marked fish captured in each trap by injecting anal fins with visible implant elastomer (Northwest Marine Technology, Shaw Island, Washington, USA). Each trap location had a specific colour code. I attempted to mark all individuals, but 150-200-mm fish were the smallest I was able to mark effectively. Throughout the summer months I recorded species and capture locations, and direction of movement. Fish captured moving in one direction were returned to the appropriate side of the trap to continue movement in the same direction.

In order to provide better movement resolution, I designed the sampling procedure to accommodate a multi-state model. I divided the stream into discrete sections and the annual cycle into discrete sampling intervals. By observing the locations of marked fish instantaneously on distinct sample dates, I can estimate movement probability between sections during specific time intervals.

Beginning 23 June 2000, I re-installed traps 1, 2b, and 4 (Fig. 1). The traps were placed to measure immigration-emigration or movements between reaches L and U. Traps 1 and 2b were operated continuously from 23 June to 8 October to measure
immigration and emigration during this time. I did not want to affect individuals moving between reaches L and U, so trap 4 was operated only during short sampling periods.

I defined five sampling periods in 2000-2001: 24 June-2 July 2000, 29 July-5 August, 2-9 September, 30 September-8 October, and 10-19 July 2001. The rationale for these dates was to satisfy the assumption of instantaneous sampling for capture-recapture (C-R) analysis (Seber 1982, Pollock et al. 1990, Hestbeck et al. 1991). This assumption was not fully satisfied because it was logistically impossible to capture the numbers of fish needed to analyse and model in a short time period. I chose 1-week sampling periods because they are relatively short compared to the time between sampling periods (approximately 3 weeks, except for the last interval, which was 9 months). Survival estimates may be biased because of the time lag, but I needed to find an appropriate balance between capture efficiency and bias.

I divided the entire study reach into 30 sections (Fig. 1). The boundaries were chosen based on section length, stream morphology, and habitat qualities. Stream sections varied in length from 45 to 165 m (mean 74 m).

I was concerned with the effects of multiple exposure to electricity on the short and long term behaviour of the fish. There is limited information regarding multiple shocks on the behaviour of fish, but this type of sampling design may bias results (Mesa and Shreck 1989; Hughes 1998b; Nordwall 1999). To reduce these effects, I only captured fish with an electrofisher only during 24 June-2 July 2000, 30 September-8 October, and 10-19 July 2001. Block nets were placed at the upstream and downstream ends of each section before a shocking run. I made a single pass with a backpack electrofisher (Smith-Root Type V, pulsed DC) using 500-600v output through all
sections, with the exception of the final sampling period when I made three passes in each section.

During the last four sampling periods, I used 60- and 90-cm hoop nets with 13 mm mesh to capture fish. The nets were 3 and 4 m in length and had 2 throats. I baited the nets with Berkley PowerBait® and set them in the evening for 10-12 hours. I only had 7 nets in total, so only a few sections could be sampled each night. Stream sections were chosen randomly, and the nets were set in locations with the greatest probability of catching fish. During sampling periods, I baited all three weir traps nightly with commercial trout bait, which in effect acted as large, permanent hoop nets. This alters their intended use as passive devices for capturing mobile fish. In addition to electrofishing, trapping, and netting, I angled fish throughout all sampling periods using spinners and flies.

I observed potentially high mortality with the use of sodium bicarbonate, so I anaesthetised fish with 40-mg/L solution of clove oil, as described by Anderson et al. (1997). Induction time was 1-3 minutes for most fish. Once fish were fully anaesthetised, I marked all trout over 100 mm with passive integrated transponder (PIT) tags (Biomark, Boise, Idaho, USA). Tags were implanted intramuscularly just below the base of the dorsal fin. Tags implanted in this location have a lesser tendency of being shed or extruded (R. Beck, Alberta Agriculture, Food, and Rural Development, personal communication). PIT tags were scanned with a HS6100L pocket reader (Destron Fearing Corporation, St. Paul, Minnesota, USA). In addition, I clipped the adipose fin of all marked individuals as a secondary mark. I measured the fork length to the nearest millimetre for all captured fish, and measured the mass of a random sub-sample ($n =$}
Marked individuals were allowed to recover in aerated stream water until they recovered equilibrium, usually in 5-8 minutes. The section of capture was recorded and processed fish were returned to the appropriate section. When possible, fish were returned close to their original capture location. Otherwise, fish were returned to the midpoint of the section.

In an effort to restore native cutthroat trout to the system, Parks Canada allowed the permanent removal of brook trout from the stream. During the final sampling period, I set two 38- and 64- mm gill nets (50 m long) throughout both reaches. I set nets in the evening for no more than 12 hours per set. Nets were placed mostly in deep ponds and runs that were difficult to electrofish or sample with hoop nets. I euthanized trout by overdosing them in a 200 mg L⁻¹ solution of clove oil. In addition to fork length and PIT tag number, I removed otoliths from a sub-sample of captured trout (n = 50) for age analysis.

Multi-State Modeling Procedures

The basic model for studying open populations is the Cormack-Jolly-Seber (CJS) model (Pollock et al. 1990; Lebreton et al. 1992). Apparent survival (ψ) may be estimated, and is the probability of survival for all individuals, given that they are available for recapture (have not permanently emigrated). The parameter p estimates the encounter probability (re-capture) for all marked individuals (Pollock et al. 1990). Moreover, given the following parameter estimates:

\[ \phi_{jik} \]  
the probability an individual alive and present in region j during the time period i survives and is present in region k during time i+1, and

\[ p_{ij} \]  
probability an individual in region j during time i is observed or encountered
it is possible to break apparent survival into a movement \( \Psi \) and a true survival \( S \) component. We can write movement probabilities as:

\[ \phi_{ijk} = S_{ij} \Psi_{ijk} \]

where \( S_{ij} \) is the probability an individual alive at time \( I \) in region \( j \) survives and is at one of the sampling sites at time \( i+1 \), and \( \Psi_{ijk} \) is the probability an individual at time \( i \) in region \( j \) moves to region \( k \) at time \( i+1 \), given that the fish is alive and at one of the sampling sites (Hestbeck et al. 1991; Brownie et al. 1993; Nichols and Kendall 1995; Spendelow et al. 1995).

Multi-state models require five assumptions: 1) time- and area- specific encounter and movement probabilities are the same for all marked fish during the sampling period in that area; 2) all individuals are independent in regards to encounter probability, survival, and movement; 3) marked fish retain their marks; 4) samples are obtained instantaneously; and 5) losses through emigration are permanent (Hestbeck et al. 1991).

I had to first define what constitutes movement. Each sampling period was a snapshot in time for each individual. I labelled a stream section where an individual was first encountered as its section of origin. I defined initial captures to be in state A. Upon recapture, the marked individual’s position of recapture was compared with the home section location. If a marked trout was recaptured in its home section, I considered it to have remained in state A. If the marked trout was recaptured in any section upstream from its home section, I considered it to have moved to state B. If the marked trout was recaptured in any section downstream from its home section, I considered the individual to have moved to state C. The parameter definition for movement is:

\[ \Psi_{AA} \quad \text{Probability the individual did not move} \]
\[ \Psi_{AB} \quad \text{Probability the marked individual moved upstream} \]
\( \Psi_{AC} \) Probability the marked individual moved downstream

The distance travelled was measured from the midpoint of the home section to the midpoint of the adjacent upstream or downstream section. The mean distance between midpoints was 74 m (range 39-120 m). This is an average number for movement into one section above or below the home section, and may be considered the minimum distance moved. Trout that were recaptured further than one section away from home were still designated as \( \Psi_{AB} \) or \( \Psi_{AC} \), but may have moved more than 74 m.

I organised the capture history for all trout as a list of individual numbers followed by five columns (Appendix). Each column represents a sampling period. A “0” indicates a trout was not encountered during the sampling period. An “A” denotes capture in state A, a “B” indicates state B, and a “C” indicates state C.

Before inputting the file into program MARK (White and Burnham 1999), I compiled a list of possible models. The candidate set of models includes possible biologically significant scenarios. The letter “t” after a parameter indicates the parameter is time dependent. The letter “g” designates a group-specific parameter (i.e. -reach L or U). A capital “T” denotes a trend in a parameter. The term “g*t” indicates an interaction between group and time. The term “.ud” stands for upstream-downstream, designating a difference between upstream and downstream movement. The term “strat” refers to stratum, and was only applied to survival parameters. The term represents a difference in survival between “stayers” (individuals remaining in state A) and “movers” (individuals moving into state B or C). Program MARK calculates maximum likelihood estimates (MLEs) for parameters in each model; it also calculates Akaike’s Information Criteria
(AIC). Models are ranked according to ΔAIC, with the lowest number indicating the most parsimonious model (Lebreton et al. 1992).

Results

In 1999 I captured 111 brook trout and 118 longnose suckers. The majority of captures occurred at trap 4 (49 brook trout, 83 longnose suckers). I suspect the suckers were spawning in the riffle habitat upstream from this trap, because most movement was upstream within three weeks and because most adults were in spawning condition.

The number of recaptures was low (2 brook trout, 7 longnose suckers). The low recapture rates may be attributable to mortality associated with my sampling and anaesthetising technique or trap avoidance by previously sampled fish. Although the preliminary results are insufficient to draw strong conclusions, they indicate that individual suckers and trout have the ability to travel long distances relatively quickly. For example, four suckers travelled 900 m in a 2-3 week period. Furthermore, beaver dams apparently were not a barrier to migration or movement. One brook trout moved approximately 1.25 km upstream over at least two beaver dams in less than a month. Alternate methods were required to document fish movement within this stream.

Immigration and emigration

Traps were operational for 64 days in 1999. At the downstream boundary (trap 1), 18 brook trout were captured travelling upstream. No fish were captured in the downstream compartment. At the upstream boundary (trap 2b), 25 brook trout were captured travelling upstream and none were captured travelling downstream. This is a common problem when using weir traps and may be the result of differential escapement...
due to a fish’s orientation to the current. This may bias estimates of upstream and downstream movement (Gowan and Fausch 1996a).

During 2000, the upstream and downstream boundary traps were operational for 107 days. At trap 1, 61 brook trout were captured travelling into the study area and 31 captured leaving the study area. At the upstream boundary (trap 2b), 4 brook trout were captured leaving the study area. However, because traps were baited during the sampling period, there may be potential bias in estimating immigration and emigration. After removing the captures occurring during the baited sampling periods, the adjusted totals were 28 individuals entering and 4 leaving at trap 1. The adjusted trap time was 77 days.

**Long-distance movement of brook trout**

The multi-state modelling procedure pooled individuals as moving a minimum of one section above or below their home section. However, several individuals were re-captured more than one section away from their home section (Table 1). Movement averaged 680 m (range 97-2145 m) and mean movement rate was 33 m day\(^{-1}\) (range 0.5-429 m day\(^{-1}\)). One individual displayed complex movement by travelling upstream, then downstream, moving 1342 m over 352 days. These results demonstrate that long-distance movement is common.

**Age and growth**

Results of length-frequency analysis \((n = 825)\) and otolith aging \((n = 50)\) reveal that there are at least five age classes of brook trout in this population (Fig. 2a). Brook trout in reach U are composed predominantly of individuals less than age 3, whereas most brook trout in reach L are older (Fig. 2b).
Multi-state modelling

Of 482 brook trout marked with PIT tags, 188 trout were marked in period 1. During period 2, 49 new trout were marked, and 5 were recaptured from the previous occasion. During period 3, 89 trout were marked, and 8 were recaptured. In period 4, I marked 126 new trout within the study area and an additional 30 downstream to determine if movement originated from outside the study site boundaries. Thirty-eight marked trout were recaptured from previous occasions. I captured 616 trout greater than 100 mm during period 5, 28 of which were recaptures. For period 5, fish younger than age 2 were not available to be marked in 2000 because they would have been less than the 100 mm limit (Fig. 2a). When fish younger than two years are removed from the sample, the number of available marked fish in period 5 is adjusted to 354.

Program MARK was not able to successfully model the data set with five sampling periods because of insufficient data for parameter estimation. The number of estimated parameters increases substantially (from 36 to 48 for the global model) when the number of sampling periods increases from four to five. Therefore, I eliminated the least successful sampling period (period 2, July 29- August 5) from the data set. I adjusted the input file to include only four sampling periods, with recaptures from period 2 reclassified as new captures (Appendix). The adjusted sample size was 433.

The most parsimonious model based on \( \Delta AIC_c \) was \( S(g^T)p(g^t)\Psi(g^t) \). This model states that survival varied between group U and L, and there was a trend over time. Capture probability and movement probability varied between group U and L over time. However, there was evidence of overdispersion in the model. Overdispersion results from two main departures from the assumptions of the model. First, survival, capture, or
movement probabilities are not constant among individuals. Second, fate is not independent among individuals (Burnham et al. 1987; Anderson et al. 1994).

Alternatively, substantial overdispersion may indicate a lack of model fit to account for the structure of the data (Lebreton et al. 1992; Anderson et al. 1994). Goodness-of-fit testing is currently unavailable for multi-state models. One way to measure overdispersion is the variance inflation factor (\( \hat{\sigma} \); Burnham et al. 1987; Lebreton et al. 1992; Anderson et al. 1994). Preliminary results indicate overdispersion was present in the data set, because \( \hat{\sigma} \) (deviance/ degrees of freedom) for the global model \( (S(\text{strat}*g*t)p(g*t)\Psi(g*t)) \) was 5.70, although this method of estimating the variance inflation factor is biased high (Anderson et al. 1994). Values of \( \hat{\sigma} \) are not expected to exceed 4, and large values (6-10) indicate a lack of model fit (Lebreton et al. 1992; Anderson et al. 1994). Furthermore, if there is no correction for overdispersion, AIC will select overfitted models (Anderson et al. 1994).

To account for overdispersion, I adjusted the levels of \( \hat{\sigma} \) from 2-4 and observed the corresponding change in \( \Delta \text{AIC}_c \). When \( \hat{\sigma} \) was adjusted to 2 and 3, the best model selected was \( S(T)p(g*t)\Psi(.) \), indicating a slight increase in survival over time and a constant movement probability. When \( \hat{\sigma} \) was adjusted to 4, the best model selected was \( S(.)p(g)\Psi(.) \), indicating constant survival and a capture probability that differs between group U and L. For the purpose of simplicity and because of model selection uncertainty, I determined that estimation of the parameter \( \Psi \) was more important than model structure. As \( \hat{\sigma} \) increases, a general pattern of constant movement probability becomes apparent (Table 2). Point estimates for \( \Psi \) remain the same at 0.165 per month across
both groups and all time intervals when $c$ is adjusted from 2-4. However, as $c$ increases, so does the standard error for parameter estimates (Fig. 3).

**Mobile vs. static dichotomy**

Seventy-three fish were recaptured at least once, of which 36 were classified as mobile. Analysis of the frequency of individuals versus the distance travelled indicates a right skewed, leptokurtic distribution (Fig. 4). The distribution remains skewed even when the distance travelled is log-transformed or when the reciprocal of distance is plotted. There was no relation between fish length (mm) and distance travelled (m) (regression; $n = 73$; slope = 0.016; $r^2 = 0.045$, $P = 0.79$). In addition, there were no differences in the length distribution of mobile and static groups (Kolmogorov-Smirnov test; $D = 0.12$; $P = 0.21$). There is no evidence that movement is size dependent.

**Discussion**

The multi-state modelling procedure outlined here is applicable when evaluating the restricted movement paradigm. Studies supporting the restricted movement paradigm typically do not comment or report on the component of the population that was not recaptured. Any discussion of missing individuals is usually attributed to handling mortality or movement due to handling or marking stress, even if mortality is unlikely to account for all the missing individuals (Gowan et al. 1994). The advantage of the multi-state model is that survival, recapture, and movement probabilities are estimated and recaptures are modelled as a probability rather than as a percentage of the population. Gowan and Fausch's (1996a) hypothesis that low recapture rates were the result of marked fish moving beyond the boundaries of the study site was probably not applicable here due to low rates of emigration. It is more likely that low recapture rates were the
result of low encounter probability, which is expected in this complex environment.

Finally, the quantification of movement probability provides evidence to support or refute the RMP. In this study, marked fish had a 0.165 month\(^{-1}\) probability of moving at least 74 m upstream or downstream from their original capture location. The probability is significantly greater than zero.

Parsimonious model selection is dependent on the amount of data available. A small sample size will only account for a certain number of parameters and a limited model structure. As the amount of data increases, more model structure becomes apparent (Anderson et al. 1994; Buckland et al. 1997). The sample size in this study was not large enough to indicate a clearly best approximating model. There were no obvious patterns in the survival and encounter probabilities of the best models, so a model averaging procedure did not seem appropriate. One problem with this study was low sample size and low capture probability. The complexity of the system and the heterogeneous nature of fish habitat in the beaver ponds made it extremely difficult to capture fish. If this study design were replicated in a simpler, more “typical” trout habitat, capture probability could be increased substantially. With a larger data set, it would be possible to quantify both survival and capture probability, and the utility of the model for evaluating movement.

The problem of overdispersion results from a lack of independence, or that parameters are heterogeneous across individuals. The assumption of homogeneity may be violated if individuals are grouped inappropriately (Burnham et al. 1987; Anderson et al. 1994). For example, if several cohorts of fish are grouped together, mortality may have a greater impact on younger age classes. In this case, apparent survival will not
apply equally to all individuals in the group, resulting in overdispersion. The probable cause of overdispersion is that $\Psi$ is heterogeneous among individuals. It is quite possible that some individuals exhibit high rates of movement, while others do not. This may be explained by the static and mobile dichotomy within fish populations described by others (Funk 1955; Stott 1961, 1967; Solomon and Templeton 1976; Harcup et al. 1984; Smithson and Johnston 1999; Skalski and Gilliam 2000; Kahler et al. 2001; Rodriguez 2001). Assuming that this population is made up of static and mobile components, then $\Psi$ would more accurately represent the transition probability of a static fish becoming a mobile fish. Results presented here illustrate a highly skewed distribution of the frequency of movers and the distance travelled. In this population, there appears to be a small number of extremely mobile fish. Size does not seem to account for differences in the mobile and static groups. On the other hand, movement may be a continuum rather than a dichotomy. Radio-telemetry studies indicate heterogeneous movement behaviour, but not necessarily a sedentary and mobile dichotomy (Clapp et al. 1990; Young 1994, 1996). A sedentary or mobile label may be an arbitrary classification given that, over time, static individuals can eventually become mobile (Kennedy 1981; Gatz and Adams 1994; Smithson and Johnston 1999). It may be more appropriate to model continuous variation in displacement rather than to specify movement parameters to discrete sub-populations (Rodriguez 2002).

The leptokurtic movement distribution observed in this study, with high modes near the mean and tails and few individuals in intermediate regions, seems to be quite common in stream fish movement studies (Harcup et al. 1984; Heggenes et al. 1991; Gowan and Fausch 1996a; Skalski and Gilliam 2000; Gilliam and Fraser 2000;
Rodriguez 2002). Leptokurtosis can result due to heterogeneity of movement within the population (Okubo 1980; Skalski and Gilliam 2000; Rodriguez 2002). Sources of heterogeneity may include temporal and spatial heterogeneity or morphology (Skalski and Gilliam 2000; Gilliam and Fraser 2001). One interesting hypothesis is that boldness, a behavioural trait expressed as the tendency to explore new habitat, is the source of leptokurtic distributions (Fraser et al. 2001).

The modelling procedure classifies \( \Psi \) in terms of a minimum average distance moved. However, long distance movement greater than 74 m was observed. With a richer data set, it may be possible to add more states to further classify mobile individuals into short- and long- distance movers (individuals recaptured more than one section from their home section). Of the 30 records of long-distance movement (Table 1), 19 travelled upstream, which indicates that long distance movement is not the result of fish passively drifting downstream with the current. Another observation is that individuals are capable of moving long distances in a relatively short time. The extreme case of an individual moving 429 m day\(^{-1}\) may be a response to shocking and handling stress, so it is difficult to generalise this extreme to the rest of the population. Similar movement responses to electrofishing have also been observed in brown trout (Nordwall 1999).

An organism’s ability to disperse is most important in relation to patchiness of the distribution of food, habitat, and other animals (Andrewartha and Birch 1954). Dispersal processes between ponds and streams are critical elements that determine fish assemblage dynamics in stream ecosystems (Schlosser 1995a). Ponds may be source areas, particularly for brook trout, which exploit the abundant benthic fauna (Gard 1961). Schlosser (1995a) observed temporal variation of community structure in adjacent stream
sections caused by changes in the abundance and composition of dispersing fish. Factors affecting dispersal include pond age and morphology, boundary permeability, and species-specific life history processes. Dispersal from source areas affects population dynamics substantially more than environmental abiotic variability (Pulliam 1998; Schlosser 1995a, 1998). Factors influencing whether dispersing fish survive and reproduce or act as reproductive sinks include spatial distribution of suitable habitat (Schlosser 1995a), density and competition, temporal abiotic variability that affects resource supply, and periodical bottlenecks to juvenile survival (Schlosser 1998). A distinction should be made between long distance movement in search of resources and true dispersal, which results in colonisation of new habitats (Andrewartha and Birch 1954).

Of the 30 long-distance movement records (Table 1), 21 individuals had to pass over one or more large beaver dams. Of these 21 individuals, 12 travelled upstream through these dams. Beaver dams marked the boundary of an adjacent section in 8 out of 30 stream sections. Dams may not be significant barriers to upstream movement, considering that \( \Psi \) was constant for upstream and downstream movers. Three large individuals (259 mm, 210 mm, and 210 mm) were first captured in upper T pond, then were later recaptured upstream, in reach U. Other smaller upstream movers (129 mm, 149 mm, 167 mm, 133 mm, and 222) were first captured in the stream section entering upper T pond (Fig. 1) and were recaptured upstream. In both of these cases, fish were able to bypass a relatively new yet large dam approximately 2 m high. Schlosser (1995a) suggested that dams are semi-permeable boundaries between ponds and streams. Significant downstream dispersal may only occur during periods of high discharge. Here,
upstream movement through dams occurred during relatively low discharge. Furthermore, $\Psi$ was equal in both upstream and downstream directions. These observations demonstrate that dams may be more permeable than Schlosser (1995a) suggested. Beaver dams may be significant obstacles to brook trout movements, but not necessarily complete barriers (Rupp 1954). Gard (1961) found that dams were not barriers to migration because trout were able to penetrate the interstitial spaces, bypass the dams using side channels, or jump over them.

It is likely that the upstream movers were travelling upstream to spawn. Aside from a few isolated patches of gravel, reach L is generally unsuitable for spawning. Reach U is a high quality spawning and rearing habitat, and the higher abundance of age one and two fish compared with reach L supports this. Spawning fish may also exit reach U at the downstream end, outside the study site boundary to spawn. As fish mature, they travel downstream and take up residence in the lentic environment of reach L. Large spawners probably travel into reach U, then possibly return to overwinter in reach L. Increased trapping for a longer duration would probably detect this movement trend. However, due to logistical constraints and the possibility of altering fish behaviour that would affect the modelling procedure, I decided to reduce trapping effort. However, trapping trends for both brook trout and longnose sucker in 1999 provide some support for this hypothesis. Gard (1961) observed that larger trout were in ponds, while more fry were found in the adjacent stream. Older ponds silt over, eventually losing spawning substrate over time. As a result, older ponds produce larger trout because of reduced competition (Call 1970). Rabe (1970) observed high standing crops of small brook trout in spawning areas and lower numbers of fish in seep ponds with inferior spawning
substrate. Pond size and the degree of natural recruitment are major influences on standing stock and densities. Ponds with suitable spawning habitat where recruitment was occurring tended to have high standing stocks of stunted fish (Winkle et al. 1990).

Several processes affect populations within a heterogeneous landscape, which include habitat complementation and supplementation, source-sink dynamics, and neighbourhood effects. Landscape complementation occurs when animals travel between relatively close habitat patches to obtain non-substitutable resources. In this case, larger populations may be supported than in systems where patches are far apart (Dunning et al. 1992). Landscape supplementation occurs when resources are substitutable and animals obtain the same resource in different habitats or switch to different resources in the same habitat. A large population may persist in a patch that would be too small to support it based exclusively on the resources within the patch (Dunning et al. 1992; Schlosser 1995b). Given that movement probability for this population is 0.165 month\(^{-1}\), it is possible that individuals are travelling to nearby habitat patches to supplement or complement their resource intake. If, however, there is a mobile and static component of the population, such a generalisation is difficult to apply to the entire population. The model is not refined enough to determine if individual fish are specifically moving from reach L to reach U to obtain resources. However, it is likely that habitat complementation is occurring across both reaches. The length-frequency histogram (Fig. 3) indicates a higher proportion of young fish in reach U than reach L. Recruitment in reach L is probably low because of the lack of spawning substrate and young-of-the-year trout. Because of the timing of the sampling periods, I was not able to detect spawning...
movements from L to U for brook trout, but spawning longnose suckers seemed to move from L to U to in 1999 so it is highly probable that trout are doing the same.

The multi-state capture-recapture modelling procedure offers a practical tool to address the RMP issue. The procedure outline here can be adjusted and replicated to suit specific populations. Larger data sets can be grouped to determine movement between specific habitat patches. Fish size can be modelled as a covariate to determine if fish size affects movement probability. It may be possible to group individuals into static and mobile groups, and to estimate and compare the separate survival and movement probabilities. As multi-state theory advances, other issues regarding the restricted movement paradigm can be addressed.

Literature Cited


Table 1. Length (mm), initial capture dates and locations, recapture dates and locations, and distance moved by brook trout in Crooked Creek

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Table 2. Movement Probability ($\Psi$) for the Best Approximating Models (dAIC$_c$ < 3.0) at varying levels of $\hat{c}$

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Fig. 1. Crooked Creek Study Area
Fig. 2a. Pooled length-frequency histogram for brook trout in Crooked Creek (n = 825).

Fig. 2b. Length-frequency histogram for brook trout in Crooked Creek separated by lower and upper reaches.

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Fig. 3. Movement probability at varying levels of $\hat{c}$. 

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Fig. 4. Frequency and maximum distance travelled for brook trout in Crooked Creek ($n = 73$).
Chapter 3. Conclusions and Applications of Multi-State Models to the RMP

I was able to document significant movement of brook trout in a beaver pond complex. On average, fish had a 0.165 month\(^{-1}\) probability of traveling 74 m away from their original capture location. The 95% confidence intervals vary depending on variance inflation, but a conservative estimate ranges from 0.088 to 0.288. This distance is only a minimum classification for movement. I found evidence of frequent long distance movement. These results support a different mobility pattern than that suggested by the restricted movement paradigm.

The multi-state model used in this study requires a very large data set. Estimation of movement probability greatly increases the number of potential parameters. A model with three states has nine transition probabilities per time interval, but when the model increases to four states, the number of transition probabilities increases to 16. The number of survival and recapture parameters also increases substantially. I was able to deal with low sample sizes by constraining the number of movement parameters. By definition, individuals could only travel from one state to another (\(\Psi_{AB}\) and \(\Psi_{AC}\)), and not the reverse. Furthermore, the linear nature of the lotic system allows movement to be modeled in one dimension, decreasing the complexity of the model. The data requirements are further reduced when the number of states is limited to three. The encounter probability is the same among the three states. A further limitation caused by low sample sizes is need to pool data across the entire stream reach. As a result, I was not able to estimate movements between specific areas (i.e. from reach L to U).

Replicating this study in a simpler stream system could alleviate the problem with low sample sizes. Although I was unable to unequivocally estimate encounter
probability, point estimates for $p$ ranged between 0.04-0.66 for model $S(T)p(g^*t)^\Psi(.)$. This model had the lowest $\Delta AIC_c$ when $\hat{c}$ was adjusted to 2.0 and 3.0, and a $\Delta AIC_c$ of 0.01 when $\hat{c}$ was adjusted to 4.0. The low capture probability is a result of complexity in the entire system. There were numerous backwaters, side channels, debris piles, and undercut banks that provided trout with places to avoid capture. A study in a "typical" trout stream without extra heterogeneity associated with a beaver pond complex would increase encounter probability and therefore, increase the sample size.

Overdispersion caused by movement heterogeneity is another issue that could be improved in future studies. Mobile individuals may have an extremely high movement probability, while sedentary individuals have a zero probability. The resulting movement probability, 0.165, is a rough average for the entire population. Separating the population into homogeneous groups and modeling separate movement probabilities could potentially reduce overdispersion. The problem with this approach is how to identify or define mobile fish from sedentary fish.

Perhaps one way of looking at $\Psi$, is that it is a transition probability between physiological states. A mobile fish is one physiological state, and a sedentary fish is another. This type of model could work assuming the population is composed of static and mobile components. However, there is some evidence to suggest the static and mobile dichotomy is an inappropriate model for stream fish movement. Movement behavior may be individually plastic (Gatz and Adams 1994, Gowan et al. 1994, Smithson and Johnson 1999), or a continuum rather than a dichotomy (Kennedy 1981, Linfield 1985; Rodriguez 2002). Over time, all marked individuals may eventually move. An increase in the number of sampling occasions may detect this pattern.
Furthermore, Markovian transitions or memory models (e.g. Brownie et al. 1993) may be able to determine if movement is plastic at the individual level.

The leptokurtic movement distribution observed in this study could be the result of population heterogeneity in movement behavior (Skalski and Gilliam 2000). Other potential sources of heterogeneity include temporal or spatial (Gilliam and Fraser 2001), morphology Skalski and Gilliam 2000; Gilliam and Fraser 2001) and behavior (Fraser et al. 2001). Skalski and Gilliam (2000) found evidence that size and growth were related to movement for blue chubs (*Nocomis leptocephalus*) creek chubs (*Semotilus atromaculatus*). In this study I was not able to detect a significant relation between movement and fish size. A multi-state model using fish size or growth rate as an individual covariate may be able to determine such a relationship. Fraser et al. (2001) suggested that boldness, the tendency to explore unfamiliar habitat, is a behavioral trait that may contribute to leptokurtic movement distributions. Such a behavioral trait would be difficult to model using the approach used in this study. A study that incorporates both a multi-state model component and an observational behavioral component (for example, Bachman 1984) may perform better.

An alternative approach to multi-state modeling and the RMP is to estimate movement between geographic states. Specific reaches of stream, tributaries, habitats, or other physical features would define the states. It may be possible to test the specific hypotheses regarding habitat complementation and supplementation and their effect on movement and survival probability (Dunning et al. 1992; Schlosser 1995b). There is a problem with the linear movement parameters. Individuals in close proximity to a state boundary would have a higher transition probability than individuals far away. Including
the distance from the boundary as an individual covariate could alleviate this. One other problem under this strategy is the assumption that stream reaches are considered independent units (Gowan et al 1994).

Future research should address mechanisms that affect the frequency and extent of fish movement (Gowan and Fausch 1996a). Applying quantitative measurements of movement is the first step to examine the more important issue of how movement variation responds to ecological factors and evolutionary consequences. Research into these issues will yield more information than focusing on stream salmonids and their conformity to the RMP (Rodriguez 2002). I was able to successfully quantify mobility for brook trout in a stream. With further refinement, it will be possible to address these questions.

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