Integration and Application of Radio Telemetry Data Collected on a Mobile Fish Species: a Synthesis of Bull Trout Movement Research

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Abstract

Bull trout *Salvelinus confluentus* are a species of char that have been intensively studied since they were listed as threatened under the U. S. Endangered Species Act in 1998. Much of the research on bull trout has involved the use of radio telemetry to monitor the movements of this highly mobile species. This project was initiated to compile information on completed and ongoing radio telemetry studies as a predicate to a synthesis of the state of knowledge about bull trout movement and habitat use. Additionally, predictive models of bull trout post-spawn habitat use were developed in the Boise River, Idaho, a system in which the bull trout population has been intensively studied using radio telemetry. In that system, large, migratory bull trout were distributed throughout the downstream portion of the watershed during winter; however, the most plausible predictive model highlighted the importance of Arrowrock Reservoir as the “hub” of winter habitat use. Field studies based on radio telemetry data can differ in the point of fish capture, the primary method of location, and the sampling intensity. The last section of this report contrasts three studies that differed in these respects highlighting the strengths of each approach. Several important questions about bull trout movement and seasonal distribution remain unanswered. Future telemetry studies should be designed to address specific, testable hypotheses about bull trout movement and habitat use in order to facilitate meta-analytical approaches to developing species-level inferences.

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Executive Summary

Bull trout *Salvelinus confluentus* are a species of char native to western North America. Populations are characterized by diverse life histories which often involve long-distance movements between spawning and overwintering habitats. The mobility of bull trout is a manifestation of the diverse life history of the species that presents a problem to professionals charged with the conservation of the species. As the human population has increased within the historic range of bull trout, the connectivity of spawning and overwintering habitats has decreased or been eliminated. One approach to the species' conservation has been the identification of spawning habitat in order to ensure that connectivity is maintained between these critical areas and downstream areas.

Because of the spatial scale of movements that are undertaken by migratory individuals, researchers have used radio telemetry to monitor movements and identify spawning and overwintering habitat. Radio telemetry can be used in a variety of ways in order to ask specific questions about animal movement, habitat use, resource selection, and population dynamics. The technology is particularly suited to mobile animals because individuals can be tracked over long distances using aerial monitoring. As mentioned above, major objectives of telemetry-based bull trout research have been the identification of spawning and rearing habitat for bull trout through the repeated location of large, migratory individuals. Such methods have enabled researchers to identify the timing and magnitude of spawning migrations in basins throughout the current species' range.

This report describes the results of a project designed to synthesize the existing knowledge about bull trout movements that has been gleaned from the use of radio telemetry. The project was conducted in two phases. The first phase involved the compilation of a database of research projects that have used radio telemetry to monitor bull trout movements. The purposes of the database were to identify the specific basins in which bull trout have been studied using radio telemetry and to catalog the methods associated with those studies. Additionally, the database is intended to facilitate dialogues between researchers who are embarking on telemetry studies and those that have conducted telemetry-based research in the past. In order to compile the information in the database I used a combination of web-based surveys and interviews with researchers. In many cases I used technical reports to complete entries in the database.

The telemetry database contained information on 72 studies of bull trout movement that involved the capture and tagging of over 3,000 bull trout. Bull trout have been studied using radio telemetry in Washington, Oregon, Montana, and Idaho in the United States and in Alberta and British Columbia in Canada. To date telemetry has not been used to study bull trout in the Jarbridge River, in Nevada. Telemetry studies have been conducted since 1991. Most of the information contained in the database describes objectives and methods associated with each project. Specifically the database included information on the following: 1) research objectives, 2) cooperators and funding; 3) information on collection, tagging, and tracking; 4) data analysis; and 5) reporting. Despite the litany of telemetry studies conducted in the last 16 years, relatively few have been published in peer-reviewed journals.

Bull trout in the Boise River, located in southern Idaho, have been well studied in the last 15 years and the analytical portion of the project began with the analysis of adult bull trout distribution during the post-spawn period based on data collected by the U. S. Bureau of Reclamation. The data used in this analysis were collected by Reclamation as part of a multi-year project investigating bull trout movements in the basin with specific interest in how a repair project at Arrowrock Reservoir might impact the migratory population. A suite of candidate models describing environmental factors associated with bull trout distribution during winter were evaluated using model-selection criteria. This approach differs from the traditional paired hypothesis approach to the scientific method in that I was evaluating the relatively plausibility of several candidate models designed to predict the presence of bull trout during winter. The plausibility of a particular model is evaluated against that of competing models. A highly plausible model doesn't "reject" the plausibility of competing models as would be expected under the hypothesis-testing paradigm. The models included several site-scale and landscape-scale variables that described characteristics of a target stream segment and that segment's position in the stream network. No single best model was identified during the analysis; however, bull trout presence was most influenced by the distance of an occupied stream segment from Arrowrock Reservoir. The results of this analysis led to the development of several hypotheses about the wintertime distribution of migratory bull trout in watersheds with and without reservoirs or lakes.

Telemetry studies can differ in three important aspects: 1) the location of fish collection and tagging; 2) the method of location; and 3) the intensity of sampling. The third chapter of the report begins with a description of three telemetry studies that were designed to collect data on the movement and distribution of bull trout but used different field methods to do so. The three studies described in this portion of the report were conducted in the Boise River, Idaho, the Clearwater River, Idaho, and the Wenatchee River, Washington. Different research objectives and logistical constraints in each watershed led to the adoption of differing field methods. While each of the studies collected data sufficient to describe the seasonal movements of their respective bull trout populations, the way in which the data were collected resulted in slightly different information. For example, intensive aerial and ground-based tracking in the Boise River yielded relatively fine spatial resolution of fish locations. The use of acoustic tags in the Clearwater River study facilitated the description of movement through Dworshak Reservoir. In the Wenatchee study, fixed telemetry stations identified the diel timing of movement by migratory bull trout. No single study was intensive enough to collect all of this information; therefore, the purpose of this exercise was to highlight the need for matching field methods to research objectives and the importance of employing a variety of data collection techniques during a telemetry study.

An original goal of the synthesis project was to use data from across the species' range to conduct a large-scale analysis of bull trout movement and distribution. This exercise was intended to be an extension of the Boise River analysis described in Chapter 2 of this report. The third chapter of the report concludes with a discussion regarding why this goal is unachievable at the current time. Most studies were excluded from consideration because of small numbers of tagged fish or limited spatial scale of the target watershed. However, coarse temporal and spatial resolution resulted in the exclusion of all the existing telemetry datasets considered for analysis. Temporal resolution refers to the frequency at which individual fish were located. Most telemetry studies greatly reduced sampling frequency in the post-spawn period; therefore, the resulting datasets included too few observations for use in a regression-based analysis. Spatial resolution refers to the precision of specific telemetry locations. The Boise River analysis was based on the presence of bull trout in individual stream segments (a portion of stream bounded on the upstream and downstream end by a tributary junction). Aerial tracking or the reliance on fixed stations eliminated the possibility of identifying occupied stream segments during the winter. Variation in temporal and spatial resolution of telemetry data highlights the need for coordination of future telemetry studies to ensure sample sizes and sampling intensities sufficient for incorporation into a dataset sufficient for species-level analysis.

Despite the wealth of data collected on bull trout in over 16 years of telemetry-based research, several questions remain unanswered. This report concludes with a discussion of unanswered questions about bull trout movement and why the answers to those questions are important for the conservation of the species. During the course of telemetry-based research on bull trout we have rigorously identified migration timing and spawning locations for many populations. However, the data we have collected are insufficient to address questions on resource selection, mortality rates, overwinter movement and activity, differences in migratory behavior between female and male bull trout, and dispersal behaviors. Additionally, with a foundation of descriptive studies it is necessary to begin addressing "why" questions about the movement patterns we have identified in order to develop a fuller picture of bull trout metapopulation dynamics and conservation needs.

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Integration and Application of Radio Telemetry Data Collected on a Mobile Fish Species: a Synthesis of Bull Trout Movement Research

Matthew R. Dare

Introduction

The salmonine (trout and salmon) fishes of the northwestern United States and western Canada are defined by their mobility. Migratory populations have been identified in every species of trout and salmon native to the northwestern United States (Scott and Crossman 1973; Northcote 1992). Migrations range in magnitude from 10-100 km in inland species such as cutthroat trout *Oncorhynchus clarki* to 100-1,000 km for anadromous species such as steelhead *Oncorhynchus mykiss* or Chinook salmon *Oncorhynchus tschawtschya*.

The mobility of salmonine populations has resulted in a wealth of information regarding the evolutionary and ecological implications of long-distance movements away from natal streams. The evolutionary trade-off between the increased risk associated with migration and the potential return in greater fecundity when compared to a non-migratory life history has been explored in great detail (Hendry et al 2004; see also Northcote 1978, 1992, 1997). The advent of new technologies, such as stable-isotope analysis, has allowed researchers to quantify the ecological role of salmon carcasses in the surrounding terrestrial landscape (Bilby et al. 1996). Research such as this increases our understanding of how these behaviors and the related anatomical and physiological adaptations first appeared and what forces have shaped migratory behavior over evolutionary time.

Populations of highly mobile stream fishes also create interesting, and arguably more challenging, management issues. Mobile animals require interconnected habitats in order to fully express their life history. Habitat connectivity has progressively decreased in the 200 years of substantial human influence in western North America. Resource managers, therefore, have to balance a local need for infrastructure, such as water, power, and roads, with a societal desire to preserve migratory species. Bull trout *Salvelinus confluentus* are a species of char that have been intensively studied since the species was listed as threatened under the U. S. Endangered Species Act. Bull trout currently occur in five U.S. states and two Canadian provinces where considerable efforts have been made to document their habitat preferences and seasonal movement patterns. Because of relatively specific habitat requirements, particularly for water temperature, bull trout have been negatively impacted by progressive urbanization in their native range. In particular, decreased connectivity and the degradation of spawning habitat are believed to be major factors in the decline of the species' range. An important management consideration is the fact that bull trout life history is very diverse (Rieman and MacIntyre 1993). Diversity, by definition, defies generality; therefore, it is difficult to ascertain the current state of our knowledge about this species. This project was undertaken in an attempt to synthesize the existing knowledge about bull trout that has been gained using a particular method: radio telemetry. Radio telemetry involves the physical attachment of an electronic transmitter to an animal. The movements of the tagged animal can then be documented over the life of the transmitter by tracking using ground-based or aerial techniques.

The purpose of this paper is to describe my attempt to integrate the disparate information collected on bull trout since 1990. The paper is organized into three chapters. Chapter 1 describes the contents of a database of radio telemetry studies in the United States and Canada. The database includes information on the objectives, location, timing, and methodology of nearly all of the bull trout studies that have used radio telemetry in the last 16 years. In Chapter 2 I use data from three bull trout studies in Idaho in an attempt to develop predictive models of post-spawn habitat use. This period in the life of a migratory bull trout has been rarely studied and this is the first attempt to develop models of their distribution and habitat use during winter. In Chapter 3 I integrate the first two chapters into a discussion of how to design a telemetry-based study to answer specific research questions. The contents of Chapter 3 are not a critique of existing research. Instead, I focus on important research questions that have not been addressed to date and discuss which of the myriad experimental designs that have been employed in telemetry research are amenable to answering specific questions. For example, the movement patterns of young migratory bull trout, often called "sub-adults", have not been intensively studied. However, some experts believe that metapopulation dynamics are facilitated by the movements of this age class of fish. How might one design a study to explore this age-class of fish and define the extent of their movements?

Chapter 1: A Database of Research Projects that have used Radio Telemetry to Study Bull Trout

Bull trout *Salvelinus confluentus* presently occur in five U. S. states and two Canadian provinces and with the exception of Nevada, the species has been studied with radio telemetry in every state and province in which it is found. Radio telemetry is not the only method suitable for monitoring movement by stream fishes; however, the large spatial scale of stream networks used by bull trout and the importance of identifying seasonal habitat, particularly spawning habitat makes radio telemetry an appropriate observational technique. This project was undertaken because managers and researchers interested in bull trout recognized the importance of defining the current level of understanding of the species as a predicate to developing future research questions.

The objectives of this report are to 1) provide and overview of the methods associated with the collection of metadata and the structure of the database; 2) highlight important and interesting information about bull trout research that was identified using the metadata; and 3) summarize future research associated with the synthesis project.

Methods

Data collection

Data were collected using an on-line questionnaire that was linked to a project website, www.northwestbulltrout.com. I interacted with researchers using email requests, phone solicitation, and personal contact. Each contributor was given instructions on how to access the form and complete the questionnaire. None of the questions were formatted so that answering them was required; however, in most cases, I followed up with the contributor to get information regarding the study. Upon completion of the on-line form, each submission was uploaded to me via email. The metadata were transferred into the formatted database by a technician. I reviewed each entry for completeness and clarity. In instances where formatting or grammatical mistakes were obvious, the entries were edited. However, I refrained from making substantial changes to statements in the submissions.

In several cases, I used technical reports to submit information from studies where the principal investigator was unavailable. When using technical reports, it was not possible to accurately answer every question in the form. This was particularly true in instances where contributors were asked to provide their opinion. Therefore, submissions from these studies are incomplete; however, the pertinent information regarding when, where, and why the project was undertaken was included. In cases where the contribution was made using a report or publication, the contributor is listed as "Matthew Dare."

Metadata collection was initiated in January 2004 and was suspended on July 1, 2004. Based on a thorough search of information on the internet, in libraries, and through discussion with bull trout researchers, I can confidently state that the 66 studies in this database constitute at least 98% of the telemetry data available on bull trout. If additional metadata become available, I will update the database and submit the revisions to the funding agencies.

Database organization

There are four components to a database: tables, forms, queries, and reports. This database contains a single table and a single form. Because of the small size and descriptive nature of the database, I did not develop specific queries pertaining to the metadata. The form is organized into eight sections (Table 1), with each section containing information on a particular aspect of each study. The primary use of the form was to facilitate transcription of the metadata into the formatted database. However, it is also the most direct way to review information within a particular submission.

Each contribution was assigned a unique identification number when it was transferred into the database. This number is the first column in the database and is labeled ProjectID. I use the identifying number from this field when referring to specific studies in this report.

When working with contributors who had metadata for large samples or projects conducted over multiple years, I advised them to make a submission for each "distinct" part of that project. I defined distinct as being separated by geographic scope or timeframe. Additionally, distinct parts could be delineated if research objectives differed among the subsets of the tagged sample. For example, the U. S. Bureau of Reclamation has been conducting a telemetry-based study of bull trout movement in the Boise River watershed in southern Idaho for three years. Tagged fish are being used to address three distinct questions about movement and habitat use. In this case, a submission was made for each of these parts of the study (Projects 9, 31, and 41).

Analytical methods

The analysis associated with the database focuses summarizing important and interesting aspects of the dataset. My objective was to provide an overview of the information contained in the database. Therefore, I used frequency distributions to describe the similarities and differences among the studies. Much of the analysis focuses on describing the proportion of respondents that answered particular questions in a similar way. For example, what proportion of the respondents said that identifying habitat use was an objective of their study? For the majority of these questions, respondents were able to select multiple answers. Consequently, most frequency distributions do not sum to 100 percent. The results are organized so that they parallel the structure of the database.

Results

Location

The first study that used radio telemetry to examine bull trout movements was conducted from 1989 through 1994 in the Lewis River in Washington (Project 23). This study was undertaken by PacifiCorp in cooperation with the Washington Department of Fish and Wildlife. This project began in 1989; however, radio telemetry was not used until 1991. Since then, radio telemetry has been used in a number of systems in four U. S. states and two Canadian provinces (Table 2). There are at least 21 on-going studies in the U. S. and Canada. On-going projects can be identified in the database in the field "EndReason".

Cooperators and funding

While many contributors did not provide specific information about how their study was funded, it is evident that a myriad of federal, state, academic, and private entities participate in bull trout research (Figure 1). State agencies, the U. S. Forest Service, and the U. S. Fish and Wildlife Service were most often cited as participating in radio telemetry studies. Academic institutions were well represented as cooperators in bull trout research: nearly one-fifth of the research described in the database was conducted by students pursuing graduate degrees at U. S. and Canadian Universities.

Most contributors cited multiple sources of funding. State and federal agencies were the cited as most often contributing funding to radio telemetry studies (Figure 2). Twelve studies were at least partially funded through some type of private, non-academic institution. The most common source of private funding was utility companies including Idaho Power, Avista, and Public Utility Districts in Washington. Contributors selected the "Other" category of funding for 26 studies. Examples of other types of funding include academic contributions associated with graduate research and governmental funding from Canada. Section 6 funding available through the Endangered Species Act was rarely cited as a source of funding for telemetry projects. However, it remains unclear whether this was due to the infrequent use of Section 6 money for telemetry studies or a lack of clarity on the questionnaire.

Contributors were asked to describe any form of expert advice or consultation that they sought out prior to beginning a project. The vast majority of studies involved some form of expert advice (Table 3). The researchers most often sought advice from experts within their own office or agency or the tag manufacturer. Inter-agency advisory groups were also common having been employed in 33 of the 66 studies. Details describing the extent to which researchers sought expert advice in the design and execution of their projects were not included in the questionnaire. Therefore, what constituted an "advisory group" or "in-house advisory group" was unclear. However, some contributors provided additional details regarding expert consultation. Professional colleagues were most commonly sought out for consultation. One contributor stated that he had sought "expert advice at professional meetings." Others contacted state, federal, or provincial biologists that had conducted studies using telemetry in the past.

Objectives

Radio telemetry studies of bull trout were most often initiated to meet multiple objectives. Only two of the 66 studies in the database cited a single research objective. The identification of migration timing and migration distances were the most often cited research objectives (Figure 3). Several contributors described research objectives that were unique to their study. Some examples of these other objectives include evaluating winter habitat use and distribution (4, 9, 42, 60), description of anadromous behavior (5, 49), evaluation of diel movement patterns (9, 11, 13), the investigation of illegal harvest (25) and the evaluation of losses into irrigation diversions (45 and 56).

When a contributor identified the evaluation of passage through a barrier as one of the research objectives of their study, they were asked to identify the type of barrier they studied and how they evaluated passage. While the loss of connectivity due to impoundment, road crossings, and diversion has been identified as a potential limiting factor to bull trout populations (Rieman et al., 1997), relatively few studies were initiated to expressly look at barriers (Figure 3). Most studies that looked at barriers were evaluating entrainment through a dam or movement through an upstream passage structure (Figure 4).

Sample information

The average sample size of tagged fish in these studies was 51 (SD: 48.2). The median sample size was 42 tagged fish. There was a wide range in sample sizes. An on-going project on the Lewis River in Washington has a sample size of five fish (Project 10); while the "largest" study involves 309 tagged fish in the North Fork of the Clearwater River in Idaho (Project 62).

Most studies used radio transmitters that were designed to last at least 6 months. Only three of the 66 studies used transmitters that had battery lives of less than 6 months. Forty-eight studies used transmitters that were designed to last over a year. A majority of studies used multiple transmitter models with different life expectancies. For example, three studies used transmitters that had battery lives of 1-3 months, 3-6 months, 6-12 months, and greater than 12 months. In instances where studies employed only one transmitter, these most often had life expectancies greater than 12 months.

Surgical methods did not appear to vary much among the studies. One of the 66 studies implanted transmitters orally (Project 49). When transmitters were implanted in the body cavity, MS-222 was the most common anesthetic and the incision was almost always closed using sutures (10 of the 65 studies that surgically implanted transmitters used surgical staples). Most contributors reported that they followed some guideline related to a tag-to-body weight ratio. It has been suggested the weight of a surgically implanted transmitter should not exceed some percentage of a fish's body weight. Limiting the tag-to-body weight ratio is believed to minimize the affects of tagging on the behavior of the fish being studied (Winter 1996). The most commonly cited tag-to-body weight ratio is 2 percent; however, there is empirical evidence that transmitter weights can exceed this rule (Brown et al. 1999). Thirty-nine of the 65 studies employed tag-to-body weight ratios of 2 percent or less.

Tagged bull trout were typically given a very short amount of recovery time before being released after surgery. The majority of studies allowed less than 30 minutes of recovery time following surgery (Figure 5). A study using orally implanted acoustic transmitters (Project 49) allowed fish to recover for at least 24 hours of recovery time; however, this was primarily to insure that fish did not regurgitate the transmitter.

Additional data

During surgery, most researchers collected other types of data on the fish or the environment. All of the studies collected some form of size data on captured fish. Fork length (n = 44) and weight (n = 58) were the most often collected types of size data. Thirty studies collected tissue samples in order to age the fish. Scales were the most frequently collected tissue for aging (n = 25). Seventeen studies collected fin rays or otoliths in order age fish. Contributors did not specify how the otoliths were collected; however, in the Boise National Forest, in Idaho, otoliths are collected from all radio-tagged mortalities (T. Salow, USBR, personal communication) and it is likely that a similar approach to collecting otoliths is used by other researchers. Two types of environmental data were typically collected during surgeries: water temperature and time of surgery. Several studies collected unique types of environmental data including physical habitat measurements, pH, alkalinity, and weather conditions.

Thirty-three contributors described their approaches to collecting information on the sex of tagged fish. The most common approach was to examine the sex organs during transmitter implantation; however, a number of contributors noted that this approach was not as effective as they had hoped. For example, one contributor assessed the efficacy of the internal examination this way: "Sometimes it worked, sometimes it didn't." Another common technique was to strip fish for the presence of eggs or milt. In one study (12) this approach was effective at identifying the sex of less than half of their sample (19 of 45 tagged fish).

Tracking

Contributors had four choices when identifying tracking methodology: ground, air, fixed station, combination. If contributors selected combination it was often impossible to determine which of the three tracking methods were used. In cases where contributors described their tracking methodology in greater detail, I selected the specific methods used rather than the "combination" option.

When tracking tagged fish, most studies employed a combination of tracking methods including aerial, ground-based, or fixed stations. Six studies only tracked fish from the air and six studies tracked fish only from the ground. Fifty-four studies used a combination of methods that was most often complementary aerial and ground-based tracking.

Forty-nine of the 66 studies included visual identifications of tagged fish during tracking. Visual identifications were made for a variety of reasons including confirmation of spawning behavior and the measurement of microhabitat at fish locations. However, fish were most often visited in order to confirm mortality. Visual identification was the most common way researchers identified spawning habitat; however, eight studies used mapping of fish locations in order to determine where tagged fish were spawning. Additionally, nine studies used mapping as a supplementary technique for identifying spawning habitat.

While 29 contributors stated that they had quantified the accuracy of their locations, only 11 of these conducted some sort of systematic test to validate the assumption that location accuracy was less than 1 km. Tracking from the air incorporates the most amount of measurement error because of the speed of the aircraft and distance between the receiver and the transmitter. However, in most cases, aerial tracking was followed by ground-based tracking to confirm a fish's position.

When evaluating the quality of the data collected during a study there are at least two important variables: the number of tagged fish, and the number of locations per tagged fish. The median sample size for studies included in the database was 42 tagged fish (see above). The questionnaire asked researchers to identify the number of times per month an average fish was located. Forty-one studies included location data on individual fish collected at least three times per month. However, only 24 studies tagged and tracked fish for more than 2 years. The intensity and duration of tracking is dependent on the research objectives (Millspaugh and Marzluff 2001), therefore, it is not possible to make a defensible evaluation of "high-quality" versus "low quality" data. However, approximately one-third of the studies monitored tagged fish for at least one calendar year and made at least three locations per month during the field component of the project. Based on an median sample size of 42 fish and three locations per month this would mean that the average study includes data for 36 discrete fish locations per tagged fish per study year. Based on previous telemetry work, I would consider this amount of observation necessary to evaluate the distance of seasonal migrations. However, the raw data will be necessary to evaluate the feasibility of examining variation in the timing of migration.

Fifty-four of the 66 studies included references to sources of mortality that were observed while tracking. Predation by avian or terrestrial predators was cited as a suspected cause of mortality in 33 studies. Interestingly, the same number of studies cited angling or poaching as a suspected source of mortality. The extent to which researchers went to confirm angling as a source of mortality is unknown. However, if these data accurately reflect causes of mortality in bull trout populations, then the anthropogenic rate of mortality may be virtually identical to the natural rate of mortality in some bull trout populations. Almost one-third (20 studies) of the studies cited transmitter implantation as a source of mortality. This proportion was slightly greater than the number of studies that identified spawning as a source of mortality (19 studies); however, this is proportion is possibly deflated due to the fact that some studies targeted juvenile fish.

Reporting

Technical reports are the most common format for reporting done during and upon completioof bull trout research projects. Forty-six of the studies used annual reports to communicate results while the studies were ongoing. Relatively few studies used email or other forms of communication during the execution of the project. Fifty-four studies used project completion reports to communicate their results to the funding agency. Researchers routinely use professional conferences as venues for communicating the results of their work on bull trout. Over half the contributors stated that results from their work were presented as posters or oral presentations at professional meetings. Peer-reviewed publication, however, was relatively rare, with only 14 contributors stating that their results were submitted for publication in a professional journal.

Discussion

The metadata contained in the telemetry database could be used by researchers currently studying bull trout as well as those intending to initiate a study in the future. The compilation of information about field methods was intended to serve as a catalog of techniques that have been used to study bull trout successfully in the past. While the questionnaire did not explore in great detail the “success” or “failure” of particular methods, I hope that researchers will use the database as a starting point for study design. Dialogue between researchers is a powerful tool for avoiding pitfalls and mistakes made during previous work. Because the database contains information on methods as well as contact information for contributing researchers, it is intended to facilitate communication between people studying bull trout movement and habitat use.

The goals of the bull trout radio telemetry synthesis project were to inventory the extent of telemetry-based research on the species and to use this information to conduct a large-scale evaluation of the species' movement patterns during the post-spawn period. Most of the telemetry-based research that has been conducted in the past was initiated to observe when and where bull trout migrated to spawn. Consequently most of the studies that incorporated post-spawn tracking greatly reduced the intensity of observation during the post-spawn period. For example, a study in British Columbia monitored bull trout movements from the air every 4-7 days in August and September but reduced sampling intensity to one flight per month during winter (Bahr and Shrimpton 2004). Therefore we know much less about bull trout movement and habitat use during the post-spawn period. The published literature contains only one study that was specifically designed to examine the movements and habitat use of bull trout during winter. This study was conducted in Montana and was focused on the habits and habitat associations of sub-adult bull trout (Muhlfeld et al. 2003).

The reality is that most of the information contained in the database has been shared among researchers at professional conferences and through publications and other forms of reporting. However, having all of this information in an accessible format represents a step toward greater coordination of future bull trout research. It is apparent that we have studied these animals throughout their current range and have collected large amounts of data on their spawning movements. These studies were initiated because of a management problem within the target basin; however, each study generally addressed the same research objectives. It is important to point out that while we know a lot about some aspects of bull trout movement patterns, a closer inspection of the data may reveal the need for additional work to address unanswered questions.

Following spawning migratory bull trout return to their feeding areas. Many of the populations that have been studied return to reservoirs following spawning. Therefore, the management of these populations must consider connectivity between the reservoir and spawning grounds but also the reservoir conditions during the time of year in which bull trout reside in the reservoir.

For fluvial populations that migrate between large rivers and tributary streams connectivity is an important management issue; however, the movement patterns and habits of migratory bull trout while they reside in their overwintering habitats are also of importance. A detailed study of bull trout movements and habitat use that incorporates data from systems containing a variety of post-spawn habitat types and migration patterns will greatly enhance our understanding of the seasonal population dynamics of this mobile species.

Table 1. Components of the database form.

Component	Description
Project information	Located at the top of the form. Includes a project number and contact information for the contributor.
Location	Includes descriptions of the system in which the study was conducted. Also includes a section for general study coordinates.
Cooperators and funding	Includes information of the entities that participated in the planning and execution of the project, including sources of funding.
Objectives	Project objectives are selected and described in this section. Includes a subset of questions pertaining to barriers.
Sample information	Information on the sample size, capture methodology, tags, and surgical methodology used in a study.
Additional data	Information on size, age, and environmental data are found in this section.
Tracking	Describes the methodology and frequency associated with fish tracking. Includes a section on habitat-related methods.
	Information on whether or not growth was calculated from recaptured individuals is found in this section.
	Includes information on the types of mortality observed during the study.
Reporting	Describes the types of reporting associated with the project and includes a section that allows the contributor to describe the contribution of the project to bull trout management.

Table 2. Sixty-six studies that have used radio telemetry to monitor bull trout movements and habitat use in the United States and Canada.

Study location	Principal investigator	Stream system
Alberta	Paul Hvenegaard	Kakwa River
Alberta	Kevin Gardiner	North Saskatchewan River
Alberta	Terry Clayton	Belly River
British Columbia	Bill Westover	Kootenay River
British Columbia	Karen Bray	Arrow Lakes Reservoir
British Columbia	Karen Bray	Lake Revelstoke Reservoir
British Columbia	Dave O'Brien	Duncan River
British Columbia	Brendan Anderson	Muskwa River
British Columbia	James Baxter	Pend D'Orielle River
British Columbia	Melinda Bahr	Morice River
British Columbia	Dave O'Brien	Fraser River
British Columbia	Jeff Burrows	Peace River
British Columbia	Ted Zimmerman	Davis River
Idaho	Joe DuPont	Pend Oreille River
Idaho	Matthew Dare	Boise River
Idaho	Dennis Scarnecchia	Salmon River
Idaho	Brian Flatter	Boise River
Idaho	Dennis Scarnecchia	Salmon River
Idaho	Peter Koetsier	Boise River
Idaho	Patrick K. Koelsch	Little Lost River
Idaho	Tammy Salow	Boise River
Idaho	Greg Schoby	Salmon River
Idaho	Danielle Schiff	Clearwater River
Idaho	Danielle Schiff	Lochsa River
Idaho	David Geist	Pend Oreille River
Idaho	Avista	St. Joe River
Idaho	Steve Elle	Salmon River
Idaho	Karen Frank	Boise River
Montana	Ladd Knotek	Clark Fork River
Montana	Ladd Knotek	Clark Fork River
Montana	Mike Hensler	Kootenai River
Montana	David Schmetterling	Clark Fork River
Montana	Clint Muhlfeld	Flathead River
Montana	Chris Clancy	Bitterroot River
Montana	Mike Jakober	Bitterroot River
Montana	Ron Pierce	Blackfoot River
Montana	Lynn Kaeding	St. Mary River
Montana	Larry Lockard	Clark Fork River
Montana	Gary Carnefix	Rock Creek

*Denotes submission completed using technical report

Table 2. Continued

Study location	Principal investigator	Stream system
Oregon	Jason Fenton	Malheur River
Oregon	Paul Sankovich	Grande Ronde River
Oregon	Paul Sankovich	Umatilla River
Oregon	Paul Sankovich	Walla Walla River
Oregon	Paul Sankovich	Grande Ronde River
Oregon	Paul Sankovich	Imanha River
Oregon	Vince Tranquilli	McKenzie River
Oregon	Craig Bienz	Sprague River
Oregon	Jason Seals	McKenzie River
Oregon	Brian Mahoney	Walla Walla River
Oregon	Eric Schulz	Metolius River
Oregon	Allen Hemmingson	John Day River
Oregon	Colden Baxter	Snake River
Oregon	Jim Chandler	Snake River
Oregon	Jim Chandler	Hells Canyon Reservoir
Oregon	Jim Chandler	Snake River
Washington	Jim Byrne	Lewis River
Washington	Frank Shrier	Lewis River
Washington	R. D. Nelle	Columbia River
Washington	John Stevenson	Columbia River
Washington	Barb Kelly Ringel	Columbia River
Washington	Larry Ogg	Dungeness River
Washington	Larry Ogg	Skokomish River
Washington	Mike Faler	Tucannon River
Washington	Fred Goetz	Puget Sound
Washington	Steve Corbett	Hoh River
Washington	Ed Connor	Skagit River

Table 3. Sources of expert advice and consultation for studies of bull trout using radio telemetry. Most contributors cited multiple sources of expert advice.

Type of advice	Number
Inter-agency advisory group	32
In-house consultation	37
Tag manufacturer	34
Other	8
None	8

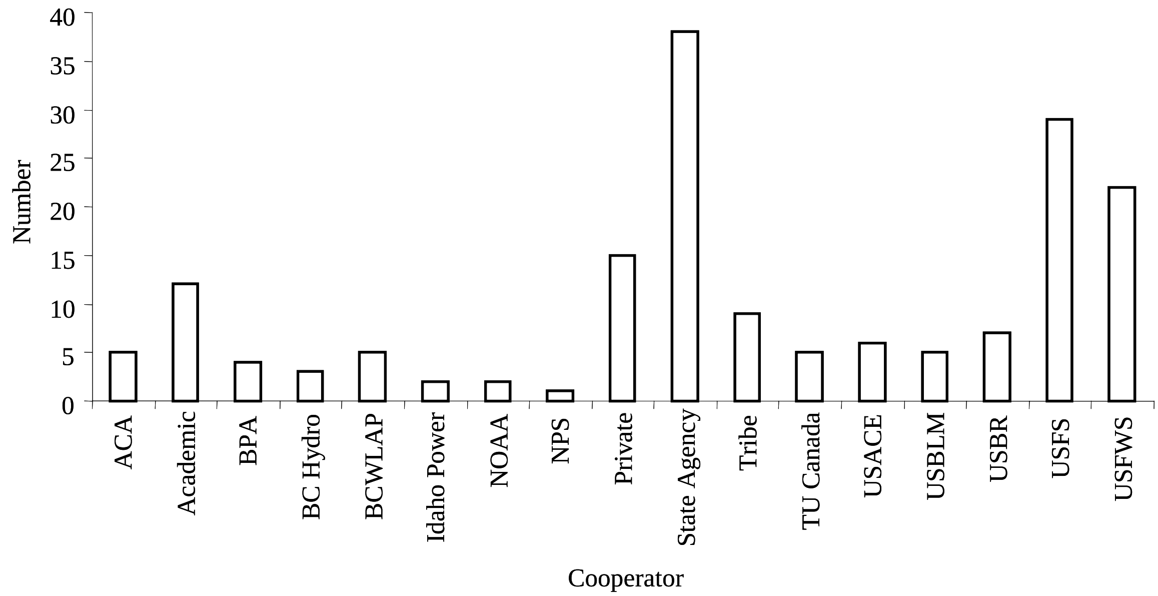

Figure 1. Cooperators in bull trout research using radio telemetry.

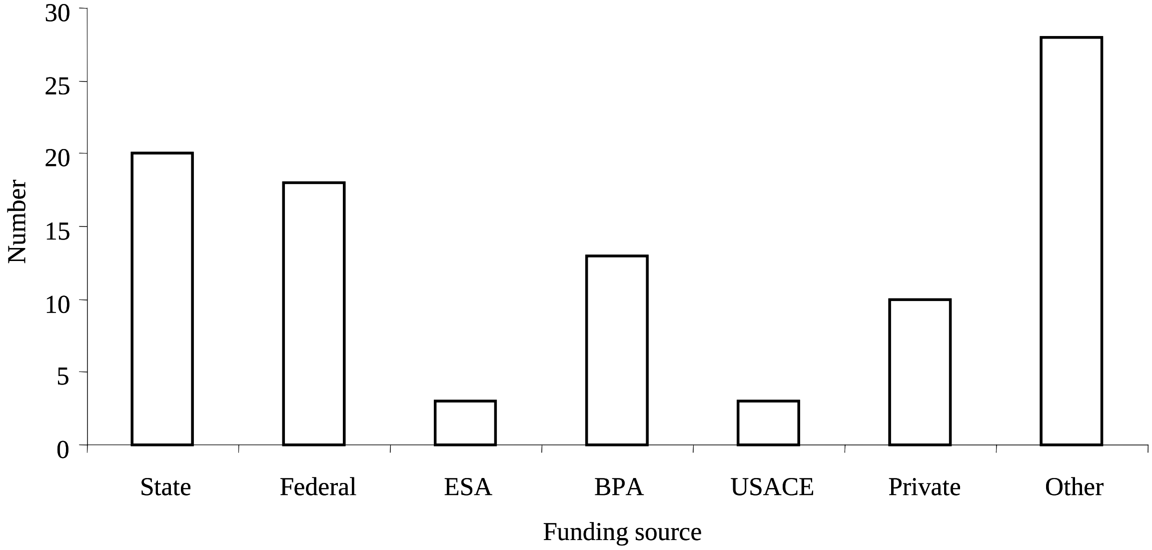

Figure 2. Sources of funding for bull trout research using radio telemetry.

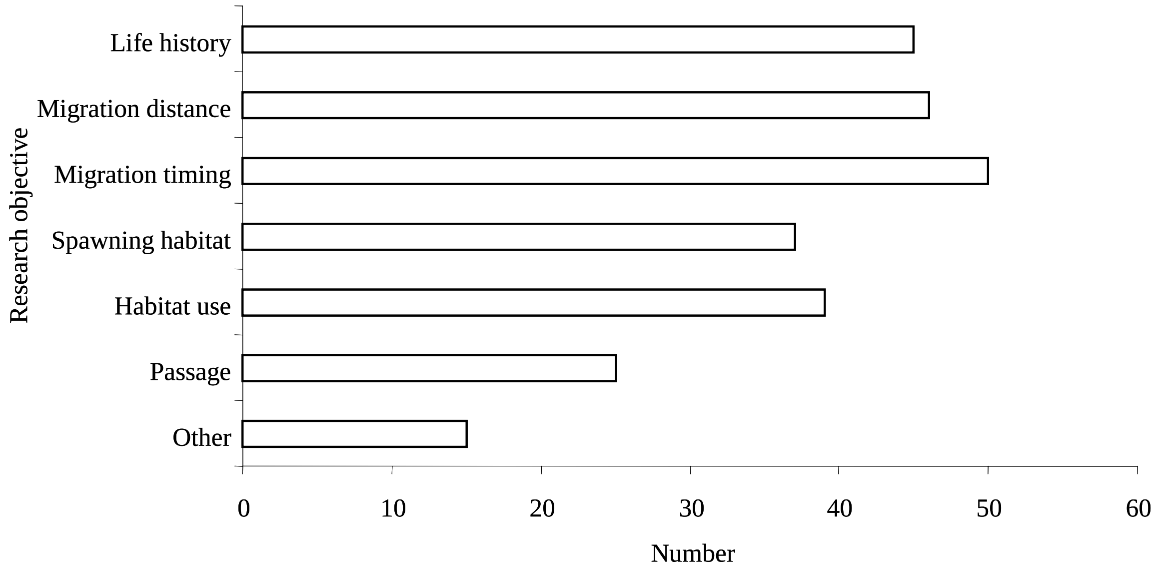

Figure 3. Objectives identified for bull trout research projects using radio telemetry.

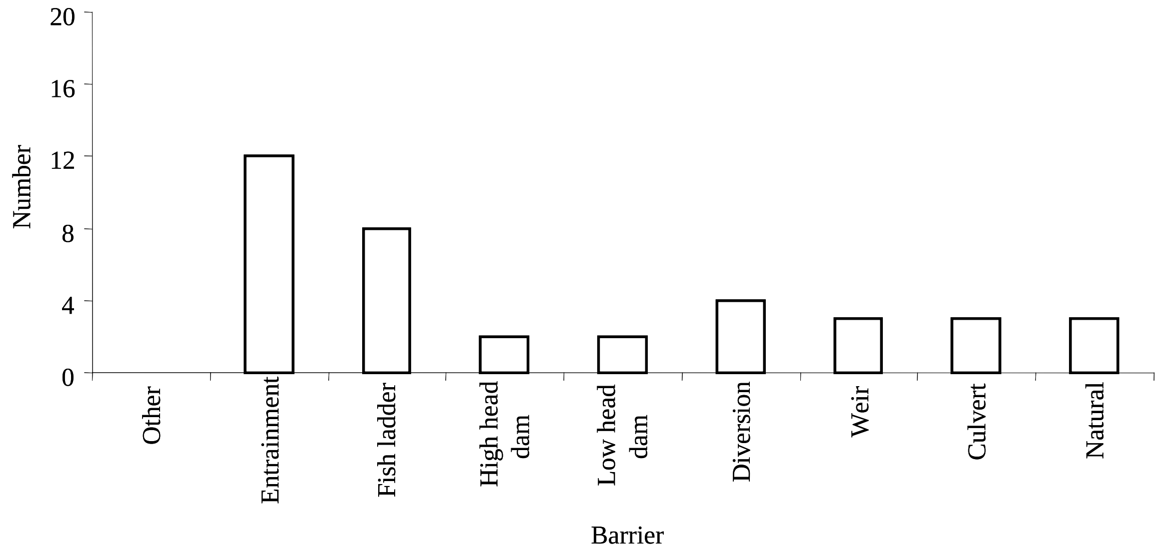

Figure 4. Frequency of barriers identified as research objectives for bull trout research projects.

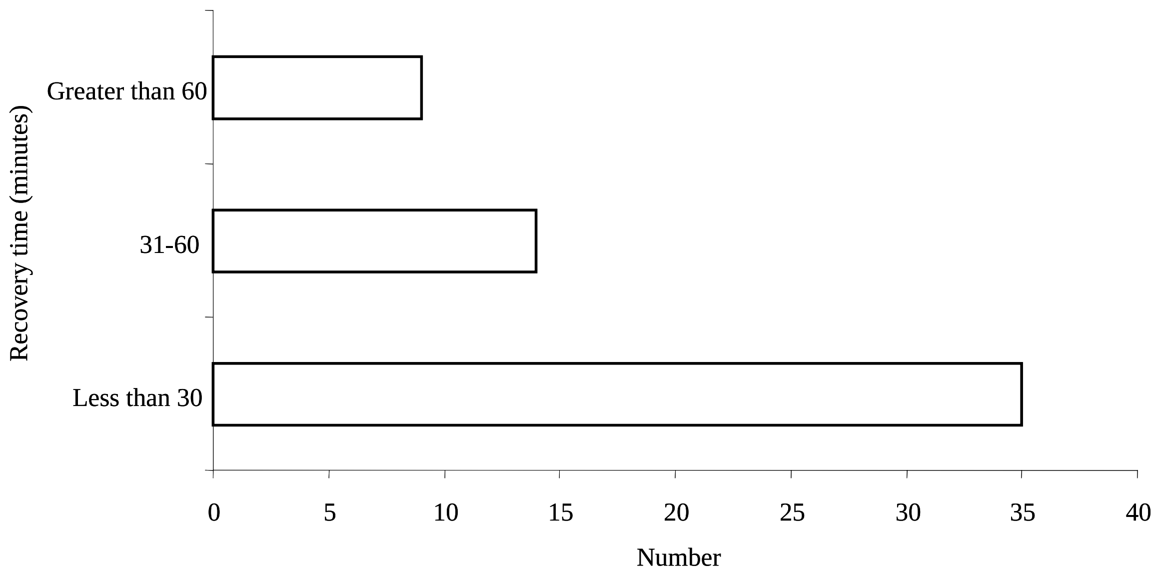

Figure 5. Length of recovery time following surgical implantation of radio transmitters in bull trout.

Chapter 2: Defining Environmental Variables for an Analysis of Bull Trout Post-Spawn Habitat Use

Animal migration is a process by which populations move among connected habitats over a predictable time period (Endler 1977, cited in Hendry et al. 2004). Stream fishes typically migrate between spawning locations and downstream habitats containing adequate food resources. For migrating fish populations these habitats are typically distinct and may be separated by long distances (Northcote 1978; Northcote 1997). Migratory behavior is believed to involve increased risk of mortality as an individual moves across the landscape (Hendry et al. 2004). For successful migrants this risk, however, is annulled by increased food availability and resulting increased growth and fecundity (Gross 1987; Northcote 1992; Hendry et al. 2004). While the impetus for migration is understood, the choices made by a migrating individual to bypass or occupy certain habitats is not. This is particularly true for the migration away from spawning areas where there most likely is not a discrete endpoint recognizable by the migrating individual. The mystery regarding habitat use during and after a migration away from spawning grounds probably stems from the fact that migratory individuals have to weigh a variety of factors when selecting a particular location (Chapman 1966; Chapman and Bjornn 1969). Undoubtedly, these include site-scale features related to habitat, food availability, and predation risk (Hughes 1992; Gowan and Fausch 2002; Railsback and Harvey 2002). However, the location of the position within the stream network (e.g., the distance between a wintering location and spawning habitat) may also be important.

Bull trout *Salvelinus confluentus* are a migratory char that have been intensively studied since they received protection as a threatened species under the U.S. Endangered Species Act (USFWS 1998). Most research has focused on identifying the movement patterns of migratory individuals during upstream spawning migrations in the fall (Dare, unpublished data). Target populations have been classified as "fluvial" or "adfluvial" based on the type of post-spawn habitat used: stream fishes that migrate between headwater spawning areas and large, downstream rivers have been called fluvial populations; whereas migratory individuals moving between spawning streams and a lake or reservoir are called adfluvial (Varley and Gresswell 1988; Rieman and McIntyre 1993). Within the published literature, studies of bull trout distribution within a watershed have focused on movement patterns and timing (Fraley and Shepard 1989; Swanberg

1997; Muhlfeld et al. 2003; Muhlfeld and Marotz 2005) and more recently on linkages between life history and movement (Bahr and Shrimpton 2004; Downs et al. 2006).

While the rationale for focusing on the spawning migration and associated habitat use patterns is logical based on the management objectives for the species, the question of why a bull trout selects one location over another following spawning remains unanswered. My objective was to determine if there were identifiable environmental correlates to the distribution of migratory bull trout in the habitats they used following their migration downstream from spawning areas in the fall. In hypothesizing about the post-spawn distribution of migratory bull trout in the upper Boise River Basin I assumed that the microhabitat selection by individual bull trout would be closely tied to energy acquisition (Fausch 1984; Hughes and Dill 1990; Railsback and Harvey 2002). The distribution of the migratory population; however, would be correlated to larger-scale features of the landscape. Such landscape-scale features include distance of a particular location from spawning areas and the reservoir. This idea stems from the work by Gowan and Fausch (2002) who studied feeding position choice by large brook trout *Salvelinus confluentus* in Colorado streams. In that study individuals that were displaced from a preferred position in a pool tended move to a secondary feeding location out of the home pool. The authors concluded that these large individuals monitored habitat conditions at a larger spatial scale than they typically occupied within a season and were able to move from their home pool to known alternative feeding areas. My hypothesis is that as the scale of movement increases so too does the scale at which an individual monitors habitat conditions around it. Therefore, within the context of seasonal migration and habitat use, landscape-scale parameters will be important factors in individual position choice. I used logistic regression analysis to determine the probability of bull trout occupancy of a stream segment based on three parameters: road presence, segment distance from Arrowrock Reservoir, and connectivity to spawning areas. I predicted bull trout occupancy would be negatively correlated with roads and positively correlated with decreasing distance from Arrowrock Reservoir and increasing connectivity to spawning areas. The last section of this chapter describes my effort to replicate this analysis using data collected during other bull trout studies. One of the major research objectives of the synthesis project was a multi-basin analysis of bull trout post-spawn movement and habitat use. I was unsuccessful in obtaining data of sufficient resolution for another round of analysis and I describe several factors that contributed to my failure to meet this objective.

Methods

Bull trout location data

I used location data collected by the U.S. Bureau of Reclamation during a multi-year study of bull trout movement and distribution associated with the repair of Arrowrock Dam (see Salow and Hostettler 2004 for a summary). The response variable used in this project was based on location data for 50 adult bull trout surgically implanted with radio transmitters during their post-spawn, downstream migration (Table 1). A detailed description of the collection and tagging methodology can be found in Salow and Hostettler (2004). I used location data based on aerial and ground-based observations from 27 September 2002 to 30 April 2003. I only included individuals for which there were at least 10 observations, which meant an individual was tracked for approximately two months.

Watershed delineation

The upper Boise River basin encompasses an area of approximately 5,700 km^2 and contains three major subbasins: the North Fork, Middle Fork, and South Fork (Figure 1). Detailed descriptions of the basin can be found in Rieman and McIntyre (1995) and Salow and Hostettler (2004). For this analysis I considered the portion of the basin upstream from Arrowrock Dam, including the South Fork of the Boise River upstream to Anderson Ranch Dam. Stream segments were identified and attributed using U.S. Geological Survey 30 m Digital Elevation Models (DEM) obtained through the TauDEM (Terrain Analysis Using Digital Elevation Models) database (Tarboton 1997). Within a TauDEM data layer a stream network is divided into segments based on tributary junctions. For this analysis I only considered stream segments downstream from potential spawning areas (patches) and therefore, I truncated the full stream network based on elevation and contributing area. Rieman and McIntyre (1995) found that bull trout presence in the Boise River basin was most common at elevations greater than 1,600 m; therefore, I removed stream segments at elevations less than 1,600 m from consideration. Streams having widths less than 2 m have a low probability of bull trout presence (Rieman and MacIntyre 1995) and Dunham and Rieman (1999) reported that most streams in the Boise basin with contributing areas less than 400 ha were too small to support bull trout. Upon review of a map of the watershed truncated based on contributing areas less than 500 ha I opted for a more liberal contributing area criterion of 250 ha which retained several tributary streams necessary for segment delineation. The truncation procedure resulted in a stream network containing 304 stream segments (Figure 2; Table 2).

Initial inspection of the distribution of bull trout presence in the network revealed that bull trout locations were restricted to the mainstem sections of the Middle Fork, North Fork, and South Fork subbasins, and Arrowrock Reservoir (Figure 3). This resulted in a substantial skewing of the response variable: bull trout were not observed in the 230 tributary stream segments. Therefore, I used the stream segments that were classified as mainstem segments for further consideration (Table 2). This resulted in a dataset including 74 stream segments with 39 occupied segments and 35 unoccupied segments.

Environmental variable derivation

For each of the original 304 stream segments I derived a number of site-scale and watershed-scale variables (Table 3) in order to compare these attributes to bull trout presence and frequency. The site-scale variables included segment length, segment slope, segment elevation, and road presence. Segment length, calculated as the stream distance (km) between tributary confluences, was included in the TauDEM database file. For analytical purposes, this variable was treated as a nuisance variable designed to account for the idea that the probability of presence in a segment may be related to segment size. The elevation of a stream segment was calculated by averaging the upstream and downstream elevations (m) of the stream segment. These data were available in the TauDEM data file. The presence of a road within 100 m of a stream segment was determined by overlaying a shapefile that included roads onto the TauDEM layer and creating a 100-m buffer around the target stream segment. Segments were coded 1 if a road was present within 100 m and 0 if a road was absent. In order to account for first-order autocorrelation in the response variable, I developed a categorical variable to account for the possibility that a fish present in an adjacent segment would increase the probability of a fish being present in a target segment. If a fish was present in segment directly upstream, downstream, or in both segments adjacent to a target segment the segment was coded 1. If no fish was present in either of the adjacent segments, the segment was coded 0.

Watershed-scale variables included contributing area, distance to Arrowrock Reservoir, and connectivity to spawning habitat. Contributing area was calculated as the area (ha) upstream of a segment that drained into that segment. Contributing area and segment slope (%) were available in the TauDEM data file. The distance to Arrowrock Reservoir was calculated by measuring the distance (km) between the midpoint of a segment and Arrowrock Reservoir. Connectivity to spawning habitat was estimated by calculating a weighted average distance between each stream segment and 13 spawning patches in the upper Boise River basin (Figure 4). I used spawning patches identified by Rieman and McIntyre (1995) and only included those spawning patches where bull trout presence had been confirmed. Connectivity was calculated based on the following formula:

$$Connectivity_i = \sum_{1}^{13} \frac{A_j}{d_j}$$

where the connectivity (km) for segment *i* is equal to the area (km^2) of spawning patch *j* divided by the distance (km) to spawning patch *j*, summed for all 13 spawning patches.

Because bull trout were occupying these stream segments in the fall, winter, and spring of the year, I did not consider a temperature variable in this analysis. While temperature has been shown to be an exceedingly important variable in bull trout habitat use at other times of the year (Fraley and Shepard 1989; Rieman and McIntyre 1993), an inspection of the stream temperatures at this time of year revealed they were well within the acceptable range for bull trout occupancy.

Data analysis

Bull trout occupancy was a dichotomous variable where a segment received a score of 1 if a bull trout resided within it for two consecutive weeks. A segment received a score of 0 if it did not meet this criterion. The relationship between bull trout occupancy and environmental variables was analyzed with binary logistic regression.

In developing a logistic regression model to explain bull trout distribution within the stream network I employed the information-theoretic approach for model selection described by Burnham and Anderson (2002). I developed a global model and a series of nested candidate models that included various combinations of the variables described above (Table 4). Two variables, SEGLENGTH and FISH, were included in all the models in order to account for the correlations between segment size and fish presence and fish presence in adjacent segments and fish presence in a target segment.

I evaluated potential correlations among predictor variables by constructing a correlation matrix and calculating variance inflation factors for each predictor variable (Phillipi 1994). Several of the potential predictors were correlated with one another and I removed variables from further consideration based on the strength of their relationship to the response variable and the ecological interpretation of the relationship. For example, I selected distance to Arrowrock Reservoir over segment elevation and segment slope because of the ecological interpretability of the former variable. The variance inflation factors for the remaining variables had values less than 10.0 and did not suggest problems with multicollinearity. I evaluated the fit of the global model using the overdispersion statistic and a goodness-of-fit test (Allison 1999; Hosmer and Lemeshow 2000).

I used Akaike's Information Criterion (AIC) and AIC weights to evaluate the plausibility of the global model and candidate models (Burnham and Anderson 2002). This approach allows the modeler to objectively evaluate the relative plausibility of a suite of candidate models. I used the 1/8th rule to evaluate the relative plausibility of the candidate models (Burnham and Anderson 2002). By this rule, models having AIC weights less than 1/8th of the maximum weight were not considered plausible. The converse was also considered true: all models whose weights were within the 1/8th cutoff were considered plausible. In cases where more than one model appears plausible, the modeler is able to average the parameter estimates to develop a composite model. I averaged parameter estimates for all plausible models. For logistic regression models these parameters include odds ratios and corresponding confidence intervals. A detailed description of the information-theoretic approach, AIC, and model averaging can be found in Burnham and Anderson (2002). Concise descriptions of the approach and specific applications are also available (Anderson et al. 2000; Thompson and Lee 2002; Hobbs and Hilborn 2006).

I evaluated the predictive power of each model by examining the proportion of concordant pairs, where a concordant pair resulted from agreement between the predicted and observed occupancy status of a stream segment. I also estimated the specificity and sensitivity of regression models (Olden and Jackson 2002). Model specificity, the ability to predict species absence, was calculated by dividing the number of segments where bull trout were predicted to be absent into the number of segments where bull trout were not observed. Model sensitivity, the ability to predict species presence, was calculated in a manner similar to specificity, except that the number of predicted and observed presences was used. In both cases, the predicted value for a segment was based on the probability of species presence calculated by a specific regression model. The cutoff for predicted occupancy status was 0.5.

Results

The best-approximating model for bull trout presence included ARROWDIST along with SEGLENGTH and FISH (Table 5). Inspection of the AIC weights revealed that all of the candidate models were plausible and parameter estimates and odds ratios for the parameters were averaged across the models (Table 6). With the exception of FISH, all of the estimated odds ratios overlapped 1.0; therefore, it is difficult to interpret the magnitude of their respective effects. An inspection of the nature of the relationship (i.e. positive or negative) between bull trout presence and the predictor variables in the composite model revealed some interesting results. Bull trout presence was negatively correlated with the presence of roads and increasing distance from Arrowrock Reservoir. However, bull trout presence was also negatively correlated, albeit weakly, with increasing connectivity.

The inclusion of segment length (SEGLENGTH) and the indicator variable for occupancy of an adjacent segment (FISH) in all models was necessary to control for the correlations between segment length and probability of occupancy and first-order autocorrelation in segment occupancy. The odds ratio for segment length supported my prediction that the probability of occupancy increased as segment length increased. This relationship, however, was not statistically significant (Table 6). Occupancy status of a segment was strongly correlated to the presence of an occupying fish in an adjacent segment and this was the only statistically significant relationship within all models. These results suggest that bull trout were patchily distributed within the stream network (Figure 3).

All of the models had high predictive power and correctly classified the status of a segment for at least 86% of the segments (Table 5). The specificity of the models ranged from 54.3 to 68.6% and the sensitivity ranged from 74.3 to 87.2% (Table 5). Model 5, the model with the highest AIC weight did not have the highest predictive power based on any of the three measurements.

Bivariate plots were useful in understanding the relationships among the predictor variables and the presence of bull trout. Bull trout occupied stream segments with contributing areas greater than 80,000 ha (Figure 5). There was not a strong demarcation between occupied and unoccupied segments with respect to segment length; however, the majority of occupied segments were less than 5 km in length (Figure 6). A strong pattern was observed with connectivity and distance to the reservoir, where bull trout occupied only segments having connectivity less than 20 km and within 58 km of Arrowrock Reservoir (Figure 6).

Discussion

With the exception of connectivity, the nature of the relationships between bull trout occupancy and the environmental variables conformed to my predictions. The least connected segments were those that were furthest from the spawning patches located in the North Fork and Middle Fork drainages. Therefore, connectivity was lowest in the most upstream South Fork stream segments. I expected that connectivity to spawning areas would be important as all of the bull trout monitored in 2002-2003 spawned in the North Fork and Middle Fork drainages (Salow and Hostettler 2004). There are at least two possible explanations for this result. First, the odds ratio for connectivity was -0.94 and 95% confidence interval for this estimate overlapped 1.0. Therefore, it is very difficult to say whether the actual relationship between bull trout occupancy and connectivity to spawning patches is accurately estimated by the value -0.94. In other words, this result could be a statistical artifact and not a biologically meaningful description of the relationship between these two variables. The second possible explanation is ecological: large, migratory bull trout are not limited by the maximum distances they travel between spawning locations and overwintering areas in this basin. The distance between the most upstream spawning patch and the base of Anderson Ranch Dam is approximately 155 km and bull trout are believed to have previously migrated between the Snake River and spawning locations in the Boise basin, a distance of at least 200 km. Bull trout have routinely been observed to move greater than 150 km during seasonal migrations (Fraley and Shepard 1989; Swanberg 1997; Muhlfeld and Marotz 2005; Bahr and Shrimpton 2004) and Baxter (2002) observed migratory bull trout to move approximately 280 km between the Wenaha and Snake Rivers in Oregon. It is not likely, therefore, that the distance between spawning tributaries and downstream habitats in the Boise basin is a limitation to migrants.

The relationship between bull trout occupancy and connectivity may have also been confounded by the frequency of use of the South Fork of the Boise River. The South Fork was occupied by a large percentage of the migratory bull trout included in this study. The South Fork is a regulated system that supports large numbers of salmonids and is managed as a trophy fishery. Bull trout most likely migrate into this system because of habitat characteristics and abundant food supply. The South Fork, however, is the least connected of the three sub-basins. This is evident in Figure 6, which bears a distinct similarity to a map of the study area (Figure 2). The pattern in Figure 6 shows the stream segments within the South Fork are less connected to spawning areas as the distance from Arrowrock Reservoir increases. This is not the same pattern for the segments in the other two subbasins where increasing distance from the reservoir reflects movement upstream within the watershed and closer to spawning patches. Unfortunately I do not know whether historical use of the South Fork by bull trout was as extensive as it is under regulated conditions. However, it appears that the frequency of use of the South Fork exerted a substantial influence on the connectivity variable and the relationship between bull trout occupancy and connectivity to spawning patches bears further exploration (see Future Research below).

I found bull trout occupancy was negatively correlated with the presence of roads. Similar conclusions were reached during previous studies of bull trout distribution (Rieman and McIntyre 1995; Baxter et al. 1999). There are at least two mechanisms by which a nearby road can negatively affect migratory bull trout. First, road crossings can lead to habitat degradation via increased sedimentation. Fine sediments are negatively correlated with the presence of a variety of salmonid species; however, this relationship generally factors into spawning habitat. Given the stream size of the target segments and the time of year in which they were occupied, the second potential mechanism is potentially more plausible: the presence of roads facilitates angler access. There is substantial angling pressure in the Boise basin, particularly in the South Fork. Bull trout are frequently captured by anglers throughout the watershed and illegal harvest of bull trout has been documented (Salow and Hostettler 2004).

My results suggest that segment occupancy is affected by a segment's spatial relationship with Arrowrock Reservoir. Despite the frequency of use of the South Fork, the migratory component of the population in the Boise basin is classified as adfluvial and I expected to detect a statistical signature reflecting the frequency of use of the reservoir. Stiefel and Dare (2006) monitored the movement patterns of bull trout within the reservoir in 2004-2005. The majority of bull trout in their sample occupied locations in the upstream section of the reservoir for approximately 80 % of the fall and winter of 2004-2005 (Stiefel and Dare 2006). These observations included individuals that were suspected to have moved into the South Fork for as long as two months.

Previous research has found that bull trout frequently move between the reservoir and the South Fork during the winter (Salow and Hostettler 2004). Bull trout are presumably migrating to Arrowrock Reservoir in search of food; however, the frequency of segment occupancy in the South Fork suggests that food availability is sufficient to support large, migratory bull trout for extended periods. Therefore, movements between the reservoir and South Fork could be a reflection of a mobile predator searching for food. A second explanation for frequent movement between the reservoir and the South Fork is that bull trout monitor the environmental conditions related to spring migration by returning to the reservoir throughout the winter (Stiefel and Dare 2006). Spring migrations from Arrowrock Reservoir are asynchronous and bull trout begin upstream movement as early as February (Salow and Hostettler 2004). Previous research, however, has failed to identify environmental correlates to departure timing (Salow and Hostettler 2004; Stiefel and Dare 2006). Regardless of the mechanism behind the pattern, previous research supports my conclusion that the post-spawn distribution of bull trout in the Boise basin is closely tied to Arrowrock Reservoir.

Despite that fact logistic regression modeling did not result in a single best model of bull trout occupancy, my results suggest that a segment's position within the stream network affected the probability that a bull trout would be present in that segment. The plausibility of a suite of candidate models can be evaluated with AIC values and their corresponding weights. The two models with the highest AIC weights included distance to reservoir and connectivity to spawning habitat. The weights of these two models were almost double that of the next most plausible models (Table 5). There is no completely objective criterion by which a modeler can exclude one or more candidate models from consideration (Burnham and Anderson 2002); however, I am confident in an ecological link between bull trout occupancy and a segment's spatial relationship to Arrowrock Reservoir. It is important to point out that the weight value for the model that considered distance to reservoir alone was almost twice that of the model that considered connectivity to spawning patches. These results are most certainly context dependent; i.e., other factors may be more important in other, particularly larger watersheds. At the same time, the importance of landscape-scale variables that I measured lend credence to Thompson's (1959) suggestion that habitat for a mobile salmonid should not be measured instantaneously: an individual's position at any one time is a single observation within a network bounded by the spatial extent of an individual's movements over their lifespan. While my results are certainly not unequivocal, I believe my hypothesis that the scale of environmental parameters that factor into decisions about which habitats to occupy is commensurate with the scale of habitat use measured, is supported by this research. Therefore, I believe the conclusions of Gowan and Fausch (2002) regarding the scale at which individuals monitor the habitat around them can be extended and applied to the post-spawn distribution of bull trout in the Boise basin.

Despite extensive review of other radio telemetry studies, I was unable to obtain data of sufficient spatial or temporal resolution to extend this analysis to another watershed. Spatial resolution refers to the ability to assign a bull trout location to an individual stream segment within a watershed. Temporal resolution refers to sufficient sampling intensity to identify localized bull trout movements following the post-spawn migration. One of the major pieces of inference from the Reclamation study in the Boise River is that bull trout do not stop moving once they reach their overwinter location. In fact these animals are quite mobile during winter (Salow and Hostettler 2004). My analysis depended upon being able to identify the small-scale (< 5 km) movements of bull trout during this period. Unfortunately most radio telemetry studies incorporated decreased sampling intensity during winter into their methodology.

Small sample sizes tended to result in studies that lacked both the spatial and temporal resolution for inclusion in this analysis. For example, Idaho Fish and Game conducted a telemetry study in the Lochsa River in 2003. Because there is not a reservoir on the Lochsa River, I hoped to contrast these results with those obtained in the Boise River where proximity to Arrowrock Reservoir was the best predictor of bull trout occurrence during the winter. Unfortunately, the 32 bull trout that were tagged as part of the Lochsa study were observed monthly over the course of the study. Therefore, because of the low intensity of observation as well as small sample size, considering the needs of logistic regression, I was not able to use these data as part of the analysis. The small number of observations of individual bull trout during the Lochsa study is not necessarily a limitation with respect to the project objectives. The investigators tagged these fish in order to collect basic life history information and identify migration patterns within the Lochsa and Clearwater Rivers. Additionally, the investigators were curious as to the extent of use of two particular tributaries to the Lochsa River. To meet these objectives it was not necessary to observe individual fish 2-3 times per week. I encountered this same problem when I reviewed data collected during a multi-year study of bull trout movement in the Clearwater River, upstream from Dworshak Dam. This study included over 300 radio-tagged bull trout collected and observed over three years (see Chapter 3 for further detail on this study). A small sample size was not a problem with this study. While there were sufficient numbers of bull trout observed during this study individuals were only observed twice a month and sometimes less during the winter. Again, the objectives of this study did not necessitate intense observation during winter (see Chapter 3).

Field methodology was also a factor in excluding data from further analysis. The U. S. Fish and Wildlife Service conducted a telemetry study in the Wenatchee River in Washington. Over 50 bull trout were observed over three years as part of this study. However, the investigators relied on fixed telemetry stations as their primary mode of field data collection. The spatial resolution of the data collected during this study was too coarse to allow for identification of occupied stream segments and therefore could not be used for my analysis.

The results of my review suggest a need for larger scale coordination of future telemetry studies in order to facilitate the study of the species at the species scale. The majority of investigators who have used telemetry to study bull trout movements feel that they met the objectives of their respective projects (see Chapter 1). However, the majority of these studies lacked the sample size or sampling intensity necessary to be melded into a dataset sufficient to ask questions about bull trout movements at the species scale. In other words, the reason I was unable to locate data sufficient to meet my project objectives is that none of the telemetry studies included in the database were designed to collect data sufficient for a larger scale analysis. If we hope to ask species-level questions in the future, it will be necessary to coordinate among researchers so that their data are similar spatial and temporal resolution to allow for consolidation into a large-scale dataset.

Table 1.—Sample size, fork lengths (mm), and weights (g) of 50 radio-tagged bull trout monitored in the Middle Fork (MFBR) and North Fork (NFBR) of the Boise River basin in the fall 2003.

Tag location	N	Fork length (SD)	Weight (SD)
MFBR	25	441 (60)	786 (288)
NFBR	25	489 (68)	999 (423)

Table 2.—Summary statistics for continuous variables measured in 304 stream segments in the truncated upper Boise River basin.

Variable	Average (SD)	Range	75th percentile
Watershed (n=304)			
CONTAREA (ha)	40,686 (72,367)	258-214,041	44,729
SEGLENGTH (m)	2,731 (1,838)	85-11,368	3,792
CONNECT (km)	12.5 (13.1)	4.8-190.0	15.1
DIST (km)	41.3 (22.8)	0.0-90.2	61.5
SLOPE (%)	0.04 (0.04)	0.0-0.2	0.07
ELEV (m)	1,289 (170)	984-1,586	1,439
Mainstem (n=74)			
CONTAREA (ha)	149,450 (71,032)	2,656-214,041	214,041
SEGLENGTH (m)	2,457 (1,744)	162-8,384	3,879
CONNECT (km)	13.0 (8.9)	4.8-53.2	15.1
DIST (km)	39.1 (20.8)	0.0 - 87.9	53.0
SLOPE (%)	0.006 (0.004)	0.000 - 0.016	0.009
ELEV (m)	1,144 (136)	984-1,539	1,235
Tributary (n=230)			
CONTAREA (ha)	5,962 (16,382)	258-214,041	4,918
SEGLENGTH (m)	2,820 (1,862)	85-11,368	3,767
CONNECT (km)	12.4 (14.2)	4.7-189.9	15.0
DIST (km)	42.0 (23.4)	2.7-90.2	64.3
SLOPE (%)	0.06 (0.04)	0.0-0.2	0.08
ELEV (m)	1,336 (153)	1,002-1,586	1,465

Table 3.—Site-scale and landscape-scale predictor variables considered in the analysis of bull trout presence in the upper Boise River basin.

Variable (Code)	Units	Description
Site-scale variables		
Segment length (SEGLENTH)	km	Segments were delineated based on tributary junctions. A stream segment was the length of stream between two tributary junctions.
Road presence (ROAD)	P/A	Presence of a road within 100 m of a stream segment.
Fish adjacent (FISHADJ)	P/A	Presence of a occupying fish in a stream segment adjacent to a target stream segment.
Segment slope (SLOPE)	Percent	The vertical drop of a stream segment expressed as a percentage of the horizontal length of that segment.
Segment elevation (ELEV)	m	The elevation of the midpoint of a stream segment.
Landscape-scale variables		
Contributing area (CONTAREA)	ha	The portion of the basin upstream of a stream segment that drains into that segment.
Connectivity (CONNECT)	km	The weighted average of the distance from the midpoint of a stream segment to 13 occupied spawning patches in the basin.
Distance to Arrowrock (DIST)	km	The distance from the midpoint of a segment to Arrowrock Reservoir.

Table 4.—Candidate model list for logistic regression analysis of bull trout presence in the upper Boise River basin. Variable designators are explained in the text.

Model	K	Variables
Global	6	FISHADJ, SEGLENGTH, ARROWDIST, CONNECT, ROAD
1	5	FISHADJ, SEGLENGTH, ARROWDIST, CONNECT
2	5	FISHADJ, SEGLENGTH, ARROWDIST, ROAD
3	5	FISHADJ, SEGLENGTH, CONNECT, ROAD
4	4	FISHADJ, SEGLENGTH, ARROWDIST
5	4	FISHADJ, SEGLENGTH, CONNECT
6	4	FISHADJ, SEGLENGTH, ROAD

Table 5.—Results of model selection procedure for analysis of bull trout distribution. Percent concordant, specificity, and sensitivity are measures of the predictive power of a model and are expressed as percentages.

Model	K	AIC	Weight	Concordant	Specificity	Sensitivity
4	4	67.904	0.27	87.7	65.7	79.5
1	5	68.005	0.26	88.7	54.3	79.5
5	4	69.226	0.14	87.0	68.6	74.3
2	5	69.274	0.14	88.0	65.7	87.2
G	6	69.854	0.10	88.5	68.6	82.1
3	5	71.224	0.05	87.0	68.6	79.5
6	4	71.241	0.05	86.3	65.7	76.9

Table 6.—Parameter estimates and odds ratios for the composite model predicting bull trout presence in the Boise River.

Parameter	Parameter estimate (SE)	Odds ratio	95% CI for Odds Ratio
Intercept	-2.270 (1.95)		
FISHADJ	3.117 (1.40)	22.58	1.46 - 348.61
SEGLENGTH	0.845 (0.54)	2.33	0.80 - 6.75
ROAD	-0.126 (0.40)	0.88	0.40 - 1.94
CONNECT	-0.061 (0.19)	0.94	0.64 - 1.38
ARROWDIST	-0.035 (0.13)	0.97	0.75 - 1.25

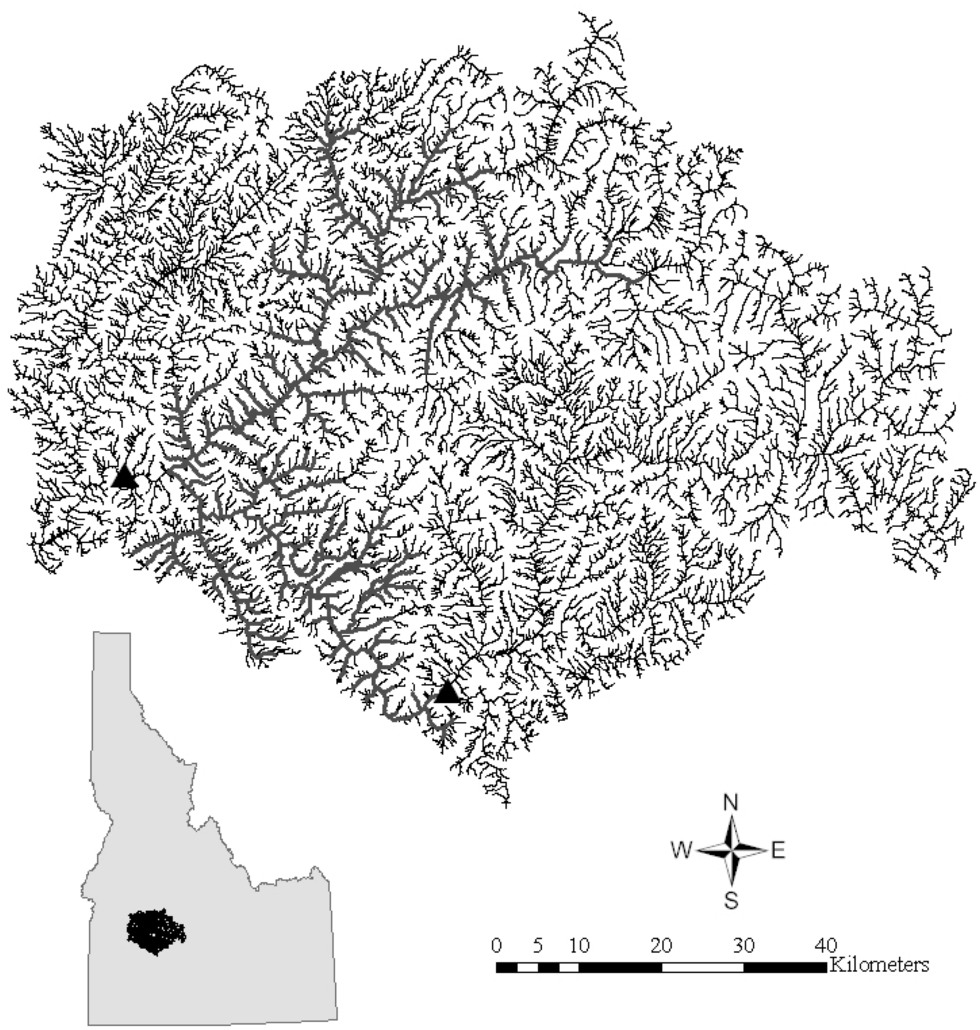

Figure 1.—The upper Boise River basin. Arrowrock Dam (left) and Anderson Ranch Dam (right) are shown with black triangles. The portion of the watershed used in this study is highlighted.

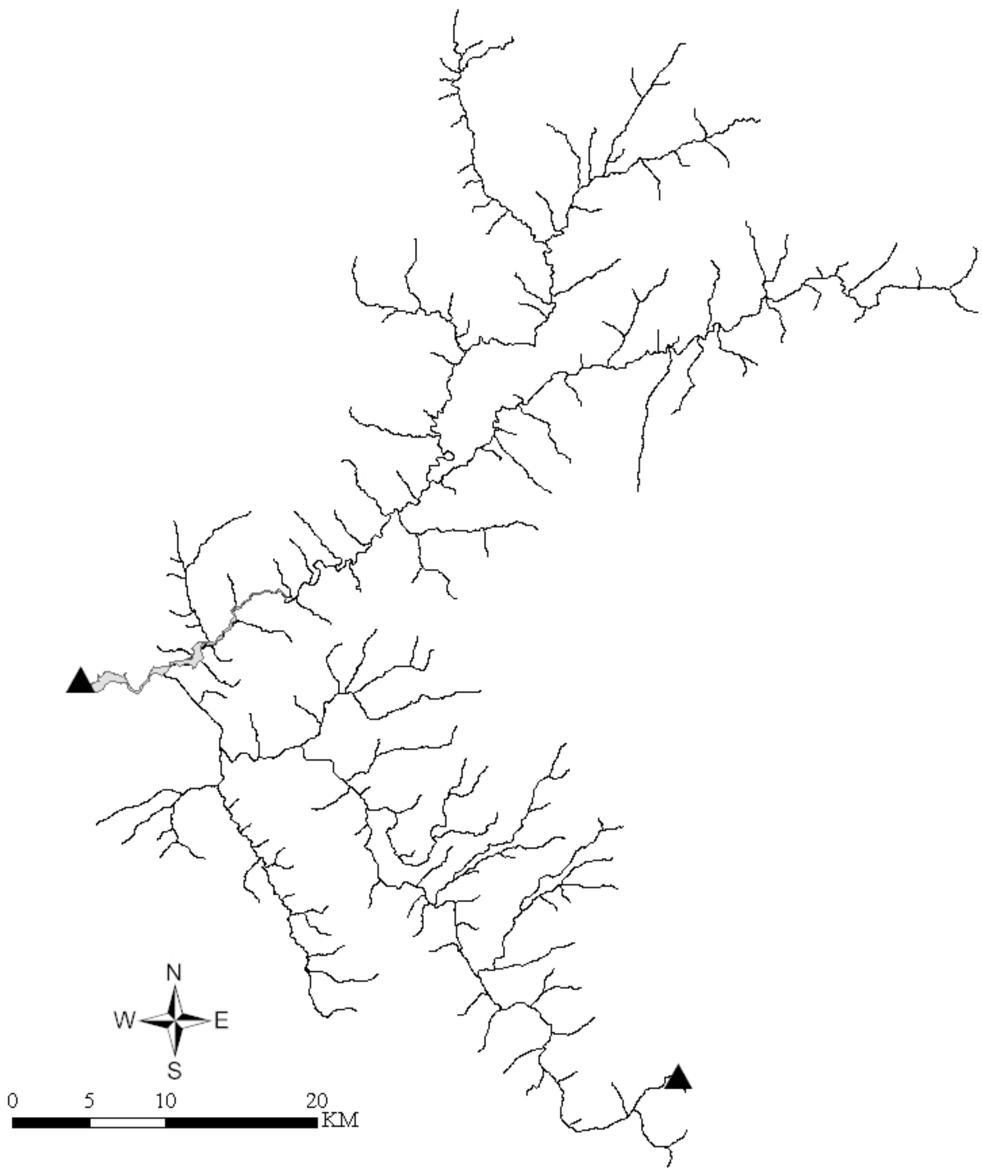

Figure 2.—The truncated watershed representing 304 stream segments. Arrowrock Dam (left) and Anderson Ranch Dam (right) are shown with black triangles.

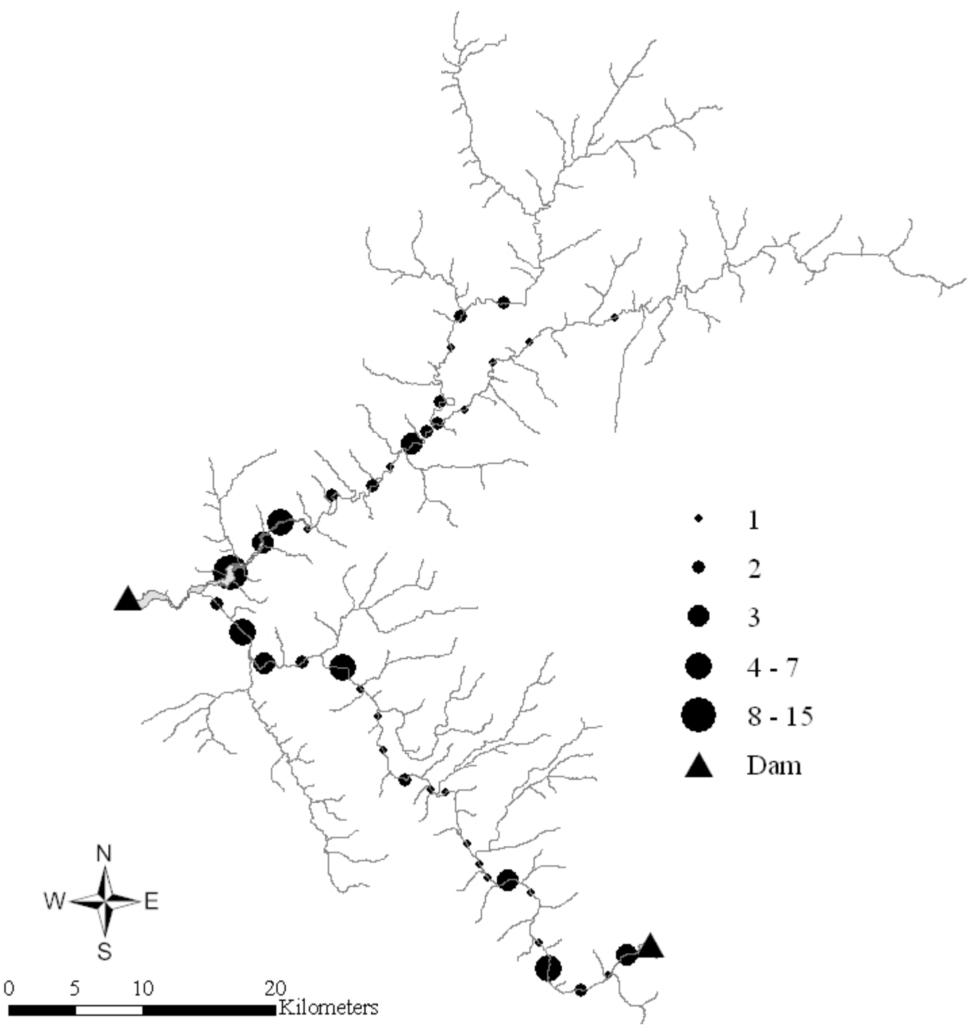

Figure 3.—Distribution of occupied stream segments. Circles represent the number of individual bull trout occupying each stream segment.

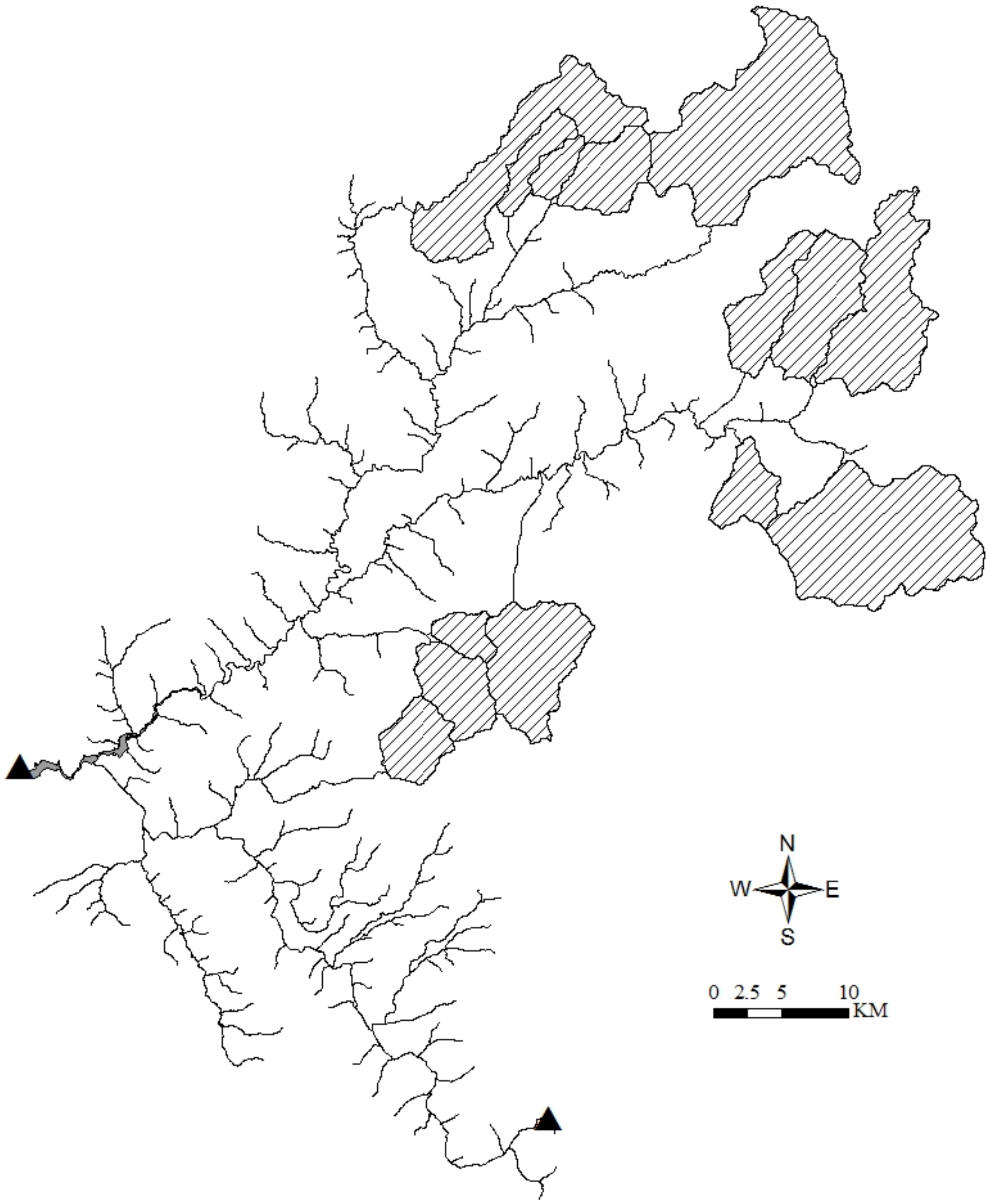

Figure 4.—Spawning patches used in the calculation of connectivity parameter.

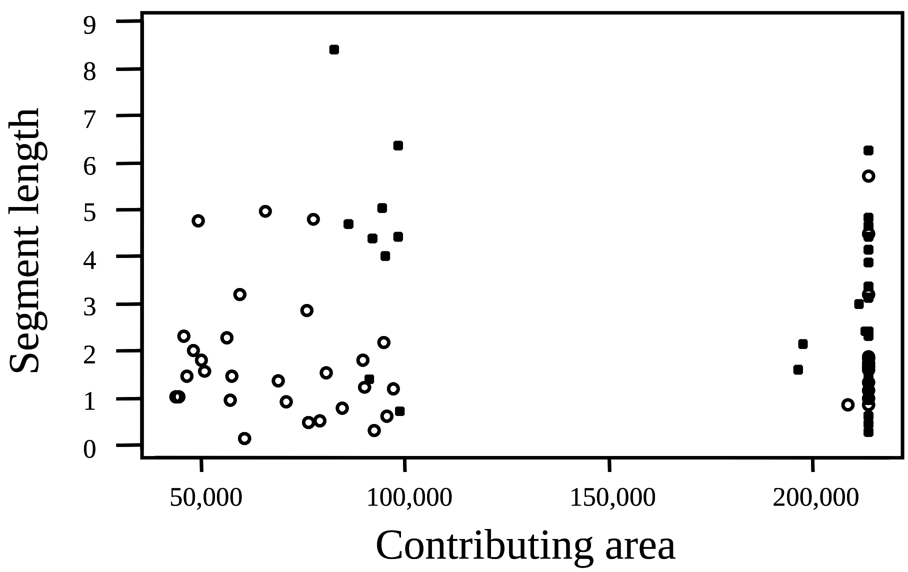

Figure 5.—The relationship between the contributing area of individual stream segments and its corresponding length. Occupied segments are denoted by closed circles.

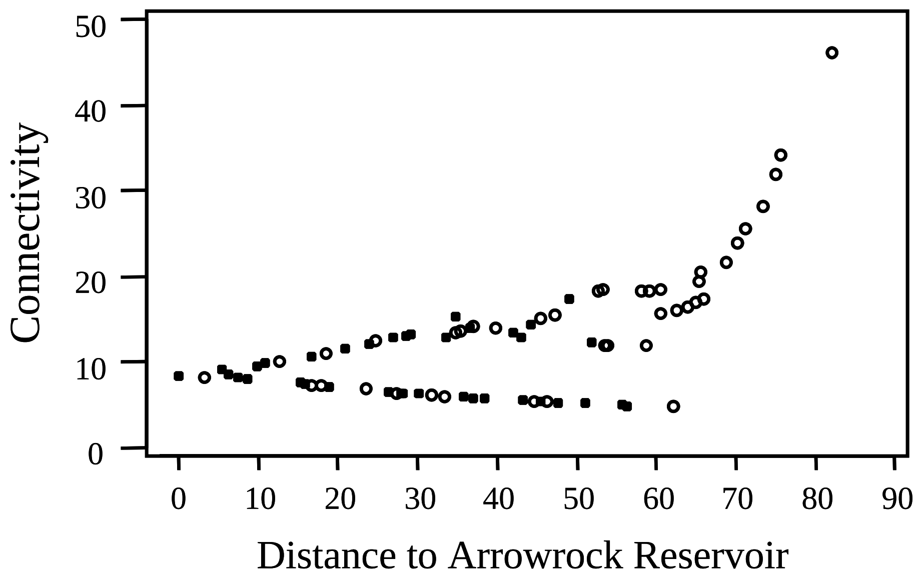

Figure 6.—The relationship between the distance of a stream segment from Arrowrock Reservoir and its corresponding connectivity value. Occupied segments are denoted by closed circles. Note the spatial relationship of the NF, MF, and SF of the Boise River is visible in this plot.

Chapter 3: Three Approaches to Monitoring Bull Trout Movement: A Case Study and Unanswered Questions

There are a variety of ways to implement field data collection with radio telemetry so that particular questions can be addressed (Millspaugh and Marzluff 2001). It is likely that we will continue to use radio telemetry to study bull trout movements in the future; therefore, it is important to highlight distinct approaches that have been used in previous work with particular attention on the types of questions that can be addressed with each approach. Ideally, each study would commence after a thorough literature review and discussion of project objectives among the investigators, discussions with researchers who have used the technology in the past, and vendors who will be supplying the telemetry equipment. The telemetry database is an excellent starting point for any group initiating a telemetry study on bull trout. Such logistics, when implemented as a predicate to data collection will greatly improve the quality of the data collected over the course of the study (Millspaugh and Marzluff 2001). My objective in this chapter is to highlight the strengths of several approaches to bull trout research using radio telemetry so that future studies have a starting point for project planning and objective setting.

In this chapter I describe three investigations of bull trout movement and the methodologies that were unique to each one. The information presented in this chapter was gleaned from project reports and discussions with investigators. The three studies differed in three key aspects: collection location of tagged fish, primary method of location data collection (air, ground, and fixed-station), and observation intensity. My objective is to highlight how each investigation was able to answer specific questions and to point out how particular methodologies are or are not amenable to answering certain research questions. This is not a critique of these, or other, telemetry studies; instead my goal is to aid future investigations in matching their research questions to particular methodologies. This chapter will conclude with a discussion of the most common research questions addressed with radio telemetry and highlight those questions that remain unanswered for bull trout.

Matching methods to questions

Radio telemetry data are amenable to use in the analysis of a number of research questions. Millspaugh and Marzluff (2001) identified three research areas for which radio telemetry could be used: 1) movements; 2) resource selection; and 3) population demographics. The analysis of animal movements includes investigations of migration and dispersal and investigations of space use and home range size. The analysis of resource selection necessitates fairly fine-scale location data paired with information on habitat availability. Studies of population demographics include estimations of population density, survival, and fecundity. The methods associated with estimating population density and fecundity were designed for use on terrestrial vertebrate populations and are not applicable to stream-dwelling fishes. However, a large sample of tagged fish may be used to estimate mortality rates.

Bull trout researchers have primarily used radio telemetry successfully to examine the movement patterns and distribution of bull trout in streams systems throughout their range. The growing body of peer-reviewed studies in fisheries journals suggests the technology is being complimented by sound analytical techniques. The following studies represent three of the most intensive telemetry-based bull trout investigations conducted to date. Each study was conducted over several years and involved tracking 51 to 300 migratory bull trout. The basis for each study was to evaluate movement patterns and seasonal distribution of migratory bull trout. The investigators, however, approached this objective in different ways. Differences in the mode, timing, and intensity of observation of individual fish resulted in datasets that could be used to describe different facets of the movement behavior of migratory bull trout. The differences among these studies represent trade-offs in the spatial and temporal resolution of the resulting datasets.

Boise River, Idaho

In 2001, the U. S. Bureau of Reclamation began a construction project to replace valves in Arrowrock Dam, located on the Boise River, northeast of Boise, Idaho. Reclamation had been studying the movements and distribution of bull trout upstream from Arrowrock Dam since 1999. The field methods used in these early studies included electrofishing in spawning tributaries, weirs in spawning corridors, and netting in reservoirs (Salow 2001). In order to address concerns outlined in Biological Opinions issued by the U. S. Fish and Wildlife Service in 1999 and 2001 (USFWS 1999, 2001), Reclamation initiated a radio-telemetry study of large adfluvial bull trout that were known to migrate between Arrowrock Reservoir and spawning tributaries in the upper Middle Fork and North Fork of the Boise River. Because the Biological

Opinions directly referenced reservoir operations and entrainment of overwintering bull trout in the reservoir, Reclamation was committed to monitoring distribution within the reservoir and entrainment rates through Arrowrock Dam. However, the study also included several objectives related to spawning movements, migration rates, and seasonal habitat use. The concept that fish size and condition affect several factors related to spawning behavior was a unifying theme of these additional objectives and built on previous research conducted by Reclamation (Salow 2001). These objectives included 1) evaluating whether fish size or condition was related to the initiation of spawning activity by migratory bull trout; 2) evaluating whether migration rate was related to fish size or condition; 3) evaluating whether the timing of initiation of spawning migrations and movement rates during migratory periods were related to fish size or condition; 4) determining whether fish size or condition and spawning behavior were related to post-spawn habitat use; and 5) determining whether temperature and discharge could be correlated to the timing of initiation of spawning migration or migration rate (Salow and Hostettler 2004).

In order to collect the data necessary to address these research objectives, Reclamation captured and radio tagged 90 migratory bull trout over 3 years[1]. The fish were collected at weirs located upstream of the reservoir in the Middle and North Forks of the Boise River. These weirs were operated from September through November of each year and the fish collected at these weirs were assumed to be first-time migrants or post-spawn adults moving downstream to the reservoir. The distribution of radio-tagged individuals was monitored using aerial and ground-based tracking, and fixed telemetry stations. Because of the size of the study area and the importance of precisely relating movement magnitude and patterns to fish condition, aerial tracking was the primary method used to monitor fish distribution during the study. Telemetry flights were conducted 4-5 times per month throughout the study. Ground-based tracking was used as a supplement to aerial tracking primarily to evaluate mortality. Ground tracking was conducted 4-5 times per month during the study. Fixed telemetry stations were used to monitor the timing of movement into and out of Arrowrock Reservoir and to monitor entrainment through Arrowrock Dam; however, additional stations were deployed in the each of the major tributaries to the reservoir.

[1] Reclamation tagged over 200 fish as part of a larger study of bull trout movement and survival in the Boise River basin. I have restricted my discussion to one component of the study involving migratory adult bull trout.

Clearwater River, Idaho

Dworshak Dam has been in place on the North Fork of the Clearwater River since 1971. The dam is located within several kilometers of the confluence of the North Fork and mainstem of the Clearwater River. The size of the dam precludes the construction of fish passage facilities; therefore, the movements of migratory fishes between the two rivers have been restricted for 35 years. It is believed that migratory bull trout moved throughout the system on an annual basis; however, current migrations are restricted to movements between the reservoir and upstream tributary habitats. In 2000 the Idaho Department of Fish and Game began studying the bull trout population upstream from Dworshak Dam (Schiff et al. 2005). Early research established the fact that migratory bull trout used the reservoir as overwintering habitat and more recent research entailed evaluating the adfluvial component of the population that moves between the reservoir and upstream tributaries in order to determine the importance of the reservoir to the larger bull trout population in the drainage (Schiff et al. 2005). As research questions were related to the adfluvial component of the population, investigators collected fish in the reservoir after they had returned from spawning tributaries in the fall.

Radio telemetry played an important role in these investigations as it enabled investigators to evaluate several research objectives. These included 1) identification of migration patterns within the North Fork of the Clearwater River, upstream from the reservoir; 2) identification of the spatial and temporal distribution of migratory bull trout within the drainage; 3) identification of bull trout spawning locations; and 4) quantification of entrainment through Dworshak Dam (Schiff et al. 2005). This study was unique compared to the others described in this report in that investigators used acoustic telemetry to monitor movements of migratory fishes through Dworshak Reservoir. The physics of radio telemetry mean that tagged fish can be “lost” in deep water due to the attenuation of the radio signal. Acoustic tags emit a sound wave akin to sonar therefore the movements of fish tagged with acoustic tags can be monitored in reservoirs and other deep-water systems. The use of acoustic telemetry allowed investigators to evaluate bull trout movements and habitat use during the post-spawn period and during winter. In fact, determining the extent and patterns of movement within the reservoir was the primary objective of the 2003 study (Schiff et al. 2005). In order to address these questions investigators collected and tagged 192 migratory bull trout within the reservoir in 2003.

Aerial and ground-based tracking surveys were conducted upstream of the reservoir approximately two times per month over the course of the study. Within the reservoir, investigators tracked fish from a boat or airplane two times per month. Movements into and out of the reservoir were monitored with two fixed stations located at the mouths of the North Fork and Little North Fork of the Clearwater Rivers, the two major tributaries to the reservoir. Five additional fixed stations were placed around the reservoir.

Wenatchee River, Washington

The objectives of the telemetry study conducted by the U. S. Fish and Wildlife Service in the Wenatchee River system in Washington State were an outgrowth of the diverse array of habitat types and relatively well connected habitats in the basin (Kelly Ringel and De La Vergne, unpublished data). The study area contains two large rivers: Lake Wenatchee drains into the Wenatchee River which flows into the Columbia River and the White River is the main tributary to Lake Wenatchee. Lake Wenatchee is an unregulated natural lake and there are numerous tributaries of various sizes to both the rivers and the lake. The U. S. Fish and Wildlife Service initiated a study of bull trout in this river system in order to gain a general understanding of the seasonal movement patterns within the system in order to put their findings into the larger context of bull trout life history diversity research. The investigators listed three research objectives: 1) describe the movement patterns of migratory bull trout in the basin; 2) identify spawning and overwintering areas for this component of the population; and 3) describe how the migration corridors are used by these fish.

A total of 51 bull trout were tagged and tracked over three years. Sixteen of the 51 fish were tracked in multiple years. Because the project objectives were focused on the distribution of bull trout and the timing of their movements, the investigators relied on an array of 11 fixed telemetry stations positioned at strategic locations throughout the basin. These stations were positioned at several points along the mainstem of the Wenatchee and the White River as well as at the confluences of six tributary streams. Because fixed stations only allow for the identification of direction and timing of movement past a station location, the investigators made several aerial and ground-based tracking surveys over the course of the study. These surveys were conducted in order to "determine locations during migrations and within spawning and overwintering areas" (Kelly Ringel and De La Vergne, unpublished data). Precise fish location data were not requisite to meeting the project objectives so aerial and ground-based surveys were not regularly done during the study. These surveys were primarily a way to determine the extent of movement into the Columbia River, downstream from the study area.

The trade-offs of sampling design

The core component of each of these studies was radio telemetry. Additionally, each of these studies monitored fish locations throughout their focal watershed using a combination of techniques over multiple seasons. Therefore, the respective datasets are similar in the kinds of bull trout "stories" each can yield. There were, however, variations in field methodology that led to differences in the inferences that could be drawn from the respective datasets. These variations included the location of capture and tagging, primary method of observation, and observation intensity. These variations represent trade-offs in the spatial and temporal resolution that can be achieved during a telemetry study.

Intensive aerial tracking yielded detailed information on the extensive seasonal movements of bull trout in the Boise River. Following tagging, bull trout observed during this study were typically located 3-4 times per month from the air. Aerial tracking enabled consistent relocation of animals distributed throughout a watershed that includes three major tributaries and a reservoir. Aerial tracking was supplemented with ground-based location information that was collected 3-4 times per month. The intensity with which radio-tagged bull trout were monitored in the Boise River was the greatest of the three studies described herein and this level of intensity allowed investigators to make detailed descriptions of the seasonal movement patterns of bull trout in this system. Additionally, fine-scale movement patterns were also described. For example, the movement patterns of fish within Arrowrock Reservoir and the weekly distribution of bull trout overwintering in the South Fork of the Boise River were captured using this approach (see Chapter 2). This intensity was necessary as the investigators were attempting to correlate movement patterns with body size and condition.

By collecting fish in Dworshak Reservoir, the IDFG investigators were able to examine the spatial extent of spawning movements by adfluvial bull trout in the North Fork of the Clearwater River. This was a major difference between the Boise River and the Clearwater River studies. The concentration of members of the target population is one distinct advantage of collecting bull trout in the reservoir. IDFG knew that the adfluvial component of this population was fairly large. During the spawning season members of this population were believed to disperse throughout the basin. Collection in even a large number of potential spawning tributaries would have probably translated to a much smaller sample size. Collecting fish in the reservoir prior to the initiation of the fall migration was advantageous for a second reason: the investigators hoped to get a representative sample of the distribution of spawning habitat in the basin. The logistics of large weirs would have limited the number of locations at which bull trout could have been collected upstream. Consequently, it would have been unlikely that a representative sample would have been collected using weirs. Bull trout were collected at two weirs in the Boise River study. Therefore, the spawning migrations of bull trout that used tributaries to the Middle Fork and North Fork of the Boise River upstream of the weirs were documented. Previous work in the Boise suggests migratory bull trout exist in other parts of the drainage. These fish were not sampled because of the limited spatial scale of the collection effort.

A centralized collection location enabled the investigators to tag a very large number of bull trout in Dworshak Reservoir each year. This study included the largest number of tagged fish in any of the telemetry studies that have been conducted on bull trout (see Chapter 1). The results of the methodology employed in this study included observations in streams tributary to the North Fork of the Clearwater River and the Little North Fork of the Clearwater River and two smaller tributaries: Floodwood Creek and Stony Creek (Schiff et al. 2005). There was a trade-off associated with the large sample size and spatial scale of the basin in which the study was conducted. The large numbers of radio-tagged fish meant that individual fish could not be located more than twice per month. Therefore, the temporal resolution of the Clearwater dataset is approximately half that of achieved during the Boise River study.

The use of acoustic telemetry allowed investigators to intensively monitor fish movements in Dworshak Reservoir. Radio telemetry signals rapidly attenuate in deep water therefore acoustic telemetry is necessary to observe fish movements and distribution in most lakes or reservoirs. Because biologists were interested in describing the extent of use of the reservoir during winter, acoustic telemetry was a necessary addition to the Clearwater study. Fish were located twice per month and their distribution among five sections of the reservoir was recorded during active tracking sessions. An array of fixed stations was also used to monitor fish locations near the dam and major tributaries. The limitations of radio telemetry in deepwater are transferred to acoustic tags when the latter is located within flowing water. The investigators, therefore, made two major assumptions when describing bull trout distributions in the reservoir and tributaries: 1) the movement patterns of radio-tagged fish reflected the movement patterns of acoustically tagged fish in tributaries, and 2) the movement patterns of acoustically tagged fish were indicative of the movement patterns of radio-tagged fish in the reservoir (Schiff et al. 2005). The use of acoustic telemetry represented an improvement over the reservoir sampling employed during the Boise River study. Arrowrock Reservoir is substantially smaller and less deep than Dworshak Reservoir. Reclamation initially relied on radio telemetry to identify the distribution of bull trout in the reservoir during winter[2]. The reliance on radio telemetry represented a trade-off for investigators in the Boise River. Movement patterns and habits in the reservoir was not a major objective of the study in the Boise River; therefore, the use of acoustic telemetry would have resulted in decreased observations in three forks of the Boise River. As reservoir movement patterns were a major objective of the study in the North Fork of the Clearwater, acoustic radio tags were an important addition to the field methodology.

Reliance on fixed stations enabled investigators in the Wenatchee River to describe variation in seasonal movement patterns and produced information on diel movement timing during migrations. From a logistical perspective, the choice of fixed stations was not a trade-off made by the investigators. Budget and labor constraints necessitated less intensive field sampling and reliance on more passive observation of bull trout movement. However, the use of 11 fixed telemetry stations allowed the investigators to characterize the variation in post-spawn habitat selection at a coarse scale as well as quantify the timing of movements into specific spawning tributaries within the basin. The fact that the fixed telemetry stations operated 24 hours a day enabled the investigators to determine that bull trout movements were primarily occurring at night. The methodologies of the studies in the Boise River and North Fork of the Clearwater River could not generate this information.

The remaining questions

Each of the above studies used the same basic array of sampling techniques therefore similar data were collected in each. Despite differences in sampling intensity and primary mode of data collection investigators in all studies were able to describe the timing and extent of movements

[2] Reclamation used acoustic tags to monitor bull trout movements in Arrowrock Reservoir in the winter of 2004-2005. Information about this study can be found in Stiefel and Dare (2006).

of large migratory bull trout within their respective basins. Bull trout initiated upstream migrations from overwintering areas as early as February and departures from overwintering areas were observed through early fall. Most fish moved considerable distances upstream to reach spawning grounds where they remained through late October or early November. After spawning, fish moved downstream to their overwintering habitat. Investigators in the Boise and Clearwater studies observed fish moving throughout reservoirs during the winter. Investigators in the Wenatchee study did not monitor movements during the winter; however, previous research on bull trout suggests short-distance (1-5 km) movements probably occurred throughout the winter (Muhlfeld et al. 2003; Bahr and Shrimpton 2004; Chapter 2). With the end of winter this pattern was repeated.

This basic approach sampling has been applied in watersheds throughout the range of bull trout and is well described in peer-reviewed literature (e.g. Muhlfeld and Marotz 2003; Bahr and Shrimpton 2004; Mogen and Scarnecchia 2006, and references contained therein). Each of these studies has successfully described the annual movement patterns of large, migratory bull trout in their respective drainages. Additionally, researchers know, on a case-by-case basis, where migratory bull trout go to spawn and where they subsequently go to spend the winter. Related research on the characteristics of bull trout spawning habitat have given us an understanding of the characteristics of these spawning locations (Rieman and MacIntyre 1995; Baxter and Hauer 2000).

“How” questions we have and have not asked about bull trout

The vast majority of radio telemetry studies on bull trout have been designed to address “how” questions as described by Gavin (1991). How questions are those that relate to how an animal or population does what it does. With respect to bull trout the most common "how" question is what is the timing and extent of seasonal movements by migratory bull trout within the drainage of interest. Since we successfully executed studies in basins throughout the latitudinal and longitudinal extent of the species' current range (see Chapter 1) we therefore understand the general seasonal pattern of migratory bull trout movements. Additionally, many studies have been conducted where bull trout movements reflect the unique characteristics of the basin of interest (e.g. downstream spawning migrations observed by Carson (2001) and Hogen and

Scarnecchia (2006)) and there is, therefore, considerable documentation of plasticity in movement patterns among populations.

Unfortunately it is arguable that despite our intensive effort related to “how” questions, we have not answered them all over 16 years of telemetry-based research. For example, there are no published studies pertaining to bull trout resource selection with respect to post-spawn habitat. Most published literature makes general inferences regarding habitat use based on observations made during radio tracking; however, none of these studies incorporated data collection on habitat availability from which they could rigorously evaluate habitat selection. Although, Goetz (1997) published a study on the habitat use of juvenile bull trout in the Cascade Mountains of Oregon and Washington (this study did not incorporate telemetry).

It is important to point out there are many excellent reports and manuscripts describing studies of bull trout spawning habitat selection. These studies have been conducted with radio telemetry (Fernet and O’Neill 1997; James and Sexauer 1997) and without radio telemetry (Baxter et al. 1999; Baxter and Hauer 2000). The impetus for these studies was pragmatic in that the management and mitigation of impacts to bull trout populations should begin by identifying and protecting spawning habitat. A similar research paradigm has been used in the management of Pacific salmon.

Rigorous evaluation of annual mortality rates is another aspect of life history for which radio telemetry could be used. Estimates of mortality rates have been evaluated by calculating the proportion of the tagged sample that died over the course of the study (Burrows et al 2001; BioAnalysts 2002; Salow and Hostettler 2004; Hogen and Scarnecchia 2006). These estimates are based on the recovery of shed tags or confirmation of mortalities; however, field methods associated with the recovery of shed tags or dead carcasses carry many assumptions. Much more rigorous methods to evaluate mortality have been developed and are commonly employed in studies of terrestrial wildlife (see Millspaugh and Marzluff 2001 for examples). Unfortunately, the sample size and sampling intensity of bull trout studies is typically well short of that needed to make more rigorous evaluations of resource selection or mortality rates. One interesting question pertaining to mortality pertains to the relative mortality rates of resident and migratory bull trout that exist in the same stream system. Movement theory suggests the migratory animals should have higher mortality rates compared with their resident cousins (Northcote 1992); however, this has not been rigorously evaluated for bull trout.

The extent of overwinter activity by bull trout is another area that has been poorly evaluated. Most telemetry studies have focused on the movements of bull trout in the fall and have, consequently, greatly curtailed sampling intensity during the winter. Because of cold water temperatures it is assumed that movement is limited during winter and most published studies have concluded that bull trout don't move appreciably during winter based on twice monthly or monthly observations (Jakober et al. 1998; Fraley and Sheperd 1989; Muhlfeld and Marotz 2005; Bahr and Shrimpton 2004). Research in the Boise River suggests that bull trout move frequently over considerable distances during winter (Stiefel and Dare 2006; Chapter 2). Based on this research and an understanding of the scope of activity of bull trout one might hypothesize that migratory fish move considerably during winter. This hypothesis is supported by the accepted evolutionary motivation for post-spawn migration: to find sufficient food resources. Migratory bull trout are large, site-feeding piscivores needing to replenish energy reserves following spawning. I expect that if future studies monitor bull trout intensively during winter my hypothesis will be supported throughout the species' range.

Previous research has determined that male and female salmonids differ in their spawning site fidelity and the documentation of such differences in bull trout could greatly enhance our understanding of bull trout spawning habitat selection and population dynamics. Neville et al. (2006) recently conducted a study of Chinook salmon (*Oncorhynchus tschawtschya*) and found that female salmon showed greater site fidelity than male salmon and this fidelity was detectable in the fine-scale genetic structure of the population. The fact that the genetic signature was not present in males was attributed to behavioral differences between the sexes on redds: females build and defend nests while males do not. While such a result may not represent information requisite to the successful conservation of a species like bull trout, Neville et al. (2006) also found that site fidelity was linked to the amount and distribution of suitable spawning habitat in the reach. Female salmon moved less in areas where spawning habitat was patchily distributed. Such a result has implications for bull trout considering the majority of the research done on the species has been related to spawning movements and spawning habitat. Unfortunately, none of the telemetry studies of bull trout incorporated the intensive monitoring and associated habitat measurements necessary to conduct such a study.

Despite the fact managers routinely invoke metapopulation dynamics as the foundation of bull trout management and recovery we know little about the dispersal behavior of these animals.

Dispersal can be simply defined as the movement of individuals between habitats (McPeek and Holt 1992). Stenseth and Lidicker Jr. (1992) expanded on this definition by specifying that movements were between homesites. Although within the confines of metapolation theory the terms dispersal and migration are synonymous (Wiens 1997) I am making the distinction here, referring to migration as the seasonal movement of bull trout between spawning and overwintering habitats. Dispersal behavior is integral to metapopulation dynamics in that it facilitates gene flow between existing populations and is believed to be the primary mechanism by which habitats are recolonized following disturbance and extinction. There are several questions related to dispersal behavior in bull trout: 1) at what rate do migratory juveniles disperse from natal habitats; 2) does dispersal behavior occur later in life, i.e., do adults outside of their spawning and overwintering habitats; 3) does dispersal behavior differ between males and females; and 4) to what extent do dispersers (migratory fish) arise from resident populations? We cannot answer all of these questions for bull trout using data collected during any of the completed telemetry studies and it is unlikely that telemetry alone will be sufficient to collect the data. The only published study that has examined the dispersal of small bull trout was conducted with the use of weirs (Downs et al. 2006). However, understanding dispersal dynamics has dramatic implications for the preservation and restoration of connectivity within and between watersheds containing migratory bull trout (Rieman and MacIntyre 1993). Therefore, the answers to these questions represent contributions to our basic understanding of bull trout movement and have a direct linkage to important management issues.

Why ask "why" questions about bull trout

It is not apparent that any of the existing research on bull trout movement has been designed to address "why" questions. Why questions are those intended to elucidate the "ultimate causation" of the physical or behavioral characteristics of an organism (Gavin 1991). According to Mayr (1961) how and why questions represent two levels of biological inquiry: functional biology and evolutionary biology. Functional biology, or how questions, involves investigations of organism or populations and are inherently descriptive in nature. Evolutionary biology, or why questions, by definition involve studies designed to define the consequences for genetic fitness of the characteristics described by asking how questions. In other words, evolutionary biology involves figuring out "how come" an individual or population functions the way it does (Mayr 1961).

Knowledge at both levels is needed for a “complete understanding of any biological phenomenon” (Gavin 1991). I can illustrate this point through an example explaining the difference between proximate and ultimate factors affecting the physical and behavioral characteristics of an animal. A juvenile bull trout may migrate from its natal stream because of environmental changes that affect its physiology. Seasonal changes in discharge, temperature, or photoperiod may provide the cues to migrate. The interaction of the environment and physiology is a proximate or direct factor and we can evaluate the relationship between environmental variables and the onset of migration through a relatively simple correlative study. With sufficient data a model relating environmental variables to the onset of migration could be developed using logistic regression. But what have we learned about why that animal left its natal habitat? The migratory behavior displayed by this individual could a genetic manifestation of a long-term lack of adequate food resources in the natal stream. Historic lack of adequate food resources in the natal stream could have promoted a genetic trigger over evolutionary time, therefore, these are ultimate factors which result in the animal responding to the physiological cues that are only tangentially related to food availability. In order to get at the ultimate causation of the onset of migration would require extensive field data collection based on multiple hypotheses related to such things as stream productivity, food availability, food quality, and fish growth and condition. In other words, there are many potential factors that may work *and* interact to “push” a migratory fish from its natal habitat. While there is a growing body of excellent telemetry studies in the peer-reviewed literature these represent the best of the observational or correlative studies of movement and habitat use and do little to address the mechanisms behind the diversity of life history and behavior observed in most bull trout populations.

The fact that we have studied bull throughout their range and developed a relatively clear picture of their movement habits suggests future studies should build on the body of correlative studies with research designed to elucidate the mechanisms underlying these habits. The current model of bull trout movement research is well described by Sinclair (1991) who discussed the incorporation of the scientific method into wildlife management. Sinclair describes one approach to understanding the diet of deer: study the diet of every population of the species in all seasons. This is an inefficient way to evaluate the diet or the movement patterns of a species for many reasons but most importantly this approach results in large amounts of data without a corresponding amount of generality. An alternative approach is a hypothesis-driven approach well described by Platt (1964) and supported by Sinclair (1991) who concluded that many studies conducted within the framework of the "case-by-case" paradigm would be unnecessary if preceding studies had been designed around hypotheses and generated predictions that could be extrapolated to the species. Another important point is that it is impossible to study every fish in every place at every time. The reality is that the logistical constraints of such a research program pale when compared to the financial constraints. Therefore, if we are to develop a greater understanding of the movements of bull trout additional research will be needed that results in data of sufficient quality for integration into large-scale analyses. To accomplish this there should be range-wide coordination of future bull trout research to ensure that important research questions are addressed in an efficient manner. There is still much room for use of radio telemetry in bull trout research as we haven't answered questions about resource selection, diet, mortality, post-spawn movements, and the dynamics of juvenile movement. However, correlative studies designed to address these questions should be components of studies designed around testable hypotheses pertaining to remaining questions described above. There are several entities through which range-wide research coordination could be accomplished. The most notable of these is the U. S. Fish and Wildlife Service through the consultation process outlined in Section 7 and the permitting process of Section 10 of the Endangered Species Act. However, there are other agencies or groups that could facilitate coordination. These include the Bull Trout Committee of the Western Division of the American Fisheries Society and the *Salvelinus confluentus* Curiosity Society. Both of these groups are in a position to facilitate interactions among bull trout researchers throughout the species' range. These interactions could facilitate a process of informal peer review at the proposal or study plan stage of a research project.

Summary and Conclusions

The goals of the synthesis project were to catalog the information that we have collected pertaining to bull trout movements and habitat use and then synthesize a portion of that information into a species-level analysis of post-spawn movements and habitat use. The compilation of the telemetry database containing information on over 70 studies and 3,000 tagged bull trout represented the achievement of that goal. Researchers can draw on the information contained in the database and initiate dialogues regarding past projects in order to achieve the highest possible data quality during field data collection. I was able to partially fulfill the objectives of the second phase of the project by conducting an analysis of post-spawn distribution of adult bull trout in the Boise River. These data were collected by the U. S. Bureau of Reclamation and probably represent the most intensive dataset in existence pertaining to large-scale bull trout movement. I am basing this assessment several factors including sample size, sampling intensity (spatial and temporal resolution), and sampling duration. It is important to point out that these data were not collected in order to conduct the analysis presented in Chapter 2; however, the spatial and temporal resolution of the data enabled the development of logistic regression models of post-spawn distribution which led to the generation of several hypotheses about bull trout distribution in winter. Unfortunately, I was unable to identify another telemetry dataset of similar quality to replicate the analysis.

The failure to develop a species-level model based on data collected from a variety of basins highlighted the importance of coordination of future research to ensure hypothesis-driven studies conducted at a level of spatial and temporal resolution necessary to facilitate meta-analytical research on bull trout at the species level. I believe the revelation that information content of the myriad telemetry datasets is not sufficient to allow for a species-level analysis is an important outcome of this project and underscores the importance of taking bull trout movement research to the next level in order to address some of the information gaps described above. In order to do this it will be necessary to institute some form of large-scale coordination of future research projects. To put Sinclair’s (1991) point into context: the basic bull trout telemetry study would be unnecessary if previous research was conducted in a coordinated manner to address specific hypotheses.

Despite the fact that most bull trout movement research is not designed around testable hypotheses within the framework of the scientific method it is not clear that widespread replication of completed studies is warranted. As Sinervo and Svensson (1998) pointed out understanding the evolutionary implications of life history traits must begin with a detailed description of the traits in question. The collected studies of bull trout movement represent a wealth of information on the timing and extent of spawning migrations. These studies are based on data collected on a continuum of spatial and temporal resolution and resulting quality of data; however, each represents an observation of movement patterns at one location within the current species' distribution. One could argue that even the results of the "best" study could not be generalized to the entire species; however, the collected observations represent a picture of bull trout spawning movement at the species level.

It still remains clear that we know very little about the "whys" of bull trout movement. To develop a complete picture of bull trout behavior additional research is needed that is designed to address unanswered questions related to resource selection, mortality, and metapopulation dynamics. These questions include the following:

1. What are the resource selection (habitat, food, etc) patterns of bull trout during the post-spawn period?
2. What are the seasonal mortality rates of bull trout? Do mortality rates differ between residents and migrants?
3. What is the extent of overwinter activity and movement by migratory bull trout?
4. How do the movement patterns and spawning activity differ between female and male migratory bull trout?
5. What are the dispersal dynamics of a migratory bull trout population?

Each of the questions contain numerous sub-questions that could be addressed within the context of a single telemetry study; however, it will be important to have large-scale coordination of these studies ensure that each can subsequently be incorporated into a species-scale analysis.

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