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Demography of the Columbia spotted frog (Rana luteiventris) in the presence or absence of fish in the Absaroka-Beartooth Wilderness Montana

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DEMOGRAPHY OF THE COLUMBIA SPOTTED FROG (*Rana luteiventris*)

IN THE PRESENCE OR ABSENCE OF FISH

IN THE ABSAROKA-BEARTOOTH WILDERNESS, MONTANA

by

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ABSTRACT

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Demography of the Columbia Spotted Frog (*Rana luteiventris*) in the Presence or Absence of Fish in the Absaroka-Beartooth Wilderness, Montana

Director: Carol A. Brewer

In this study, I examined the physical and biological influences on the Columbia spotted frog, *Rana luteiventris*, in the Absaroka-Beartooth Wilderness, Montana, USA. In particular, I examined the influence of introduced fish (*Salvelinus fontinalis* and *Thymallus arcticus*) on frog population dynamics by comparing ponds with and without fish. In contrast to several previous studies, Columbia spotted frogs co-occurred with fish in stocked ponds in the study area even using them as breeding and rearing sites. However, there was an impact on survival from egg to metamorphosis suggesting that the presence of fish could have deleterious effects on Columbia spotted frog populations over time. Unfortunately, fish introductions planned and carried out by federal, state, and local fish managers, have had impacts on native species that were never considered and are currently difficult to reverse. While introduced fish effects on native amphibians are typically attributed to direct interactions (e.g., predation), the influence of introduced fish can be subtle. The results from this study suggest that introduced fish contribute to changes in frog population dynamics, population size, and/or distribution. Data from this study provide an important baseline to test hypotheses about spotted frog population dynamics and for long-term monitoring.

ACKNOWLEDGMENTS

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Chapter 1. General Life History Patterns of Amphibians: A Literature Review

A global amphibian decline has become evident within the last decade (Houlahan et al. 2000). However, the paucity of natural field experiments has limited the ability to identify the mechanisms of decline (Fellers and Drost 1993). Data that exist typically are limited to short study periods (< 5 years) making it difficult to separate natural population fluctuations from human-caused declines (Pechmann et al. 1991, Alford et al. 2001). If amphibian populations naturally decrease more often than they increase as Alford and Richards (1999) suggest, it may be impossible to detect a real decline. Although it is important to realize that the dynamics of local populations may be poor indicators of their status, numerous studies have identified several possible elements contributing to population decline and local extinctions including: 1) introduction of alien species, 2) over-exploitation, 3) habitat loss and fragmentation, 4) increased UV radiation, 5) increased use of pesticides, and 6) emergent infectious diseases (Collins and Storfer 2003). The introduction of fish into naturally fishless waters is most commonly implicated in amphibian declines for high-elevation species (Bradford 1989, Drost and Fellers 1996, Knapp and Matthews 2000).

High-elevation, fishless waters probably once constituted major population centers for species of amphibians whose aquatic larvae are vulnerable to fish predation. Studies across many mountain ranges in North America have established that fish introductions have altered distribution of native frogs and salamanders, apparently contributing to their recent extirpation at local and,

possibly, regional scales (Bradford 1989, Bradford et al. 1993, Fellers and Drost 1993, Hecnar and M'Closkey 1997, Tyler et al. 1998). Introduced fish can also change the species composition and size structure of zooplankton, and depress or eliminate important large-bodied zooplankton (Brooks and Dodson 1965, Vanni 1988, Chess et al. 1993, Liss et al. 1995, McNaught et al. 1999). The consequences of such changes in zooplankton food webs on food supply, growth and survival of frogs are not known with certainty but could be significant (Bahls 1992, Liss et al. 1995, Tyler et al. 1998, McNaught et al. 1999).

To examine this phenomenon more closely, I initiated a study in the Absaroka-Beartooth Wilderness in 1999. Although the Wilderness falls within the potential range of several amphibian species, including the Tiger salamander *(Ambystoma tigrinum)*, Boreal toad *(Bufo boreas boreas)*, Columbia spotted frog *(Rana luteiventris)*, and Boreal chorus frog *(Pseudacris triseriata)* (Reichel and Flath 1995), the Columbia spotted frog is the only amphibian I encountered in the area chosen for study. Thus, the research results I report in this thesis will focus on this particular frog species.

This organism is of interest for several reasons related to a recent reclassification of the western North America spotted frog complex into two genetically distinct species *(Rana pretiosa, R. luteiventris)*, thus altering their conservation status (Green et al. 1997). The current range of the two species is the result of glacial retreat since the Pleistocene glacial maximum. Genetic differences considerable enough to warrant reclassification of *Rana pretiosa* into *Rana pretiosa* and *Rana luteiventris* seems to be due to geographic isolation and

fragmentation of populations (Green et al. 1996). Over this long time period, the northern range extension has been accompanied by a range contraction to the south. The range shift has resulted in several fragmented populations of *R. luteiventris* in high-mountain basins of Nevada, Utah, and Idaho that are essentially island communities. Each population is completely isolated because of the extensive desert separating them. Further genetic analysis will determine if these "relict" populations are yet another species.

Though Columbia spotted frogs (*Rana luteiventris*) are the most common amphibian in the Greater Yellowstone Ecosystem (GYE) and appear to be successfully reproducing, a 75% decline has been documented for one population near the North shore of Yellowstone Lake in Yellowstone National Park, Wyoming during the past 40 years (Patla 1997). Since the early 1900's, the Oregon spotted frog (*Rana pretiosa*) has disappeared from 78 – 90% of its historical range in Washington, Oregon and California (Hayes 1997). At this time, neither *R. pretiosa* nor *R. luteiventris* are federally listed as threatened or endangered species (Stebbins and Cohen 1995). However, *R. pretiosa* is a candidate for federal listing and a species of concern in Washington and Oregon (Leonard and McAllister 1997). *R. luteiventris* is a state candidate in Washington and a federal candidate in Idaho, Nevada, Oregon and Washington (Mizzi 1997). A federal conservation agreement was established in 1998 to protect *R. luteiventris* in the Provo River, Utah. The Bureau of Land Management has also designated *R. luteiventris* as a sensitive species in Idaho and Montana. A recent conference on the biology and conservation of the spotted frog allowed various

research biologists and natural resource managers to discuss the status of this species and to identify research needs. This meeting provided an opportunity to coordinate efforts on spotted frog research throughout its geographic range. Little work had been conducted on the Columbia spotted frog in Montana and this meeting served to connect biologists to facilitate further biological and ecological studies of the spotted frog.

The research I report on here goes beyond determining the relationship between introduced fish presence and frog presence, and investigates multiple metrics that can be used to identify the effect introduced fish may have on the frog population. All frog life stages were studied over a 3-year period. In the studies on spotted frogs in the Absaroka-Beartooth Wilderness, I examined adult frog abundance and age/size structure, reproductive biology and recruitment in the context of influences on food-webs and examined the influence of fish to test for top-down effects on the aquatic food-web. My results suggest that impacts by fish on this system are mostly indirect and include interactions between both biological and behavioral factors in the frog population.

The goal of this chapter is to provide a literature review exploring environmental and biological influences on an amphibian through its life cycle. Specifically I focused on those factors expected to be most influential on Anurans (specifically Ranidae) that deposit eggs in water in north temperate, high elevation, lentic ecosystems.

Life History

Most amphibians exhibit a complex life history, filling niches in water and on land (Duellman and Trueb 1986). Breeding activity is cued by environmental conditions, such as temperature, precipitation, or ice-out (Duellman and Trueb 1986, Bull and Shepherd 2003). Females typically lay eggs in marginal shallows of ephemeral ponds where water temperature is at a maximum (Berven 1990) and, therefore, developmental and growth rates are highest (Bizer 1978, Wollmuth et al. 1987). Hatchling larvae have a compact body and tail allowing them to exploit the aquatic environment where they develop and grow until they reach a certain body size. Eventually, free-swimming larvae metamorphose and the presence of front and hind limbs allow the movement of frogs, toads, and salamanders in the terrestrial habitat and the ability to exploit new resources. The terrestrial stage will reproduce and disperse.

Amphibians exploit various habitats throughout their life history in both terrestrial and aquatic environments. Where environmental stresses are imposed naturally and persist long-term (e.g., native predators, pond drying, density effects), species have adapted by varying larval period and size at metamorphosis, and by developing antipredatory behavior. However, recent anthropogenic influences have severely altered the ability for successful persistence. Habitat loss, fragmentation, climate change, and exotic introductions have occurred over relatively short time periods and have led to declines in many amphibian populations (Collins and Storfer 2003).

Larval Environment

Numerous studies suggest that the environmental conditions to which

larvae are exposed are highly predictive of overall individual fitness (Wilbur 1972,

Travis 1980, Berven 1981, Petranka and Sih 1986, Semlitsch et al. 1988, Berven

1990, Amezquita and Luddecke 1999). Biotic and abiotic factors that affect the

life-history in the aquatic phase may control population dynamics and

persistence, because the larval stage is most influenced by environmental

factors. In ephemeral or shallow habitats, larvae must metamorphose at the end

of the first season to avoid desiccation or freezing, to exploit terrestrial resources

or move to areas of water permanence, and/or overwinter (Berven 1990,

Newman 1998, Amezquita and Luddecke 1999). Those that cannot transform do

not survive.

Metamorphs that survive a poor larval period are at a disadvantage,

because the size of a frog or salamander at metamorphosis has direct immediate

and long-term effects (Crump 1981, John-Alder and Morin 1990, Scott 1994).

Metamorph size influences adult survival and fecundity (Pettus and Angleton

1967, Smith 1987). For example, though an individual may initially survive,

smaller frogs and salamanders may exhibit decreased fitness through reduced

reproductive output (Smith 1987, Scott 1994). Although fecundity is highly

variable among amphibian species, in general, female body size is positively

correlated with clutch and egg size (Duellman and Trueb 1986), smaller breeding

females produce smaller and fewer eggs. A delay in sexual maturity because of

small size may result in a reduction in lifetime fecundity, frogs that reach sexual

maturity at a later age may have fewer opportunities for reproduction. Degradation in adult fecundity as a result of poor larval conditions may lead to population-wide reductions in breeding success and recruitment. Elasticity analyses conducted for two amphibian species (*Ambystoma macrodactylum* and *Bufo boreas*) suggest that the effect of egg mortality on the persistence of a population may be slight, will vary with the number of eggs laid by a species and with the degree of density-dependence in the larval stage (Vonesh and De la Cruz 2002). Post-metamorphic vital rates (juvenile and adult) appear to be the most influential in elasticity analyses conducted for *Rana muscosa*, *R. temporaria*, and *Bufo boreas* (Biek et al. 2002) but again variation is apparent among species and is expected among populations. Though both studies suggest that post-embryonic vital rates are more influential and that post-metamorphic survival most influential on population trends (Biek et al. 2002, Vonesh and De la Crus 2002) repeated episodes of poor environmental conditions for developing larvae that result in reduced adult success could indeed influence population viability.

In contrast, large metamorphs tend to be less susceptible to size-limited predators (Caldwell et al. 1980) and may have more energy reserves to avoid capture (Crump 1981, Alder and Morin 1990). Moreover, large metamorphs will be larger at sexual maturity and reach maturity at a younger age. Reproductive success directly related to body size and early maturation may increase the probability of survival to first reproduction and a greater reproductive output

during an individual's lifetime (Pettus and Angleton 1967, Berven 1990, Scott 1994).

Pettus and Angleton (1967) suggest that reproductive strategies differ between high and low elevation populations in amphibians. At high elevations, the time period between hatching and metamorphosis is constrained by temperature. To compensate for a limited growing season, conspecifics in high elevation sites may be larger as adults and produce larger eggs than those in lowland areas (Pettus and Angleton 1967). Consequently, hatching tadpoles are larger and can transform more rapidly than tadpoles born from smaller eggs. Amphibians that breed in higher montane areas invest more energy into every egg so that each larvae has a greater likelihood of surviving. Those in lowland areas produce many small eggs. This strategy increases the probability that some will persist, with less parental expenditure into each egg.

Trade-Offs of Behavioral Response to Predation

Tadpole behavior and activity are influenced by resource and microhabitat quality, and by predation risk (Lawler 1989, Werner and Anholt 1993). Prey behavior and activity levels are strongly structured by predators, even when the predator impact is nonlethal (Skelly and Werner 1990). Active larvae may be able to access more food, thereby hastening development, but they are at a higher risk from visually cued predators such as trout (Skelly 1996). Under the threat of predation, individual larvae may alter behavior and shift their activity patterns to avoid predators (Caldwell et al. 1980, Holomuzki 1986, Lawler 1989, Tyler et al. 1998) and the time and energy allocated to growth and resource

acquisition is diverted to defense (Van Buskirk 2000). In some cases, daily shifts in predation pressure can cause associated shifts in microhabitat use. For example, nocturnal activity of a beetle predator (*Dytiscus dauricus*) excluded larval *Ambystoma tigrinum nebulosum* in the resource-rich littoral zone (Holomuzki 1986). Low activity levels compromise competitive ability, slow development, and prolong exposure to predators. In the absence of fish in most high mountain lakes (Bahls 1992), anuran larvae actively feed on suspended particles in the water column. However, in the presence of fish, these larvae may alter their behavior to avoid predation by fish and suffer a cost to foraging efficiency, resource quality, and survival (Petranka et al. 1987, Sih et al. 1992, Feminella and Hawkins 1994). Thus, predator presence may not affect larval survival directly but often the effect is indirect by inhibiting growth rates which leads to smaller size in metamorphs (Figiel and Semlitsch 1990).

Amphibians commonly detect predators via nonvisual cues, including chemical signals. Several experiments have documented antipredatory behavior in response to water that was conditioned by the presence of potential predators (Petranka et al. 1987, Kats et al. 1988; B. Maxell and A. Wyrick, The University of Montana, unpublished data). Amphibians may coexist with predators by constantly sampling the environment and adjusting activity level and habitat usage accordingly. Some species are unpalatable to predators, an antipredatory adaptation tightly linked with exposure to predation (Kats et al. 1988). Species that inhabit sites without fish predation (or with limited exposure) remain palatable. Although predation pressure should be less on noxious species,

amphibians with this defense mechanism also will reduce their activity levels in the presence of predators (Brodie et al. 1978). Often the presence of a predator completely excludes amphibians from lakes and ponds because the prey have not yet developed behaviors to avoid predation (Petranka 1983, Bradford et al. 1993, Tyler et al. 1998).

Amphibian populations indigenous to historically fishless waters may lack behavioral adaptations to resist predation (Bradford 1989, Liss et al. 1995, Tyler et al. 1998). Previous research in several mountain ranges in western North America has established the vulnerability of ranid frog tadpoles to trout predation (Bradford 1989, Pilliod and Peterson 2001). Fish are efficient aquatic predators and may be the greatest predation threat to amphibian larvae. The presence of introduced fish may exclude the presence of amphibians due to high predation pressure, especially in high elevation lakes where cover for amphibians is limited and overall low productivity limits availability of alternative large food items for fish. Indeed, efficiency of predators generally increases with decreased habitat complexity (Crowder & Cooper 1982, Lawler et al. 1999), such as is common in high-elevation lakes and ponds.

Food-web interactions between fish, insects, and amphibians are highly linked. In many systems, insect predation may cause significant mortality of the larval and juvenile stage of amphibians (Caldwell et al. 1980, Gascon 1992, Werner and McPeek 1994, Skelly 1996, Peacor and Werner 1997), and influence larvae behavior (Relyea 2000, Van Buskirk 2000). Insects also may compete with larval anurans for similar habitat and food resources (Morin et al. 1988,

Peacor and Werner 1997). In some cases, abundance and diversity of predatory and competing insects is reduced in fish-bearing sites thereby reducing competitive and predation pressure (Werner and McPeek 1994, Skelly 1996, Lawler et al. 1999).

Larval Period and Size at Metamorphosis

Amphibians can persist in highly variable environments because larval developmental rate and length of the larval period, size at metamorphosis, and reproductive effort vary as well. Physiological constraints influence the range in larval period and body size at metamorphosis, while environmental conditions determine exact timing (Denver 1997). Indeed, growth rates vary considerably in response to abiotic and biotic factors and during an individual's lifetime. There is a debate however. For example, Wilbur and Collins (1973) argued that growth rates affect development throughout the larval period but Travis (1984) argued that the rate of development is set early in the larval period and individual variation is due to independent responses to environmental effects. Further research suggests that tadpoles allocate resources differentially throughout the larval period (Leips and Travis 1994). Early resource conditions dictate development rate and age at metamorphosis, and food quantity and quality late in the larval period determine size at metamorphosis (Newman 1998). Early on, food resources are used for individual development. Increasing food intake at this stage will hasten development (reduce larval period) while a decrease will have the opposite effect. Later on larvae will allocate resources to growth. Consequently, changes in resource quality at this point will affect final body size.

Unfavorable conditions retard rate and development of larvae. And slowly growing tadpoles metamorphose later and at a smaller size, or perish.

Although changes in rates of growth and development affect larval period and size at metamorphosis, larvae must reach a threshold size to ensure successful metamorphosis (Wilbur and Collins 1973). Once the threshold size is reached, environmental conditions influence whether or not a larva will metamorphose to escape poor aquatic conditions (e.g., lack of water permanence) or remain in the favorable aquatic environment for awhile longer (Semlitsch and Wilbur 1988, Pfennig et al. 1991, Leips and Travis 1994, Newman 1998, Amezquita and Luddecke 1999). Scarce resources, high predation rate, and site drying are conditions that favor emergence. Once larvae reach metamorphic climaxes, they no longer feed and are completely dependent on stored energy, so successful metamorphosis also depends on energy reserves (Crump 1981). Ultimately, larvae should transform only when they have enough energy reserved for the metamorphic process.

Temperature

Studies have shown that several species of ranid tadpoles prefer microhabitats within a pond or lake that are warmer and will preferentially congregate in water at ~25° C (Lucas and Reynolds 1967, Bradford 1984, Wollmuth et al. 1987). How larvae move between various thermal habitats is one mechanism regulating larval development and growth and growth rates of larvae increase with increasing temperature up to ~30° C.

In ephemeral aquatic habitats, individuals must transform before a pond dries, therefore larvae exposed to higher temperatures will have a higher growth rate and metamorphose before desiccation. In sites where water permanence is not a limitation, higher temperatures may allow an individual to metamorphose at a larger size and increase energy reserves (Crump 1981, Alder and Morin 1990, Amezquita and Luddecke 1999). Interestingly, temperature fluctuations have major influences on larval development and growth, especially at high elevations where extreme weather fluctuations and lack of cover allow a wide range in diurnal and seasonal water temperature (Heath 1975, Bizer 1978). A study by Bizer (1978) documented that water temperature influences salamander larval growth rates more strongly than food abundance. Access to warmer microenvironments as larvae therefore increases the probability of survival to metamorphosis and through the first winter. It is important to note that high-energy reserves and large size at metamorphosis become increasingly important when individuals overwinter under stressful conditions, such as in high elevation landscapes.

Breeding Activity

Because many amphibian species preferentially breed in temporary habitats when both permanent and temporary habitats are available, the duration of the breeding and rearing season is limited for many amphibians (Woodward 1983). For amphibians that breed in ephemeral ponds, the most influential factor during larval period is the hydroperiod, or persistence of open water in the pond basin (Semlitsch and Wilbur 1988). Ephemeral sites lose volume as the season

progresses due to limited inputs (e.g., rainfall) and/or evaporation. Pond persistence varies annually and, in years of higher average temperatures and/or lower rainfall, ponds dry out more rapidly and egg masses may be stranded out of the water before the embryos hatch. In general, ephemeral sites exclude species that have a lengthy larval period (Kats et al. 1988). Because fish are able to exploit ephemeral waters only when connected to permanent waters via streams, amphibians with a larval period shorter than one season can exploit ephemeral sites to avoid direct predation by fish, thus these sites can serve as refugia for breeding and rearing. Fish must move out of these ephemeral sites before they dry or freeze, so isolated ponds rarely support fish populations unless artificially stocked.

Conspecific competition

Biological interactions with conspecifics alter habitat and resource availability. Increased larval density can lead to increased competition for existing resources and energy expenditure to obtain food. Thus, competition with conspecifics may lead to increased larval period and decreased size at metamorphosis (Petranka and Sih 1986, Scott 1994, Newman 1998). Larval density not only affects growth and developmental rates and metamorph size, but it also influences how readily an individual can store energy (Crump 1981). At high densities, larvae that expend energy in competitive interactions allocate fewer resources to storage. At low densities, individuals tend to maximize resource uptake and accumulate energy more rapidly, thereby influencing the metamorphic process. Superior larval competitors can produce growth inhibitors

that further limit the development of other tadpoles (Wilbur and Collins 1973), consequently increasing their competitive ability and decreasing predation risk (Travis 1980).

Dispersal and Connectivity

Seasonal dispersal and distribution is influenced by frog activity level, topography, dispersal corridor, and predator presence along the dispersal corridor. Populations are more sensitive to local extinction when dispersal is limited, they may disappear following the complete loss of a larval cohort due to an unsuitable aquatic environment (e.g., pond drying) before transformation or when a population becomes isolated (Corn and Fogleman 1984, Sjogren-Gulve 1994). Repeated episodes of zero recruitment severely reduce future breeding populations and lead to crashes in local populations when immigration is limited or nonexistent. Isolation and fragmentation of populations reduce the likelihood that individuals from other sites can immigrate to an isolated population. Moreover, the presence of fish in lakes and connecting streams/rivers acts to isolate and fragment remaining amphibian populations because they severely limit dispersal ability and subsequent recolonization (Bradford 1991, Bradford et al. 1993, Sjogren-Gulve 1994), thereby increasing the probability of disappearance in response to natural, random events (Sjogren-Gulve 1991, 1994; Pearman 1993).

After metamorphosing from an ephemeral site, juvenile spotted frogs (*Rana luteiventris*) migrate to sites with permanent water (Turner 1958). Predation pressure on juveniles en route to an overwintering site and/or the

presence of predators in the permanent site may reduce recruitment. At high elevations, the presence of fish in permanent sites may reduce the availability of favorable amphibian overwintering sites (Pilliod and Peterson 2001). However, frogs may overwinter away from fish predators in nearshore holes, crevices, and ledges when the oxygen supply (air or water) is adequate (Matthews and Pope 1999). In sites where alternative frog refugia are unavailable, predator effects on overwinter survival may be severe.

Conclusions

While basic natural history has been described for all species, there have been few biological or ecological studies of amphibians in the state of Montana. This study on the Columbia spotted frog (*Rana luteiventris*), provides novel information about the habitat preferences, breeding biology and the interactions among species in high elevation water bodies. Data from this study provide a baseline for continued evaluation of the global phenomena of amphibian decline and further elucidates the mechanisms that are involved in interactions between introduced predators and frogs. This research was conducted in the Absaroka-Beartooth Wilderness, thereby minimizing some of the confounding effects from human impacts more common in lower elevation habitats with more extensive human influences.

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Chapter 2. Demography of the Columbia Spotted Frog (*Rana luteiventris*) in the Presence or Absence of Fish in the Absaroka-Beartooth Wilderness, Montana

INTRODUCTION

Amphibians are an integral component of most ecosystems worldwide and link aquatic and terrestrial habitats through nutrient flow from water onto land and back. Globally, many amphibian species are on the decline with significant consequences for biological diversity and ecosystem functions. The most puzzling declines have occurred in habitats or locations that are considered pristine and relatively untouched by human impacts (Wake 1991, Drost and Fellers 1996, Knapp and Matthews 2000). Various causes have been proposed, including the loss of habitat, pesticides, increased UV exposure, infection by parasites and bacteria, and introduction of exotic species (Collins and Storfer 2003). Habitat loss is the dominant threat to persistence, but in many cases, declines are attributed to a suite of causes.

In the Pacific Northwest region of the United States, the loss of habitat and the introduction of exotic species have been the major contributors to amphibian decline (Bradford 1989, Fellers and Drost 1993, Knapp and Matthews 2000). Increased urbanization has led to habitat fragmentation, pushing frogs and salamanders out of preferred habitat, and into less favorable areas where they may contact new and novel predators (e.g., non-indigenous fish and bullfrogs; Hayes and Jennings 1986, Kiesecker and Blaustein 1998, Lawler et al. 1999). Habitat loss and fragmentation is expected to be particularly problematic for

amphibians because many species require multiple habitats for each stage of the complex life cycle (e.g., breeding areas, hibernacula, foraging areas).

Even within areas of national forests, parks, and wilderness areas considered to be less impacted by land use changes and disturbance, amphibians (primarily frogs and toads) are experiencing major setbacks (Liss et al. 1995, Drost and Fellers 1996). Particularly since the early 1900s (but as far back as the early 1800s), fish have been introduced to lakes, ponds, creeks, and rivers to provide humans with forage and recreational fishing (Bahls 1992, Knapp 1996, Pister 2001). Fish have been introduced into waters from sea-level to the highest alpine elevations. Where non-indigenous fish have been introduced, frogs and toads have experienced decreased available habitat, increased predation pressure, and alterations of the pre-introduction food web. In most cases, the introduction of fish has led to the local decline (and possible exclusion) of amphibians (e.g., Bradford 1989, Tyler et al. 1998a, Knapp and Matthews 2000). Where amphibians continue to inhabit watersheds that have been stocked with fish, population numbers are significantly lower than historical levels and rarely (if ever) does breeding occur in sites stocked with fish (Bradford 1989). Studies that examined interactions between populations of amphibians and introduced predators identified direct predation as the mechanism of the loss or decline of the amphibians (e.g., Hayes and Jennings 1986).

In response to recreation demand, fish have been introduced into naturally fishless waters with the introductions planned and carried out by federal, state, and local fish managers (Knapp 1996). Unfortunately, these fish have had

impacts on native species that were never considered and are currently difficult to reverse. Introduced fish effects on native amphibians are typically attributed to direct interactions (e.g., predation). Although the influence of introduced fish can be subtle, the results from this study suggest that introduced fish contribute to changes in frog population dynamics, population size, and/or distribution. And the introductions may have influences elsewhere in the foodwebs of the ponds, including insect and plankton communities (e.g., Pecarsky and McIntosh 1998, McNaught et al. 1999). In most cases, the characterization of these food-webs and the species that are involved are unknown.

The Absaroka-Beartooth Wilderness area has a trout fishery largely sustained by continued fish stocking with most lakes on 8-yr stocking schedules (Marcuson 1985, Marcuson and Poore 1991). However, some lakes have never been stocked or no longer support fish. Thus, the Absaroka-Beartooth wilderness is one of the few areas in the western United States where more than 10% of the large, high-elevation lakes are maintained in fishless condition (Bahls 1992).

In this study, I examined the physical and biological influences on the Columbia spotted frog, *Rana luteiventris*, in the Absaroka-Beartooth Wilderness, Montana, USA. Although spotted frogs are the most common amphibian in the Greater Yellowstone Ecosystem, a 75% decline has been documented in one part of their range during the last 40 years (Patla 1997). In particular, I examined the influence of introduced brook trout (*Salvelinus fontinalis*) and Arctic grayling

(*Thymallus arcticus*) on frog population dynamics by comparing ponds with and without fish.

The Columbia spotted frog population in this study has co-occurred with Arctic grayling for more than 20 years, and with brook trout for more than 50 years. Predation pressure may select for adaptive life history shifts in a variety of animals, and based on life history theory we can make several predictions regarding the adaptive shifts in life history of Columbia spotted frogs (Stearns 1992). The risk of predation may affect life history of these animals in at least two ways 1) predation pressure on the aquatic or juvenile stage will select for later sexual maturity, longer-lived adults and lower investment per reproductive event, and 2) predation pressure on the adult stage will select for earlier sexual maturity and higher investment per reproductive event.

In addition to conducting basic morphometric and limnological analyses, I predicted that: 1) introduced fish would have the greatest impact on the aquatic stage of the frog life cycle; 2) negative impacts during the egg and/or larval stages would be manifested in the adult population, and 3) in this system, influences of the physical environment are secondary compared to biological interactions between frogs and introduced fish.

STUDY AREA

This study was conducted in south-central Montana, USA, within the Absaroka-Beartooth Wilderness, a remote region south of Granite Peak at 2800 – 2950 m above sea level. I chose this study area because it exhibited Columbia spotted frog presence and breeding activity at a number of lakes and ponds. The

area was accessible within a day's hike and was geographically isolated by high

mountains to the north and east and a 300 m cliff to the south. All water bodies

examined were within a of 4-km^2 area, allowing regular data collection and

observation (Figure 1). The waterbodies examined ranged from lakes with little

vegetation to shallow ponds with extensive vegetation. The surrounding

landscape was dominated by subalpine fir (*Abies lasiocarpa*), Engelmann spruce

(*Picea engelmannii*) and dwarf huckleberry (*Vaccinium cespitosum*). Willow

(*Salix* spp.) and whitebark pine (*Pinus albicaulis*) were also present in some

areas. Twenty-one permanent ponds and lakes, and four ephemeral ponds

comprised the lentic environment and all runoff flowed into the Clarks Fork of the

Yellowstone River. The water in the study area is usually ice-free from early

June until late September. Based on an initial survey, ponds above 2950 m in

elevation were excluded from further study because they did not appear to

support amphibian populations.

STUDY SPECIES

The Columbia spotted frog (Ranidae, *Rana luteiventris*) is a common

anuran found in parts of Alaska, British Columbia, Washington, Oregon, Nevada,

Idaho, Montana, Utah, and Wyoming in North America (Turner 1958, Licht 1974,

Green et al. 1997). The onset of breeding activity is variable annually and

depends on elevation and temperature. In high-elevation sites, breeding occurs

immediately following ice out. Larvae hatch several weeks after eggs are

deposited and metamorphosis follows up to four months later (Turner 1958,

Morris and Tanner 1969). The larval period is constrained by habitat availability
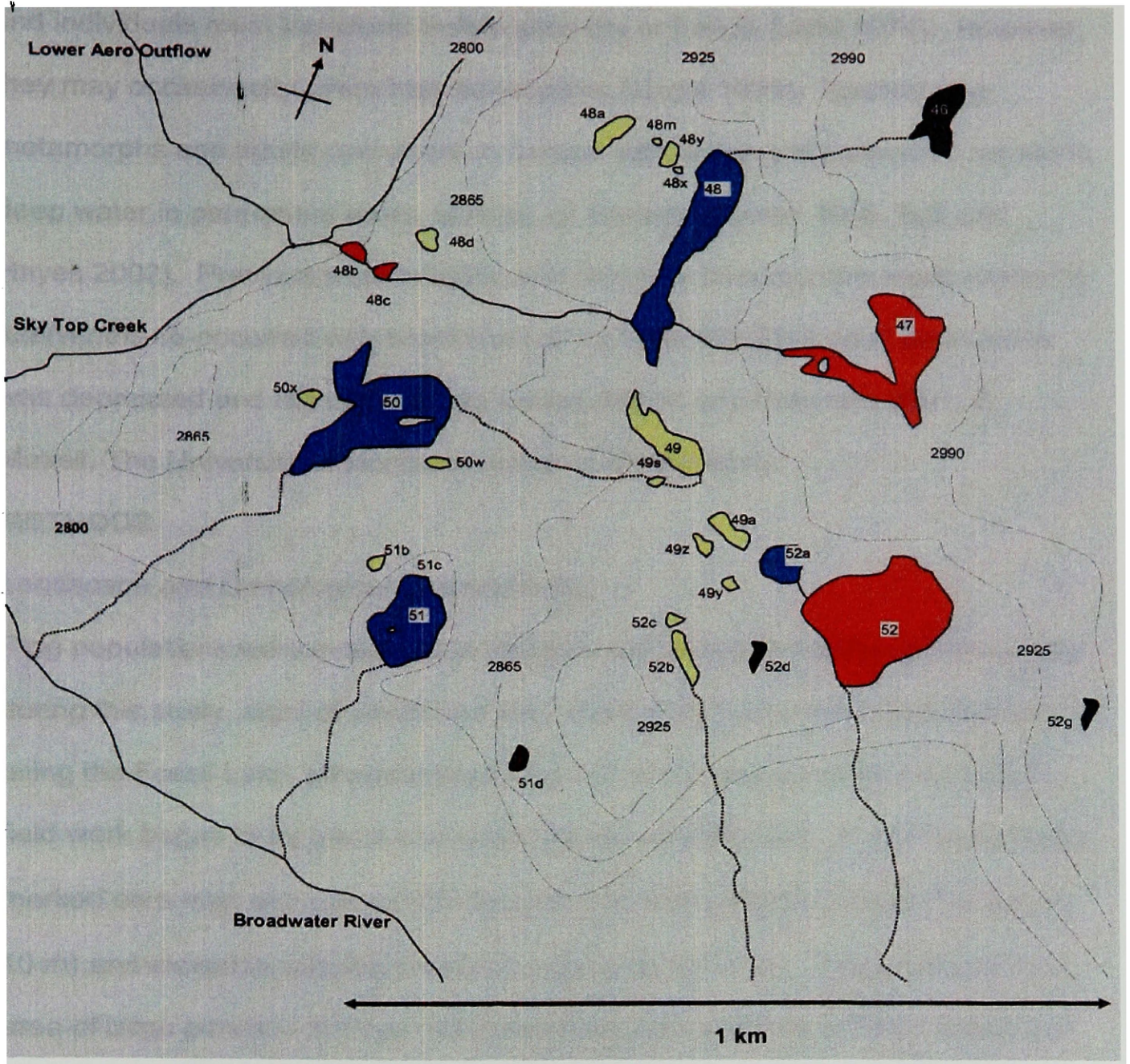
Figure 1. Map of study area. Ponds in red support fish only, in yellow support frogs only, in blue support both fish and frogs and in black support neither. Elevation contours are shown in light gray and rivers and streams are shown in black.

and individuals must transform before sites dry or freeze (Licht 1974). However, they may occasionally overwinter as tadpoles (Engle 1999). Spotted frog metamorphs and adults overwinter in contact with water and commonly retreat to deep water in permanent lakes, springs, or streams (Turner 1958, Bull and Hayes 2002). Previous work in Idaho and Montana documented areas where *R. luteiventris* co-occurred with brook trout or cutthroat trout but adult abundance was depressed and recruitment was limited (Pilliod and Peterson 2001; B. Maxell, The University of Montana, personal observation).

METHODS

Landscape and Limnological Characteristics

Frog populations were evaluated in 25 lakes and ponds (hereafter called ponds) during this study, eight of which had fish. Each lentic water body was located using the Fossil Lake, Montana-Wyoming 7.5' USGS topographic map before field work began or by visual encounter during early surveys. Pond location was marked on a map and into a GPS (Garmin International Inc., Olathe, Kansas; ± 10 m) and elevation was determined by topographic maps. The perimeter and area of large ponds (> 0.1 ha) was determined using Montana Fish Wildlife and Parks maps (P. Marcuson, Montana Fish Wildlife and Parks, unpublished data). Smaller ponds were measured with a meter tape to determine the length and width; from these data, rectangular area and perimeter were calculated using standard formulae. Maximum depth was measured (in m) in shallow ponds, or estimated visually or determined from preexisting data for deep ponds (> 2 m; P. Marcuson, Montana Fish Wildlife and Parks, unpublished data).

Conductivity was measured in each pond twice during the summer of 2001. All measurements were made 1 m from shore at 2 cm below the water surface using a handheld conductivity meter (Model WD-35653-11, Oakton Instruments, Vernon Hills, Illinois). In the summer of 2000, water temperature (°C) was measured using a HOBO H08 4-channel data logger (Onset Computer, Bourne, Massachusetts) at each of two ponds. Temperature probes were set at 0.05, 0.25, and 0.50 m deep and the fourth probe measured air temperature. In 2001, temperature was monitored in an additional 6 ponds used for breeding and rearing. At five of these ponds, a single StowAway TidbiT temperature logger (Onset Computer, Bourne, Massachusetts) was placed at a depth of 5 cm for 70 days. A HOBO H08 4-channel data logger was used at the sixth pond to measure water temperature at 1 m ("deep"), 0.3 – 0.5 m ("mid"), and 0.05 – 0.1 m ("shallow"). The fourth probe measured air temperature. All temperature data were collected at 15-min intervals. In some cases, temperature probes placed in the water became exposed to air. In these cases, only the days when probes were known to have accurately recorded water temperature were included in subsequent analyses. Degree-days (dd) were calculated for each 15-min reading and then summed for the day (equation 1). Development and growth in Ranid frogs generally does not occur below 10 °C (McDiarmid and Altig 1999, Bull and Shepherd 2003) and this temperature was used as the threshold in calculating degree-days. Cumulative degree-days were calculated by month and for the entire field season (equation 2).

Equation 1:   Daily dd = Σ [dd(15-min)/96]

If temperature > 10 °C then dd(15-min) = Temp (15-min) - 10 °C

If temperature $\leq$ 10 °C then dd(15-min) = 0

Equation 2:   Cumulative dd = Σ average daily dd

Landscape characteristics were determined using the USGS 7.5' Fossil Lake Quadrangle map. Distance between ponds was measured using a metric ruler and then corrected to actual ground distance in km. The distances (m) from each pond to the nearest pond with fish, nearest pond with frogs, and nearest pond with frog breeding were estimated. Annual precipitation data was collected from a National Weather and Climate Center SNOTEL weather station (Fisher Bridge) located 8 km southwest of the study location.

Fish Presence and Abundance

The baseline reference for fish presence and density was the 1999 Montana Fish Wildlife and Parks stocking report. Thereafter, I verified the presence and abundance of fish (1999 and 2000) using a 30 m x 1.2 m gillnet positioned across the northwestern shoreline of each pond examined (n = 8). The net was set up in the evening and removed the next morning. Length, gender, and species were determined for all caught fish; gape height and width (gape size) was measured for fish caught in 2000. All stomachs were collected to determine the degree of "stomach fullness" and stomach contents. Stomachs, kidneys, and livers were visually examined and the presence of parasites was

noted. For the other 18 ponds, the presence or absence of fish was verified by visual observation at the water surface. Finally, each pond was categorized according to whether fish are stocked on an 8-yr schedule or if they are self-sustaining populations.

Ponds with brook trout (n = 7) and arctic grayling (n = 1) were pooled for all analyses of the effect of fish presence on various frog metrics. Trout consume a wide variety of prey, feeding from the surface to benthos of ponds and streams (Moyle and Cech, 1996) and brook trout in the study area are known to be voracious feeders. Although little has been published on the biology of Arctic grayling in Montana, previous work on this species in Alaska has shown it to be an aggressive and adaptable predator, feeding from deep water to surface (Lee 1985). Brook trout have a larger gape size than Arctic grayling, but I pooled species into the category "fish present" because they occupied the same habitat in the ponds studied, and because I made the assumption that they would have comparable effects on frog demography.

Population Estimates for Adult Frogs

During the summer of 1999, frog presence and abundance were estimated by the visual encounter method (Thoms et al. 1997). At each pond, two observers walked around the perimeter of the pond (one in the water, one on shore), maintaining a distance of ~0.5 m, and recording all individuals encountered. In 2000 and 2001, I implemented a capture-mark-recapture (CMR) sampling design (Pollock 1982, Kendall and Nichols 1995, Kendall et al. 1997), and data were collected during two survey sessions annually. The initial capture-

mark session occurred during mid-July when the majority of animals were congregated at foraging sites; the other sampling session occurred during late August as metamorphs emerged and individuals prepared to overwinter. After the first capture session in July 2000, the number of recaptured individuals far exceeded the number of unmarked frogs. Therefore, CMR sampling was reduced to a single time for each subsequent survey session.

To implement CMR sampling, ponds generally were divided into 2 or 4 equal sections. To locate and capture frogs, two observers walked around the perimeter of each pond (on observer several meters behind the other), and capturing all frogs (noting when one escaped). Because the water was very clear and there were few obstructions (emergent vegetation or large-woody debris), we were able to find and capture most frogs that were present during the sampling period. Captured frogs were held in a large plastic container until the section of the pond under study was fully searched and all frogs were deemed to have been captured. Each frog was processed individually and measurements were made by the same observer. Body length (snout-vent length) was measured using dial calipers (± 0.1 mm) and body mass was measured with a Pesola spring scale (Forestry Suppliers Inc., Jackson, Mississippi; ± 0.1 g). Mature males were recognized by the presence of nuptial pads, females by the absence of nuptial pads, and juveniles by body length (< 45 mm). During the first visit to a pond, all individuals were given a unique toe-clip mark, following an alphanumeric toe-clip code modified from Waichman (1992). At least three toes were clipped but no more than two toes were clipped from any one foot. Toes

from at least 30 individuals per pond were collected and stored in 95% ethanol (these are available for microsatellite analysis). All other toes from each pond were stored in 10% formalin for use later in a skeletochronology analysis (see description below). Cuts on frogs were washed with Bactine and the frog was then released back into the water. All frogs were processed and released before observers moved on to the next pond section. During subsequent capture sessions, marked individuals were re-measured and their codes were recorded. As possible, microhabitat features were noted where frogs were captured.

Survivorship of females and males was estimated using Program MARK (Gary White, Colorado State University, Fort Collins, Colorado). Summer and overwinter survival of adult male and female frogs was estimated using the Jolly-Seber method and did not assume equal capture periods. Model selection was based on AICc weights.

Clutch density and egg production

In all years, the shoreline and littoral zone were searched for the presence of egg clusters. Pond water in this region is exceptionally clear (Secchi depth > 4 m) making the visual encounter survey the most efficient for this task. In 2001, data were collected in early June during peak breeding season. At each pond, I counted the number of egg clusters; then they were labeled and their location was recorded on a pond map. When possible, ten clusters per pond were collected to estimate the number of eggs/cluster using volume displacement. Each cluster was subdivided into 3 sub-samples and the number of eggs/subsample and the volume displacement were recorded. These data were

used to estimate the number of eggs per cluster. I estimated the date that each cluster was laid by visually examining the status of egg development (Gosner 1960) and the level of mass cohesiveness (C. Funk, The University of Montana, personal observation).

Larval Growth, Development and Metamorphosis

In 2001, size and developmental stage for 30 larvae were recorded for all breeding sites every 10 – 14 days from July 11 to August 23. Larval snout-tail length (STL) was measured using calipers (± 0.1 mm) and a Gosner (1960) developmental stage was assigned. The dates of hatching and first transformation were approximated using data collected during both early June and observations made in late August.

At the end of August 2001, all emerging metamorphs (stage 46) were counted and assigned a unique pond code (one toe was clipped). Criteria for this stage were the total emergence of hind limbs and a completely resorbed tail. For up to ten metamorphs from each pond, snout-vent length (SVL) was measured. The number of emerging metamorphs was calculated using the Lincoln-Petersen estimate.

Skeletochronology

Toes were excised, preserved in 10% formalin, and then randomly selected for skeletochronology analysis (Leclair, Jr. and Castanet 1987). As necessary, samples were adjusted to include an equal number of males and females. I used toes with the greatest bone thickness, smallest marrow cavity (medulla), and with no cartilage. Up to three cross-sections were prepared for

each toe and mounted on one slide (Figure 2). The resorption margin and first

zone (Zug 1991) were identified. Only periosteal lines of arrested growth (LAG)

(Zug 1991) were counted, with special attention focused on closely spaced LAG

at the bone periphery in older frogs (Appendix 1; method of Gary Matson, Matson

Labs LLC, Missoula, Montana, unpublished data). Typically, a peripheral area of

bone that stained darkly contained several LAG that were identifiable at other

points in the same section or in adjacent sections. Age was recorded in months

but is presented in years.
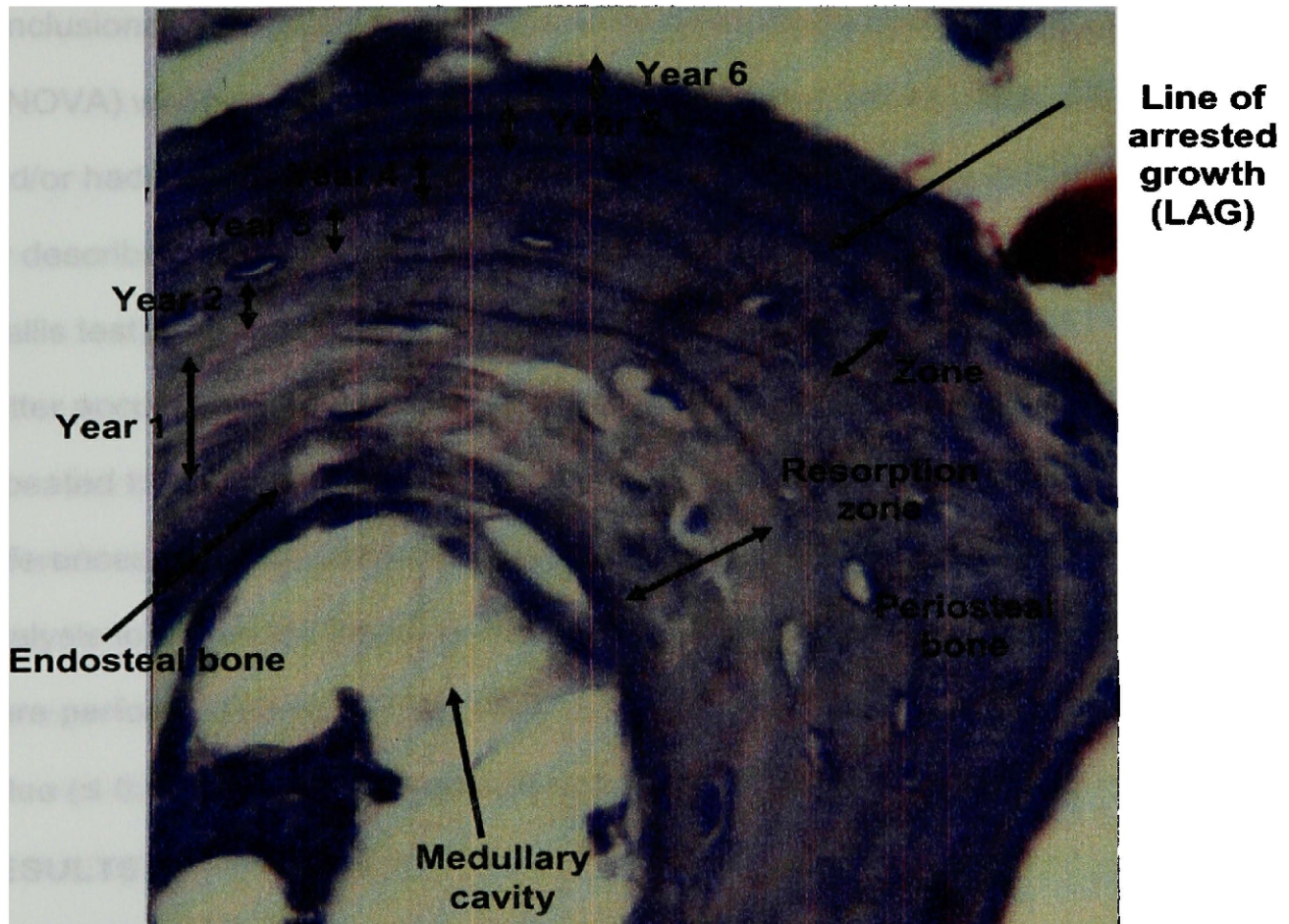
Figure 2. Skeletochronology cross-section (400 X) of an individual frog assigned an age of six years. Photo by Gary Matson 2002.

Statistical Analyses

The extent to which biological attributes of Columbia spotted frogs were correlated with physical/limnological characteristics of the landscape was examined with a Pearson correlation analysis. Chi-square analysis was used to test whether or not the presence of adult frogs and the presence of breeding activity could be attributed to fish presence or absence. Analysis of covariance (ANCOVA) was conducted to determine the influence of habitat and fish presence on various frog metrics and to account for these influences in making conclusions. Comparison of means were made using analysis of variance (ANOVA) when possible. In cases where data were not normally distributed and/or had unequal homogeneity of variance, nonparametric analyses were used for describing other attributes of frog biology (Mann-Whitney U test, Kruskall-Wallis test). As appropriate, analyses were made for all individuals, and then to better account for differences that might be related to gender analyses were repeated to compare separately males and females. The specific significant differences between ponds were identified using Games-Howell post-hoc analysis to determine which ponds exhibited the difference. All statistical tests were performed using SPSS v.10.0 (SPSS Inc., Chicago, Illinois). A standard p value ($\leq$ 0.05) was used as benchmark for statistical significance.

RESULTS

Landscape and Limnological Characteristics

Ponds in the study area were found at elevations from ~2800 to 2950 m above sea level, and ranged in area from 0.01 to ~2.8 ha (Appendix 2). The

most shallow pond was < 0.5-m deep, while the deepest pond was nearly 10-m deep. Larger ponds were deeper (r = 0.85, p < 0.001). Conductivity ranged from 6.0 to 16.5 μS, indicative of low productivity. The number of inlets and outlets were significantly positively correlated with pond area and pond perimeter.

From early July to late August, the daily air temperature ranged from < 1 °C to 24.0 °C ($\bar{x}$ = 12.0 °C in 2000, $\bar{x}$ = 10.3 °C in 2001). Water temperature was highly variable, especially in water < 0.1 m deep (< 1 °C to 34.5 °C); the greatest diurnal range was nearly 30 °C (6.6 – 34.5 °C on July 3, 2001). For the eight ponds chosen for more intensive study, maximum and minimum near-shore water temperature varied from pond to pond. In the summer of 2001, there were no significant differences in shallow water (< 5 cm) temperature among ponds. Cumulative degree day totals for the entire 2001 growing season (6/11 – 8/20) ranged from 582.59 to 798.65 (Table 1). The greatest accumulation of degree-days was experienced by 49a at the highest elevation (2908 m asl) and least accumulation in 49 (2900 m asl). There was no significant correlation between elevation and degree-days (Pearson correlation; p = 0.894). When degree-days were examined for the entire 2001 growing season, two ponds (48d and 49a) had significantly higher mean degree-days than pond 49 (p = 0.045 and 0.011 respectively).

Temperature data from a single fishless pond (49) was further examined to detect mean temperature fluctuations over a 24-hour period in the littoral (< 0.5 m) and deep (> 0.5 m) water habitats (Figure 3). The figure illustrates that littoral habitat had a greater thermal range while deep water provided less variation. In

Table 1. Shallow water (< 5 cm) temperatures and degree-days for a subsample of ponds (3 without fish, 1 with fish) from the study area. The cumulative degree-days for each pond is shown in bold.

Pond (elevation in m)	Dates	Minimum Temperature (°C)	Maximum Temperature (°C)	Mean Temperature (°C) (± SE; n)	Degree-days (°C)
51 (2801)					
	6/11-28/2001	0.00	26.69	9.68 (± 0.09; 5184)	138.57
	7/12-31/2001	8.08	26.04	15.71 (± 0.05; 5760)	342.79
	8/9-20/2001	8.94	25.72	15.49 (± 0.07; 3456)	198.08
					679.44
48d (2835)					
	6/11-28/2001	0.24	21.06	10.73 (± 0.07; 5184)	133.6
	7/12-31/2001	3.27	38.17	16.14 (± 0.07; 5760)	385.75
	8/9-20/2001	11.84	24.77	16.93 (± 0.05; 3456)	253.78
					773.14
49 (2900)					
	6/11-28/2001	0.00	26.75	8.36 (± 0.08; 5184)	98.69
	7/12-31/2001	5.52	30.60	14.34 (± 0.07; 5760)	284.32
	8/9-20/2001	12.03	22.27	15.53 (± 0.04; 3456)	199.58
					582.59
49a (2908)					
	6/11-28/2001	1.03	30.88	12.47 (± 0.08; 5184)	205.50
	7/12-31/2001	6.54	29.02	16.09 (± 0.06; 5760)	362.25
	8/9-20/2001	11.97	23.03	16.42 (± 0.04; 3456)	230.9
					798.65
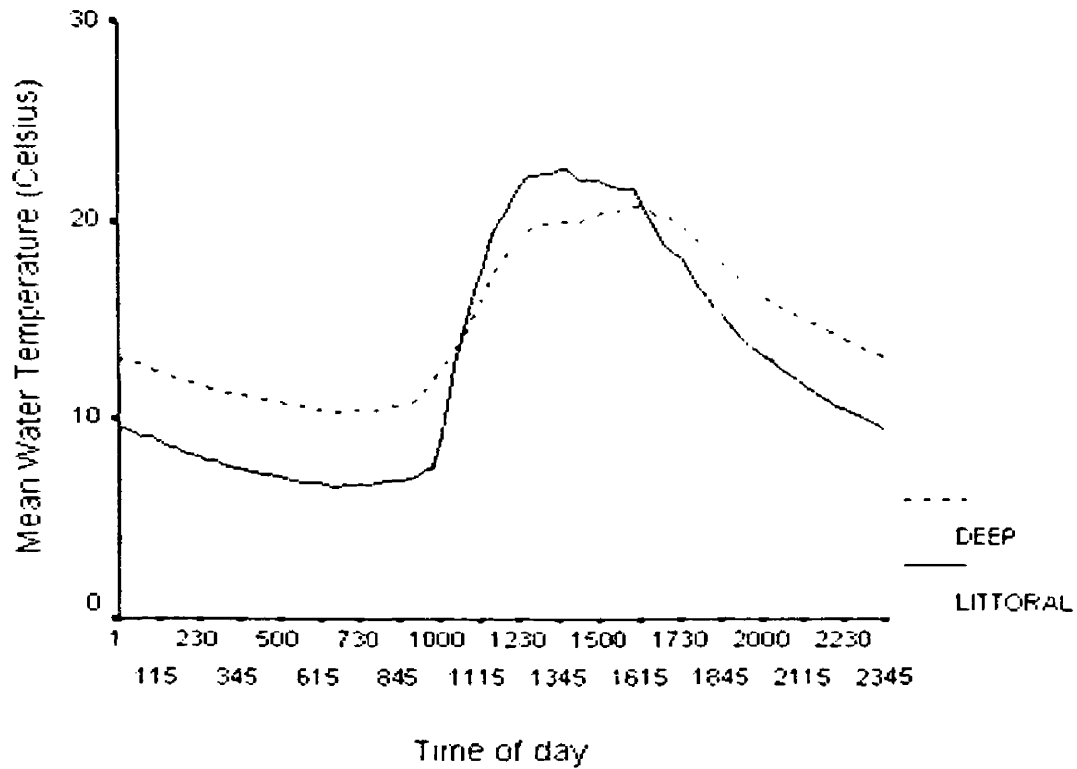
Figure 3. Mean 24-hour temperature fluctuations of the littoral (< 0.5 m) and deep (> 0.5 m) water in a fishless pond (49) between 13-July and 28-July, 2001.

all years of this study, I observed that tadpoles tended to congregate in the littoral regions between 1000 and 1600 hours, when temperatures were at a maximum and then moved into deeper water in late afternoon. Between 13-July to 28-July, 2001, tadpoles following this trend would have experienced a 35% increase in degree-days (84.5) compared to those who might have inhabited the shallows throughout the 24-hour period (62.6).

Correlation analysis was conducted on numerous physical attributes of the pond and landscape and frog population metrics (Appendices 3 and 4). Many of these correlations were significant but were not highly informative to this study.

Analysis of variance (ANOVA) was conducted to compare physical characteristics of ponds with and without frog breeding. There were no significant differences between the physical characteristics in these ponds (Table 2). Only two ponds with fish were used for reproduction by frogs and these ponds had the lowest abundance of fish. Further analysis was conducted to compare the physical characteristics between ponds with and without fish. Because of the low sample size and unequal variances, a Mann-Whitney U test was used to compare means. There were a number of significant differences in physical characteristics between ponds with and without fish (Table 3). Ponds with fish were significantly larger in area and perimeter, deeper and had higher conductivity. Frogs are present across the landscape but fish are restricted to large, deep ponds.

Table 2. Comparison of means for physical characteristics for ponds with and without frog breeding. Results shown as the mean (± SE; n) and the ANOVA F and p values.

Physical characteristic	Without breeding	With breeding	F	p value
Elevation (m)	2882.5 (± 11.0; 13)	2865.6 (± 14.9; 10)	0.882	0.358
Area (ha)	0.69 (± 0.30; 13)	0.65 (± 0.27; 10)	0.009	0.927
Perimeter (m)	292.4 (± 76.8; 13)	278.4 (± 66.0; 10)	0.018	0.895
Depth (m)	2.90 (± 0.92; 13)	3.23 (± 1.00; 10)	0.059	0.810
Conductivity (μS)	12.5 (± 1.2; 13)	11.2 (± 0.8; 10)	0.895	0.360

Table 3. Comparison of physical characteristic means for ponds with and without fish. Results shown as the mean (± SE; n) and the Mann-Whitney U p value.

Physical characteristic	Without Fish	With Fish	p value
Elevation (m)	2882.2 (± 8.9; 17)	2858.4 (± 16.8; 8)	0.157
Area (ha)	0.22 (± 0.09; 17)	1.49 (± 0.42; 8)	< 0.001
Perimeter (m)	171.1 (± 31.7; 17)	486.8 (± 99.6; 8)	0.001
Depth (m)	1.33 (± 0.42; 17)	6.02 (± 1.12; 8)	< 0.001
Conductivity (μS)	10.3 (± 0.8; 17)	14.1 (± 0.7; 8)	0.027

Analysis of covariance (ANCOVA, Type III sum of squares) was conducted to determine the influence of habitat parameters (elevation, perimeter and water depth) versus the presence of fish on various frog metrics. Main effects of habitat and fish presence influenced frog metrics differently and there were many nonsignificant effects (Table 4).

Annual precipitation (mostly as snowfall) records collected by the National Weather and Climate Center weather station (www.wcc.nrcs.usda.gov) indicate that snowfall in 1999 was near the 30-year average but 2000 and 2001 snowfall accumulation was below average (Figure 4).

Fish Presence and Abundance

Fish were present in eight ponds (Table 5) and ranged from being abundant to rare. Thirty-three brook trout (7 female, 10 male, 17 unknown gender) and four Arctic grayling (3 female, 1 male) from five different ponds in the study area, were examined in more detail in 1999 and 2000. Body length of brook trout ranged from 150 to 420 mm ($\bar{x}$ = 278.9 ± 4.0 mm). Arctic grayling body length ranged from 285 to 340 mm ($\bar{x}$ = 310.0 ± 0.8 mm). In brook trout the gape height and width (n = 7) ranged from 29 to 60 mm and from 20 to 40 mm respectively; the gape width and height in the single Arctic grayling measured 20 x 20 mm. A stomach analysis was conducted on 16 brook trout and 4 Arctic grayling. Stomachs of all but two fish were at least half-full. Contents of individual stomachs varied, but there was no distinct difference in content between species. None of the fish examined contained the remains of

Table 4. ANCOVA results for habitat and fish effects on various frog metrics. The directions of effect (positive or negative) are given for significant model parameters. Type III sum of squares.

Dependent variable	Model parameter	Degrees of freedom	F	p	Direction of effect
Eggs/clutch					
	Elevation	1	4.523	0.280	
	Perimeter	1	30.742	0.114	
	Maximum depth	1	3.588	0.309	
	Fish presence	1	16.685	0.153	
Larval growth (mm/day)					
	Elevation	1	28.436	**< 0.001**	positive
	Perimeter	1	6.752	**0.010**	positive
	Maximum depth	1	0.000	0.991	
	Fish presence	1	57.873	**< 0.001**	positive
Larval development (stage/day)					
	Elevation	1	1.991	0.159	
	Perimeter	1	0.501	0.479	
	Maximum depth	1	1.005	0.316	
	Fish presence	1	0.004	0.953	
Adult frog abundance (frog/m)					
	Elevation	1	0.978	0.334	
	Perimeter	1	2.437	0.134	
	Maximum depth	1	5.114	**0.035**	positive
	Fish presence	1	3.747	**0.067**	positive
Sex ratio (F:M)					
	Elevation	1	0.807	0.387	
	Perimeter	1	0.156	0.700	
	Maximum depth	1	0.157	0.699	
	Fish presence	1	1.123	0.310	
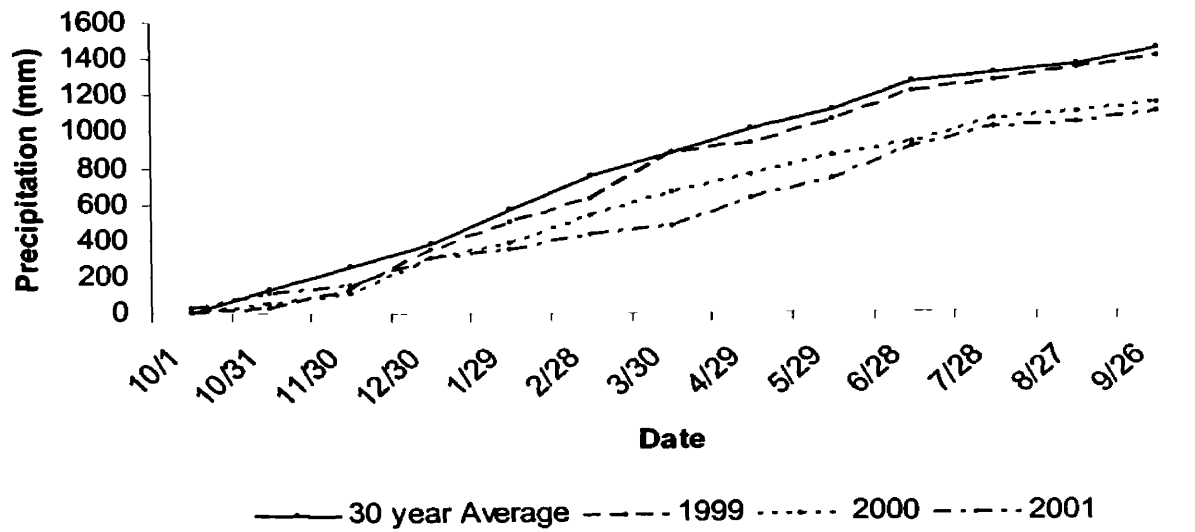
Figure 4. Annual precipitation records for all years of the study compared with the 30-year average. Data from Data from Fisher Creek SNOTEL database

Table 5. Fish and frog presence and abundance data for each pond. Fish presence is recorded as 0 (absent) or 1 (present) and permanence as 1 (stocked) and 2 (self-sustaining). Fish species are labeled as Thar (arctic grayling; *Thymallus arcticus*) and Safo (brook trout; *Salvelinus fontinalis*).

Lake or Pond	Fish Presence (species)	Fish Permanence	Female Abundance (2000)	Male Abundance (2000)	Female Abundance (2001)	Male Abundance (2001)	Number of Clutches (2001)	Number of Metamorphs (2001)
48a	0	0	23	40	16	32	7	135
48d	0	0	11	16	7	4	9	12
48m	0	0	2	2	4	2	0	0
48x	0	0	2	0	0	3	0	0
48y	0	0	11	33	6	22	6	2
49	0	0	33	58	24	47	8	85
49a	0	0	15	38	10	30	8	185
49s	0	0	6	5	5	3	1	50
49y	0	0	1	0	1	0	0	0
49z	0	0	8	19	9	17	0	0
50w	0	0	1	0	0	0	0	0
50x	0	0	2	8	2	4	0	0
51b	0	0	9	8	8	12	3	0
51d	0	0	0	0	0	0	0	0
52b	0	0	1	4	1	3	0	0
52c	0	0	0	11	2	9	1	20
52d	0	0	0	0	0	0	0	0

Table 5, continued. Fish and frog presence and abundance data for each pond.

Lake or Pond	Fish Presence (species)	Fish Abundance	Female Abundance (2000)	Male Abundance (2000)	Female Abundance (2001)	Male Abundance (2001)	Number of Clutches (2001)	Number of Metamorphs (2001)
51	1 (Thar)	1	68	66	47	49	54	38
50	1 (Safo)	1	40	39	33	30	35	21
48b	1 (Safo)	2	0	0	0	0	0	0
48c	1 (Safo)	2	0	0	0	0	0	0
52a	1 (Safo)	2	2	1	0	2	0	0
47	1 (Safo)	3	0	0	0	0	0	0
48	1 (Safo)	3	3	0	1	1	0	0
52	1 (Safo)	3	0	0	0	0	0	0

any life history stage of a spotted frog. Furthermore, none of the fish examined

harbored parasites.

Demographic Patterns for Columbia Spotted Frogs

Although there was movement between ponds during the study, most

adult frogs were recaptured at the same pond in 2000 and 2001 (Figure 5).

Thus, it was possible to compare ponds without a confounding effect of year-to-

year variation in pond populations. Lincoln-Petersen estimates were calculated

for each pond (Table 6) but overall, it was estimated that the population was

composed of 761 adult and juvenile frogs in 2000. Throughout the study,

recapture rates were high (> 75%) and were comparable for all sites. In total,

807 frogs (308 females, 446 males, and 53 juveniles) were captured and marked

during four capture sessions in 2000 and 2001 (Table 5). Female frogs captured

in ponds that were used for breeding and rearing were equally split between

ponds without fish (n = 145) and with fish (n = 145).

Fish presence had no significant effect on whether or not frogs occurred in

a pond (Table 7). Adult frogs were found everywhere, regardless of fish.

Moreover, the difference between adult frog (defined as SVL > 45 mm)

abundance as frogs per meter of shoreline in ponds without and with fish,

regardless of frog gender, was not significant. However, when fish permanence

was taken into account, the difference in the number of frogs was significant for

both females and males (Table 8). No breeding occurred in ponds where fish

populations were self-sustaining. Although adult frogs are found across the

landscape, regardless of fish presence, breeding tends to be in the absence of
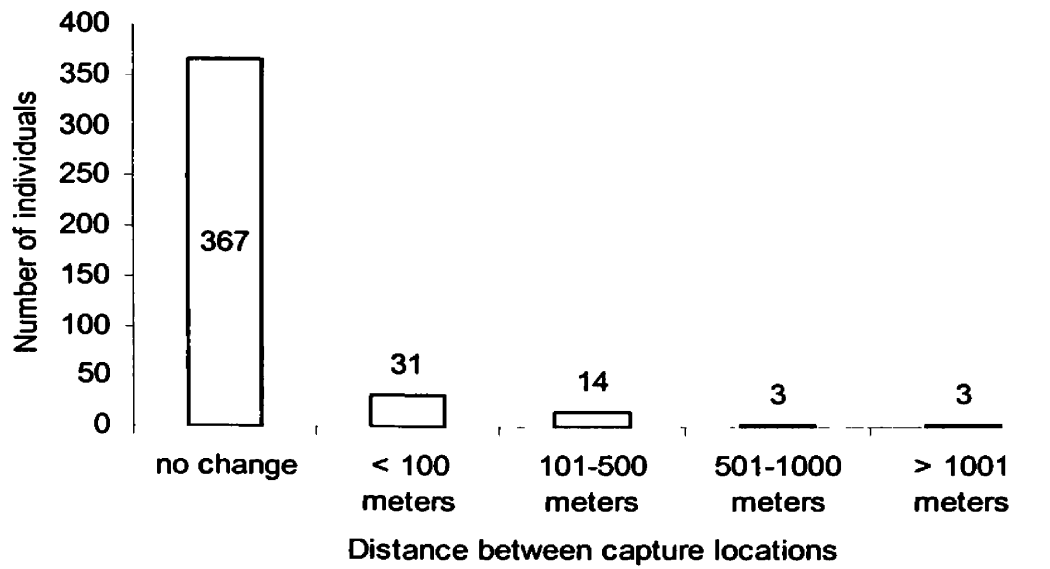
Figure 5. The distance between capture locations from the first capture in year 1 (July 2000) to the first capture in year 2 (July 2001) for individual frogs.

Table 6. Lincoln-Petersen estimates for the juvenile and adult population size at each pond.

Pond	Number of frogs caught, marked and released during capture session 1 (July 2000)	Total number of frogs caught during capture session 2 (August 2000)	Total number of marked frogs caught during sample session 2 (August 2000)	Population size
48	4	8	3	10
48a	70	75	59	89
48d	29	7	6	34
48m	4	2	1	8
48y	45	34	29	53
49	94	125	100	118
49a	54	31	27	62
49s	11	3	3	11
49z	27	24	19	34
50	90	65	61	96
50x	3	3	3	3
51	142	140	101	197
51b	17	9	8	19
52a	4	10	4	10
52b	5	1	1	5
52c	11	20	11	20

Table 7. Two-way Chi square analysis of frog presence in response to fish presence. Data are the chi-square value and significance level (p value).

Population Parameter	No Fish	Fish
Frogs Absent	3	3
Frogs Present	14	5
Total	17	8
2-Way χ^2	2.057 (0.358)	

Table 8. Comparison of means of adult frog abundance in ponds with varying fish permanence. Data are abundance #/meter ($\pm$ SE; n) Kruskall-Wallis significance level p value.

	No Fish	Stocked	Self-sustaining	p value
Adult	0.16 ($\pm$ 0.03; 17)	0.23 ($\pm$ 0.14; 3)	0.001 ($\pm$ 0.001; 5)	**0.02**

fish. Although spotted frog breeding activity occurred in 47% of ponds without

fish only 25% of ponds with fish, there was no significant effect of fish presence

on breeding activity (Table 9).

The difference between mean snout-vent length (mm) and body weight

(gm) in ponds without and with fish was significant in several cases. Female

body weight was significantly higher in ponds with fish and males were

significantly longer and heavier in ponds with fish. Fish presence did not have an

effect on juvenile body length or weight (Table 10).

To explore the effect of fish presence on spotted frog reproduction and

demography, comparisons were made to detect differences in these parameters

between ponds with and without fish (Table 11). The specific differences are

discussed more fully below.

When data for all ponds were pooled, the sex ratio of females to males

was significantly different for ponds with versus without fish, (presence vs.

absence; $p < 0.05$; Table 11; Figure 6). However, when sites were divided

according to fish permanence, the female:male ratio was skewed strongly toward

females when fish populations were stocked or self-sustaining, with males rarely

encountered in ponds with self-sustaining populations (1 male found in 3-yr).

Probability of survival and capture was modeled using Program MARK.

The most parsimonious model, a constant survival rate over time (phi(.)), was

used to estimate survival of adult frogs in ponds with and without fish (Table 12).

Overall difference in mean survival rates of frogs were not statistically significant

Table 9. Two-way Chi square analysis of 2001 frog breeding activity in response to fish presence and permanence. Data are the chi-square value and significance level (p value).

Population Parameter	No Fish	Fish
Breeding Absent	9	6
Breeding Present	8	2
Total	17	8
2-Way χ^2	3.782 (0.151)	

Table 10. Comparison of means for snout-vent length and body weight for all frogs at their initial capture reported for female, male and juvenile frogs in ponds with and without fish. Results shown as the mean (± SE; n) and the ANOVA p value.

		No Fish	Fish	p value
Snout-vent length (mm)				
	Female	71.43 (± 0.56; 161)	71.05 (± 0.46, 148)	0.605
	Male	61.90 (± 0.17; 300)	62.58 (± 0.22; 147)	0.018
	Juvenile	30.57 (± 1.12; 27)	31.32 (± 1.40; 26)	0.681
Body weight (gm)				
	Female	30.39 (± 0.67; 161)	32.47 (± 0.58; 148)	0.020
	Male	20.74 (± 0.18; 300)	22.83 (± 0.26; 147)	<0.001
	Juvenile	2.68 (± 0.35; 27)	2.91 (± 0.42; 26)	0.665

Table 11. Comparison of means of population metrics in ponds with and without fish. Data shown are the mean (± SE; n), and the significance of the comparison.

| Population Parameter	Without Fish	With Fish	p value
Adult Frog Abundance (#/m)	0.16 (± 0.03; 17)	0.09 (± 0.06; 8)	0.307
Female:Male Sex Ratio	0.586 (± 0.146; 12)	1.185 (± 0.322; 3)	**0.031**
Adult Frog Size:Age (mm/year)	8.947 (± 0.408; 44)	9.013 (± 0.363; 53)	0.789
Female Frog Size:Age (mm/year)	8.554 (± 2.126; 22)	9.210 (± 2.427; 26)	0.350
Male Frog Size:Age (mm/year)	9.340 (± 0.679; 22)	8.824 (± 0.551; 27)	0.520
Eggs (eggs/clutch)	618.9 (± 48.8; 17)	730.5 (± 34.7; 26)	0.136
Larval Growth (mm/day)	1.023 (± 0.0.14; 202)	0.825 (± 0.205; 208)	**< 0.001**
Larval Development (stage/day)	0.867 (± 0.017; 202)	0.734 (± 0.010; 208)	**< 0.001**
Metamorph Body Size (mm)	22.57 (± 0.20; 49)	21.74 (± 0.19; 27)	**0.002**
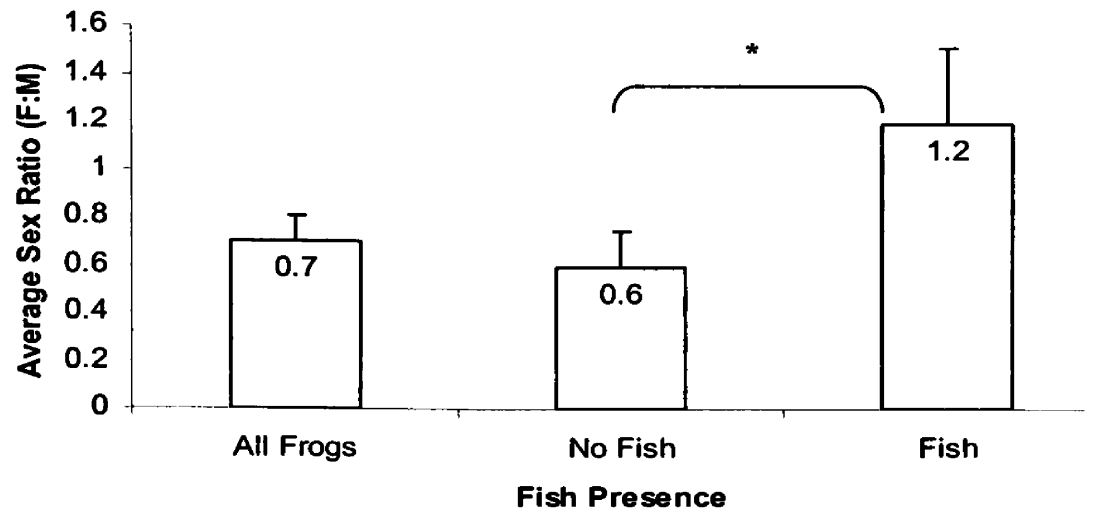
Figure 6. Effect of fish presence and abundance on female:male sex ratio. Error bars represent ± SE and significance (p value) is shown as * p < 0.05.

in ponds with and without fish (t-test), nor was survival of male frogs. However, females had higher survival rates in ponds with fish (Table 13).

Clutch Density and Egg Production

The presence of breeding was noted in 1999-2001 and breeding metrics were recorded in 2001 (Table 5). Based on visual estimation of clutch aggregation and egg development, in 2001 the first eggs were laid in pond 50 (2816 m elevation) between June 3-8. This pond supported brook trout.

The absolute density of eggs laid ranged from ~7900 – 47,000 eggs/ha in ponds without fish versus ~10,000 – 38,000 eggs/ha in ponds with fish. The difference between the average number of eggs laid per clutch at ponds with and without fish was not significant; however almost three times as many total eggs were laid in sites where fish were present (Table 11; Figure 7). It was not possible to test for the effect of fish abundance on clutch or egg metrics because breeding only occurred in ponds with no fish or where fish were stocked.

Larval Growth, Development and Metamorphosis

As expected, the difference between overall larval growth and developmental rate at ponds without versus with fish was significant. Larvae grew faster at ponds without fish, and larval developmental rate was significantly faster at ponds without fish (Table 11). Indeed, when growth and developmental rates were examined graphically by pond, larval growth and developmental rates were visibly greater in ponds without fish versus rates In ponds with fish throughout the growing season (Figure 8). No statistical comparisons of larval

Table 12. Probability of survival and capture model likelihood.

Model	AICc	Delta AICc	AICc Weight	Model Likelihood	# Parameters	Deviance
No Fish						
Phi(.)p(t)	1365.860	0.00	0.38147	1.0000	4	17.831
Phi(t)p(.)	1366.587	0.73	0.26530	0.6955	4	18.557
Phi(t)p(t)	1367.527	1.67	0.16575	0.4345	5	17.473
Phi(.)p(.)	1408.992	43.13	0.00000	0.0000	2	64.998
Fish						
Phi(t)p(.)	963.222	0.00	0.65222	1.0000	4	12.582
Phi(t)p(t)	965.198	1.98	0.24292	0.3724	5	12.519
Phi(.)p(t)	968.871	5.65	0.03872	0.0594	4	18.230
Phi(.)p(.)	975.945	12.72	0.00113	0.0017	2	29.359

Table 13. Survival rate (phi; ± SE) of adult frogs in ponds with and without fish.

	No Fish	Fish
All Frogs	0.87 ± 0.02	0.88 ± 0.03
Female	0.82 ± 0.03	0.89 ± 0.03
Male	0.90 ± 0.03	0.87 ± 0.04

Figure 7. The total number of eggs laid in ponds without fish and with fish in 2001.
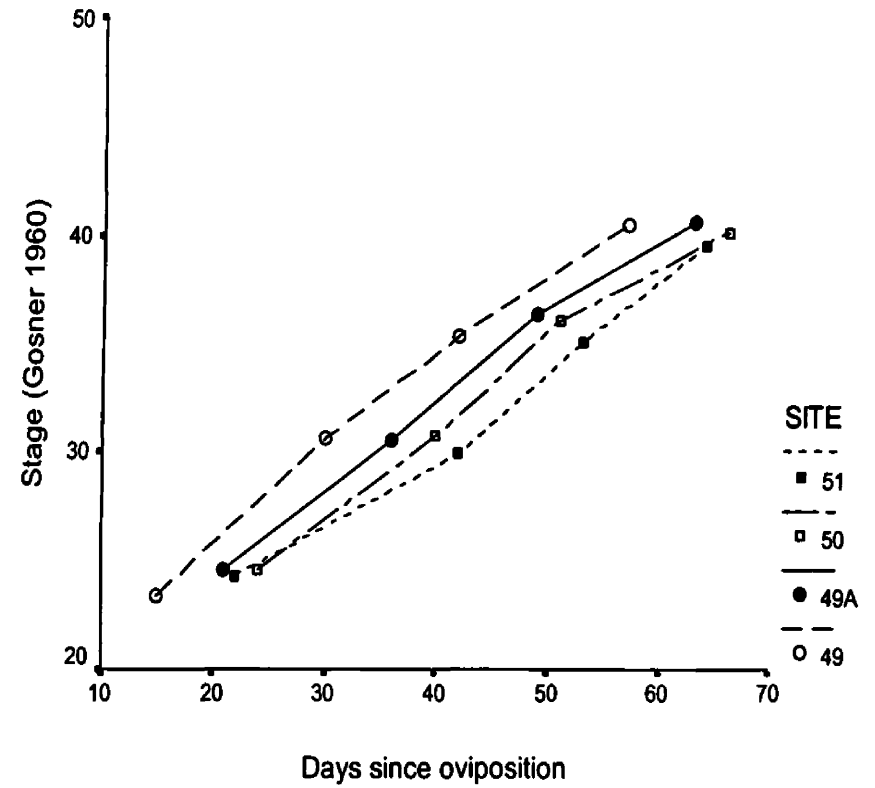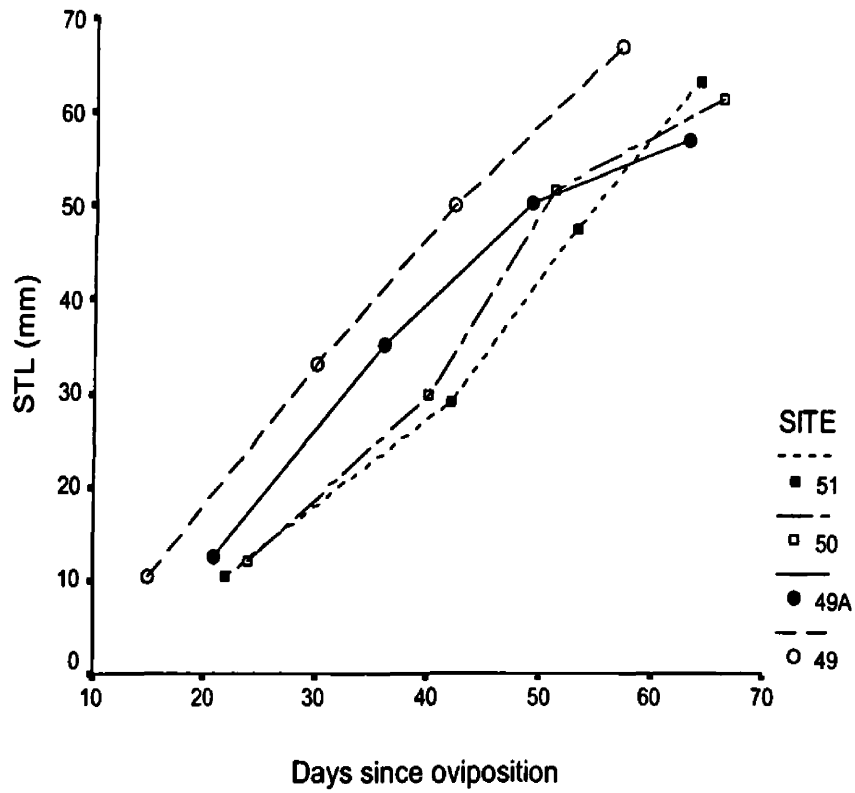
Figure 8. A comparison of growth and development rates of larval Columbia spotted frogs in ponds without fish (49 and 49a) and with fish (50 and 51).

growth or development could be made as a function of fish abundance because breeding only occurred in ponds without fish or where fish were rare. The first metamorphic frogs (stage 46) were captured from several sites (48a, 49, 49a) on August 17, 2001, nine weeks after the first eggs were laid in the study area. More metamorphs successfully emerged from ponds without fish (Figure 9) and these metamorphs were significantly larger (Table 11). Metamorphs emerging from ponds with fish were smaller than those emerging from ponds with fish ($p < 0.05$; Table 11). No comparison of metamorph number or size of emerging metamorphs as a function of fish permanence could be made because breeding only occurred in ponds without fish or where fish were stocked.

The number of days between the oviposition of the first eggs and the capture of the first metamorphs can be used as an index of the length of larval period (Table 14). Unfortunately, oviposition data was not collected for all ponds and the first metamorphs captured did not necessarily reflect their date of first emergence. Therefore the data should be interpreted with caution. In general, the larval period (oviposition to emergence) was slightly longer in ponds with fish but by a few days only (Table 14).

Skeletochronology Analysis

Although metamorphosis did occur earlier in most cases, for age analysis uniformity, a standard metamorphosis date of September 30 was used. Age was counted in months (but has been reported in years for ease of comparison) from the last day of latest metamorphosis month. An additional full month was
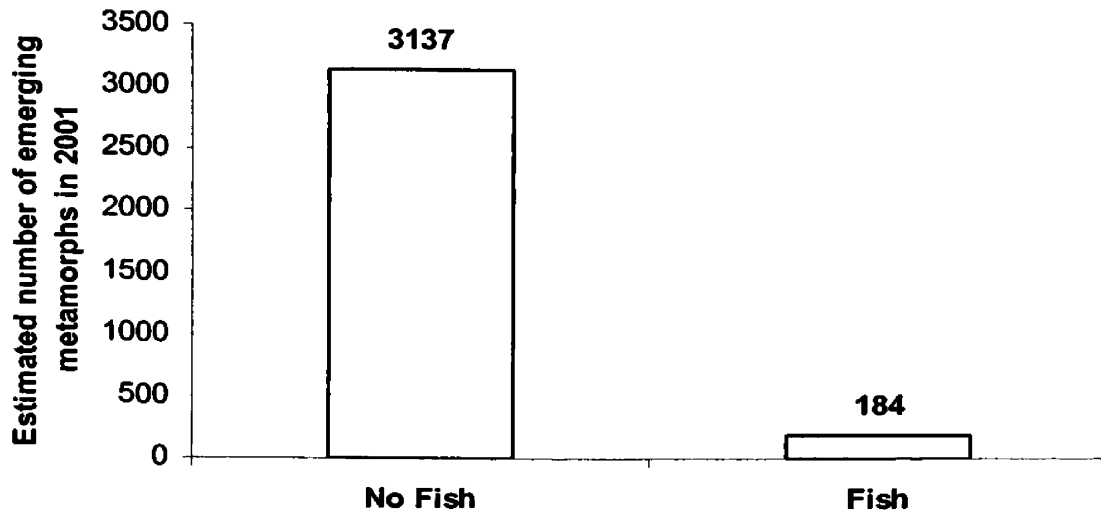
Figure 9. The estimated number of metamorphs that emerged from ponds with and without fish in 2001.

Table 14. The number of clutches and index of the length of the larval period by pond.

Pond	Number of clutches	Dates of oviposition	Date of capture of first metamorph (stage 46)	Days (1st eggs to 1st metamorphs)
No Fish				
48a	7	unknown	17 August	unknown
48d	9	unknown	23 August	unknown
48y	6	unknown	21 August	unknown
49	8	11 June	17 August	67
49a	8	5-8 June	17 August	73
49s	1	5-8 June	19 August	73
51b	3	6-8 June	none	74
52c	1	unknown	19 August	unknown
Fish				
50	54	3-8 June	18 August	75
51	35	5-7 June	18 August	73

included in the count when a toe was excised past the fifteenth day of that

month. Population and individual variation in the first zone thickness were

expected and measurements varied among different points along the length of

the bone. Moreover, the same zone may have differed in thickness at different

points (Figure 2). For all specimens, the resorption margin was characteristically

wavy and irregular (Figure 2), with irregular cellular clusters and translucent

spots. The first zone stained uniformly, had generally low cellularity, and was

bordered by a line of arrested growth (LAG) that was smoothly circular and

stained with regular density.

Frogs in my study had many bone layers suggesting they were long-lived.

Sometimes LAG zones were absent from more than one year. In these cases,

the technician assumed that no more than three zones would be removed by

resorption (cases with extensive resorption were noted) (method of Gary Matson,

Matson Labs LLC, Missoula, Montana, unpublished data).

In frogs older than 5 – 6 years, the oldest LAG zones were thin and

closely spaced and accurate LAG counting may not have been possible because

of the lack of visual separation between lines. In some older frogs, the bone

periphery contained a darkly stained area in which several zones and LAG were

condensed together and spaced too closely for accurate counting. However,

sections adjacent to the one analyzed often revealed peripheral areas where the

LAGs were more identifiable. Evidence in the toe sections suggested that the

extent of resorption taking place in older frogs varied among individuals. In some

animals, all the first zone and LAG were resorbed but this was not the case in others. The first LAG outside a thick (20 – 30 μm) zone in an older frog with extensive resorption was counted as having been laid down after the first summer. For those individuals marked early in the summer (n = 7), the assumption was made that a periperal LAG was present, but not visible, because new bone had not yet formed at the periphery by the date of excision.

Analysis of covariance (ANCOVA, Type III sum of squares) was conducted to determine the effect of age, pond type (fish vs. fishless) and the interaction (age*pond type) on female and male size (SVL) (Table 15). Male size was not significantly affected by age or pond type but age, pond type and the interaction were significant model parameters when analyzing female size. Linear regression was independently conducted on female size in ponds with and without fish to further identify the effect of age on size. Age was a significant model parameter for female size, but only in ponds without fish (Table 16, Figure 10A). The relationship of size to age was weak for females in ponds with fish and for males in both ponds with and without fish (Figure 10B-D). Sexual dimorphism in adult size is apparent in this population. The females are significantly larger than males (Table 17).

Frog age (in years) was examined to determine the overall age structure of the population (Figure 11A). Setting the most recent capture year as age 0 (2001), a calendar year was connected with individual age. Data represent only individuals who were identified as male or female. In some cases, small (< 45 mm) individuals could not be assigned as male or female because they had not

Table 15. ANCOVA results for the effect of age and pond type on male and female size (SVL). The directions of effect (positive or negative) are given for significant model parameters. Type III sum of squares.

Dependent variable	Model parameter	Degrees of freedom	F	p	Direction of effect
Female size (SVL)					
	Age (yr)	1	4.607	0.037	positive
	Pond type (fish vs. fishless)	1	9.097	0.004	positive
	Age*Pond type	1	8.431	0.006	positive
Male size (SVL)					
	Age (yr)	1	0.634	0.430	
	Pond type (fish vs. fishless)	1	1.115	0.297	
	Age*Pond type	1	1.051	0.311	

Table 16. Linear regression results for the effect of age on male and female size (SVL), controlling for pond type. Significant results are indicated in bold.

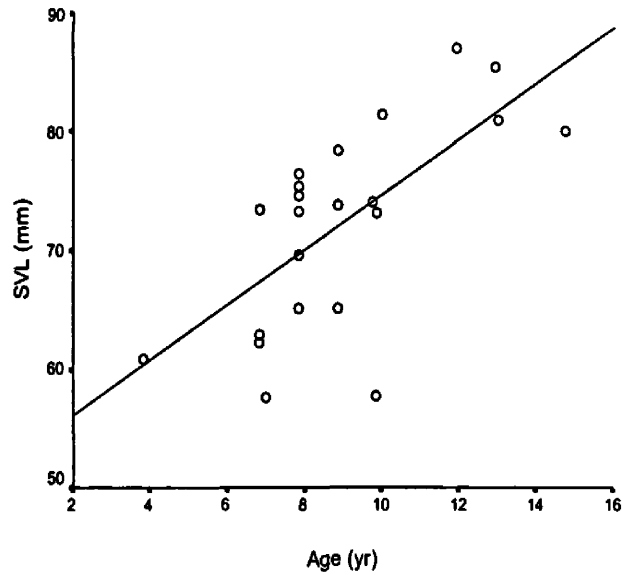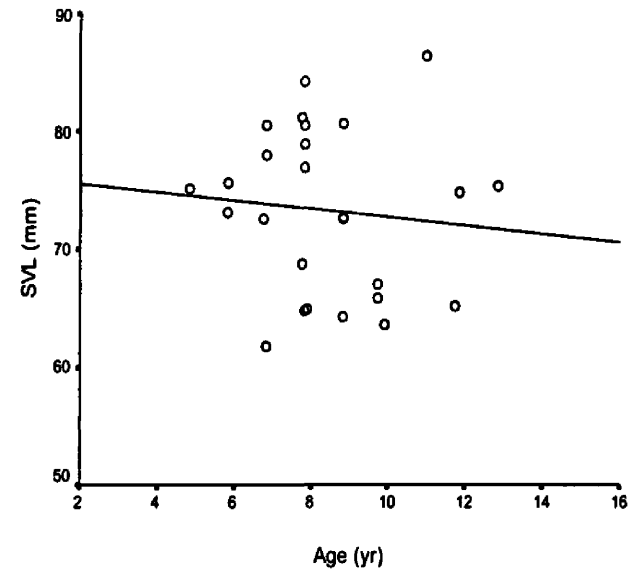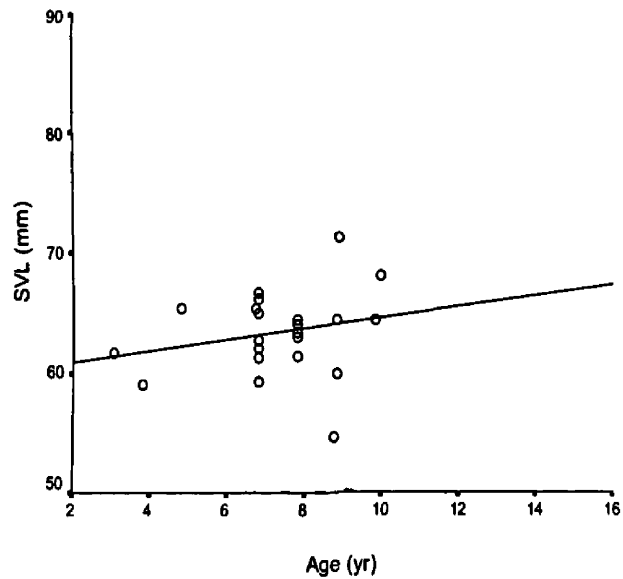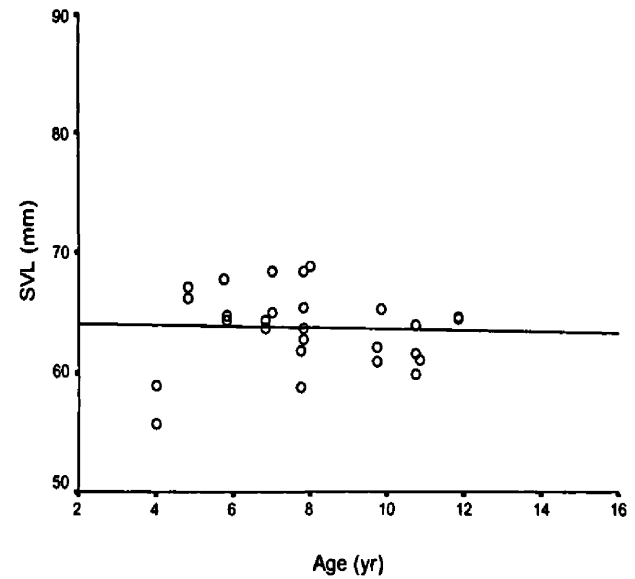| Dependent variable	Pond Type	Degrees of freedom	F	p
Female size (SVL)				
	Fishless	21	16.657	**0.001**
	Fish	26	0.230	0.636
Male size (SVL)				
	Fishless	21	1.114	0.304
	Fish	26	0.045	0.833

Figure 10. The effect of adult frog age, controlling for frog gender and pond type. A) females in ponds without fish (R^2 = 0.427), B) females in ponds with fish (R^2 = -0.032), C) males in ponds without fish (R^2 = 0.005), and D) males in ponds with fish (R^2 = -0.038).

Table 17. Comparison of means for snout-vent length and body weight for all female and male frogs in the total population, and from ponds with and without fish. Values under subheadings are sample size. Results shown as the mean (± SE). The t-test significance p value is shown for the total population and the ANOVA significance p value is given for values compared for ponds with and without fish.

Size metric	Total Population			Without Fish			With Fish		
	Female (309)	Male (447)	p value	Female (161)	Male (300)	p value	Female (148)	Male (147)	p value
Snout-vent length (mm)	71.25 (± 0.37)	62.12 (± 0.14)	< 0.001	71.43 (± 0.56)	61.90 (± 0.17)	< 0.001	71.05 (± 0.46)	62.58 (± 0.22)	< 0.001
Body weight (gm)	31.39 (± 0.45)	21.43 (± 0.16)	< 0.001	30.39 (± 0.67)	20.74 (± 0.18)	< 0.001	32.47 (± 0.58)	22.83 (± 0.26)	< 0.001

yet reached sexual maturity. Overall, age was normally distributed with the greatest number of individuals at ages 6 – 8 years (Figure 11A). This age range corresponds to hatching between 1993 to 1995. Most frogs were 6 – 11 years old. The oldest individual captured was a 14 year old female while the youngest individual was a 3 year old male. In ponds without fish, females ranged in age from 3 to > 14 years old, while the age distribution for males was 4 to ~12.5 years (Figure 11B). In ponds with fish, the overall age distribution ranged from 3 to ~12 years (Figure 11C). Most frogs were 6 – 11 years old. In ponds with fish, no females older than ~10.5 years were captured. Thus, older females were most common in ponds without fish.
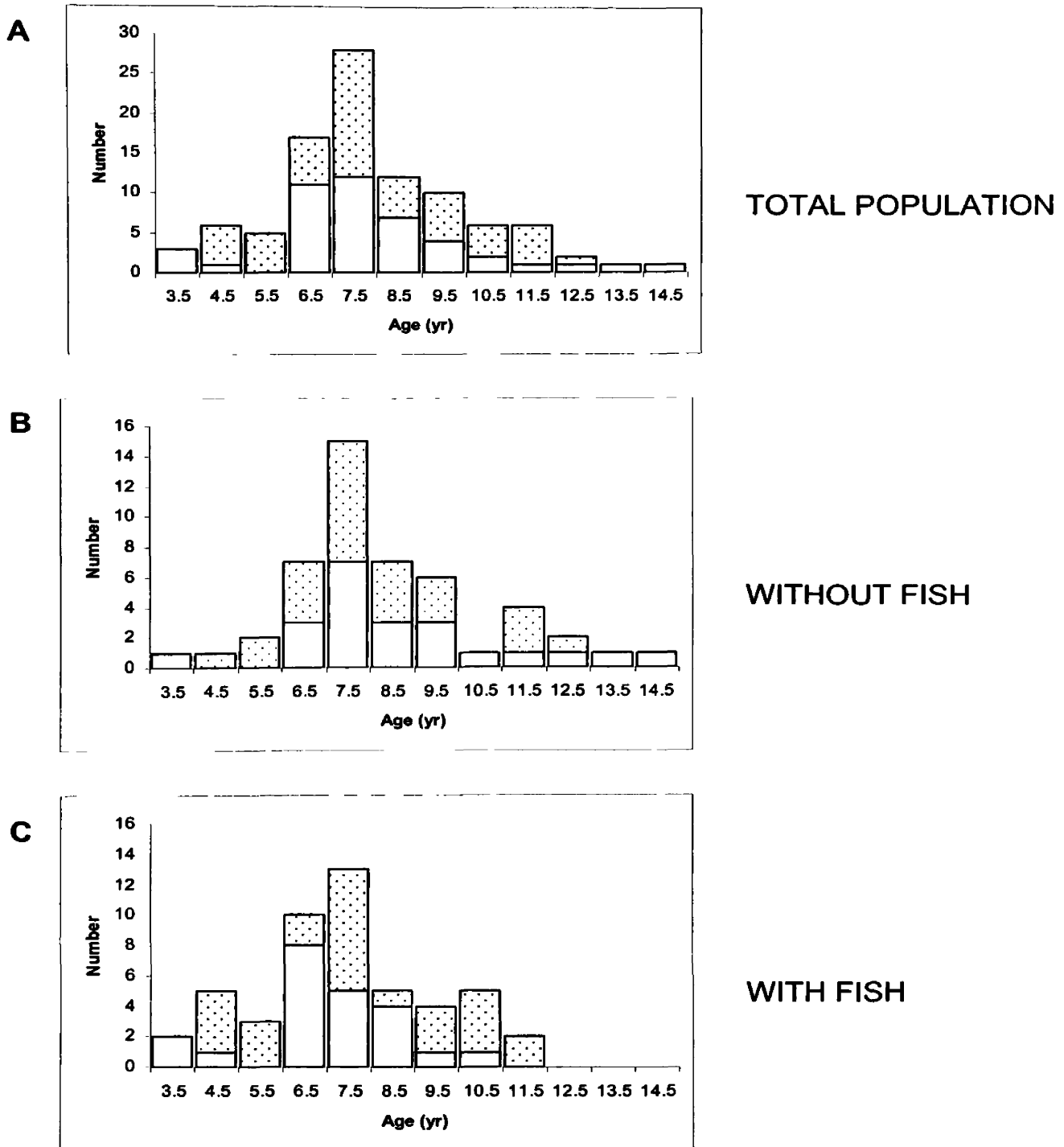
Figure 11. The overall age distribution of adult frogs (A) as well as a comparison of ponds without (B) and with (C) fish. Number of females represented in gray bars; males in dotted bars.

DISCUSSION

When fish are introduced to ponds supporting breeding populations of frogs, one potential expectation is that the local population will decline or disappear (Bradford et al. 1993, Hecnar and M'Closkey 1997). Contrary to this expectation, Columbia spotted frogs co-occurred with fish in stocked ponds in the Absaroka-Beartooth Wilderness (ABW) and used some ponds with fish as breeding and rearing sites. However, there were effects on both the adult and larval frogs suggesting that the presence of fish could have negative population-level effects on Columbia spotted frogs over time.

The Physical Environment

In the ABW, the period when frogs are active is short, ranging from early June to early September. The physical environment defines the overall conditions for frog presence or absence in the landscape and it is difficult to sort out the fish effects from the habitat effects. Elevation, pond area and depth were significant model parameters but did not fully explain observed differences in several frog metrics (e.g., larval growth and development rates, size at metamorphosis, adult abundance and number of eggs per clutch).

The physical factor expected to be most influential in the aquatic stages was water temperature, especially at high elevations (Bizer 1978). Shallow water temperatures varied widely on a daily and seasonal basis. However, the available temperature data indicates that shallow water provide essentially the same thermal habitat in all ponds studied.

In general, frogs concentrated egg-laying and rearing in shallow pond areas with emergent vegetation. No eggs were laid in ephemeral ponds in this study area though most shallow areas in these ponds were subject to potential dessication as the shoreline receded. Breeding and rearing activities were confined to ponds where fish were absent or had small populations sustained by stocking every 8 years.

Population Demographics

The greatest number of frogs in the ABW were 6 – 8 years old (born in 1993 to 1995) when annual precipitation (as snowfall) was well below average (National Weather and Climate Center). In general, recruitment trends correspond well to snowfall records; a low snowfall year corresponds to higher recruitment. Although 10% of frogs did move farther than 100 m from their original pond of capture, there was a high degree of site fidelity, which facilitated seasonal and year to year comparisons among ponds. Spotted frogs in the ABW lived up to 14 years. This is long compared to reports in other studies (Reaser 2000), but is expected from what is known about life-history variation in high-elevation populations of frogs (Morrison and Hero 2003). The hypothesis is that frogs living at high elevations require more years to reach sexual maturity because of a limited growing season and are therefore longer lived (Morrison and Hero 2003).

In amphibians in general, body size is strongly associated with reproductive capacity. For females, this can be translated into the number and/or size of eggs. For males, size influences amplexus with females. A study of

spotted frogs in northwestern Montana showed that successful mating males tended to be smaller in body length (SVL) with larger nuptial pads and thicker forearms than unsuccessful males (A. Greene, The University of Montana, unpublished data). Reproductive maturity is cued by a threshold body size and the age at which an individual reaches maturity influences lifetime reproductive success (Crump 1981).

In the population of spotted frogs I studied, the overall relationship between age and size in adults was only significant for females from ponds without fish. This suggests that these females continued to grow throughout their lifetime in fishless ponds. On the other hand, male (with and without fish) and female (with fish) age:size relationships suggest that once sexual maturity is attained, individuals do not experience further growth. Females from ponds with fish did appear to reach sexual maturity at an earlier age, potentially allowing for increased lifetime reproductive output. Males with higher growth rates reach sexual maturity at a younger age, after which it may no longer be adaptive to have a larger body (Jorgenson 1992), unless it confers some advantage to attracting females. In comparison, female frogs may benefit from continued growth throughout their lives if being larger translates into larger and/or more eggs. Fish may be a selective factor favoring larger body size for both males and females to escape gape-limited predation. A younger age at sexual maturity is one outcome predicted by life-history theory when adults experience high levels of predation pressure. Although it was not possible to determine the influence of

fish on size of frogs in the ponds I studied based on the data I collected, this could be interesting to investigate in the future.

The overall ratio of females to males in the ABW ponds I studied was slightly male-biased. Sex ratios in frogs can certainly vary temporally. For example, the female:male sex ratio in spotted frogs can be extremely male biased (0.2) during mating activity in small, shallow ponds (Morris and Tanner 1969). This skew towards more males at the time of mating is expected because Columbia spotted frogs participate in a scramble mating system (A. Greene, The University of Montana, unpublished data). However, a very intriguing result of this study was that the sex ratio of female:male differs spatially in ponds with (1.2:1) versus without (0.6:1) fish. Males were much more common in ponds without fish compared to ponds with fish. One hypothesis to explain this result is that because females were larger than males, their risk of predation by gape-limited fish predators was reduced. Unfortunately, there are few published studies examining the influence of predation on frog sex ratios for comparison. In a demographic analysis of a several populations of *Rana luteiventris* in the Toiyabe Range in west-central Nevada, the female:male sex ratio ranged from 0.7 to 3.8 (Reaser 2000). The female:male sex ratio was significantly different among sites in Reaser's study, and females dominated most ponds. The lowest ratio of females:males (0.7) occurred in a pond without fish. In ponds with fish where both males and females were found, the sex ratio ranged from 1.3 – 3.8. Reaser concluded that the difference in the observed sex ratios may be affected by gender-based site selection criteria. Female frogs tended to congregate in

terrestrial vegetation and not along the shoreline in this particular study (Reaser 2000).

In comparison with the results reported by Reaser (2000), few frogs were found more than 1 m from ponds in the ABW. However, the explanation of differential selection of habitats in males versus females cannot be ruled out. Another ranid species (*Rana japonica*) studied in a marsh in Japan had a sex ratio that ranged from 0.3 to 1.0 in the years between 1995 and 1999 but no explanation for the variation was offered (Marunouchi et al. 2002).

Determining the relative importance of gape limitation, habitat preference, and resource availability for explaining the differences in female:male sex ratios in the spotted frog populations in the ABW cannot be resolved based on the data currently available. Though survival estimates show that female frogs had a higher survival rate in ponds with fish there is an overall lack of old frogs in ponds with fish, suggesting a predation risk. These conflicting data are difficult to interpret which make this is an important and interesting area for future experiments and follow-up.

Reproductive Effort in Ponds With and Without Fish

Even though overall female frog numbers were the same in ponds with and without fish, females laid nearly three times as many eggs in ponds with versus without fish. However, fewer metamorphs emerged from ponds with fish and they were significantly smaller compared with ponds without fish. Several nonmutually exclusive factors may explain the disparity between reproductive investment and recruitment including differences in intraspecific competition

between tadpoles, influences of female size on reproductive effort, physical differences in breeding ponds, and direct and indirect influences of fish.

In this study, there was not sufficient data to address the effect of female body size on the number and size of eggs laid, nor the number and size of clutches. Although neither female body length nor weight was significantly different between ponds with or without fish, age was unknown for most individuals. Without this information, it is difficult to form conclusions about the influence of fish on female reproductive output. First, because more eggs were laid in ponds with fish, emerging tadpoles may have experienced higher levels of intraspecific competition. The absolute density of eggs laid ranged from 7930 – 47,000 eggs/ha in ponds without fish versus 10,113 – 38,000 eggs/ha in ponds with fish. Although visual estimates of tadpole density in ponds overall was comparable, intraspecific competition was not measured, and therefore this explanation cannot be ruled out. Intraspecific competition among tadpoles could greatly reduce the availability of better-quality resources and could have a large influence on larval rates of growth and development.

The physical environment of ponds used for breeding and rearing in the ABW were more similar than different based on the variables I measured with just a few exceptions. Ponds with fish tended to be deeper and have a larger area. Furthermore, temperature in the lower elevation ponds was slightly higher, but this did not fully explain differences in growth and developmental rates of tadpoles. These oligotrophic ponds are expected to exhibit low nutrient (e.g., nitrogen) levels, low levels of photosynthesis by algae and macrophytes, low

productivity and high oxygen levels (Wetzel 1983). In this study, conductivity, the measure of dissolved ions in water, was used as a rough estimate of pond productivity. Unfortunately, these data were not useful in determining how resource level differences among ponds might affect tadpole growth and development. More intensive limnological sampling is needed to completely rule out the influence of the physical environment on maternal investment and larval biology.

An interesting potential explanation is that females may be laying more eggs per clutch in ponds with fish to compensate for the negative effect of fish presence. To fully determine the impact of fish presence on female reproductive output and success, data is needed on the clutch size that each female lays and analysis should be controlled for body size. However, the data that was collected, a greater investment per clutch measured in ponds with fish, fits with life-history prediction; an increase in reproductive investment when adults are at risk from predation. By laying more eggs per reproductive event the individual increases its lifetime fecundity and increases the likelihood that some will survive to metamorphosis. The survival rate to metamorphosis from ponds with fish was only 0.03% (compared to 14% from ponds without fish). Therefore, this greater maternal investment in egg-laying in ponds with fish is resulting in very few recruits and provides evidence that these ponds with fish are demographic sinks. Although no remains of tadpoles or adult frogs were found in the fish stomach contents analyzed in this study, numerous lines of evidence suggest that predation does occur.

My data suggest that indirect effects of fish may influence larval biology. For example, there was a significant difference in overall developmental rates in ponds with and without fish. Tadpoles developed more slowly in ponds with fish. Larvae in ponds without fish exhibited higher mean growth rates from weeks 4-7 and overall. Tadpoles in ponds without fish grew at the same rates during weeks 9 and 10 suggesting that these tadpoles had entered into metamorphosis and were allocating all resources toward development.

Even when direct predation is rare, the presence of fish may alter tadpole behavior in ways that influence growth rate. For example, other studies have documented reduced activity of larval amphibians in the presence of fish predators (Petranka et al. 1987, Kats et al. 1988, Feminella and Hawkins 1994; B. Maxell and A. Wyrick, The University of Montana, unpublished data) which is expected to influence growth rates (e.g., Chivers et al. 1999, Kiesecker et al. 2002). Frogs appear to be able to detect chemical cues from fish, even from water where fish have been removed. This "scent of death" (Kats and Dill 1998) triggers a behavioral response whereby tadpoles limit their movement to reduce the likelihood that they will encounter a predator. In a preliminary laboratory study we tested the response of Columbia spotted frog larvae to chemical cues from a variety of potential predators (e.g, brook trout), but the results were inconclusive (B. Maxell and A. Wyrick, The University of Montana, unpublished data). Although the tadpoles reduced swimming activity and increased time spent under cover, we did not measure long-term effects of this behavior on tadpole growth and development. Tyler et al. (1998b) found that larval

survivorship of two salamander species (*Ambystoma macrodactylum* and *A. gracile*) was significantly reduced when raised in experimental ponds with fish as compared to those raised in ponds without fish. Not only was survivorship lower in ponds with fish, but emerging metamorphs were smaller. These effects were attributed to both direct predation by fish and the reduction in foraging opportunities for tadpoles when exposed to predation threat (Tyler et al. 1998b). Although few studies have examined the long-term effects of reduced ranid tadpole activity levels in response to fish presence, response to non-fish predators (e.g., insects and predatory salamanders) have been well-documented (e.g., Altwegg and Reyer 2003). These studies suggest potential outcomes of tadpole behavioral response to introduced fish. In some species, active tadpoles developed more rapidly, enabling them to reach metamorphic climax, transform, and exit the aquatic habitat earlier than tadpoles in ponds where tadpole activity levels were reduced in response to predators (Lawler 1989). Studies have been conducted to further test the influence of predator diet on tadpole behavioral response. In some species, the smell of a predator combined with a diet of conspecifics, led to an increase in development and they transformed earlier than those tadpoles exposed only to predator presence (Chivers et al. 1999; Kiesecker et al. 2002). However, the effect of predator presence and diet on emerging metamorph size varied; western toads (*Bufo boreas*) emerged at similar sizes regardless of predator diet (Chivers et al. 1999) while red-legged frogs (*Rana aurora*) emerged smaller when exposed to chemical cues from predators fed larval red-legged frogs (Kiesecker et al. 2002).

The presence of fish in a pond may have an effect on the thermal environment of tadpoles may explain differences in growth. It could be that the presence of fish in deeper water excludes tadpoles from making a daily movement from shallow to deep water to maximize exposure to highest temperatures. In all years of this study I observed a daily movement of tadpoles from shallow to deep water in fishless ponds. Tadpoles tended to congregate in the littoral habitats between 1000 and 1600 hours and then moved into the deeper, offshore waters at other times. I never observed this trend in ponds with fish however, the fewer number of tadpoles might have influenced the lack of such an observation. A tadpole that is free to move from shallow to deep water as needed to maximize the thermal environment will accumulate more degree-days and subsequently be able to develop and grow more rapidly to metamorphosis. In fact, if a tadpole had followed this trend (as observed in several fishless ponds) it would have accumulated 30% more degree-days in the span of two weeks than a tadpole confined to the shallows. This effect on larval period is unknown but is expected to be great. To clearly understand the role that chemical cues from fish may play in larval survival and success, future work is needed to examine costs (or benefits) of a behavioral response to the sublethal presence of a predator on habitat use (e.g., resource uptake, temperature preference), and the ultimate effects on growth and development.

Conservation and Management Implications

Columbia spotted frogs are persisting in the ABW despite the presence of fish in many of the ponds. Although these frogs co-occur with fish and use

several ponds with fish for breeding and rearing areas, they are not successfully coexisting in these ponds. There are several possible ways to explain how the Columbia spotted frog population in the ABW co-occur with introduced fish compared to other high elevation amphibians: 1) life history differences and 2) access to refugia and fishless migration corridors.

One important difference between spotted frogs in the ABW and the amphibians in other high elevation settings, is that the time spent as larvae is shorter and they do not over winter as tadpoles. The extent of the impact on species in high elevation waters of the Sierra Nevada depended on the length of the larval period; those species that overwintered at least once as a tadpole were much more negatively affected by fish presence (Bradford 1984, 1989). More time spent as a larva increased the risk of predation, especially over winter when pond size was reduced by freezing. In contrast, amphibian species for which the time from hatching to metamorphosis occurs over a single season such as Columbia spotted frogs, spend less time in the presence of fish predators.

Another explanation for the co-occurrence of fish and frogs in the ABW is that there are many ponds within a relatively small geographic area without fish, and these ponds may serve as refugia. It may be that frogs were better able to use these fishless waters for breeding and rearing larvae and inhabit stocked sites only as adults. The impact of the presence of at least a few ponds without fish may be substantial for frog population recruitment and persistence. Other studies have reported that several species (mountain yellow-legged frogs, long-toed salamanders, Columbia spotted frogs) attempted to breed and rear young in

ponds and lakes where fish have been introduced, but few if any frogs survived to the metamorph stage (Bradford 1989, Pilliod and Peterson 2001). My study was different in that the level of breeding investment in ponds with fish in the ABW was very high (> 60,000 eggs), but similar in that successful recruitment was very low (0.03%). It may be that ponds with fish are population sinks and it is the landscape that determines the level of frog resilience (e.g., the extent of fish-free ponds and movement corridors).

Very few frogs in the ABW area I studied traveled far seasonally or between years. Fewer than 10% of frogs were recaptured more than 100 meters from the original pond of capture, but I did document movement up to 1.2 km between 2000 and 2001. In other studies, Columbia spotted frogs have been known to travel up to 6.5 km (Engle 2001), but seasonal movement is typically less than 2 km (Pilliod et al. 2002). Persistence of spotted frogs in landscapes with fish may depend on the ability of individuals to migrate between ponds.

Few of the ponds included in this study were connected by rivers or streams, thus reducing the potential for fish to invade fishless ponds without human assistance. Moreover, the presence of numerous "predator-free" movement trajectories between and among ponds reduces at least one obstacle to between pond migration by frogs. In the Sierra Nevada in California lakes and ponds are connected by streams and rivers where fish are present (Bradford et al. 1993). The presence of fish in these waterways can be a major barrier to successful movement and recolonization, due to either the direct loss of migrating individuals to predation or the unsuccessful movement of individuals

through alternate routes with more hostile (e.g., drier) conditions. In the ABW, it may be that migration of frogs in a season or over time is not limited by predators to the same extent as reported by Bradford et al. (1993). Fishless refugia and movement corridors may be the key to success of this population, highlighting the importance of protecting complementary habitats and movement corridors (Pilliod and Peterson 2001, Pilliod et al. 2002).

Frog populations of conservation concern, such as the Columbia spotted frog (Leonard and McAllister 1997, Mizzi 1997), can be aided by direct efforts to remove introduced fish. The removal of fish eliminates predation risk by fish on amphibians. Where adequate numbers of frogs persist to recolonize these areas, the expectation is that population sizes may recover to pre-introducion sizes. For example, after fish were removed, mountain yellow-legged frogs (*Rana muscosa*) recovered in some high elevation lakes of the John Muir Wilderness and Kings Canyon National Park (Knapp et al. 2001). However, Knapp et al. predicted that recovery of these populations of frogs may require at least 10 years. In the Bitterrroot Mountains of Montana, long-toed salamanders (*Ambystoma macrodactylum*) recolonized high elevation lakes following the extinction of introduced trout populations (Funk and Dunlap 1999). In Mt. Rainier National Park, Washington, some lakes have been returned to fishless condition to facilitate recovery of amphibian populations but the impact of this management activity on amphibians was not described (Drake and Naiman 2000). While several case studies have shown that amphibian species can recolonize lakes that are returned to a fishless state (e.g., Knapp et al. 2001, Funk and Dunlap

1999), it may be unreasonable to expect that fish removal is feasible for all areas. For example, in the Sierra Nevada Mountains, conservation efforts were in conflict with recreationalists who had fished in these restored areas for many years.

In 1980, a fisheries management plan was developed for the ABW (Marcuson 1985, Marcuson and Poore 1991). Since then, the Montana Department of Fish, Wildlife and Parks (MFWP) has maintained a database with information on stocking schedules, fish species composition and fish population densities in the ABW lakes and ponds. Lakes in the ABW are unique when compared to wilderness areas in the Rocky Mountains, Pacific Northwest and Sierra Nevada mountain ranges. Only about 34% of lakes have been stocked (12% on 5-8 year stocking schedules; 22% with self-sustaining fisheries). The presence of a large number of fishless lakes and ponds (~66%) allows more refuge areas than is typical of high mountain landscapes in other wilderness areas. The low number of stocked sites may also facilitate the opportunity for successful fish removal from core frog areas (Knapp and Matthews 1998). If the results of other studies on the impact of fish removal are generalizable to the case of the Columbia spotted frog in the ABW, extirpation of fish would, over time, allow the population of spotted frogs to increase toward pre-introduction levels. A compromise management alternative would be to limit fish stocking to lakes that do not provide adequate habitat for all stages of the amphibian's life history. For example, lakes and ponds above 2950 m in elevation in the Absaroka-Beartooth Wilderness do not provide appropriate habitat for any life-

history stage of Columbia spotted frogs. These waters are nutrient poor, rarely have emergent vegetation, and are the last to ice-off in the spring and first to freeze in the fall. Lakes or ponds that provided preferred amphibian habitat (extensive shallows shores, emergent macrophytes) could be returned to a fishless state. Consequently, lakes for angling would still be available, but the availability of suitable refugia and predator-free migration corridors would be maximized, thereby contributing to the conservation of this amphibian species. Most importantly, public education about the benefits of restoring lakes to a fishless condition should be a priority (see Chapter 3).

Conclusions

The amphibian life cycle is complex and an introduced predator can influence a number of points from egg laying through metamorphosis. The results presented here suggest that Columbia spotted frogs co-occur in the ABW landscape with introduced fish largely due to the availability of refuge ponds without fish and fish-free movement corridors. Although frogs appeared to use ponds with fish for breeding, the subsequent poor recruitment from these ponds suggests that individuals reared in these lakes are at a disadvantage from egg to metamorph. To better understand the direct and indirect influences of fish on frog population dynamics experiments are needed to examine predator feeding preferences, non-lethal effects on larval growth and development, and effects on activity levels and microhabitat use.

It may be that predation pressure on adults in ponds with fish is selecting for a shift in life-history traits. In ponds with fish, adult frogs were larger at a

younger age (suggesting a younger age at sexual maturity), had shorter life-spans and laid more eggs per clutch. While all of these results fit with life-history theory predictions in response to predation pressure on adults, it is difficult to make conclusions based on these data. First, these general trends may be more influenced by habitat differences than predation pressure. Furthermore, while survival rates of male frogs was slightly lower in ponds with fish, female frogs had a significantly higher probability of survival in ponds with fish, an outcome that does not correspond well to expectation of increased predation risk in ponds with fish. Even though most frogs remained at the original site of capture, suggesting site fidelity, 10% of individuals did move. This level of movement and dispersal may be blurring not only the effects of predation selection but also the distinction assigned to frogs from ponds with and without fish. A long-term study is needed to test the hypothesis that fish may be selecting for a population-level shift in life history.

Although Columbia spotted frogs in this study area of the Absaroka-Beartooth Wilderness are currently living and reproducing in the presence of fish, this does not mean that the population is safe from declines and extirpations. Finally, it is imperative for federal and state wildlife managers to acknowledge the documented negative effects that fish introductions have on the aquatic food-web, especially the negative effect on many high-elevation frog species. Ideally, future fish-stocking should be eliminated in wilderness areas, or as a compromise, occur only where these negative effects can be minimized. Data

from this study provide an important baseline to test this and other hypotheses

about spotted frog population dynamics and for long-term monitoring.

ACKNOWLEDGMENTS

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Appendix 1. Protocol for skeletochronology (method of Gary Matson, Matson Labs LLC, Missoula, Montana)

To begin the analysis, the thickness of the first growth zone, formed before the first winter of life, was measured (μm). A zero was recorded if the entire first zone was absent due to resorption. Hence, the first zone encountered when "0" as noted in a section actually corresponded to the second layer of bone laid down (unless otherwise noted). Where the new bone at the periphery was just barely visible, the thickness of new bone was measured (μm). To aid in judging the amount of bone formation expected for different populations/ages during the season of toe excision, a different bone thickness was measured when this periphery was a very thick.

The first LAG was counted as being from the second winter when 1) resorption was extensive, 2) the preceding zone was fairly thick (~ 10 μm) all the way around the circumference or was very thick in one spot, 3) subsequent zones were thinner than expected for second or third growth seasons, and zone compression that is characteristic of older years began within one or two years after the LAG in question.

Frogs younger than three years had an identifiable zone formed before the first winter of life and at least a remnant of this zone and the first LAG were present in younger frogs. As frogs age, initial LAGS may be reincorporated into the endosteal bone. In older frogs, it was assumed that all of the first zone might be resorbed, but not all of the second zone. The assumed identity of the first

visible LAG was a potential error source, because the extent of resorption probably varied among individuals. It was assumed that the margin of resorption was identifiable, with endosteal zones proximal to the margin and periosteal zones distal.

In older frogs, zone thickness was an unreliable identifier for the first visible line of arrested growth and zone thickness reflected rate of growth and varied among individuals. Periodically, the first two to three zones were of different thickness due to variable genetic and environmental factors and this thickness variation was a potential source of error. Other possible sources of error were the identification of the first zone of growth, LAG that did not reflect annual growth, and low visibility LAG.

Appendix 2. Landscape and limnological characteristics for each lake or pond. Missing data is indicated as "nd".

Pond	Elevation (m)	Area (ha)	Perimeter (m)	Maximum depth (m)	Conductivity (µS)	Number of Inlets	Number of Outlets	Distance to nearest pond with fish present (m)	Distance to nearest pond with frog present (m)	Distance to nearest pond with breeding present (m)
48a	2890	0.53	350	4.6	13	0	0	219	31	70
48d	2835	0.44	274	3.1	15	0	0	94	242	242
48m	2920	0.02	57	0.5	nd	0	0	172	23	31
48x	2920	0.02	54	0.3	nd	0	0	39	39	63
48y	2920	0.10	132	0.6	9	0	0	133	23	70
49	2900	1.58	550	6.4	10	0	1	109	78	76
49a	2908	0.16	170	0.9	7.5	0	0	141	31	141
49s	2865	0.01	30	0.3	nd	1	1	320	78	78
49y	2871	0.05	98	0.3	nd	0	0	188	31	31
49z	2871	0.07	122	0.9	9.5	0	0	188	31	31
50w	2865	0.07	160	0.6	8	0	0	125	125	125
50x	2819	0.03	92	0.6	nd	0	0	39	39	39
51b	2807	0.04	106	0.5	10	0	0	70	70	70
51d	2865	0.09	120	0.5	6	0	0	500	500	500
52b	2914	0.30	290	0.9	10	0	0	219	16	16
52c	2914	0.07	112	0.8	10.5	0	0	164	16	242
52d	2914	0.11	192	0.9	15	0	0	94	39	39

Appendix 2, continued. Landscape and limnological characteristics for each lake or pond.

Pond	Elevation (m)	Area (ha)	Perimeter (m)	Maximum depth (m)	Conductivity (μS)	Number of Inlets	Number of Outlets	Distance to nearest pond with pond present (m)	Distance to nearest pond with frog present (m)	Distance to nearest pond with breeding present (m)
51	2801	0.89	400	9.1	13.5	0	1	305	70	70
50	2816	2.67	660	6.1	12	1	1	172	39	125
48b	2835	0.24	214	1.5	nd	1	1	16	141	141
48c	2835	0.16	150	2.7	nd	1	1	16	94	94
52a	2867	0.32	230	3.4	16.5	0	1	47	55	141
47	2946	2.06	600	9.5	nd	1	1	305	305	406
48	2902	2.79	940	6.7	14.5	1	1	305	39	133
52	2865	2.75	700	9.1	14	1	1	47	47	234

Appendix 3. Pearson correlation coefficients between landscape variables. Data represent the correlation coefficient, significance level and sample size (n). Significant correlations are indicated in bold face.

	Pond elevation (m)	Distance to nearest pond with fish present (km)	Distance to nearest pond with frog present (km)	Distance to nearest pond with breeding present (km)	Area (ha)	Pond perimeter (m)	Maximum depth (m)	Conductivity (μS)	Number of Inlets
Distance to nearest pond with fish present (km)	0.254 p=0.243 (23)								
Distance to nearest pond with frog present (km)	-0.002 p=0.994 (23)	0.025 p=0.910 (23)							
Distance to nearest pond with breeding present (km)	0.167 p=0.445 (23)	0.117 p=0.594 (23)	**0.717 p < 0.0005 (23)**						
Area (ha)	0.013 p=0.951 (25)	0.293 p=0.175 (23)	0.160 p=0.467 (23)	**0.456 p=0.029 (23)**					

Appendix 3, continued. Pearson correlation coefficients between landscape variables.

	Pond elevation (m)	Distance to nearest pond with fish present (km)	Distance to nearest pond with frog present (km)	Distance to nearest pond with breeding present (km)	Area (ha)	Pond perimeter (m)	Maximum depth (m)	Conductivity (µS)	Number of Inlets
Pond perimeter	0.043	0.339	0.157	0.410	0.964				
(m)	p=0.837	p=0.113	p=0.474	p=0.052	p<0.0005				
	(25)	(23)	(23)	(23)	(25)				
Maximum depth	-0.074	0.345	0.271	0.507	0.853	0.860			
(m)	p=0.726	p=0.106	p=0.211	p=0.013	p<0.0005	p<0.0005			
	(25)	(23)	(23)	(23)	(25)	(25)			
Conductivity	-0.169	-0.039	0.178	0.260	0.386	0.455	0.538		
(µSiemens)	p=0.516	p=0.887	p=0.510	p=0.330	p= 0.126	p=0.066	p=0.026		
	(17)	(16)	(16)	(16)	(17)	(17)	(17)		
Number of	-0.141	0.163	0.333	0.419	0.599	0.510	0.444	0.312	
Inlets	p=0.522	p=0.457	p=0.121	p=0.047	p=0.003	p=0.013	p=0.034	p=0.240	
	(23)	(23)	(23)	(23)	(23)	(23)	(23)	(16)	

Appendix 3, continued. Pearson correlation coefficients between landscape variables.

	Pond elevation (m)	Distance to nearest pond with fish present (km)	Distance to nearest pond with frog present (km)	Distance to nearest pond with breeding present (km)	Area (ha)	Pond perimeter (m)	Maximum depth (m)	Conductivity (µS)	Number of Inlets
Number of	-0.251	0.175	0.232	0.330	0.629	0.592	0.687	0.478	0.754
Outlets	p=0.248	p=0.425	p=0.286	p=0.125	p=0.001	p=0.003	p<0.0005	p=0.061	p<0.0005
	(23)	(23)	(23)	(23)	(23)	(23)	(23)	(16)	(23)

Appendix 4. Pearson correlation coefficients between physical attributes of the landscape and ponds and frog population metrics. Data are the correlation coefficient, significance level and sample size (n). Significant correlations are indicated in bold face.

	Pond elevation (m)	Distance to nearest pond with fish present (km)	Distance to nearest pond with frog present (km)	Distance to nearest pond with breeding present (km)	Area (ha)	Pond perimeter (m)	Maximum depth (m)	Conductivity (µS)	Number of Inlets	Number of Outlets
Adult Frog	-0.263	0.309	-0.245	-0.186	0.201	0.245	**0.459**	0.051	-0.267	0.174
Abundance	p=0.214	p=0.161	p=0.273	p=0.408	p=0.346	p=0.248	**p=0.024**	p=0.846	p=0.229	p=0.439
	(24)	(22)	(22)	(22)	(24)	(24)	**(24)**	(17)	(22)	(22)
Female Frog	-0.372	0.337	-0.186	-0.151	0.282	0.317	**0.520**	0.129	-0.154	0.294
Abundance	p=0.067	p=0.116	p=0.395	p=0.491	p=0.172	p=0.123	**p=0.008**	p=0.622	p=0.483	p=0.174
	(25)	(23)	(23)	(23)	(25)	(25)	**(25)**	(17)	(23)	(23)
Male Frog	-0.201	0.315	-0.256	-0.171	0.153	0.210	**0.415**	-0.016	-0.308	0.108
Abundance	p=0.335	p=0.143	p=0.238	p=0.434	p=0.467	p=0.314	**p=0.039**	p=0.951	p=0.152	p=0.622
	(25)	(23)	(23)	(23)	(25)	(25)	**(25)**	(17)	(23)	(23)
Frog Sex Ratio	-0.298	-0.279	-0.121	-0.249	-0.052	-0.152	-0.091	**0.695**	0.101	0.291
(F:M)	p=0.246	p=0.278	p=0.644	p=0.335	p=0.843	p=0.561	p=0.728	**p=0.012**	p=0.699	p=0.256
	(17)	(17)	(17)	(17)	(17)	(17)	(17)	**(12)**	(17)	(17)

Appendix 4, continued. Pearson correlation coefficients between physical attributes of the landscape and ponds and frog population metrics.

	Pond elevation (m)	Distance to nearest pond with fish present (km)	Distance to nearest pond with frog present (km)	Distance to nearest pond with breeding present (km)	Area (ha)	Pond perimeter (m)	Maximum depth (m)	Conductivity (µS)	Number of Inlets	Number of Outlets
Adult Frog Age- Size Relationship	0.036 p=0.730 (97)	-0.175 p=0.086 (97)	-0.014 p=0.890 (97)	0.111 p=0.278 (97)	0.167 p=0.101 (97)	0.059 p=0.565 (97)	-0.229 p=0.240 (97)	-0.175 p=0.094 (93)	0.297 p=0.003 (97)	-0.077 p=0.453 (97)
Female Frog Age- Size Relationship	-0.063 p=0.670 (48)	-0.074 p=0.617 (48)	-0.053 p=0.723 (48)	0.101 p=0.494 (48)	0.229 p=0.117 (48)	0.153 p=0.299 (48)	-0.049 p=0.742 (48)	-0.079 p=0.603 (46)	0.286 p=0.048 (48)	0.104 p=0.481 (48)
Male Frog Age- Size Relationship	0.109 p=0.457 (49)	-0.246 p=0.089 (49)	0.038 p=0.796 (49)	0.130 p=0.373 (49)	0.126 p=0.390 (49)	-0.010 p=0.943 (49)	-0.361 p=0.011 (49)	-0.244 p=0.099 (47)	0.320 p=0.025 (49)	-0.216 p=0.137 (49)
Cluster Density	-0.474 p=0.022 (23)	0.331 p=0.123 (23)	-0.161 p=0.463 (23)	-0.071 p=0.747 (23)	0.274 p=0.205 (23)	0.271 p=0.211 (23)	0.473 p=0.023 (23)	0.112 p=0.679 (16)	-0.031 p=0.888 (23)	0.281 p=0.194 (23)

Appendix 4, continued. Pearson correlation coefficients between physical attributes of the landscape and ponds and frog population metrics.

	Pond elevation (m)	Distance to nearest pond with fish present (km)	Distance to nearest pond with frog present (km)	Distance to nearest pond with breeding present (km)	Area (ha)	Pond perimeter (m)	Maximum depth (m)	Conductivity (μS)	Number of Inlets	Number of Outlets
# Eggs/Cluster	-0.488	-0.405	0.521	0.658	0.644	0.733	0.489	0.793	-0.018	-0.041
	p=0.327	p=0.426	p=0.289	p=0.155	p=0.168	p=0.098	p=0.325	p=0.110	p=0.973	p=0.938
	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(5)	(6)	(6)
Larval Growth (mm/day)	0.055	**-0.133**	**0.185**	**0.142**	-0.035	0.006	-0.033	-0.58	**-0.086**	**-0.077**
	p=0.087	**p<0.0005**	**p<0.0005**	**p<0.0005**	p=0.283	p=0.861	p=0.303	p=0.072	**p=0.007**	**p=0.016**
	(957)	**(957)**	**(957)**	**(957)**	(957)	(957)	(957)	(957)	**(957)**	**(957)**
Number of Emerging Metamorphs	0.139	0.203	-0.172	-0.047	-0.008	0.047	0.089	-0.196	-0.191	-0.083
	p=0.509	p=0.353	p=0.433	p=0.832	p=0.968	p=0.824	p=0.671	p=0.450	p=0.384	p=0.706
	(25)	(23)	(23)	(23)	(25)	(25)	(25)	(17)	(23)	(23)
Metamorph Body Size (mm)	0.093	-0.192	**0.361**	0.101	0.006	0.145	0.090	**0.333**	0.156	-0.085
	p=0.427	p=0.097	**p=0.001**	p=0.386	p=0.956	p=0.212	p=0.440	**p=0.003**	p=0.179	p=0.464
	(76)	(76)	**(76)**	(76)	(76)	(76)	(76)	**(76)**	(76)	(76)

CHAPTER 3. Introduced Species, Wilderness, and Amphibian Decline

"Plants, vertebrates, invertebrates, and pathogens all interact in synergistic and complex ways, and any alien that is released into the natural environment becomes a part of this interconnected web." Daniel Simberloff (1996)[1]

It is a cool morning as I hit the trail; it usually is at 9000 feet above sea level. My pack is bursting at the seams with supplies for the next week, so the first half-mile feels like a climb up Mount Everest. Huffing and puffing I make my way through the forest, concentrating too much on the trail hazards, a rock here, a tree root there. The forest is quiet except for my heart beating in my chest and the wind blowing through the tree-tops. I concentrate on the calming sound of the wind and it reminds me to enjoy the amazing landscape that surrounds me. The trail rises and dips. At times I feel like I can barely make another step, at others I want to run down the trail. Eventually, I reach a sparkling meadow filled with marsh marigolds. A Clark's nutcracker squawks as I approach his lookout tree near the rock where I will take a break. This is my favorite rock! The height is perfect for leaning up against it to remove my back-pack or strap it back on without much effort. After my break, I have to cross several creeks before reaching my final destination. The creek waters are crystal clear, and when I first go to these mountains each summer, it is early enough in the season that little algae is growing on the rocks, so the crossing is not too slippery. And at each

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[1] **Simberloff, Daniel. 1996. impacts of introduced species in the United States. Consequences 2 (2). You can read this article in its entirety at www.gcrio.org/CONSEQUENCES**

creek, the water is so cold I leave my hiking boots on to insulate my feet and toes, and the water-logged feeling afterwards is worth it! The hike into the wilderness area is six hours of pure joy and pure torture, but waiting for me when I reach my usual campsite are the trees for hanging my hammock and one for hanging my bear bag, and just over a slight rise is the pond I will use to collect drinking water. As soon as I get my tent and camp situated I grab my fly rod and walk a few steps to beautiful Sliver Lake. Choosing a pale morning dun fly, I make my first cast. Immediately I get a nice hit, and land a brook trout. I swear he is "this big".

More than 1000 lakes and ponds and numerous other small wetlands, streams and rivers are found in the Absaroka-Beartooth Wilderness in south-central Montana. The area, inhabited by high-alpine trees, shrubs, and flowers, is a spectacular place to hike, backpack and camp. In a number of these lakes and ponds, you also can find a variety of fish: Eastern brook trout, cutthroat trout, rainbow trout, arctic grayling, and more. In fact, if you were to explore high-mountain areas of the Sierra Nevada Mountains in California, the Cascade Mountains in Oregon, or other high-elevation regions of the Rocky Mountains in Montana, Wyoming and Colorado you would find a similar scenario - in most lakes, fish are plentiful. While the presence of these fish is a boon to the weary backpacker or camper hungering for a fresh-caught meal of trout, it is a bust to the other organisms that live in the same water. In most cases, the fish are not supposed to be there! Historically, high elevation lakes and ponds were without fish for a very simple reason - the fish could not swim into them. These various

fish species have been introduced (or stocked) into high elevation waters to serve a recreational role – such as fishing – for the outdoors adventurer.

The movement of species among continents has occurred since the beginning of human travel. How introduced species interact with their new environments can be described as the good (or at least indifferent), the bad, and the ugly. Species introductions that benefit the human condition (e.g., food crops) tend not to "escape" and run wild in their new habitats. And introductions of plants and animals into cities, towns and surrounding areas are also common. We all want beautiful flowers in our gardens and pet dogs and cats and parakeets in our homes. Their influence may be indifferent if they never leave the house, or they can have negative effects if they prey on native animals such as birds.

Indeed, introducing new species to places we live is nothing new, and, in many cases, there is little or no detectable change to the environment into which they are placed. In fact, the idea of introducing new species to the places we move can seem logical. The success of human culture is largely based on the introduction of exotics, and the intentional introductions of most of these plants and animals seemed innocuous at the time. For example, tomatoes are not natural to Montana and there are few among us who worry about this species escaping to take over the native habitats in our state. But are all introduced species as innocuous as the garden tomato plant? For the most part, the introduction of species was thought to be a "win-win" situation historically. Now

that we have lived with introduced species for decades or even centuries, we have ample evidence that many exotics can have great effects on the native landscape when they escape. You do not need to go much further than your own yard to see introduced species. Actually, most plants you see when you take a walk in a typical neighborhood are introduced. Depending on where you live in Montana, few of the original species of the native Palouse Prairie or forest understory vegetation remain today. In fact, many of us battle introduced species, such as spotted knapweed and toadflax, in our own gardens and fields. For example, spotted knapweed, a close relative of bachelors buttons, is a species that has been introduced from Eurasia and has extended its range into most of the Pacific Northwest. This species has few natural enemies where it has escaped in North America and it out-competes the native prairie grasses of the Intermountain West. Along many road- and trail-sides in Montana, knapweed swamps the scenery with its purple blooms. The spread of this plant is blamed for the loss of native grasses and the subsequent loss of plant diversity in many areas of Montana and beyond.

Our aquatic habitats also have been changed by the introduction of new species. Historically, the bull trout inhabited many of the rivers and lakes in Montana. However, the introduction of Eastern brook trout into these same waters has been very detrimental, and is closely linked to the current endangered status of bull trout in the state. Brook trout have a negative influence in two ways. First, the brook trout out-compete the native bull trout for habitat and food. Second, brook trout can breed with bull trout and, because offspring from this

mating of two different species are sterile (a result of genetic incompatibility), bull trout populations, and the integrity of the gene pool, are becoming compromised.

How do introductions influence an entire ecological community? Flathead Lake presents an excellent example. Historically, Flathead Lake supported a diverse suite of fish; west-slope cutthroat trout, bull trout, lake whitefish and several others, with bull trout acting as the top aquatic predator. As people moved from east to west in the U.S. in the mid 1800's, many longed to catch and eat familiar fish species from their home states. To meet the demand from homesteaders and tourists, Burlington Railroad introduced lake trout, a large game fish, into Flathead Lake in the late 1800's. The lake trout fast became the new top predator, preferentially feeding on bull trout and cutthroat trout. In 1916, again in response to recreational demand, kokanee salmon were introduced into the lake and became a food source for both lake trout and bull trout, as well as a major sport fishery for anglers. Kokanee salmon also migrated from Flathead Lake into rivers and tributaries to spawn and then die. These dead fish served as a major food source for Bald eagles.

In the early 1980's, *Mysis* shrimp made their way into Flathead Lake, invading from upstream lakes where they had been introduced in earlier years. The introduction of *Mysis* shrimp into Flathead Lake had effects that had not been observed before, and certainly were not anticipated. *Mysis* shrimp eat zooplankton, the same food as the kokanee. They also migrate to very deep water during the day and are present in more shallow water only at night.

Kokanee would eat *Mysis* if they could see them, but because they feed by sight, the shrimp were rarely captured by kokanee. Interestingly, the tiny *Mysis* are responsible for the rapid disappearance of the kokanee salmon because *Mysis* shrimp won the competition for zooplankton. But that's just half of the story. When the kokanee fishery collapsed, the Bald eagle population that depended heavily on these fish for food during and after spawning suffered as well. Bull trout also lost a major prey item in the kokanee and soon experienced population declines. But also, there was another winner. Lake trout inhabit deep water and during the daily migration of the *Mysis* shrimp to deep water, they served as an excellent new food source for lake trout. In fact, the availability of *Mysis* as forage is believed to be responsible for the significant increase in lake trout numbers and size, further impacting populations of bull trout and cutthroat trout. How have introductions of lake trout, kokanee and *Mysis* influenced the ecological community in Flathead Lake? The answer is simple. Today the fishery is much less diverse and native trout populations are severely threatened. What has been done to improve conditions for the populations of native fish? Fall Mack Days, a three-week fishing derby, is held annually to encourage anglers to catch and keep as many lake trout as possible in order to harvest the over-abundant fish. Time will tell if this strategy is successful.

Although new species have been introduced into low elevation lakes, ponds, streams and rivers for hundreds of years, stocking fish into high elevation waters in Montana that were historically fishless has occurred only since the early 1900's. The number and pervasiveness of these introductions has

increased throughout the twentieth century as our technology for moving fish has improved. But, what about purposeful introductions into places we have set aside to let nature take its course, such as the introductions of fish into areas deemed "wilderness"? To understand why such introductions may be particularly insidious, it is necessary to look back at why we have this act in the first place.

The Wilderness Act of 1964[2] states "A wilderness, in contrast with those areas where man and his own works dominate the landscape, is hereby recognized as an area where the earth and its community of life are untrammeled by man, where man himself is a visitor who does not remain. An area of wilderness is further defined to mean in this Act an area of undeveloped Federal land retaining its primeval character and influence, without permanent improvements or human habitation, which is protected and managed so as to preserve its natural conditions and which (1) generally appears to have been affected primarily by the forces of nature, with the imprint of man's work substantially unnoticeable; (2) has outstanding opportunities for solitude or a primitive and unconfined type of recreation; (3) has at least five thousand acres of land or is of sufficient size as to make practicable its preservation and use in an unimpaired condition; and (4) may also contain ecological, geological, or other features of scientific, educational, scenic, or historical value." Long before remote high elevation landscapes were declared wilderness areas in 1964, many

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[2] **The Wilderness Act of 1964 can be read in its entirety on Wilderness.net website (www.wilderness.net)**

rivers and lakes had already been stocked with fish. Ironically, stocking practices have continued in the present.

"A civilization which destroys what little remains of the wild, the spare, the original, is cutting itself off from its origins and betraying the principle of civilization itself." Edward Abbey (Desert Solitaire 1990)[3]

Introductions in Wilderness Areas: Recreation Versus Ecological Integrity in the Absaroka-Beartooth Wilderness

Figure 1. The Absaroka-Beartooth Wilderness, an area located in south-central Montana. In the distance you can see Granite Peak, the highest point in Montana.

Today there are 662 designated wilderness areas in the United States and 14 of these areas occur in Montana. These areas are the last stronghold of primeval landscapes, and are important for their biological diversity. For an example of the influence of introduced species in a wilderness area let's look at

[3] Abbey, Edward. 1968. Desert Solitaire: a Season in the Wilderness. McGraw-Hill, New York, 269 pp.

the Absaroka-Beartooth Wilderness. Portions of the Absaroka and Beartooth mountain ranges were designated as primitive areas in 1932, and as Wilderness in 1975. In the early 1930's, state fishery managers first introduced fish into numerous high alpine lakes carrying them in by horseback and this practice of stocking into wilderness area by horseback continues today. It is also very likely that many lakes were stocked by "bucket biologists", that is, individual anglers who purposefully moved fish from lake to lake. Stocking "mistakes" also occurred; there is at least one example of cutthroat trout mistakenly being introduced into the aptly named Wrong Lake, instead of the target lake.

In many lakes and ponds of the Absaroka-Beartooth Wilderness, initial stocking efforts resulted in self-sustaining fish populations where fish were able to successfully reproduce. Hence, these lakes are no longer stocked by Montana Fish Wildlife and Parks (MFWP). Other lakes that are more hostile to fish, for example, those that regularly freeze and/or provide insufficient winter resources, occasionally become fishless. These lakes and ponds can be repopulated by fish without stocking if they are connected, upstream or downstream, to a lake from which fish can migrate. Those lakes and ponds where fish populations are not self-sustaining, or where fish cannot recolonize by migration, are replenished by MFWP on an eight-year stocking schedule.

Why are we becoming more concerned about these repeated introductions of fish to wilderness lakes? How does stocking affect the native species inhabiting the lakes and ponds of these high-elevation landscapes? We

can find answers to these questions by examining the life cycle of other species that are native to these habitats. Historically, these high elevation fishless waters once constituted major population centers for species of amphibians such as frogs, toads, and salamanders. Believe it or not, species of these groups of animals can be found in high elevation landscapes if you know where to look. What is life like for an alpine amphibian such as the Columbia spotted frog (*Rana luteiventris*)? As soon as the near-shore habitat thaws in early to late June, spotted frogs begin to breed. Male frogs grab onto females in an embrace known as amplexus and hold on for dear life. The male frog fertilizes the eggs externally; that is, as females deposit the eggs into water, the male releases sperm and eggs are fertilized. Eggs are laid in clusters of several hundred to more than a thousand eggs in shallow water near shore. There, where water temperature gets a little warmer, eggs are supported by emergent vegetation. Frogs also will congregate to lay their eggs communally, probably helping to insulate eggs.

Eggs develop and hatch into tadpoles after 3 – 4 weeks and these tadpoles are completely aquatic and primarily feed on algae. Tadpole development and growth is greatly affected by water temperature, food quantity, and food quality. Although the exact length of time a tadpole spends in the water is affected by these habitat conditions, they typically transform into frogs 4 – 6 weeks after hatching. Tadpoles at high elevations must metamorphose in one summer because they cannot survive as tadpoles over winter. In early September, the emerging "metamorphic" frogs and adult frogs migrate to areas

they will inhabit through the winter months. How do they survive when their pond is frozen for 8 months a year? Little is known about the specific winter habitats of Columbia spotted frogs because few people have braved the cold temperatures and deep snow to look for them during the winter. We expect that they likely over-winter in deep water or in underground seeps or springs, and that they are mostly inactive during this hibernation. At high elevations, most adult frogs reach sexual maturity by age 4 and some are known to live 14 years! Because high elevation conditions are so harsh and individuals can be so long-lived, female frogs do not breed every year. Females need to accumulate resources over several years to produce a viable cluster of eggs several times over the course of their lives.

What happens when fish appear in these systems? Many studies have shown that fish introductions have altered the distribution of frogs, toads and salamanders wherever they are introduced. The introduction of fish into waters where they were not found historically can influence an amphibian population in several ways including 1) direct predation, 2) indirect interactions, and 3) alteration of the aquatic food web. In California, Oregon and Washington, for example, fish introductions are known to have caused local population decline and extinction for species such as the mountain yellow-legged frog, boreal toad, and long-toed salamander. The most obvious explanation for declines in amphibian populations after fish are stocked is predation. Hungry fish will feed on amphibians throughout their life cycle, but predation of tadpoles is especially

high. When tadpoles do not survive to maturity, they cannot reproduce and,

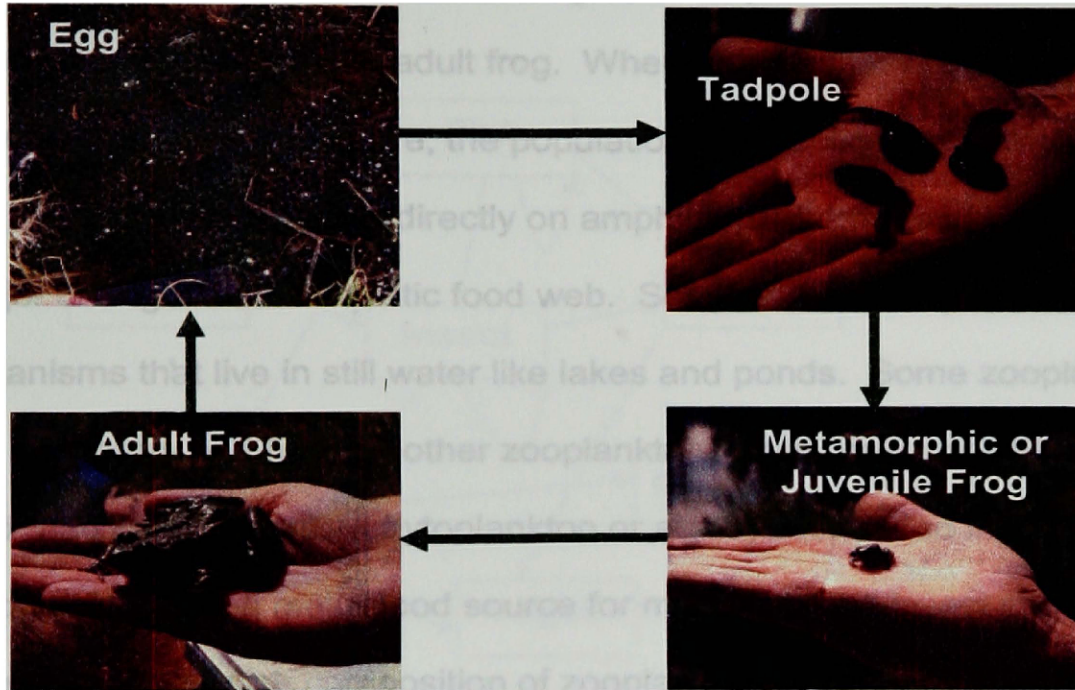eventually, the overall population of frogs in a particular habitat suffers.

Figure 2. The life cycle of the Columbia spotted frog. Each arrow represents growth and development to the next life history stage. The arrow from adult frog to egg represents successful reproduction which will not occur until sexual maturity (> 3 years of age). Some individuals may reproduce only several times or not at all during their life time.

But direct predation is not the only reason amphibians may disappear from

stocked waters. The reasons for reduction in an amphibian population can be

much more indirect and difficult to determine. Interestingly, a number of studies

have shown that tadpoles can sense the presence of a fish predator by "smelling"

its scent in the water. So the fish does not have to be actively hunting a tadpole;

the mere presence of fish may be enough to scare a tadpole into inactivity or

hiding out so it does not attract unwanted attention. And when hiding out leads

to decreased time spent eating, or the inability to move to an area that is rich in food or warmer water, tadpoles do not thrive. In other words, hiding out in poorer quality habitat and/or reduced feeding can compromise the size and rate at which a tadpole matures into an adult frog. When tadpoles do not survive, or are not as robust when they do mature, the population can decline over time.

Aside from preying directly on amphibians, introduced fish also can cause major changes in the aquatic food web. Some fish eat zooplankton, very small organisms that live in still water like lakes and ponds. Some zooplankton species are predatory and feed on other zooplankton, while other species are vegetarians and feed on tiny plants (phytoplankton or algae) suspended in the water column. Zooplankton are a major food source for many fish and insect species, and fish can change the size composition of zooplankton community by preferentially eating the largest species. The consequences of such changes in the zooplankton community on food availability, growth, and survival of frogs are not known with certainty but could be significant. To understand why this is the case, we need to understand how a food web works in these lakes and ponds. In the diagram in Figure 3, the arrows point to the food being eaten. For example, adult frogs primarily feed on terrestrial insects, many of which have aquatic larval stages that feed on zooplankton. If fish are more successful in capturing zooplankton, fewer are available for insect larvae, thereby influencing the number of insects that will be available for adult frogs. Fish also directly prey on insects, which can influence insect density and diversity. Consequently, the alteration of the insect population in a lake or pond can affect a frog population because 1)

adult frogs eat insects, 2) aquatic insect stages can compete with tadpoles for resources, and 3) some aquatic insect larvae can actually eat tadpoles.
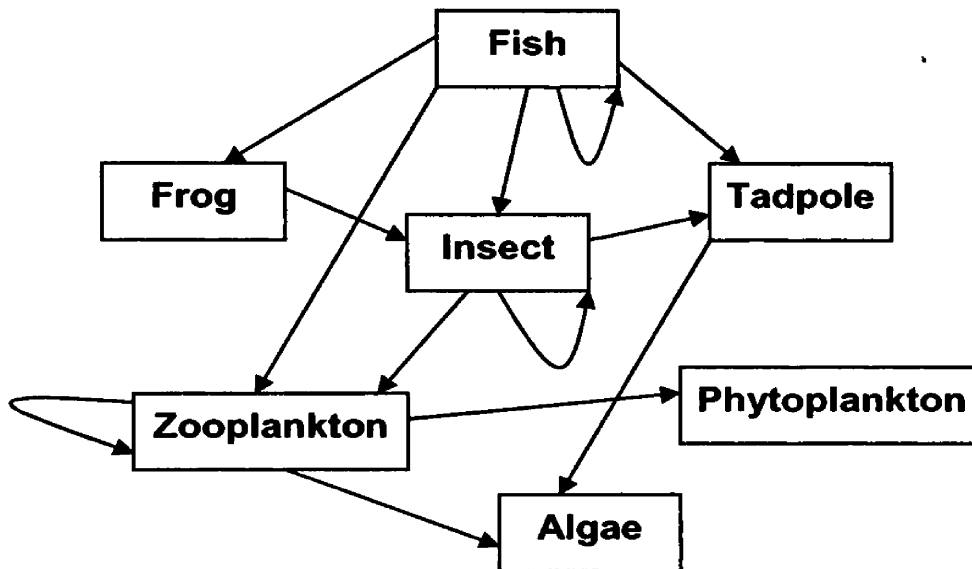

Figure 3. Food web of high elevation ponds in the Absaroka-Beartooth Wilderness. Each box represents a component of the food web. Arrows point from the feeding organism to one or more of its prey.

Aside from the ecological influences, stocking native and non-native fish into previously fishless lakes in wilderness areas, an historical artifact related to recreation, is inconsistent with the 1964 Wilderness Act. Today we have a much better understanding of the ecological consequences of these repeated introductions, and we have better tools to weigh the social and ecological costs of this practice. What is a benefit of repeated stocking of fish? Recreationalists can catch their dinner after a long hike into the wilderness. But what are the costs of stocking wilderness lakes with fish. Obviously there is the actual dollar

expenses of raising and transporting fish on a regular basis to these remote areas. And then there is the ecological cost in terms of alterations to the natural food web.

What would happen if we stopped artificially stocking ponds and lakes in the Absaroka-Beartooth Wilderness today? Could they return to a more natural state? There is good news from other wilderness areas. For example, in the Muir Wilderness of the Sierra Nevada Mountains in California, biologists have observed that amphibians return to lakes and ponds in these areas when fish are removed. Indeed, based on studies that documented the potential for re-establishment of amphibian populations, the California Department of Fish and Game stopped stocking lakes, and began to actively remove fish from these areas. There is another mechanism that, over time, can help in this process. When ponds and lakes freeze from top to bottom over winter, fish die. Without stocking, fish eventually disappear from all but the deepest high elevation lakes. Perhaps managers could be convinced to only stock lakes where amphibians cannot live. In the Absaroka-Beartooth Wilderness, lakes and ponds above 9750 feet in elevation do not provide appropriate habitat for any life-history stage of Columbia spotted frogs. These waters are nutrient poor, rarely have emergent vegetation, are the last to ice-off in the spring and first to freeze in the fall. Columbia spotted frogs prefer lakes with extensive shallow water shores and a lot of grasses and sedges. These areas are used for breeding and rearing and also provide a warm safe place for frogs to hide out. Lakes or ponds that provide the preferred amphibian habitat could be returned to a fishless state, while lakes

for angling would still be available when important frog habitat was not compromised. The effectiveness of this solution would be maximized if streams and rivers used by frogs to move from one lake to the next were also fishless.

The Wilderness Act of 1964 challenges us to protect and manage in ways that are consistent with preserving natural conditions and functional relationships in our Wilderness areas. Clearly, we have an opportunity to do this better in our treasured high elevation lakes and ponds. In reality, the resources are probably not available to accomplish the total removal of introduced fish from all wilderness area lakes, ponds, streams, rivers and marshes. However, federal and state wildlife officials and policy makers can help us better meet the requirements of the Wilderness Act of 1964 by stopping further stocking efforts and, when possible, encouraging back-country travelers to play a role in reducing fish numbers. This is one circumstance where we should catch and eat (versus catch and release!).

Back at the campsite, the trout I caught in the wilderness is delicious, simply seasoned with olive oil and rosemary. As my first big meal since I started hiking early in the morning, it is truly satisfying. I lick my fingers and then wonder...at what cost has this meal been supplied to me? Why do hikers and back-packers travel such long distances by foot to reach back-country wilderness areas? Is it because they value wilderness for the angling opportunities? Or do we hike into wilderness areas to get "back to nature", to a place where one can forget about the scars on the landscapes of our everyday lives? Perhaps it is for a more spiritual reason, a place to meditate, or simply to enjoy the pristine state

of nature and its processes. Maybe we hike into the wilderness for a combination of all of these reasons. Ultimately, the future of wilderness integrity and management is interconnected with the values we place on wilderness, and the suite of the experiences that wilderness affords. And perhaps to retain the "primeval character" of these places, as the Wilderness Act challenges us to do, it is time to rethink why we introduce species into them. I think I can probably enjoy the experience just as much if I don't catch my dinner at my favorite campsite next time I head up the mountain.