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Translocation Mortality and Local, Regional, and Continental Diet of the Northern River Otter (*Lontra canadensis*)

Casey C. Day

A thesis submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of

Master of Science

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ABSTRACT

Translocation Mortality and Local, Regional, and Continental Diet of the Northern River Otter (*Lontra canadensis*)

Casey C. Day
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Master of Science

The northern river otter (*Lontra canadensis*) is a semi-aquatic carnivore whose range extends throughout most of the United States and Canada. The northern river otter experienced a severe range contraction post-European settlement, but due to widespread management has in recent decades begun to recover much of its former range and habitat.

We translocated 27 river otters from Utah and Idaho to the Provo River, Utah from November 2009 through January 2012 in a reintroduction effort to restore the northern river otter to its native range. Of these 27 otters, 6 died as a result of effects related to the translocation. We used linear regression and model selection to determine what factors had the most influence on the immediate mortality of translocated otters. We found that body mass was the most important factor, followed by sex. Indeed, otters at the high end of the body mass spectrum were 4 times more likely to survive a translocation than otters at the low end of body mass.

Along with the reintroduction project, we determined the food habits of the northern river otter in the Provo River watershed. We located and monitored otter latrine sites from February 2010 through February 2012, collecting scats on a monthly basis. We identified prey items in otter scat and recorded data as the frequency of prey items per total number of scats, presented as a percentage. Fish was the primary class of prey taken by otters (96.5%), followed by crustaceans (16.9%). Otter diet varied among seasons for nearly all classes ($G = 127.8$, d. f. = 24, $P < 0.001$) and families ($G = 132.94$, d. f. = 18, $P < 0.001$) of prey. We conclude that otters are potentially selecting prey in the main channel according to their abundance and in inverse proportion to their swimming ability. However, with multiple habitat types that vary in species richness and diversity, it was difficult to determine which prey items otters are selecting for without direct behavioral data on location of foraging.

We examined the diet of the northern river otter at the regional and continental scale. We examined 100 publications and 106 prey lists in order to determine the food habits of the northern river otter among ecoregions and seasons. Fish was found to occur in otter diet more often than any other class of prey, followed by malacostracans. At the family level, Astacoidea contributed more to otter diet than any other family of prey. Multiple classes and families varied by ecoregion and/or by season. Crayfish, while not the primary component of otter prey throughout North America, was found to be the primary component when readily available. Furthermore, we developed a model of river otter prey selection which includes factors that may have an impact on the availability of prey to otters. Otter prey selection is likely due to a variety of factors, including the habitat, detectability, catchability, and palatability of prey.

Keywords: river otter, *Lontra canadensis*, translocation, reintroduction, diet, food habits

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Finally, I thank my family for all of their love and support throughout the years of not only my graduate education, but from my kindergarten years to the present. None of this is possible without them.

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CHAPTER 1: FACTORS INFLUENCING MORTALITY OF TRANSLOCATED NORTHERN RIVER OTTERS (*LONTRA CANADENSIS*) IN UTAH

ABSTRACT

Reintroductions and translocations of northern river otters have been a common occurrence throughout the United States from the 1970's to the 2000's. In Utah, managers are actively working with otters to try to reestablish their presence throughout the state. From 2009 through 2012, we translocated 27 radio-marked otters into the Provo River watershed in northern Utah. Many of these otters, however, did not survive the translocation and died from various causes within the first two weeks of release. Our objective was to develop a model to determine what factors had the most impact on the translocation-related mortality of otters. We developed a series of *a priori* models and used linear regression to determine what factors were the most important. We used Akaike's information criterion to evaluate relative model support. We found that the univariate models that included body mass bore the most model weight, and that body mass was the most important factor influencing the initial survival of translocated otters. Model averaged β estimates indicated that otters at the large end of body mass were 4 times more likely to survive the translocation than otters at the low end of body mass. Sex was the next most important factor influencing survival, as odds ratios indicated that males were more likely to survive the translocation than females. We urge ecologists and managers to delay the trapping and translocating of otters until young of the year are likely large enough to have a high probability of survival.

INTRODUCTION

Reintroduction biology is a growing field. The number of reintroduction projects and reintroduction-related publications in existence has drastically increased from the 1970's to the 2000's (Seddon et al. 2007). While reintroductions have had various uses in the past such as restocking hunted populations (Griffith et al. 1989) and solving human-wildlife conflict, reintroductions are more commonly being used as a tool for conservation (Fischer and Lindenmayer 2000, Seddon et al. 2007) and have proved increasingly successful over time (Seddon et al. 2007). Reintroductions, translocations, and supplementations can be effective methods for preserving and increasing biodiversity, strengthening the structure and function of an ecosystem, and rehabilitating populations of threatened or vulnerable species (Wolf et al. 1996). Furthermore, the reintroduction of keystone species could serve as a major step toward rehabilitating a disturbed ecosystem.

Carnivores have regularly been the focus of reintroduction projects (Breitenmoser et al. 2001). Often seen as charismatic symbols of conservation (Gittleman et al. 2001) and indicators of ecosystem health (Ray 2005), these predators also tend to have a widespread trophic impact on the systems they inhabit (Estes and Palmisano 1974, Paine 1980, Beschta and Ripple 2011). Indeed, it has been argued that the conservation of top predators can yield greater biodiversity and more effective conservation of entire ecosystems (Boutin 2005). In addition, carnivores are notorious for existing in low densities and having large home ranges, making them relatively more susceptible to becoming threatened or endangered and therefore natural targets of management programs. Accordingly, at least 165 carnivore reintroduction projects took place worldwide from 1950 – 1999, with the majority in North America where carnivores have often been displaced by human activity (Breitenmoser et al. 2001). As a result of these efforts, many carnivore species have experienced recent range expansions and population increases, including wolves (Lowry 2009), black-footed ferrets (Jachowski and Lockhart 2009), and northern river otters (Melquist et al. 2003).

The northern river otter (*Lontra* canadensis) is a highly social (Reid et al. 1994, Gorman et al. 2006), nocturnal (Martin et al. 2010), carnivore that has undergone a number of reintroductions since the 1970's (Raesly 2001). Originally, its range extended east to west across North America and from Mexico to Alaska (Hall 1981, Polechla 1988, Melquist et al. 2003). However, during the 19th and 20th centuries, the northern river otter experienced a severe range contraction (Deems and Pursley 1978, Melquist et al. 2003) that was most likely due to unregulated harvest and habitat degradation (Polechla 1990). Following the recent trend toward species conservation (Seddon et al. 2007), however, the otter's range is once again expanding with at least 22 states having conducted reintroduction projects since the 1970's.

Unfortunately, reintroduction projects are often unsuccessful due to poor planning and little or no monitoring post-release (Breitenmoser et al. 2001). A failed reintroduction or translocation can still be beneficial to the ecology of a species, however, if monitoring is able to reveal factors associated with the reasons behind the failure, such as cause-specific mortality. This information can include both immediate causes related to the translocation, and general causes that would affect an established population. For river otters, incidental trapping and collisions with vehicles have been cited as common causes of mortality (Gorman et al. 2008). Due to the high mortality rate of otters within two weeks of release in our study site, however, were interested in what might affect the survival rate of river otters immediately after translocation.

Our objective, therefore, was to determine what factors had the most influence on the translocation-related mortality of northern river otters during a reintroduction conducted in northern Utah from 2009 - 2012. Specifically, we wanted to determine what life history traits (e.g. age, sex) or environmental factors (e.g. season, temperature) contributed to the translocation-related mortality of reintroduced individuals.

METHODS

We translocated 27 river otters from various locations in Utah and Idaho to another Utah location from November 2009 to January 2012. During the first year of the reintroduction, we trapped otters on A Section of the Green River in northeastern Utah. The second year of the reintroduction we trapped otters in coordination with the Utah Division of Wildlife Resources (UDWR) and Idaho Fish and Game (IDFG) on Sheep Creek which feeds the southwest corner of Flaming Gorge Reservoir in Utah; Montour Wildlife Management Area, Idaho; the Payette River near Garden Valley, Idaho; and the IDFG Clearwater Region. Some otters were also provided to us by private trappers in exchange for a fee. During the third year of the reintroduction, trapping was conducted solely by IDFG, and otters were provided from the Clearwater Region, IDFG. We translocated all otters to the middle section of the Provo River between Deer Creek Reservoir and Jordanelle Dam. Located in the Heber Valley of northern Utah, this area was recently restored by the Utah Reclamation Mitigation and Conservation Commission, and is home to a wide diversity of fish species. The area has not had a stable population of river otters since the 19th century (Maxfield et al. 2005).

To capture otters for translocation, we surveyed for otter sign such as tracks and latrine sites by walking, kayaking, and rafting rivers; and boating lakes and reservoirs. Once sign was located, we trapped for otters using Sleepy Creek #11 leg-hold traps (Sleepy Creek

Manufacturing, Berkley Springs, WV), supplemented by Victor #1 traps and Victor #1 soft-catch traps (Oneida Victor, Inc., Cleveland, Ohio). All traps that we used were modified in some way (e.g. spaced jaws, double-jawed, padded jaws) to reduce the risk of injury or discomfort to the otter. We also included other modifications such as inline springs to reduce shock to the otters' appendages, several inline swivels in each trap to allow otters to roll freely, and 2-4 feet of additional chain length to allow the otter to comfortably move around the area and maintain body temperature. We instructed private trappers and agency personnel who assisted in trapping to use similar trap modifications. Once traps were in place, we monitored them each morning.

When an otter was successfully caught, we followed several specific steps to ensure the successful capture and transportation of the animal. We secured the otter around the mid-section in a Ketch-All pole. We then guided the otter into a transport tube made from 12-inch PVC which was capped on one end with PVC and on the other end with a metal door. Once the otter was inside the tube, we closed the door while leaving it open enough to extract the trap still holding the otter's foot. We then released the otter from the Ketch-All pole as well as the foot-hold trap. Once securely inside the tube, we transported the animals to the ORCA Veterinary Facility at Brigham Young University.

We transported otters to BYU the same day they were trapped in most cases, occasionally holding them overnight for logistical purposes or in anticipation of obtaining additional otters to transport the following day. If held overnight, we transferred the otter to a 1 x 1 x 0.6 meter cage built from wire mesh with a polyurethane coating to protect otters' teeth against gnawing on the cage. If transported to BYU the same day, otters were transferred to the wire cage at the veterinary clinic and left overnight, with surgery scheduled to take place the following day. We fed captive otters thawed fish and water throughout their stay. BYU veterinarians chemically immobilized the otters with an intramuscular injection of ketamine (x = 15 mg/kg) and Midazolam (x = 5 mg/kg). While under anesthesia, BYU veterinarians performed surgery to insert a radio transmitter into the peritoneal cavity of the otter. These radio transmitters (Models 56934-03 and 56934-02; Advanced Telemetry Systems, Inc., Isanti) contain a mortality sensor that is activated after eight hours of complete animal inactivity. The veterinarians also administered Convenia (8mg/kg), an antibiotic, Meloxicam (5mg/ml), an analgesic, Ivermectin (0.2mg/kg), a parasiticide, as well as distemper and clostridium vaccines. We extracted a small vestigial upper premolar for purposes of aging via cementum annuli (Matson 1981, Kuehn and Berg 1983), extracted a blood sample for genetic work, and inserted no. 1 Monel ear tags (National Band and Tag Company, Newport, KY) in the left ear of each otter. We collected a hair sample for a toxin screen and genetic material, and we monitored body temperature with an anal thermometer. We allowed the otters to recover naturally from anesthesia and then released them from within a few hours to a few days, depending on the veterinarian's level of concern for the recovery of the otter. We released all otters on the Middle Provo River between Deer Creek Reservoir and Jordanelle Dam, with the exception of one female that was released below Deer Creek Dam.

To determine what factors were most associated with translocation-related mortality of river otters we used logistic regression. We first developed 23 *a priori* models from a set of variables that included sex, body mass, body mass squared, occurrence of injury, minimum average temperature at the release site, season, source population, and number of days in captivity. For average minimum temperature we used two weeks of data from the date of release of the otter, which we obtained from the Utah State University Climate Center (http://climate.usurf.usu.edu/). We used a body mass squared variable because we predicted an exponential relationship between survival and mass rather than a linear relationship. For the response variable, we considered any otters that survived beyond two weeks of the translocation to be a successful release. We tested for multicollinearity among variables using the "cor" command in program R (R Development Core Team 2011), and did not include any two variables having a correlation coefficient > 0.6 or < -0.6 in the same model. To evaluate relative model support, we judged models based on minimization of Akaike's adjusted Information Criterion (AICc) (Akaike 1974, Hurvich and Tsai 1989, Burnham and Anderson 2002) for small sample sizes. We considered models within 2 ΔAICc units to be top competing models. To evaluate effect sizes, we looked at model-averaged β estimates for each parameter and calculated odds ratios.

RESULTS

We captured and released 27 northern river otters into the Provo River. However, only 23 otters underwent surgery to implant a radio-transmitter in the peritoneal cavity. Of these 23, 6 otters died as a result of complications related to the translocation. Two otters died while under anesthesia; one while recovering from the anesthetic, the other while still in the preparatory stages of surgery. One otter was found dead suffering from severe peritonitis and a dehisced surgical site. The other three mortalities all occurred within two weeks of release but from unknown specific causes.

We had five competing models within 2 ΔAICc units (Table 1). The top two ranked models were univariate, comprised of body mass squared and body mass, bearing 15.2% and 12.2% of the model weight, respectively. The next two models included two variables, being comprised of body mass squared and sex, and body mass and sex, bearing 11.7% and 10.6% of the model weight, respectively. The final competing model contained a single variable, sex, and had 6.6% of the model weight. Combined, the univariate models containing body mass squared and body mass bore 27.4% of the model weight. The variables body mass and body mass squared were highly correlated (r = 0.99), and therefore we did not combine them together in any single model. The bivariate models comprised of sex and body mass squared, and sex and body mass contained 22.3% of combined model weight. These results indicated that the most important variables factoring into translocated otter survival over the initial two weeks were body mass squared, body mass, and sex. Model averaged β estimates for these three variables were 0.25kg (SE = 0.030), 0.79kg (SE = 0.015) and 2.2 (female was assigned 0, male 1, SE = 0.099), respectively. Odds ratios indicated that males were roughly 8 times more likely to survive the initial two weeks following translocation than females, although this statistic may be inflated due to small sample size. According to the top model, probability of survival for otters on the large end of body mass (10.6 kg) was 99%, over 4 times higher than for those on the low end (4.31 kg, 24%). The median body mass (7.71 kg) had a probability of survival of 80% (Figure 1).

DISCUSSION

Our findings indicate that body mass is clearly the most important factor influencing the survival of translocated river otters, probably followed by sex. Despite the fact that we were unable to accurately age the otters, these findings may show mortality to be linked to age because it is, of course, correlated with mass. River otters gain weight rapidly during their first year, and are 3-4 years old by the time they reach weight capacity (Melquist and Hornocker 1983). Sexual dimorphism among the species may reveal why 83% of our mortalities were female, as female otters weigh less than male otters at all age classes (Jackson 1961, Melquist and Hornocker 1983). This may also be an indication of why models including variables for body mass and sex filtered toward the top of our model set.

Given these findings, it is possible to develop some guidelines about how and when to conduct river otter translocations. Clearly, it would be imprudent to move otters during denning season, when pups have yet to permanently emerge, are highly dependent on their mothers, and are not yet weaned. But with weaning occurring at 12 weeks, how soon is too soon to begin trapping and translocating? Several of our otters died from unknown causes. It is possible, however, these otters suffered from starvation as a result of being separated from the mother prior to being capable of independent foraging. Shannon (1991) showed that otters will provide food for their offspring for up to 8 – 9 months, at which point gestation could begin again. While there will probably never be a solid rule of governance timing the movement of otters, we recommend conducting translocations prior to and as near to denning season as possible, keeping in mind that otters gestate for approximately 2 months prior to parturition. In Utah, this would mean translocations occurring some time in December – February to avoid causing stress to full-term females and light, young juveniles. This would vary spatially, however, as reproductive cycles have been shown to vary geographically in river otters (McDaniel 1963, Crait et al. 2006).

When conducting translocations for any animal, it would be prudent to gauge what circumstances may result in a higher mortality rate. These circumstances and variables may carry even more significance as handling time (Baxter et al. *In review*) or length of captivity increase, or if surgical procedures are involved. The combination of multiple stressors can likewise compound the risk of mortality. Otters, for example, were most vulnerable at low body mass, but releasing otters at low weight into areas with a relatively low prey base could compound the effect of low weight. In any case, we call for further investigations into the mortality of any animal that, like the northern river otter, has been commonly reintroduced and translocated. Reintroductions can be an effective tool of conservation, yet all too often end in failure (Breitenmoser et al. 2001). By understanding and then limiting the effects of those variables that can have a significant influence on the mortality of reintroduced individuals, we maximize the likelihood of successful reintroductions in the future.

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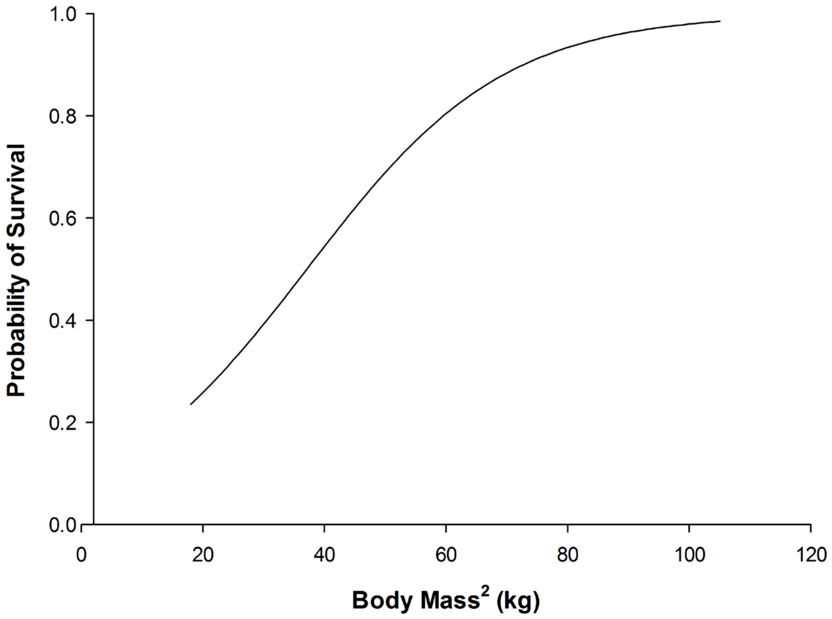
Table 1. Model structure and corresponding weights for factors influencing the mortality of river otters translocated to the Provo River, UT, from November 2009 to January 2012. (MinTemp is the mean temperature low for two weeks post-release; TimeCap is number of days spent in captivity; Source is the source population, Utah or Idaho.)

Model	Parameters	k	AIC	AICc	ΔAICc	Weight
18	BodyMass^2	2	24.38	24.98	0.00	0.152
3	BodyMass	2	24.81	25.41	0.43	0.122
19	Sex, BodyMass^2	3	24.23	25.49	0.52	0.117
8	Sex, BodyMass	3	24.43	25.69	0.72	0.106
2	Sex	2	26.04	26.64	1.67	0.066
20	BodyMass^2, Injury	3	25.78	27.04	2.07	0.054
23	BodyMass^2, MinTemp	3	25.91	27.17	2.19	0.051
13	BodyMass, Injury	3	26.18	27.45	2.47	0.044
21	BodyMass^2, TimeCap	3	26.37	27.64	2.66	0.040
16	BodyMass, MinTemp	3	26.44	27.70	2.73	0.039
14	BodyMass, TimeCap	3	26.80	28.07	3.09	0.032
12	Sex, MinTemp	3	26.82	28.08	3.10	0.032
9	Sex, Injury	3	27.36	28.63	3.65	0.024
22	BodyMass^2, Season	3	27.60	28.86	3.88	0.022
10	Sex, TimeCap	3	27.68	28.94	3.97	0.021
15	BodyMass, Season	3	28.00	29.27	4.29	0.018
7	MinTemp	2	28.72	29.32	4.34	0.017
4	Injury	2	29.83	30.43	5.45	0.010
11	Sex, Season	3	29.54	30.80	5.83	0.008
1	Source	2	30.37	30.97	5.99	0.008
5	TimeCap	2	30.39	30.99	6.01	0.007
6	Season	2	30.95	31.55	6.58	0.006
17	TimeCap, MinTemp	3	30.72	31.98	7.00	0.005

LIST OF FIGURES

Figure 1 - Logistic regression function displaying the probability of survival of river otters based on the square of their body mass. Data from 23 river otters translocated to the Provo River in Utah from November 2009 through January 2012 were included.

Fig. 1


1.0
0.8
0.6
0.4
0.2
0.0
Probability of Survival
0
20
40
60
80
100
120
Body Mass^2 (kg)

CHAPTER 2: DIET OF THE NORTHERN RIVER OTTER (*LONTRA CANADENSIS)* ACROSS MULTIPLE HABITAT TYPES: SEASONAL VARIATION AND PREY SELECTION

ABSTRACT

The northern river otter is a semi-aquatic carnivore whose native range extends throughout North America. The diet of the otter has been studied throughout much of its range and across many different habitat types. Few studies however, have provided information on otter diet in diverse mountain stream systems, nor on prey selection based on prey abundance estimates. The purpose of this study was to examine the diet of a reintroduced population of otters in a diverse Rocky Mountain stream system of northern Utah. We determined the composition, seasonal variation, and prey selection in otter diet. We predicted that diet would vary among seasons, particularly with the increase in crayfish availability during the summer months. We further predicted that otters would take prey according to abundance and in inverse proportion to swimming ability. We surveyed latrine sites monthly from February 2010 through February 2012 on the Provo River, Utah. We reported otter prey as frequency of occurrence in scats, recorded as a percentage. Fish was the primary class of prey taken by otters (96.5%), followed by malacostracans (16.9%). Among families, otter diet was mostly comprised of Salmonidae and Cottidae, the two families that dominate the main channel fish community. Otter diet varied among seasons for nearly all classes ($G = 127.8$, d. f. = 24, $P < 0.001$) and families ($G = 132.94$, d. f. = 18, $P < 0.001$) of prey. In particular, fish occurrence was lower during the summer than during other seasons ($P \leq 0.05$), while crustacean (crayfish) occurrence was higher ($X^2 = 83.4$, $P < 0.001$). At the family level, occurrence of Salmonidae was greatest during fall ($X^2 = 15.5$, $P < 0.001$). Otters appeared to select prey based on habitat, as

composition of otter diet correlated more closely with the river main channel than the river side channels according to Bray-Curtis similarity results between composition of diet and habitat. Reservoir species appeared to be selected against, except for crayfish which made seasonally significant contributions to otter diet. When based on the composition of the main channel, we found otters to select for prey in proportion to its abundance and in inverse proportion to its swimming ability. However, the complexity of habitat types and varying prey communities in the Provo River made it difficult to determine specific mechanisms behind otter prey selection. Without behavior data to reveal specifically where otters are foraging, it may be impossible to determine which prey items otters are selectively preying on or avoiding.

INTRODUCTION

The northern river otter (*Lontra canadensis*, hereafter otter) is a nocturnal (Martin et al. 2010) semi-aquatic predator whose original range extended across the United States and Canada from the Pacific Ocean to the Atlantic (Hall 1981, Polechla 1988, Melquist et al. 2003). During the 19th and 20th centuries, the otter experienced a severe range contraction that continued until the 1970's (Deems and Pursley 1978, Melquist et al. 2003). At that time, a concerted effort began across the United States to restore the otter to its once native range. From 1976 to 2012, at least 22 states conducted reintroduction programs for river otters (Raesly 2001), which subsequently led to an increase in research. In particular, the number of studies published on otter diet dramatically increased in the 1980's and continued into the 2000's (Day et al. *In review*).

The diet of the otter has been studied extensively and in many different habitat types. Specifically, otters have been studied in both the Pacific and Atlantic coasts (Larsen 1984, Bowyer et al. 1994, Cote et al. 2008, Penland and Black 2009, Guertin et al. 2010), eastern temperate forests (Wilson 1954, Hamilton 1961, Knudsen and Hale 1968, Tumlison and Karnes 1987, Serfass et al. 1990), boreal forests (Gilbert and Nancekivell 1982, Reid et al. 1994), pacific forests (Toweill 1974), great plains (Stearns and Serfass 2011), southern marshes (Chabreck 1982), and western mountain ranges (Greer 1955, Melquist and Hornocker 1983, Manning 1990). Relatively few studies have been conducted in diverse Rocky Mountain stream systems (Melquist and Hornocker 1983, Mack 1985, Mack et al. 1994), particularly with a reintroduced population of otters (Findlay 1992). Results from these studies have been inconsistent as Catostomidae, Cyprinidae, and Salmonidae have each been reported as the most commonly taken family of prey. Therefore, we do not have an adequate understanding of food habits of otters in the Rocky Mountains.

Seasonal variation in otter diet has been examined by some in an effort to understand the mechanisms behind otter prey selection and diet preferences (e.g. Grenfell 1974, Pierce 1979, Serfass 1984, Route and Peterson 1988, Lizotte and Kennedy 1997). As seasons change, often the habitat and the wildlife community undergo changes that can alter the abundance and/or presence of prey availability. For example, crayfish and amphibians may burrow or hibernate during colder or drier months, and are thus less available to otters as prey items (MacArthur and Dandy 1982, Hamr and Sinclair 1985, Irwin et al. 1999). Likewise, changes in habitat such as seasonal ice cover or flooding can alter availability of habitat and influence the richness and diversity of available prey species (Tumlison and Karnes 1987). Otter diet can also vary with the seasonal migrations of potential prey. For example, otters may take more cutthroat trout and Kokanee salmon during spawning seasons in Yellowstone Lake and the Payette River, Idaho, respectively (Melquist and Hornocker 1983, Crait and Ben-David 2006). Therefore, if the diet of otters fails to fluctuate with the patterns and/or availability of its prey, then it can be assumed that they are preferentially selecting for certain prey items. However, otter diet does tend to fluctuate with seasons. In particular, levels of fish and crayfish in otter scats often fluctuate from summer to winter (Tumlison and Karnes 1987, Miller 1992, Noordhuis 2002, Roberts 2008). At more specific taxonomic levels, there are often significant differences between families of fish across seasons (Greer 1955, Sheldon and Toll 1964, Anderson and Woolf 1987, McDonald 1989, Reid et al. 1994, Cogliano 2003, Roberts 2003, Roberts 2008, Wengeler et al. 2010). Yet despite having considerable seasonal data for otter diet, many of the mechanisms behind what drives that temporal variation are still not well understood.

Understanding the preferences of predators for particular prey items, as well as the mechanism behind those preferences, aids in understanding and predicting predator ecology and trophic cascades. A prevailing notion is that otters take prey according to their abundance and in inverse proportion to their swimming ability (Ryder 1955). While some have shown otters to be opportunistic, flexible predators that will prey switch based on season and availability of prey (Quinlan 1983, Dubuc 1987, Noordhuis 2002, Roberts 2008), many that have examined diet of otters have only speculated on what prey items otters were selecting. A relative few have utilized actual abundance data to determine the significance of such preferences. When availability data were available, results of prey selection have been mixed ranging from little or no selection, to strong selection for and against various prey types (Griess 1987, Crait and Ben-David 2006). Centrarchids and crayfish were selected for in western New York, Catostomids were selected for and Salmonids selected against in Colorado, and Catostomids and Centrarchids were selected for in eastern Virginia (Mack 1985, Cogliano 2003, Skyer 2006). Taken together, the complexity of various habitat types and composition of prey communities make it difficult to produce a model of prey selection that fit otters across their range. The parameters of the initial theory that otters take prey according to abundance and agility (Ryder 1955) have since been widened to include habitat of the prey, time of day of foraging, fish spawning, ice cover, variable water levels, and fishing methods of otters (Sheldon and Toll 1964). The most appropriate way to test these ideas and produce a model, however, is to use prey abundance data measured against these other variables to determine what does or does not influence an otter when selecting its prey, a method that has been used sparingly in the literature.

Our objective was to examine the diet of a reintroduced population of otters in a study area mixed with both lentic and lotic habitats in a rocky mountain system. We investigated not only what otters were eating and in what proportions, but how proportions varied by season in a landscape that undergoes dramatic changes as reservoirs freeze seasonally and water levels in the system fluctuate drastically between spring (i.e. snow melt) and late summer. To understand potential mechanisms of food habits, we tested for selective foraging by comparing the abundance of prey items found in otter scat to estimated prey abundance data. We predicted that otter diet would vary by season, particularly with the increase in availability of crayfish during the summer months when lentic habitats were more accessible. We further predicted that otters would select for fish in proportion to their abundance and in inverse proportion to their swimming ability, thereby selecting against more agile prey (e.g. Salmonidae, Centrarchidae).

METHODS

Study area

Our study area included a 64km portion of the Provo River and its tributaries in north-central Utah along the Wasatch Range at the intersection of the Great Basin and the Rocky Mountains (Figure 1). The Heber Valley region in which the river is located has an annual average temperature of 8.1°C with an average of 19.2°C in the summer and -3.3°C in the winter.

The region has an annual average precipitation of 412.0mm, which is mostly comprised of snow from late fall to early spring (National Oceanic and Atmospheric Administration 2000). The headwaters of the Provo River are located in the Uintah Mountains, roughly 32 linear kilometers northwest of the upper end of our study site, and ends in Utah Lake after dropping approximately 1,660 meters in elevation. The Provo River has a drainage area of 1,823 km^2 and an average annual discharge of roughly $0.18km^3$ (Billman et al. *In press*). Within the study area, the river channel itself is twice interrupted by large dams and reservoirs, namely Deer Creek Reservoir and Jordanelle Reservoir. Both reservoirs are consistently iced over from December through March/April. They are also popular destinations for fishing and recreation, and are home to a number of fish families, including Centrarchidae, Catostomidae, Cyprinidae, Ictaluridae, Percidae, and Salmonidae (Nielson and Slater 2008). Crayfish (Cambaridae) are also present in the reservoirs. Within our study area the river runs through several small towns and agricultural areas above Deer Creek Reservoir, and through a narrow canyon for approximately 16 kilometers below the Deer Creek Dam. Fish composition in the main river channel consists primarily of members of the families Salmonidae and Cottidae, with families Catostomidae and Cyprinidae inhabiting side channels and backwater areas (Billman et al. *In press*). These areas are recognized for their Blue Ribbon fisheries (Utah Division of Wildlife Resources 2012) and recreational opportunities. Terrestrial vegetation along the shores of the reservoirs is sparse, while along the river channel it consists mostly of Fremont cottonwood (*Populus fremontii*), willows (*Salix* spp.), red osier dogwood (*Cornus cericea*), and various grasses.

From 1999 to 2008, the Utah Reclamation Mitigation and Conservation Commission conducted the Provo River Restoration Project (PRRP) to restore 14 kilometers of the river within our study area (Utah Reclamation Mitigation and Conservation Comission 2007), effectively increasing the diversity of flora and fauna within our study area. As a culmination to this restoration the Utah Division of Wildlife Resources planned an otter reintroduction to the Provo River. Accordingly, in the fall of 2009, a reintroduction began with the transplanting of radiomarked otters from the Green River in northeastern Utah and Idaho to the Provo River near Heber, UT, with releases continuing through 2011. Each otter that was released in the Provo River underwent surgery to have a VHF radio-transmitter (Advanced Telemetry Systems, Inc.) placed in the peritoneal cavity (For detailed trapping and surgical methods, see Day et al. *In review*).

Latrine surveys

We initially surveyed for latrine sites by walking the banks of our study area. When we discovered a latrine site, any fresh otter scat was collected. We identified otter scat from that of other species by its size, shape, odor, contents, and the presence of mucous (Greer 1955). Fresh scat was identified by a soft, wet appearance and more pungent odor. We then recorded a GPS location and cleared the site of any remaining scat. We picked up and stored scat using individual plastic bags which were then sealed to avoid cross-contamination, labeling each bag with the date and site of collection. We stored scats at -12°C until they were processed.

After the initial river bank survey, we continued to search for and locate latrine sites via radio-telemetry of otters from February 2010 through February 2012. After the first group of otters was released in the fall of 2009, we monitored the population by searching our entire study area 2-3 times per week. We used an omnidirectional whip antenna mounted on our vehicle to conduct general scans with an R-1000 telemetry receiver (Communication Specialists, Inc.). Once an otter was located, we recorded several azimuths using a 3-element Yagi folding antenna from both sides of the river in order to triangulate its location. When we found an otter to be in the same general location on several occasions, we walked in to pinpoint the position of the otter and to search for latrine sites. The majority of our sites were found in this manner. After we found a latrine, we cleared all scat and monitored it on a monthly basis for three months. If no scat was found again within those three months we discontinued the monitoring of that site. If scat was found in the initial three months we continued to monitor the latrine site monthly for the duration of the study, regardless of the amount of time that passed between uses.

Scat washing and processing

We placed collected scats in a 2-layer pouch of fine nylon mesh fabric with a laminated number and sealed it with a plastic cable tie. We then soaked the pouch in a mixture of water and laundry detergent for at least one hour to break up the scat fragments and mucilaginous material (Bowyer et al. 1994, Cogliano 2003). After they had soaked, we ran the scat through a single cycle on a Whirlpool Thintwin washing machine and allowed them to air-dry for 24 hours. We then transferred each scat to a plastic dram vial labeled with the scat number, site, and date of collection. We subsequently spread individual scat contents across a gridded petri dish and examined them under a dissecting scope (Leica EZ4HD) for identification.

We identified prey items to class (excluding mollusks and bivalves), and fish prey were identified to family whenever possible. We identified fish scales using a dichotomous key provided by Lagler (1947), as well as a guide to the vertebrae of Utah fish families (Findlay 1992). We also created a scale and vertebra reference collection by collecting samples of each species of fish that occurred in our study area by gill-netting both reservoirs, electro-shocking 3 100-meter stretches of river channel, and placing baited minnow traps in backwater sloughs. Once collected, we removed 10 scales at equidistant locations both above and below the lateral line from at least 4 individuals of various sizes of each species. We then mounted these scales to microscope slides for comparison to prey items that we extracted from scat. We also dissected fish from each family and removed and cleaned their vertebrae for comparison purposes, as some fish in the Provo River watershed lack scales (Cottidae, Ictaluridae). As the scales of the common carp (*Cyprinus carpio*) were difficult to distinguish from the Utah sucker (*Catostomus ardens*), we included carp in the family Catostomidae. We used various texts to aid in identification of remains from other prey classes (Aves, Mammalia, Reptilia, etc.) (Romer 1968, Hildebrand 1988, Pough et al. 2004, Gill 2007, Saxena and Saxena 2008). As we analyzed prey remains, we removed and stored samples of any items used to positively identify prey for future reference and comparison. In the case that a scale or vertebra was unidentifiable, we recorded images of the items for future consultation and analysis. We entered all identified prey items into a Microsoft Access database along with the latrine site number, date of collection, and any additional notes needed for further review (e.g. foreign objects, problems with identification).

Data analysis

We recorded all prey items as a frequency of occurrence (number of scat samples containing a given prey item divided by total number of samples; Day et al. *In review*), reported as a percentage. As scats were collected monthly, we assigned each of them to one of the four seasons as defined by the Gregorian calendar (mid-March through mid-June for spring, mid-June through mid-September for summer, etc.) for temporal analysis. We used a G-test to determine whether the proportional composition of overall diet varied among seasons, as well as which of the four seasons varied from one another ($\alpha = 0.05$). We used chi square analysis ($\alpha = 0.05$) to determine which prey items varied in composition among seasons. We performed two-tailed proportional z-tests to determine which seasons varied significantly from the mean for each prey taxon, as well as which seasons differed from each other individually. We used a G-test as well as the Bray-Curtis similarity index (Bray and Curtis 1957) to compare composition of diet to availability in various habitats using electroshocking data collected by the Utah Division of Wildlife Resources for the main channel (Nielson and Slater 2008), and snorkeling data conducted by Billman et al. (*In press*) for the side channels. To conduct these analyses, we converted our data to relative percent occurrence (number of scats containing a certain prey item divided by the total number of prey items recorded among all scats (Tumlison 1986)) converted to whole numbers. Additionally, we used pooled z-tests to compare our results to these datasets to determine if otters selectively forage. To estimate fish agility we used the speed tables at fishbase.org (Froese and Pauly 2012).

RESULTS

Scat collection

We collected 943 scats from 23 different latrine sites along the Provo River and its tributaries from February 2010 through January 2012 (Table 1). Despite our searches, we found no latrine sites along the banks of the reservoirs. We collected and analyzed scat monthly for 24 concurrent months except for March of our first year of sampling. The amount of scat that was present at latrines varied by season ($G = 292$, $P < 0.001$), as we collected 98 scats in the spring , 119 in the summer, 356 in the fall, and 370 in the winter. We found that scats were better preserved during the colder months when a permanent snowpack protected them from human and animal traffic, weather, exposure, etc. We collected 463 scats through the first year of sampling, and 480 during the second year.

Composition of prey

The mean number of fish families recorded per scat that contained fish was 1.39 (*SE* ± 0.020), with a range of 1 to 6. The mean number of prey classes per scat was 1.70 (*SE* ± 0.023) and ranged from 1 to 5. Mean number of prey items per scat (fish family or prey class) was 3.06 (*SE* ± 0.032) with a range of 1 to 7.

Diet varied among prey classes ($G = 3306$, $P < 0.001$) and was dominated by fish (97.5%). This was followed by insect at 44.8%, although the vast majority of instances of insect were in trace amounts, likely due to secondary or incidental ingestion (Lagler and Ostenson 1942). A literal few scats were composed primarily of insect parts. The only other prey class that appeared in more than 5 percent of total scats was Malacostraca, crayfish being the only member of that class to appear in otter scats at 12.2%. However, the mean seasonal percent occurrence of crayfish in otter diet was 16.9%, as summer scats were underrepresented when compared to other seasons ($G = -303.9$, $P < 0.001$). Other prey classes that were present in less than five percent of total scats in order of frequency of occurrence were mollusks (trace amounts), reptiles, mammals, birds, bivalves (trace amounts), and amphibians.

Diet varied among fish families ($G = 1656$, $P < 0.001$). Diet was comprised of Salmonidae (69.5%) more than of any other family. This was followed by mottled sculpin (*Cottus bairdii*, Cottidae) at 30.4%, which is the only other family along with Salmonidae that dominates the main channel of the Provo River. Other fish families that made up significant portions of otter diet included Catostomidae (17.6%) and Cyprinidae (8.2%). Interestingly, Centrarchids (1.6%) and Percids (2.5%), which occur mainly in the reservoirs and in ample numbers, made very little contribution to otter diet.

Seasonal variation

Otter diet varied seasonally both at the prey class level ($G = 127.8$, d. f. = 24, $P < 0.001$, Figure 2), and at the fish family level ($G = 132.94$, d. f. = 18, $P < 0.001$, Figure 3). In addition to this overall temporal variation, each season varied from every other season at both the class and family levels (d. f. = 8, $P \leq 0.05$). Several individual classes also varied by season (d. f. = 3, $P \leq 0.05$, Table 1, Figure 2) including Crustacea ($X^2 = 83.4$, $P < 0.001$), which increased drastically during the summer, Reptilia ($X^2 = 35.1$, $P \leq 0.001$), which also increased during summer, and Aves ($X^2 = 9.3$, $P = 0.026$), which peaked during spring (Figure 2). Fish occurrence in the summer was lower when compared with any other season ($P \leq 0.05$). Seasonal variation also occurred at the individual family level ($P \leq 0.05$, d. f. = 3, Table 1, Figure 3). Catostomidae ($X^2 = 59.7$, $P \leq 0.001$) and Cyprinidae ($X^2 = 18.8$, $P \leq 0.001$) both displayed peaks during the winter months, while Cottidae ($X^2 = 18.8$, $P \leq 0.001$) and Percidae ($X^2 = 14.0$, $P = 0.003$) saw peaks during the spring. Occurrence of Salmonidae ($X^2 = 15.5$, $P < 0.001$), the most common family of fish in the system, rose significantly during the fall (Figure 3).

Prey selection

When we compared the composition of otter diet on the Provo River to the availability of prey in the main channel and side channels of the river (Table 2), the G statistic for each habitat type was significant (d.f. = 6, $P < 0.001$, $G = 1163.4, 3402.1$ for main channel and side channel, respectively). Both tests displayed a significant level of difference ($\alpha = 0.05$) between otter diet and fish community composition, though the main channel composition correlated better than the side channels (Figure 4). We did not have reliable data for relative abundances of fish species in Deer Creek Reservoir nor Jordanelle Reservoir. The high level of independence of variables in the side channels may be due to high availability of Cyprinids (67.7%) relative to occurrence in otter diet (6.3%), and lower availability of Salmonids (25.1%) and Cottids (0.2%) relative to occurrence in diet (53.3% and 23.3%, respectively). Prey abundance in the main channels was likewise different from that of diet composition. Percent occurrence of Cyprinidae was much higher (6.3%) than sampling of the main channel would predict (0.4%), however, this difference may have been less stark were reservoir densities able to be included in the analysis. The main channel dataset showed percent occurrence of Salmonidae (53.3%) was lower than sampling of the main channel would predict (74.1%). Based on the fact that otter diet correlated better with the main channel prey abundances, it is possible that otters were selecting for Catostomidae ($X^2 = 1685.8$, $P < 0.001$) and Cyprinidae ($X^2 = 720.2$, $P < 0.001$), against Salmonidae ($X^2 = 54.7$, $P < 0.001$), and selecting Cottidae according to its abundance ($X^2 = 0.60$, $P = 0.44$). It is important to note, however, that electro-shocking data often underestimates Cottid densities (J. Nielson, *pers. comm.*); therefore, otters were potentially selecting against Cottidae as well. Were we able to include reservoir abundances, however, the strength of these results would likely be weakened in each case, as the reservoirs are abundant in Catostomidae and Cyprinidae, and less dominated by Salmonidae.

DISCUSSION

Diet composition

Fish was the most dominant class of prey in the overall diet of otters on the Provo River (Table 1). This finding is consistent with previous reports on otter diet (Wilson 1954, Greer 1955, Knudsen and Hale 1968, Melquist and Hornocker 1983, Penland and Black 2009). Fish were followed in abundance in otter diet by crustaceans, which in the diet of otters on the Provo River were represented solely by crayfish (Cambaridae spp.). Again, this is consistent with previous reports on otter diet, particularly in studies conducted in western North America (Toweill 1974, Christensen 1984). In the Provo River watershed, crayfish are only available in the reservoirs, which make up a small portion of the total habitat available to otters. In the eastern United States, where crayfish are available year-round and in both lotic and lentic habitat, crayfish were the most commonly found prey item of otters (Pierce 1979, Tumlison and Karnes 1987, Noordhuis 2002, Beverly and Elliott 2006, Roberts 2008). In Arizona crayfish were reported to be the most common prey item of otters in a system that had been heavily invaded by exotic crayfish (*Orconectes* spp.) (Taylor et al. 2003). The only other prey class that made up a significant portion of otter diet (> 5%) was insect. The majority of instances of insects, however, were in trace amounts and probably due to secondary or incidental ingestion.

At the family level the most abundant families in the main channel of the Provo River, Salmonidae and Cottidae, dominated the composition of fish in otter diet (Table 1). These two families have rarely been reported in the literature as the main components of otter diet, though this is probably due to so few studies having been conducted in similar habitat (Melquist and Hornocker 1983, Mack 1985, Mack et al. 1994). This results lends support to the notion that otters are opportunistic predators, taking prey according to their abundance (Ryder 1955), although these otters certainly spent time foraging in the reservoir habitat as evidenced by the amount of crayfish in their summer diet. Other fish families, Catostomidae and Cyprinidae, made up significant portions of otter diet (> 5%) as well, and occurred in greater numbers in habitats other than the main channel (i.e. side channels, reservoirs). Catostomidae, which for identification purposes included the common carp (*Cyprinus carpio*), was more abundant in the reservoirs, while Cyprinidae was more abundant in the side channels. These two families were not well-represented in otter diet, which may suggest that otters on the Provo River preferred to forage in the main channel habitat over side channels or reservoirs. This notion is further supported by the results that Centrarchidae and Percidae, families exclusive to the reservoirs, contributed little to the diet composition of otters (1.6% and 2.5%, respectively). This is particularly relevant as Centrarchidae has often been found to be the most commonly taken family of prey (Lauhachinda 1977, Lauhachinda 1978, Pierce 1979, Cooley 1983, Tumlison and Karnes 1987, McDonald 1989, Lizotte and Kennedy 1997, Cogliano 2003), which may lend support to the idea that in the Provo River otters avoided foraging in the reservoirs. The exception appears to be Cambaridae (crayfish), which were found only in the reservoirs and made up 12% of total otter diet, and 41% of otter diet in the summer. It is likely, therefore, that during the summer months, otters did forage in the reservoirs to select for Cambaridae over other lake-dwelling prey.

Seasonal variation

Birds, crustaceans, and bivalves, were the only prey classes that displayed overall seasonal variation (Table 1). However, variation between individual seasons occurred for nearly all prey classes (Figure 3). Fish contributed significantly less to otter diet in the summer when compared to any other season, dropping from ~99% to 88%. This result is likely due to the increased availability of other classes of prey during the summer (e.g. crustaceans, reptiles). During the summer, crayfish may be less active or migrate to habitat less available to otters (Armitage et al. 1972, Flint 1977). Crayfish also are found exclusively in the reservoirs along the Provo River watershed; therefore, they are more available in the open waters of summer. This pattern of a tradeoff between fish and crayfish consumption in the summer is common throughout the otter's range, and in several instances the percent occurrence of crayfish is higher than that of fish (Berg 1999, Cogliano 2003, Skyer 2006). Reptiles also displayed a significant increase in percent occurrence during the summer months when they are most available, from ~1% in spring, winter, and fall, to 11% in the summer. Likewise, birds were taken as prey more often in the spring, likely correlating with the rearing of waterfowl chicks. Otters have been known to predate heavily on nesting birds (Hayward 1975, Footit 1977, Quinlan 1983, Speich and Pitman 1984), and young waterfowl chicks may similarly be easy prey for otters. These examples give further support to the idea that otters are opportunistic, and will take prey as it becomes available. In the Provo River, this could mean a change in method and location of foraging.

Otter diet also displayed seasonal variation among nearly all fish families. Some of these changes may be due to changes in habitat on the Provo River. For example, Deer Creek and Jordanelle Reservoirs are generally frozen from December through March. This may be the cause of the increase in Catostomidae during the winter months, as these fish may be migrating toward the mouth of the river to feed on primary production, thus making them more available to otters and in higher densities. Physiological and life history cycles may also influence the seasonal percent occurrence of various fish families. For example, percent occurrence of Salmonidae was particularly high during the fall, possibly correlating with spawning season of brown trout (*Salmo trutta*) and mountain whitefish (*Prosopium williamsoni*) when these fish become lethargic and emaciated while devoting most of their energy to the spawn. This would make trout and whitefish, generally very agile species, potentially easier prey for otters. Melquist and Hornocker (1983) found similarly elevated levels of Salmonidae in both the fall and winter months, and noted that otters were less likely to move during the Kokanee salmon spawning run. Likewise, Cottid consumption was higher in the spring during their spawning season than it was during summer or winter. Consumption of Cottidae was also greater in the fall, a possible byproduct of otters foraging for spawning Salmonids in the same habitat occupied by Cottids.

Prey selection

Prey selection by otters can be difficult to determine in a system with widely varying habitat types, particularly when the prey community in each habitat varies by richness and diversity. Our results indicate that otters in the Provo River likely spent more time foraging in the main channel than in the side channels or reservoirs (Table 2, Figure 4). Regardless, composition of otter diet was significantly different from the fish composition of either the main channel or side channels. The side channels contained high densities of Cyprinidae and Salmonidae, while the main channel was nearly void of Cyprinidae and was dominated by Salmonidae and Cottidae, much like otter diet. Furthermore, while we were unable to estimate abundances in the reservoirs, families exclusive to the reservoirs (e.g. Centrarchidae, Ictaluridae, and Percidae) made minor contributions to otter diet. Only Cambaridae was commonly present in otter scat, likely a result of otters selectively foraging for crayfish and against reservoir fish species during the summer. These results likely indicate, along with low percent occurrences of Catostomidae and Cyprinidae, that most of the otters' time was spent foraging in the main channel, except when foraging for crayfish. Alternatively, it is possible that latrines existed along the reservoirs but went undetected despite our efforts to locate them, and so recovered scats from river latrines were only composed of main channel species. These findings are particularly relevant as 18 different studies have found otters to prey on Centrarchidae, which only occur in the reservoirs in our system, more than any other family of fish.

Our results lend some support to the hypothesis that, in the case of the main channel community composition only, otters take prey according to their abundance and in inverse proportion to their swimming ability (Ryder 1955). This may be most apparent for Salmonidae and Centrarchidae, which have relatively high burst speeds, meaning good escapability. When the relative percent occurrence of Salmonidae in otter diet was compared to the relative abundance of Salmonidae in the main channel, otters were found to select against this family. And while otters were found to select for Centrarchidae when compared to main channel relative abundances, their low percentage indicates that even when foraging in reservoirs for crayfish otters were not selecting for Centrarchidae. Some of our results do not, however, support the above hypothesis. For example, the only species of Cottidae in the Provo River is mottled sculpin (*Cottus bairdii*), a relatively slow-moving and sedentary fish found on river floors (Etnier and Starnes 1993). We would predict, therefore, that otters would select for this slow-moving species, but we found them selected in proportion to their abundance. Furthermore, with Cottid densities often underestimated by electroshocking, it is possible that otters selected against Cottidae. This may provide evidence for the hypothesis that habitat of prey is also an important factor for otters when selecting prey species (Sheldon and Toll 1964). If otters are unable to locate or detect mottled sculpin due to their habitat, then they will most likely be under-represented in otter diet. Likewise, Cyprinids were found in great abundance in the side channel habitat of the Provo River, but were found in very low percentages in otter diet. Again, a slow-moving family of fish that is under-represented, possibly because their habitat is not conducive to otter foraging.

While we do agree that there may be a relationship between otter diet and prey abundance and agility, we contend that there are several other factors involved that influence the selection of prey and the ability to analyze prey selection data. Our conclusions, for example, are highly dependent upon the habitat in which otters are foraging. In addition, changes in otter habitat (i.e. flooding, icing) can limit or expand otters' available forage (e.g. crayfish). Life history cycles of prey may also influence prey selection, as otters selected for Salmonidae (brown trout, *Salmo trutta*; mountain whitefish,) during spawning season. Furthermore, density of prey, habitat, and palatability of prey can influence otter prey selection. For example, otters have been known to inhabit lakes with lake trout, though lake trout made up very little of their diet, possibly because lake trout prefer habitat deeper than otters are willing to forage (Crait and Ben-David 2006). Conversely, fish species occurring in high densities could possibly be selected for by otters more than groups of the same species in lower densities. Fish in high densities could be selected for by otters that use cooperative foraging to prey on schools of fish (Blundell et al. 2002). There are likely other factors as well that influence prey selection of otters, and predicting what effect a population of otters may have on individual prey species may prove quite complicated. To compound these issues, multiple habitat types and varying prey communities spread throughout the range of a population of otters makes prey selection difficult to determine. In our case, for example, each of our three habitat types (river main channel, river side channel, reservoir) have distinctly different prey communities. While we were able to estimate relative abundances for two of these habitat types, testing for prey selection by otters proves complicated without specific knowledge of where otters are foraging. While we were able to make inferences as to foraging locations based on diet composition (presence of crayfish indicated selective foraging in reservoirs, lack of Cyprinidae in diet indicated avoidance of side channels), the actual selectivity numbers become blurred as otters are likely foraging somewhat across all three habitat types. The complexity in aquatic habitat and prey communities may very well account for the inconsistencies in prey selection thus far reported in the literature. Selection in one habitat type in one study area may be influenced by factors that are non-existent in a similar study with different habitat and thus a different prey community. While some general principles may apply, realizing the application of those principles across such complex habitat is daunting at best. Therefore, it would be prudent for future research on otter prey selection to be conducted in areas of uniform habitat and prey composition, thus minimizing the complexity of dealing with multiple prey communities. In addition, due to the difficulty of predicting the prey selection of otters, we urge managers to use caution when translocating and/or reintroducing otters to areas devoid of them. We further encourage the implementation of prey community monitoring programs to gauge the impacts of otters on their fisheries and/or ecosystems.

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Table 1 - Percent occurrence of prey items of northern river otters in the Provo River in northern Utah from February 2010 through February 2012. Asterisks indicate significance in overall seasonal variation. (*P < 0.05, **P < 0.01).

Prey	Spring	Summer	Fall	Winter	Total	Seasonal Mean
Fish	100.0	88.2	98.3	99.5	97.5	96.5
Catostomidae**	18.4	16.0	5.6	29.5	17.6	17.4
Centrarchidae	3.1	1.7	2.0	0.8	1.6	1.9
Cottidae*	45.9	25.2	35.7	23.0	30.4	32.4
Cyprinidae*	8.2	10.9	3.1	12.2	8.2	8.6
Ictaluridae	1.0	0.8	0.3	0.5	0.5	0.7
Percidae*	7.1	1.7	3.7	0.5	2.5	3.3
Salmonidae*	55.1	57.1	80.1	67.0	69.5	64.8
Coregoninae	12.2	5.9	10.4	11.4	10.4	10.0
Salmoninae*	40.8	43.7	65.4	54.3	55.8	51.1
Amphibians	0.0	0.8	0.3	0.5	0.4	0.4
Birds*	6.1	0.8	1.4	1.6	1.9	2.5
Bivalves	4.1	2.5	1.1	0.5	1.4	2.1
Crustaceans**	11.2	41.2	10.1	5.1	12.2	16.9
Insects	57.1	47.9	41.6	53.8	48.8	50.1
Mammals	0.0	4.2	2.2	2.2	2.2	2.2
Reptiles**	0.0	10.9	0.8	1.4	2.2	3.3
Mollusks	4.1	8.4	4.2	1.9	3.8	4.6
Sample Size	98	119	356	370	943	

Table 2 - Percent abundances of fish families found in 2 habitat types on the Provo River, Utah, as well as relative percent occurrence of prey composition in otter diet on the Provo River. Main channel abundances were determined by electroshocking in 2009, side channel abundances were determined by snorkeling in 2009, and otter diet was determined by gross fecal analysis from 2010 to 2012.

	Catostomidae	Centrarchidae	Cottidae	Cyprinidae	Ictaluridae	Percidae	Salmonidae
Main Channel	0.89	0.00	24.58	0.45	0.00	0.00	74.07
Side Channels	7.03	0.00	0.15	67.70	0.00	0.00	25.13
Otter Diet	13.51	1.23	23.33	6.29	0.38	1.92	53.34

LIST OF FIGURES

Figure 1 - Map of the portion of the Provo River included in our study. Latrine sites (marked with dark circles) were located and monitored monthly from February 2010 through February 2012.

Figure 2 - Seasonal variation in prey composition by class presented as percent occurrence of northern river otter diet from February 2010 through February 2012. Bars sharing the same letter are not statistically different ($P \leq 0.05$).

Figure 3 - Seasonal variation in prey composition by family presented as percent occurrence of northern river otter diet from February 2010 through February 2012. Bars sharing the same letter are not statistically different ($P \leq 0.05$).

Figure 4 - Bray-Curtis similarity index on a 0 – 100 scale, measuring the similarity in composition between the river main and side channels, and the composition of otter diet. A score of 0 is when there is no similarity between samples, and 100 represents exact similarity. The Provo River channels were sampled in 2009, and otter diet was determined by gross fecal analysis from 2010 to 2012 in northern Utah.

Fig. 1

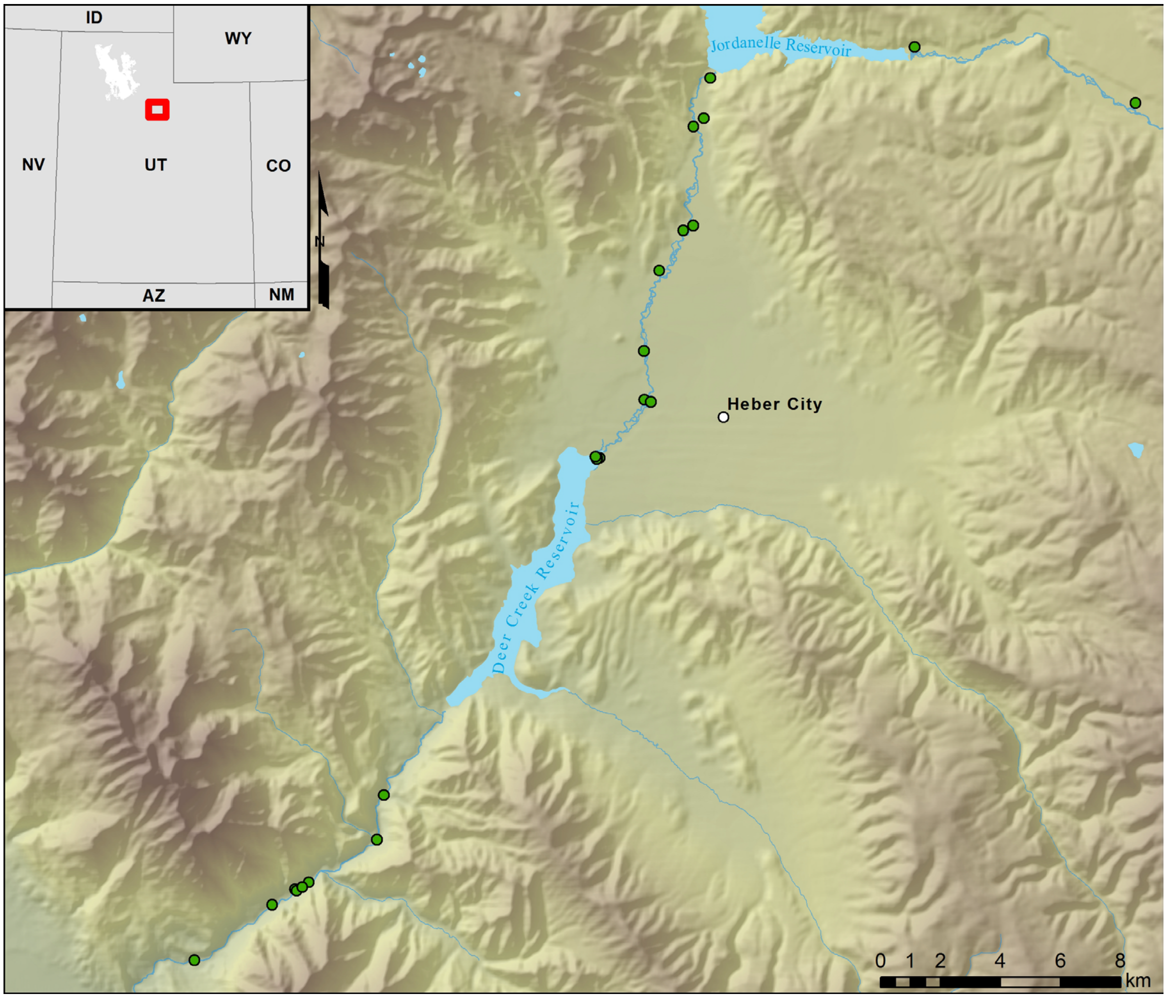
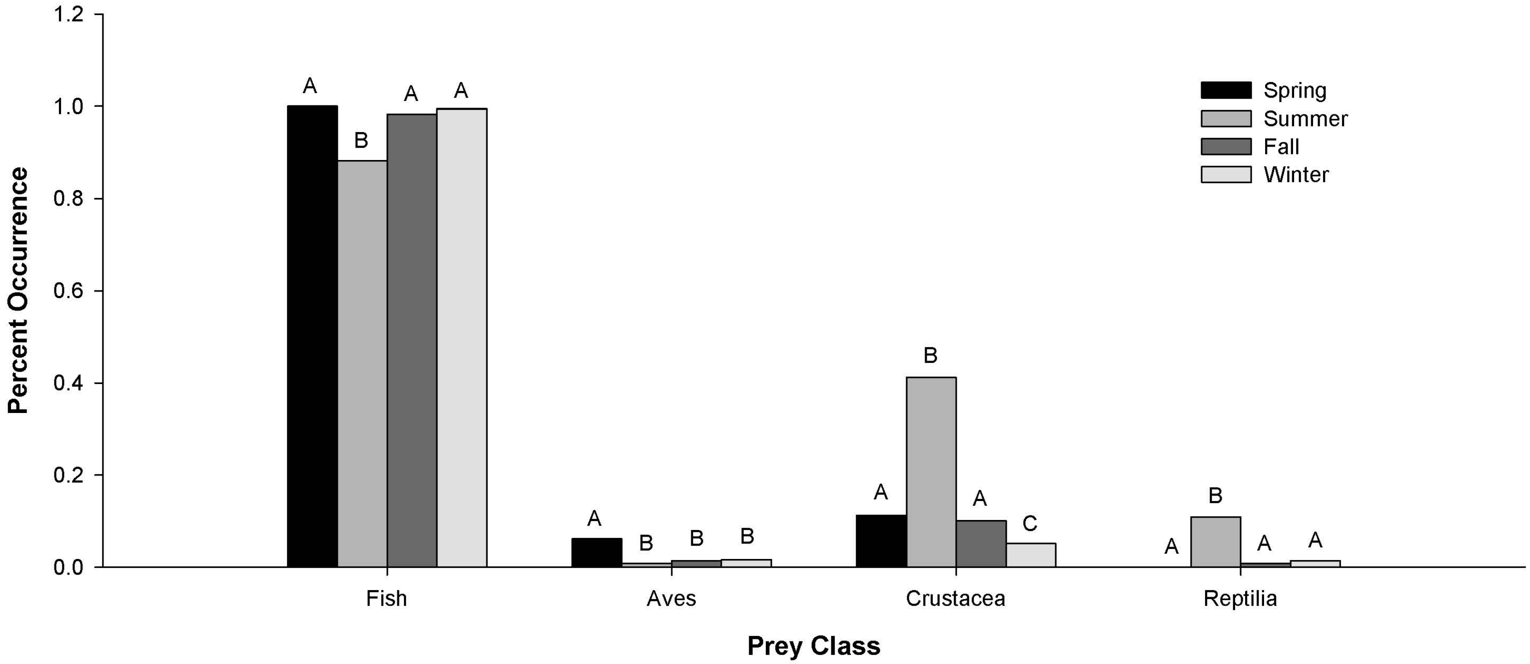
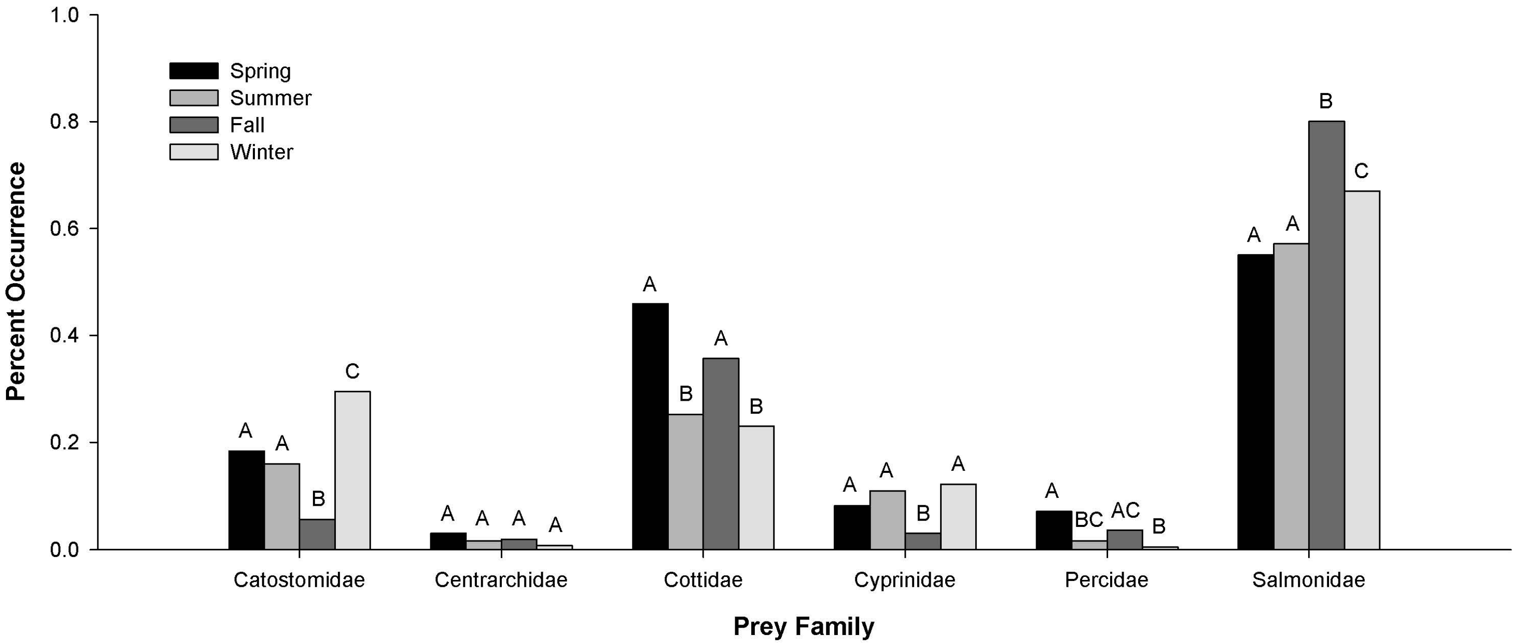

ID
WY
NV
UT
CO
AZ
NM
N
Jordanelle Reservoir
Heber City
Deer Creek Reservoir
0 1 2 4 6 8
km

Fig. 2



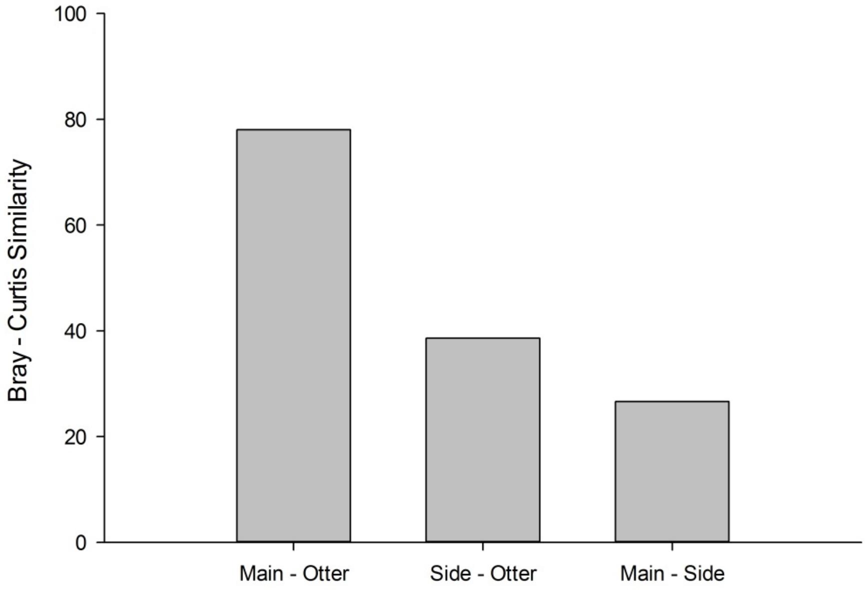
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Percent Occurrence
A
B
A
A
A
B
B
B
A
B
A
C
A
B
A
A
Spring
Summer
Fall
Winter
Fish
Aves
Crustacea
Reptilia
Prey Class

Fig. 3



1.0
0.8
0.6
0.4
0.2
0.0
Percent Occurrence
Spring
Summer
Fall
Winter
A
A
B
C
A
A
A
A
A
B
A
B
A
A
B
A
A
BC
AC
B
A
A
B
C
Catostomidae
Centrarchidae
Cottidae
Cyprinidae
Percidae
Salmonidae
Prey Family

Fig. 4



100
80
60
40
20
0
Bray - Curtis Similarity
Main - Otter
Side - Otter
Main - Side

CHAPTER 3: A SYNTHETIC REVIEW OF THE DIET OF THE NORTHERN RIVER OTTER (*LONTRA CANADENSIS*)

ABSTRACT

The diet of the northern river otter has been studied extensively throughout much of its range, though no comprehensive synthesis of otter diet has yet been produced. We examined 100 publications and 106 prey lists in order to determine the food habits of the northern river otter among ecoregions and seasons. Fish was found to occur in otter diet more often than any other class of prey, followed by malacostracans. Other classes that occurred in otter diet but at much lower levels include amphibians, birds, gastropods, insects, mammals, and reptiles. At the family level, Astacoidea contributed more to otter diet than any other family of prey. Fish families contributed a major portion to otter diet in at least one ecoregion include Catostomidae, Centrarchidae, Cottidae, Cyprinidae, Gasterosteidae, Ictaluridae, Percidae, Salmonidae, and Umbridae. Multiple classes and families varied by ecoregion and/or by season. Crayfish, while not the primary component of otter prey throughout North America, were found to be the primary component when readily available. We developed a model of river otter prey selection and what factors might have an impact on the availability of prey to otters. Otter prey selection is likely due to a multitude of factors, including the habitat, detectability, catchability, and palatability of prey.

INTRODUCTION

Diet is a fundamental component of the basic ecology of any species of wildlife. The dietary needs of an individual often dictate every aspect of that individual's life such as health, recruitment, habitat, daily activity patterns, foraging behavior, social behavior, daily movements, and seasonal migration. For example, 100% of winter diet of the sage-grouse (*Centrocercus* *urophasianus*) is composed of sagebrush (*Artemisia spp.*), and so their food habits confine them to living in areas with an ample sagebrush food supply (Wallestad and Eng 1975). Animals that pursue large prey, such as wolves (*Canis lupus*), maintain a social structure that optimizes the foraging efficiency of the individual (Nudds 1978), while black bears (*Ursus americanus*) benefit from solitary foraging of widely dispersed food (Rogers 1987). Mountain lions (*Puma concolor*) move great distances while hunting to maximize encounters with prey (Seidensticker et al. 1973), and humpback whales (*Megaptera novaeangliae*) migrate thousands of kilometers each year (Palsboll et al. 1997) to return to nutrient-rich waters that provide a necessary diet. Clearly, animals go to great lengths to maintain their food habits, yet they are hardly the only species affected by those food habits.

The diet of any species is part of a more complex food web, and can have a sizeable impact on the structure and function of its ecosystem. Therefore, a change in one species such as an increase or decrease in population size, an introduction or reintroduction, or a recolonization can alter the dynamics of many species in a system. These impacts have been shown to occur through both top-down and bottom-up mechanisms and can be brought about either artificially or naturally. For example, leaf beatles (Chrysomelidae) have been used for biological control of salt cedar (*Tamarix* spp.) based on their singular feeding habits (Dudley 2005). Walleye have also historically been stocked to control populations of yellow perch, which tend to breed aggressively in the absence of predators (Forney 1974). From a bottom-up perspective, Whittaker (1975) proposed that diversity among the primary producers fosters diversity at higher levels. One example is the invasion of cheatgrass (*Bromis tectorum*) reducing the diversity of arid plant communities, and thus limiting the diversity of small-mammal communities in the same ecosystem (Hall et al. 2009, Ostoja and Schupp 2009).

Trophic cascades are often more pronounced when initiated by an apex predator, usually having a broader impact on ecosystem structure and function than a similar change to a species at a lower trophic level (Estes et al. 1998). This is due to either direct effects on prey densities known as density-mediated cascades (Estes and Palmisano 1974) or indirect effects by altering prey behavior known as behaviorally-mediated cascades (Abrams 1984, Kauffman et al. 2010). Classic examples of these trophic cascades include the correlations between reintroduced wolves in Yellowstone and elk on various tree species (Ripple and Beschta 2007, Beschta and Ripple 2011), and the effect of the absence or presence of sea otters on kelp forests and sea urchins in coastal ecosystems (Estes and Palmisano 1974). In the latter example, both humans and orcas have served as the top predator that initiated the trophic cascade. As these cascades always begin with direct predation, an understanding of the apex predator's food habits is foundational to the ability to predict its impact on a system, particularly when that predator's demographics are in constant flux.

The northern river otter (*Lontra canadensis*) is a predator that has been widely managed in recent decades in an effort to restore otters to their native geographic range (Raesly 2001). It is likely that more reintroductions, translocations, and/or recolonizations of river otters are forthcoming, and a more clear understanding of patterns in otter food habits will be useful not only for managing the species, but working with the public to support conservation efforts. The river otter's current range extends latitudinally across North America and over many different habitat types, though it has still not been restored to pre-colonial levels (Melquist et al. 2003). The river otter inhabits both lentic and lotic areas in eutrophic and oligotrophic systems (Humphrey and Zinn 1982, Melquist and Hornocker 1983, Reid et al. 1994). It also inhabits coastal tributary areas, utilizing a much different prey base than it depends on further inland

(Testa et al. 1994, Cote et al. 2008b). It is difficult to accumulate a complete comprehension of the overall dietary habits of the northern river otter due to wide variation in prey composition, habitat types, elevations, and ecoregions.

Food habits of the river otter, have been widely investigated throughout their range (Greer 1955, Knudsen and Hale 1968, Loranger 1980, Bowyer et al. 1994, Noordhuis 2002). In addition, some have investigated concepts beyond basic diet such as how food habits vary seasonally (Grenfell 1974, Serfass 1984) and what preferences are exhibited in otter diet (Crait and Ben-David 2006, Stearns and Serfass 2011). Taken together, however, these papers do not yield the same conclusions about how river otters select their diet. Due to the variability among studies that provide only local results, it is difficult to gauge what prey species will be most affected by the presence of otters, and therefore how any given system will respond to changes in the density and behavior of those prey.

The purpose of this paper is to provide a quantitative synthesis of the literature on the diet of the North American river otter. Specifically, we will provide a comprehensive synopsis of the otter's general food habits, of prey selection due to food preferences, and of changes in food habits due to seasonal variation. Additionally, we will provide a synthesis of the variation in otter food habits by ecoregion throughout their geographic range, as well as a general model of otter prey selection. We predict that the northern river otter is an opportunistic predator whose food habits vary based on the availability of prey due to community composition, the natural history traits of their prey (e.g. agility, habitat), and environmental factors (e.g. ice cover, drought).

METHODS

Literature review

We searched bibliographies and databases for literature with information on otter diet. In addition, we scanned the literature cited list for every paper included in the analysis for additional references. We created a database to house the various data from each paper. Data that we recorded include latitude and longitude, dates of collection, region, habitat type, collection method, measurement method, sample size, and number of total prey items.

Data collection

We assigned an ecoregion of North America to each study based on work provided by the United States Environmental Protection Agency (Omernik 1987). To maintain the most appropriate sample size for each ecoregion, we used the broadest ecoregion level. Accordingly, we labeled our ecoregions as Eastern Temperate Forests, Marine West Coast Forests, Northwestern Forested Mountains, Great Plains, Northern Forests, Mediterranean California, and Temperate Sierras (Figure 1). We divided habitat type into four categories: lentic, lotic, mixed, and coastal. Collection method refers to how the data itself was collected, usually through gross fecal analysis or by stomach and intestinal contents. We recorded measurement method as percent occurrence, relative percent occurrence, or volume. We conducted separate analyses for each type of method used for measuring the relative abundance of prey in otter diet.

In addition to these metadata, we recorded percentages of prey items at each available taxonomic level, although we mainly restricted our analysis to the class and family levels. We combined the families Cambaridae and Astacidae in the superfamily Astacoidea, as 99% of crayfish species in North America are of Cambaridae (Taylor et al. 2007), and usually no distinction was made in the literature as to which family was recorded. When a higher taxonomic level was not assigned a percentage, we calculated its percentages from lower taxonomic levels whenever possible. When studies used the percent occurrence method these calculations were not always possible and so not all studies include data at both the family and class levels. When available, we also recorded seasonal percentages for winter, summer, spring, and fall. If data were reported monthly, we recalculated percentages to be analyzed in the four-seasons format. The majority of studies reported data in percent occurrence (i.e. total scats/stomachs in which a certain prey item was found divided by the total number of scats/stomachs). Where data were reported in some other format (e.g. frequency of occurrence, relative percent occurrence), we recalculated the percentages to be expressed as a percent occurrence whenever possible. When one paper contained multiple prey lists, we generally entered these lists separately into the database. Lists were combined into a single list if prey were found within the same watershed, so as not to bias results toward studies with multiple lists from a small area. When publications included only anecdotal data, those data were included in the database for the purpose of listing overall diversity in river otter diet (Stophlet 1947, Duffy 1995), but not included in analyses which required reported percentages.

Data analysis

We calculated mean percentages for each reported taxon across North America and for each ecoregion. We took the average percentage for each reporting method (percent occurrence or volume) for each prey type from each study within an ecoregion. If some prey types were not reported in a study they were not assigned a 0, as omission from the prey list does not make certain the omission of that prey from otter diet. Therefore, percentages listed represent the average percentage in otter diet where that prey item occurs. To determine the primary prey group in each list and for each region, we used two-tailed proportional z-tests for significance.

We also used this test to determine if a given prey taxon exhibited seasonal variation more often than another taxon. To determine differences in percent occurrence of prey items across seasons, we performed chi-square tests across the means of each of the four seasons for each taxon in each prey list. We set our alpha level at 0.05. We used SigmaPlot to test regional data for equal variance and for normality using the Shapiro-Wilk test. When data met the normality and variance assumptions, we used a one-way analysis of variance (ANOVA) to test for variation among regions for each prey class and family. When the ANOVA assumptions were not met, we used the Kruskal-Wallis one-way analysis of variance non-parametric test. We retrieved burst speeds and critical swimming velocities of various fishes from the speed tables at fishbase.org (Froese and Pauly 2012).

Crayfish

In order to visualize crayfish density and distribution throughout the United States, we created a database to house crayfish records available from the Smithsonian National Museum of Natural History (http://collections.nmnh.si.edu). We exported these records into an Excel spreadsheet by number of individuals collected and number of sampling events per county, as GPS coordinates were not available for each record. We then joined these data in ArcMap 10 (ESRI, Redlands, California) to a shapefile of United States counties. We symbolized these data by number of individuals collected per county normalized by county area. We then compared relative importance of crayfish and fish to United States crayfish distribution to visualize the otter's crayfish feeding preference.

Primary productivity

To determine the effect of primary productivity on the diversity of prey in otter diet, we retrieved MODIS gross primary productivity data (GPP) from the University of Montana

Numerical Tetradynamic Simulation Group (http://www.ntsg.umt.edu/project/ mod17). We selected the improved MODIS product 17 dataset for the year 2006 showing annual GPP (Zhao et al. 2005). Using ArcGIS 10, we extracted mean GPP from a circular area surrounding each study site with a radius of 25 kilometers. We plotted the richness of fish families present in each study against the average GPP and calculated a Pearson's correlation value (r). For this analysis we omitted data from studies on coastal river otters, as the primary productivity of coastal land is probably not a good indicator of species richness in marine habitat.

RESULTS

Literature Review

We examined 100 publications with information related to diet of otters in North America published between 1936 and 2011. Eighty-five of these publications contained at least 1 prey list, and 77 publications contained quantitative data that were included in our database. Many of these publications contained multiple lists of otter prey, and our final analysis included 106 individual lists (Figure 2). All of these prey lists combined yielded a total of 24,352 samples that we analyzed with an average of 286.5 samples per study (*SE* = 43.7, Table 1). By ecoregion, the number of publications was greatest in the Eastern Temperate Forests and Marine West Coast Forest. Sample size for an entire ecoregion ranged from 120 from 1 study in Mediterranean California to 10,164 in the Eastern Temperate Forests ($\bar{x}$ = 274.7 ± 70.9). By decade, the number of publications with information on otter diet increased dramatically in the 1980's and continued into the 2000's (Figure 3). This increased interest in otter food habits may be related to an increase in the number of states that were conducting reintroductions at the time, which also peaked in the 1980's and 90's (Figure 4).

Diversity of Prey

Across North America, a total of 7 phyla, 24 classes, 79 orders, and 123 families (7.3 families per study, *SE* = 0.55) were represented in otter diet. Genus and species were rarely reported in prey lists, and were never listed comprehensively. Of the 7 ecoregions that contained otter diet studies, the region with the most diverse prey base was Eastern Temperate Forests (70 families), followed by Marine West Coast Forest (66 families, Table 2). Per prey list, Eastern Temperate Forests averaged 8.0 families (*SE* = 0.88), Marine West Coast Forest averaged 7.5 families (*SE* = 1.45), and the Great Plains' two publications averaged 9.8 families (*SE* = 0.49) per list For the diversity of fish families, Eastern Temperate Forests had 27, and both Marine West Coast Forest and Northern Forests had 22 (Table 3). And while Eastern Temperate Forests, Northern Forests, and Great Plains all averaged over 8 fish families per prey list (8.0 ± 0.54, 8.4 ± 1.17, 8.8 ± 0.49, respectively), Marine West Coast Forest only averaged 5.8 (*SE* = 1.10).

Composition of Prey

Analyses of mean percent occurrence revealed that fish were the primary class of prey found throughout North America, followed by malacostracans. In decreasing order of importance amphibians, insects, reptiles, birds, gastropods and mammals represented a much less significant portion of otter diet (Figures 5, 6). At the family level, the crayfish superfamily Astacoidea was found to be the most important prey item for studies using the percent occurrence method, followed by several fish families including Centrarchidae, Cottidae, Catostomidae, Cyprinidae, and Salmonidae (Figure 7). For studies that measured prey abundance by volume, Cottidae made up the largest proportion of prey among studies that recorded their presence. Only 3 of 18 studies that measured volume, however, reported Cottids in the prey of river otters, and mean Cottid volume was not significantly different from Astacoidea and Catostomidae. Cottidae was followed in average volume by Astacoidea, which was recorded in 12 of the 18 studies, more than any other family of prey. In decreasing order of abundance, other families that represented significant portions of otter diet across their range included Catostomidae, Cyprinidae, Centrarchidae, and Salmonidae (Figure 8).

Otter diet varied among ecoregions ($P < 0.05$) as reported using the percent occurrence method at the class level (Figures 1, 9). Fish varied by ecoregion ($H = 11.56$, *d. f.* = 5, $P = 0.041$) and was the main prey class in all regions except for Mediterranean California and Temperate Sierras, which contained only two prey lists each and were led by malacostracans. Malacostracans also varied by ecoregion ($F = 2.66$, *d.f.* = 5, 49, $P = 0.03$). When malacostracans weren't the primary prey class in a region, they were the secondary prey class. Malacostracans were found to be most prevalent in Eastern Temperate Forests and Northern Forests. Birds also varied by ecoregion ($H = 17.85$, *d.f.* = 4, $P = 0.001$), occurring in 15.8% of samples in the Marine West Coast Forest. Other classes that made significant contributions in at least one region (> 10% occurrence) were amphibians, insects, and mammals. None of these classes, however, varied by ecoregion ($H = 1.37$, *d.f.* = 4, $P = 0.849$; $H = 8.183$, *d.f.* = 4, $P = 0.085$; $H = 0.90$, *d.f.* = 4, $P = 0.93$, respectively). While these classes occurred regularly in many regions, only amphibians and insects occurred in more than 10% of samples in multiple regions. It is likely, however, that the majority of occurrences of insects were due to secondary or incidental ingestion. Amphibians did not vary among ecoregions and were present in studies from all regions except Mediterranean California. Mammals and birds tended only to occur in samples in low percentages.

The average percent occurrence in otter diet also varied by ecoregion among families ($P < 0.05$, Figure 10). Only fish and malacostracans were commonly reported to the family level, and only six of the seven ecoregions that contain otter diet studies reported data to the family level. Of those six ecoregions, the most commonly reported families in each region were Astacoidea in Eastern Temperate Forests, Cyprinidae in Great Plains and Northern Forests, Cottidae in Marine West Coast Forest, Salmonidae in Northwestern Forested Mountains, and Catastomidae in Temperate Sierras. Astacoidea did not vary among ecoregions ($H = 5.87$, *d.f.* = 5, $P = 0.31$). Catastomidae was present in all regions but varied dramatically ($F = 3.64$, *d.f.* = 4, 38, $P = 0.31$), from 90% in Temperate Sierras, to 17% in Eastern Temperate Forests. Centrarchidae was also present in all regions, and was the most commonly taken family of fish in Eastern Temperate Forests. Cottidae varied among ecoregions ($H = 8.76$, *d.f.* = 2, $P = 0.013$), only contributing a significant portion to otter diet in Marine West Coast Forests (46.9%) and Northwestern Forested Mountains (29.6%). Cyprinidae did not vary by ecoregion ($H = 7.27$, *d.f.* = 4, $P = 0.122$) but was the top family in two regions and occurred at less than 20% in three other regions. Salmonidae did vary by ecoregion ($H = 17.21$, *d.f.* = 3, $P < 0.001$) and was the primary prey family of otters in the Northwestern Forested Mountains (43%), but did not have an average occurrence of more than 20% of samples in any other ecoregion. Other families that contributed > 10% to any ecoregion in at least one study included Amiidae, Cyprinodontidae, and Gasterosteidae in Northern Forests; Esocidae, Cyprinodontidae, and Sciaenidae in the Eastern Temperate Forest; Esocidae and Gadidae in the Great Plains; Batrachioididae, Embiotocidae, Gasterosteidae, Gobiesocidae, Hexagrammidae, Liparidae, Pholidae, Pleuronectidae, Scorpaenidae, and Stichaeidae in Marine West Coast Forest, which had more endemic families than any other ecoregion.

Seasonal variation

Thirty-four studies reported seasonal variation in otter diet. We tested each of these studies to determine if there was any significant seasonal variation in prey consumption by class or family ($\alpha = 0.05$). Malacostracans and amphibians exhibited significant seasonal variation ($P \leq 0.05$) in 85% and 83% of published reports on otter diet, which was significantly more seasonal variation than all other prey classes ($Z = 2.21$, $P = 0.0271$) but insects. All other classes displayed seasonal variation in a portion of publications as well, but none of those classes displayed significantly more or less seasonal variation than others. Forty-eight percent of studies reported seasonal variation in fish consumption, while insects were the only other class with seasonal variation reported over 50% of the time (Figure 11). At the family level, all families that were reported in at least five publications were found to have significant variation among seasons in at least 50% of reports ($P \leq 0.05$). Centrarchidae (91.7%), Cyprinidae (88.9%), and Astacoidea (88.2%) were the only families found to vary seasonally more often than any other families ($P \leq 0.05$, Figure 12).

We also examined each season individually by both class and family ($\alpha = 0.05$). Prey item occurrence varied more often in the winter and summer seasons at the class level. For example, percent occurrence of fish varied from the seasonal mean more often during the summer (83% of publications) than during any other season ($P \leq 0.05$), and varied more during the winter (53%) than either spring or fall ($P \leq 0.05$). Likewise, malacostracans exhibited more seasonal variation in the winter and summer months than in the spring and fall months ($P \leq 0.05$). While amphibians displayed an increase the frequency of temporal variation in fall and summer, these seasons were not significantly different from winter or spring (Figure 13). No other classes exhibited a significant increase in percent occurrence during a given season. All families that were included in analyses showed significant seasonal variation for two seasons in at least one publication. Astacoidea displayed seasonal variation more often during the summer and winter than during the spring and fall, as did Centrarchidae ($P \leq 0.05$). Catostomidae displayed seasonal variation more often in the summer and winter than in the spring ($P \leq 0.05$), and Salmonidae nearly displayed more seasonal variation in the fall than in the winter and spring ($Z = 1.51$, $P = 0.065$). All other families were consistent across seasons as to the occurrence of significant seasonal variation (Figure 14).

Astacoidea (crayfish) in otter diet

In order to evaluate the importance of Astacoidea in otter diet, we directly compared the top-reported prey item of each study against the distribution and density of Astacoidea within the United States (Figures 15 – 19). We found that at the class level Astacoidea was consistently reported higher than fish where Astacoideans were found to be the densest, particularly in the southeastern United States. When we compared percent occurrence of Astacoidea to other families of prey in otter diet, Astacoidea was found to be the top-reported prey family throughout most of the eastern United States. When we examined top-reported prey items during the summer season, the range where Astacoideans were reported as the top prey item continued to expand and eventually included studies located in western states such as Colorado, Arizona, California, and North Dakota.

Food preferences

Twelve publications made some report of otter prey being taken according to their abundance. Of those 12, 8 utilized some kind of abundance data, and 7 conducted statistical tests to determine whether there were significant differences between prey abundances and prey occurrence in diet. According to these 7 publications, Catostomids were selected for 4 times and selected against once, Centrarchids were selected for 5 times, Cyprinids were selected against 1 time, and Salmonids were selected for 1 time and against 1 time. Each of these four families was found to be taken according to their abundance twice. Other families selected for once included Percidae and Esocidae. All other families that were reported were found to be taken according to their abundance.

Many publications have speculated on size of fish taken by otters, but only a few studies have documented size selection based on methods to assess the size of fish from bones and scales found in scat. In a marine environment, otters were found to select prey larger than expected based on the size structure of existing fish populations, selecting for larger fish than expected, but only up to 25cm in length (Cote et al. 2008a, Cote et al. 2008b). In North Dakota, fish prey selection ranged in size from 3.5cm to 71cm, and most fish were between 10 and 20 cm, though this trend varied seasonally as smaller fish were taken more often in the summer. The relative number of fish taken in 10cm increments outward from the 10-20cm rank decreased in a stepwise fashion (Stearns and Serfass 2011). Similar results to those found in North Dakota were found in a reintroduced otter population in Pennsylvania (Giordano 2005).

Productivity and diversity of prey

Average primary productivity of the area around a study site was positively correlated with the richness of fish families present in diet of otters ($r^2 = 0.25$, $P < 0.001$ Figure 20). Family richness ranged from 2 to 17 families, though this may be a result of sampling effort.

DISCUSSION

Current literature on the diet of the northern river otter covers most of its current range and habitat types. The United States has far better coverage than Canada, however, and large areas within Canada have not been studied at all including Saskatchewan, Manitoba, Ontario, Quebec, Nunavut, Yukon, and the Northwest Territories. Additionally, the only studies that have been conducted in Alaska are on coastal otters, therefore knowledge of food habits of otters in much of northern North America is lacking. Additionally, there are gaps in knowledge of otter diet in areas where otters were extirpated and have not yet recovered, such as the Great Plains of the United States and Canada, and the southwestern United States. As otters continue to be translocated to and naturally colonize these areas, it will be important to monitor their food habits to be able to predict what impact they might have on the structure and function of those ecosystems.

Otter diet varied by ecoregion among several prey classes and families. Regional variation in otter diet is likely a result of a combination of the composition of available prey community and variation in habitat types. For example, the dominant prey family in the Eastern Temperate Forest and the Northwestern Forested Mountains was Centrarchidae and Salmonidae, respectively. Both of these families are native to their respective ecoregions, and both dominate the aquatic landscape (Berra 2007). While both families now occur throughout both ecoregions through introductions and range expansions, otters are feeding primarily on the native families which tend to be more successful in their native habitats. Salmonids dominated otter diet in and are more suited to thrive in the stream habitats of the Northwestern Forested Mountains, and Centrarchids are likewise more suited to thrive in the high-productivity systems of the Eastern Temperate Forests where they dominated otter diet. Therefore, if habitat is ultimately driving the community composition of fish, it is likewise driving the diet of river otters. This idea then lends support to the notion that otters are flexible and opportunistic, thus able to survive in habitats, freshwater or marine, throughout North America regardless of the fish community composition.

We found otter diet to vary by season at the class level, particularly among malacostracans and amphibians. All families that we tested also displayed seasonal variation, but none more than Centrarchidae, Cyprinidae, and Astacoidea. Seasonal variation in otter diet is likely due to a combination of factors including temporal variation in available habitat and prey types. Regions with drastic fluctuations in climate or periods of otherwise severe weather could result in greater seasonal changes in habitat than areas with more moderate climates. These changes in habitat, such as ice cover, temperature fluctuations, and flood cycles, then affect what prey is available to river otters (Tumlison and Karnes 1987). In addition to these effects, the life history cycles of prey also affect their availability to otters. For example, in Utah and Idaho Salmonids were found to be eaten most in fall and winter (Melquist and Hornocker 1983, Day et al. *Unpub. Data*). This could be correlated with the life history cycle of the more abundant Salmonids in those systems, which generally spawn in the fall. It could also be a result of river habitat being more available to otters than lake habitat during the colder months of the year. Likewise, amphibians showed consistent deviation from mean seasonal occurrence in the summer months, likely due to hibernation in the colder months and their activity level being at its highest in the summer.

Crayfish (Astacoidea) appear to be the primary prey of river otters when and where they are readily available. While the majority of studies on otter diet reported fish to be the primary prey component of otters, crayfish were the top prey item in several studies. Crayfish also had the highest mean percent occurrence by family across all North American studies (Figure 16). Additionally, the majority of studies that reported crayfish as the primary diet component were located in the southeastern United States, where crayfish are known to be the most diverse and the most abundant relative to the rest of North America (Taylor et al. 2007; Figure 15). This regional trend becomes even more apparent when you look at prey on the family level and/or at the seasonal trends of the prey (Figures 17-19). Seasonally, an increase in crayfish in diet relative to fish in diet occurs during the summer months throughout the United States at both the class and family level. During the summer, the majority of studies in the eastern half of the United States found crayfish to be the most common prey item (Figure 18). This increase in crayfish consumption in the eastern United States and in the summer months may indicate that otters prefer crayfish over fish, as fish availability is fairly constant throughout the year. Otters are therefore appear to be switching their prey base from fish to crayfish whenever and wherever they are available. Indeed, even in Arizona where crayfish are not natively abundant, otters have switched from primarily consuming fish to primarily consuming crayfish. In the early stages of an exotic crayfish invasion, Christensen (1984) reported otter diet composed of 90% fish and 22% crayfish. Twenty years later from the same watershed, Taylor et al. (2003) reported only 19% fish and 100% crayfish occurrence in otter scats, indicating the otter's ability and willingness to change prey base.

The hypothesis that otters are opportunistic predators is supported by our results that the primary productivity of a study area is positively correlated with richness of fish families found within otter diet. We found that primary productivity moderately correlated with fish richness in otter diet (Figure 20), lending support to the notion that otters will opportunistically feed on any prey that is available to them. This is based on the oft-quoted idea that "diversity begets diversity" (Whittaker 1975), assuming that in areas of high productivity and diverse vegetation, higher trophic levels such as fish communities, will likewise increase in richness and diversity. Based on our results, otters apparently do not specialize on one or even a few prey types. Although selection may occur, it is not so extreme that otters would ignore other available prey.

In fact, in the study area with the highest primary productivity in northern Florida, otters consumed 17 different fish families (Cooley 1983).

Based on our results, we believe prey selection by river otters is influenced by environmental and prey-related factors (Figure 21). It has been speculated that otters take prey according to their abundance and in inverse proportion to their swimming ability (Ryder 1955). However, from the little abundance data that exists in the literature, it is difficult to assess whether this is truly the case. Additionally, prey availability should be defined not only by abundance in a given ecosystem, but by all factors that might influence an otter's ability to take that prey item. Sheldon and Toll (1964) expanded on the idea of availability by including such factors as habitat, time of day of foraging, fish spawning, ice cover, flood cycles, and otter fishing methods. We have developed a model of otter prey selection factors that influence otter prey selection in a stepwise fashion.

The first factor in the model that impacts what prey items an otter will take is the presence/absence of that particular item. If a prey item is indeed present, the habitat of that prey item is the next factor that influences otter selection. Lake trout, while often abundant, occupy habitat too deep for otters to consistently and successfully forage (Crait and Ben-David 2006). In contrast, Centrarchids were commonly reported as the top prey family in otter diet, possibly because they inhabit shallow and muddy areas that provide predatory advantages for otters (Tumlison and Karnes 1987). Prey habitat can change throughout the year as well, accounting for seasonal variation in otter diet. Ice cover can cause lake and reservoir species to be more or less available to otters, depending on the wintering strategies of the prey. Annual flooding cycles can widen the habitat available to otters, along with the prey base, as reptiles, amphibians, and crayfish become more active and available. If, therefore, prey occupy habitat that is available to otters for foraging, the next factor that influences their prey selection is detectability.

The ease of which an otter is able to detect a prey item certainly influences its decision to pursue it. Prey motility and camouflage may very well play a role in detectability (Cote et al. 2008b), as mottled sculpin (*Cottus bairdii*), a sedentary bottom-dwelling river-fish, was likely selected against in a study in northern Utah (Day et al. *Unpub. data*). Likewise, fish that may share the right habitat with otters may be undetectable due to vegetative or sedimentary cover. Time of day during which an otter forages might also influence an otter's ability to detect prey items. This may explain why the usually nocturnal river otter (Martin et al. 2010) rarely preys on diurnal waterfowl.

Once prey is detected, the next factor in our model that influences prey availability is its catchability. In the fish literature, there exist two primary measures of fish agility: burst speed and critical swimming velocity (CSV; Brett 1964, Beamish 1978, Plaut 2001). Both of these measures potentially influence the ability of an otter to catch a prey item, as burst speed is an indicator of initial escapability from predators, and CSV is an indicator of sustained escapability during pursuit. Assuming that some fish indeed require more effort from otters to catch, those fish families with the highest measured burst speeds and CSV's, and therefore the most difficult to catch, are the piscivorous Salmonidae and Centrarchidae (Froese and Pauly 2012). We would therefore expect these families to be consistently selected against and found in low numbers in otter diet, while slower families such as Catostomidae and Cyprinidae would be expected to be selected for and represented in high numbers in otter diet. This is not often the case however, as Centrarchidae and Salmonidae were the most abundant prey families in many studies, and were each selected for in at least one study. Similarly, Catostomidae and Cyprinidae were each selected against in at least one study. This may indicate that otters are able to catch members of any family of fish with relatively little effort and are driven more by palatability, or it could mean that selection of these particular prey families is a result of factors previously mentioned. Catchability may also be influenced by otter foraging methods. In marine ecosystems, schooling fishes have been found to be preyed upon more frequently by groups of otters foraging collectively, while intertidal and demersal fishes have been found to be foraged upon more often by solitary otters as schooling fishes may be less catchable (Blundell et al. 2002, Ben-David et al. 2005).

The final factor in the stepwise model of prey selection is palatability. Indeed, assuming that an otter is able to detect and catch any prey item that is in the proper habitat, preference based on palatability could potentially be one of the driving forces behind otter food habits. This would include not only taste preferences, but also the effort it takes to consume the prey once caught (suckers are known to have tough skin) and the nutritional value of various prey items. In addition to the factors detailed above, density of prey items can influence how detectable and/or catchable a prey item may be. For example, schooling fishes in high densities may be easier for groups of otters to catch and would also make them more detectable. Overpopulated fish will likewise have difficulty maintaining protective cover and escaping predation.

Overall, prey selection is indeed influenced by availability of prey when it is thought of in terms broader than mere abundance and includes the complexities of factors such as prey habitat, detectability, catchability, and palatability. While many studies have been conducted on river otter diet, gaps in the literature remain. To better understand otter prey selection, more studies are needed that test food habits against actual prey abundance data obtained using sound methodology. Many studies speculate on prey selection, or report prey abundance data without conducting statistical tests for significance. Additionally, as the river otter's range continues to expand, food habits studies should be conducted by managers of the ecosystems into which the otters are expanding. This will not only further the knowledge of otter food habits, but also further the understanding of the impact that this top predator has on aquatic systems.

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Table 1 - Number of publications, number of prey lists, and sample size analyzed for each region of North America from 1939 – 2011.

Region	No. of Publications	No. of Prey Lists	Total Sample Size	Mean	*SE*
North America	85	106	24352	286.5	43.7
Eastern Temperate Forests	30	41	10164	274.7	70.9
Great Plains	2	5	651	130.2	109.8
Marine West Coast Forest	30	34	2950	163.9	33.5
Mediterranean California	1	2	120	120	0.0
Northern Forests	9	12	3877	387.7	110.9
Northwestern Forested Mountains	11	14	6190	515.8	175.5
Temperate Sierras	2	2	400	200	147.0

Table 2 - Richness (by taxon) of prey items as well as mean number of families reported throughout North America in 85 publications on food habits of otters from 1939 – 2011. n represents the number of prey lists that reported families.

Region	Phyla	Classes	Orders	Families	Mean families per list	*SE*	*n*
North America	7	24	79	123	7.3	0.55	90
Eastern Temperate Forests	5	15	54	70	8.0	0.88	38
Great Plains	2	4	10	12	9.8	0.49	5
Marine West Coast Forest	5	18	45	66	7.5	1.45	21
Mediterranean California	3	8	11	6	6.0	0.00	1
Northern Forests	6	10	33	31	6.5	1.40	11
Northwestern Forested Mountains	3	10	22	21	5.3	0.69	12
Temperate Sierras	3	6	6	6	3.5	2.50	2

Table 3 - Richness (by taxon) of fish prey throughout North America as reported in 85 publications on food habits of otters from 1939 – 2011. N/A means studies did not report fish to that taxon. n represents the number of lists that reported fish families.

Region	Orders	Families	Mean families	*SE*	*n*
North America	21	40	6.8	0.42	71
Eastern Temperate Forests	18	27	8.0	0.54	29
Great Plains	8	11	8.8	0.49	5
Marine West Coast Forest	12	22	5.8	1.10	17
Mediterranean California	N/A	N/A	N/A	N/A	0
Northern Forests	15	22	8.4	1.17	7
Northwestern Forested Mountains	5	7	3.9	0.45	12
Temperate Sierras	5	5	5.0	0.00	1

LIST OF FIGURES

Figure 8 **-** Mean composition of prey of otter diet (± *SE*) throughout North America from published accounts that used volume measurements from 1954 - 2011. Families with a mean proportion greater than 5% and represented by at least 3 prey lists were included. Sample size (*n*) is displayed above each bar.

Figure 9 – Average percent occurrence of prey items at the class level (± *SE*) for each ecoregion of North America.

Figure 10 – Average percent occurrence of prey items at the family level (± SE) for each ecoregion of North America. Families that made contributions to Marine West Coast Forest and were seldom reported elsewhere include Pholidae (85.8%), Pleuronectidae (52.6%), Stichaeidae (68.7%), Liparidae (24.6%), and Gobiesocidae (49.3%).

Figure 11 **-** Percent of publications that showed seasonal significant variation in otter diet for each class as determined by chi square tests across the four seasons (spring, summer, winter, fall) that were reported by studies throughout North America from 1954 - 2011. Classes represented by at least five studies were included. Sample size is displayed above each bar.

Figure 12 **-** Percent of publications that showed seasonal significant variation in otter diet for each family as determined by chi square tests across the four seasons (spring, summer, winter, fall) that were reported by studies throughout North America during 1954 - 2011. Families represented by at least five studies were included. Sample size is displayed above each bar.

Figure 13 **-** Percent of publications showing significant seasonal variation for each prey class in otter diet throughout North America from 1954 - 2011. Significance was determined by z-test against the mean for all seasons ($P < .05$). Classes represented by at least five studies were included.

Figure 14 **-** Percent of publications showing significant seasonal variation for each prey family in otter diet throughout North America from 1954 - 2011. Significance was determined by z-test against the mean for all seasons ($P < .05$). Families represented by at least five studies were included.

Figure 15 **-** Map showing number of individuals per county extracted from records in the Smithsonian Museum of Natural History database normalized by county area. We used this as a surrogate for crayfish density and distribution in the United States.

Figure 16 **-** Map showing the importance of crayfish and fish in otter diet at the class level as reported by publications throughout North America from 1939 - 2011. Symbols denote the primary prey class per study based on z-tests (NS = not significant, $P < .05$). Note the regional importance of crayfish in the eastern United States.

Figure 17 **-** Map showing the importance of crayfish and fish in otter diet at the family level as reported by studies throughout North America from 1939 - 2011. Symbols denote the primary prey family per study based on z-tests (NS = not significant, $P < .05$).

Figure 18 **-** Map showing the importance of crayfish and fish in otter diet as reported by publications throughout North America from 1939 - 2011. Symbols denote the primary summer prey class for each study based on z-tests (NS = not significant, $P < .05$).

Figure 19 **-** Map showing the importance of crayfish and fish in otter diet as reported by publications throughout North America from 1939 - 2011. Symbols denote the primary family of prey in the summer for each study based on z-tests (NS = not significant, $P < .05$).

Figure 20 - Number of fish families (± 95% C.I.) present in otter diet studies based on the primary productivity of the study area ($r^2 = 0.25$, $P < 0.001$). Data was collected from studies conducted in North America from 1936 – 2011.

Figure 21 - This model provides a framework for a basic stepwise progression that leads to river otter prey selection. These steps refer to characteristics of the prey. Density does not result in the predation or lack of predation of any given prey type, but does influence detectability and catchability.

Fig. 1

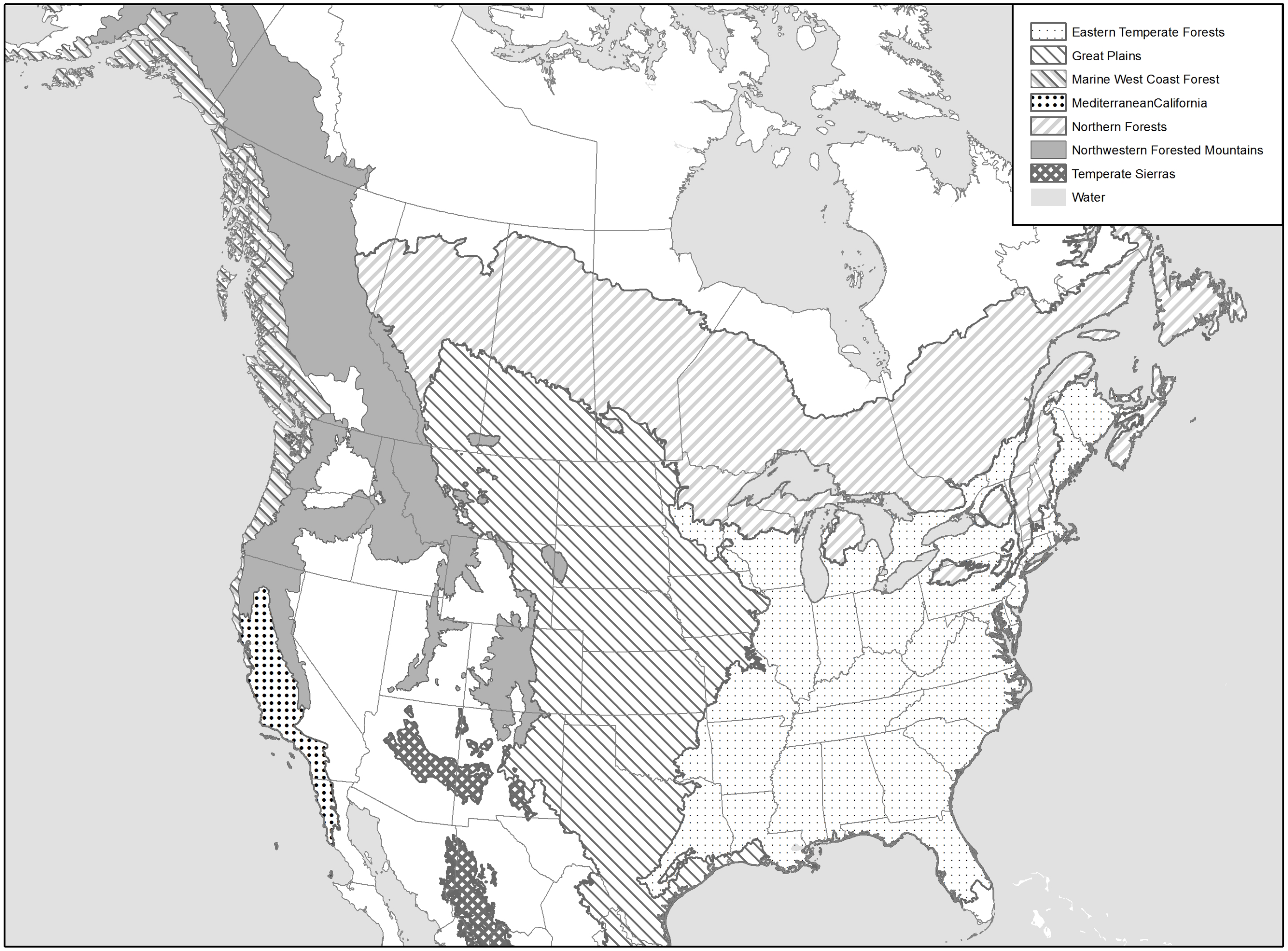

Eastern Temperate Forests
Great Plains
Marine West Coast Forest
MediterraneanCalifornia
Northern Forests
Northwestern Forested Mountains
Temperate Sierras
Water

Fig. 2

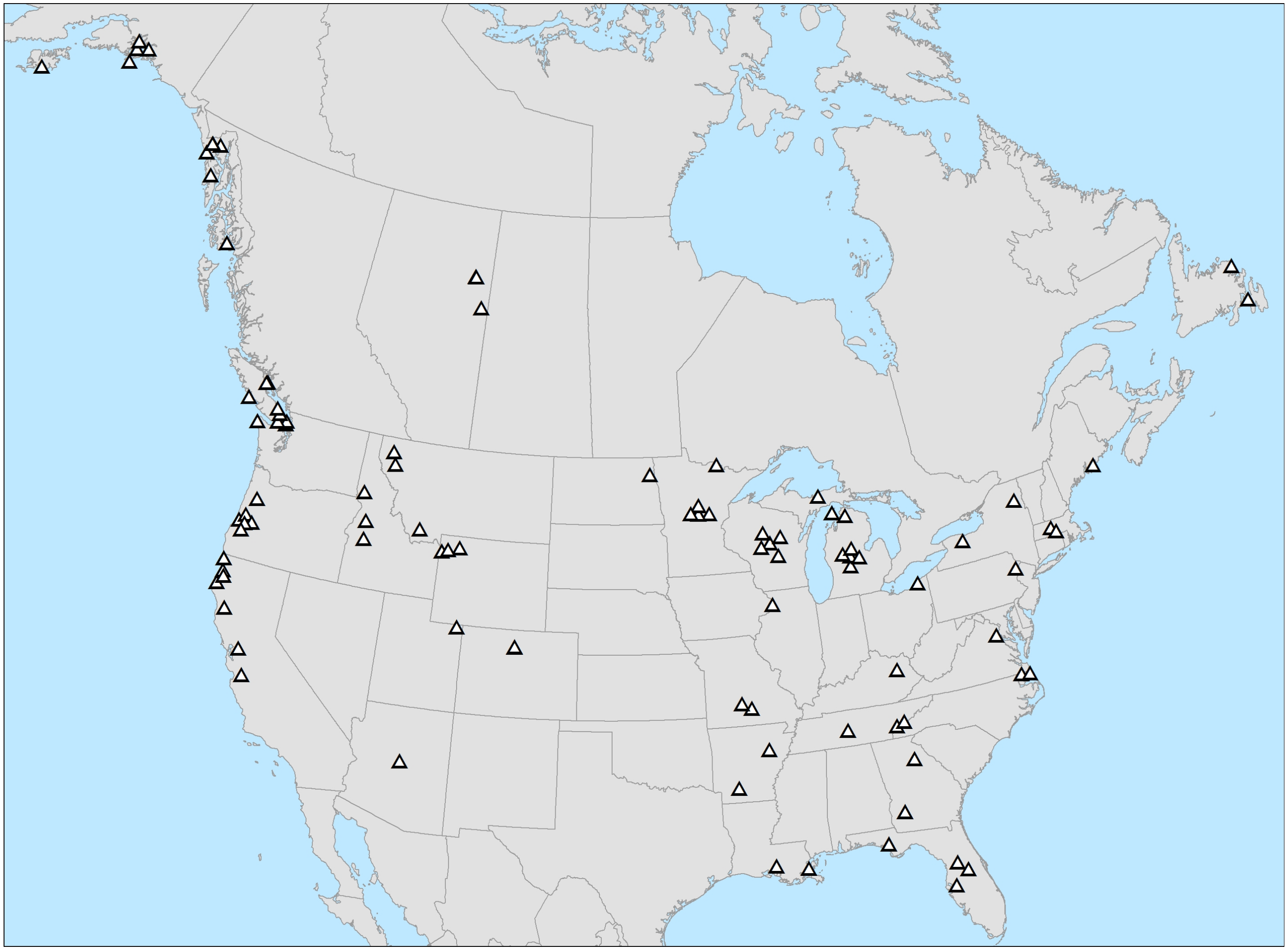
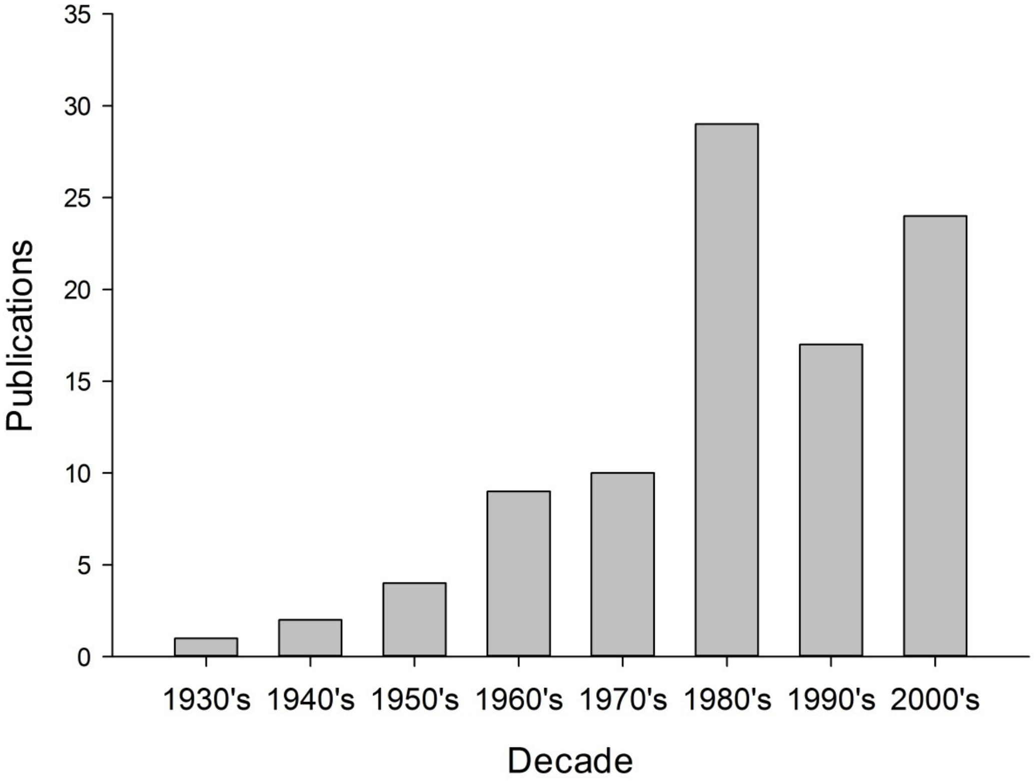
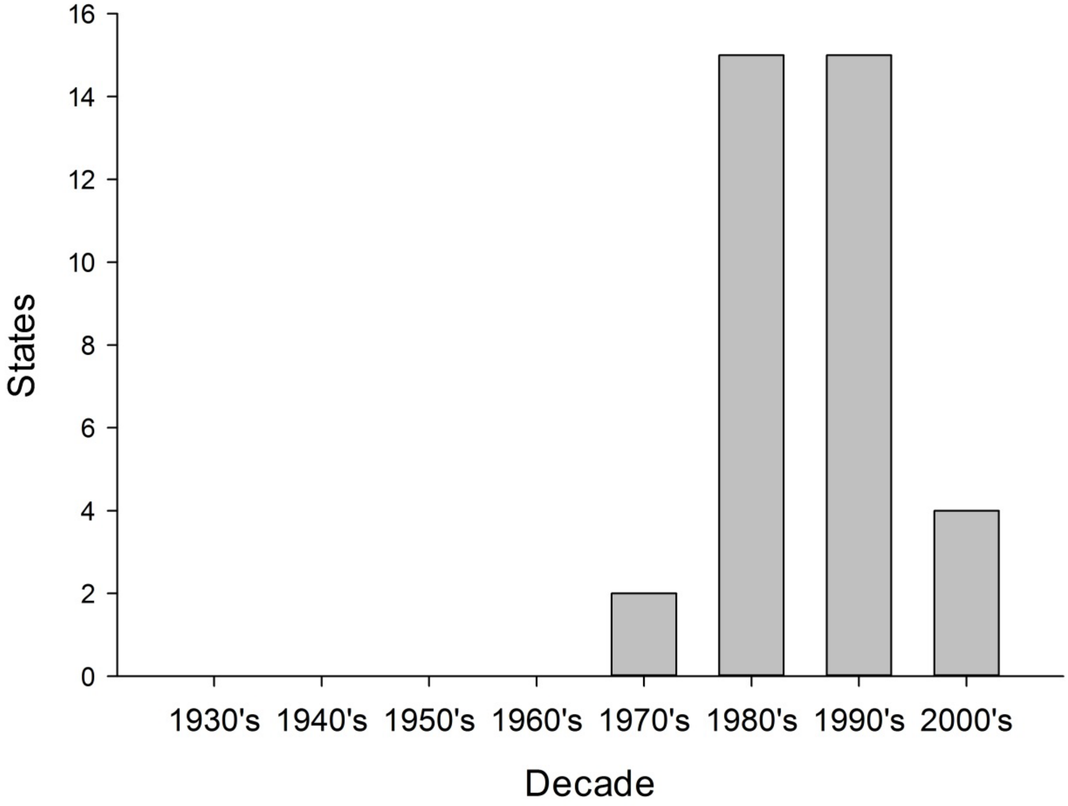


Fig. 3



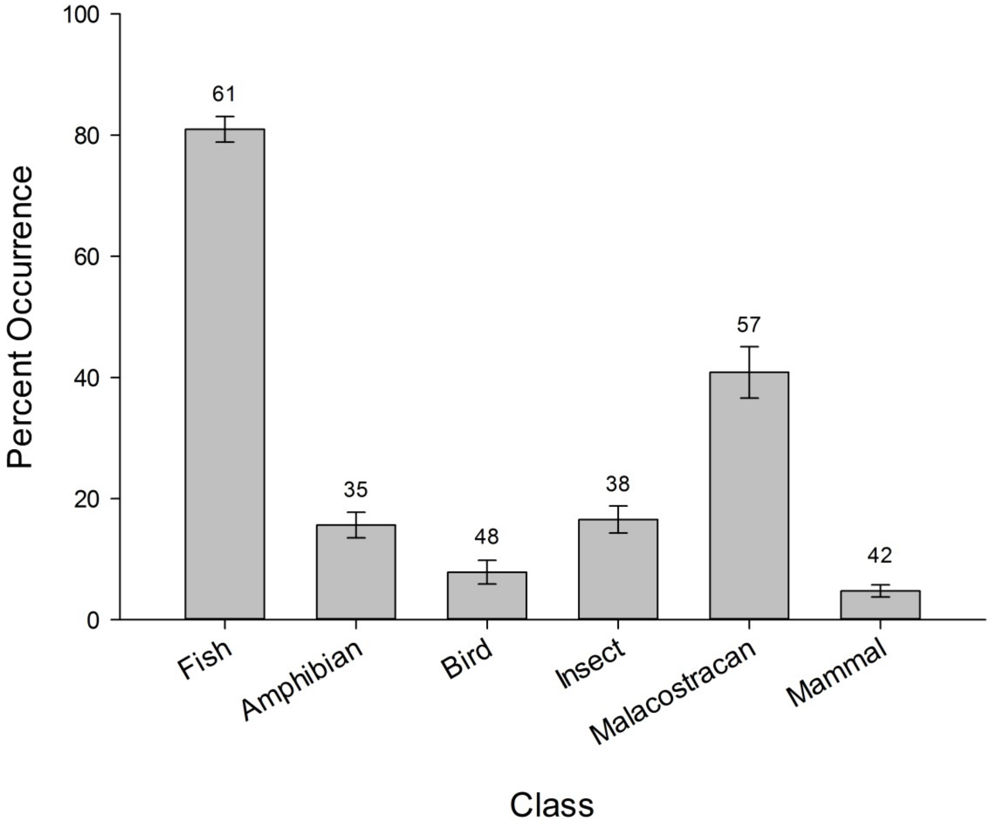
35
30
25
20
15
10
5
0
Publications
1930's
1940's
1950's
1960's
1970's
1980's
1990's
2000's
Decade

Fig. 4



16
14
12
10
8
6
4
2
0
States
1930's
1940's
1950's
1960's
1970's
1980's
1990's
2000's
Decade

Fig. 5



100
80
60
40
20
0
Percent Occurrence
61
35
48
38
57
42
Fish
Amphibian
Bird
Insect
Malacostracan
Mammal
Class

Fig. 6

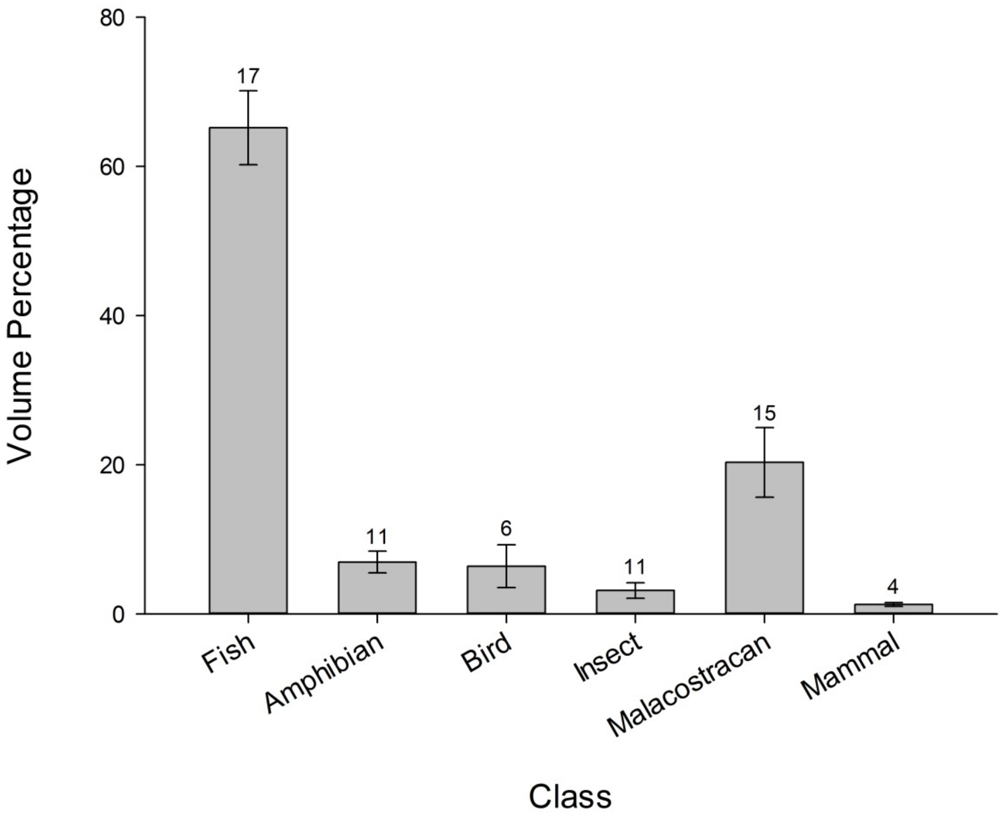

80
60
40
20
0
Volume Percentage
17
11
6
11
15
4
Fish
Amphibian
Bird
Insect
Malacostracan
Mammal
Class

Fig. 7

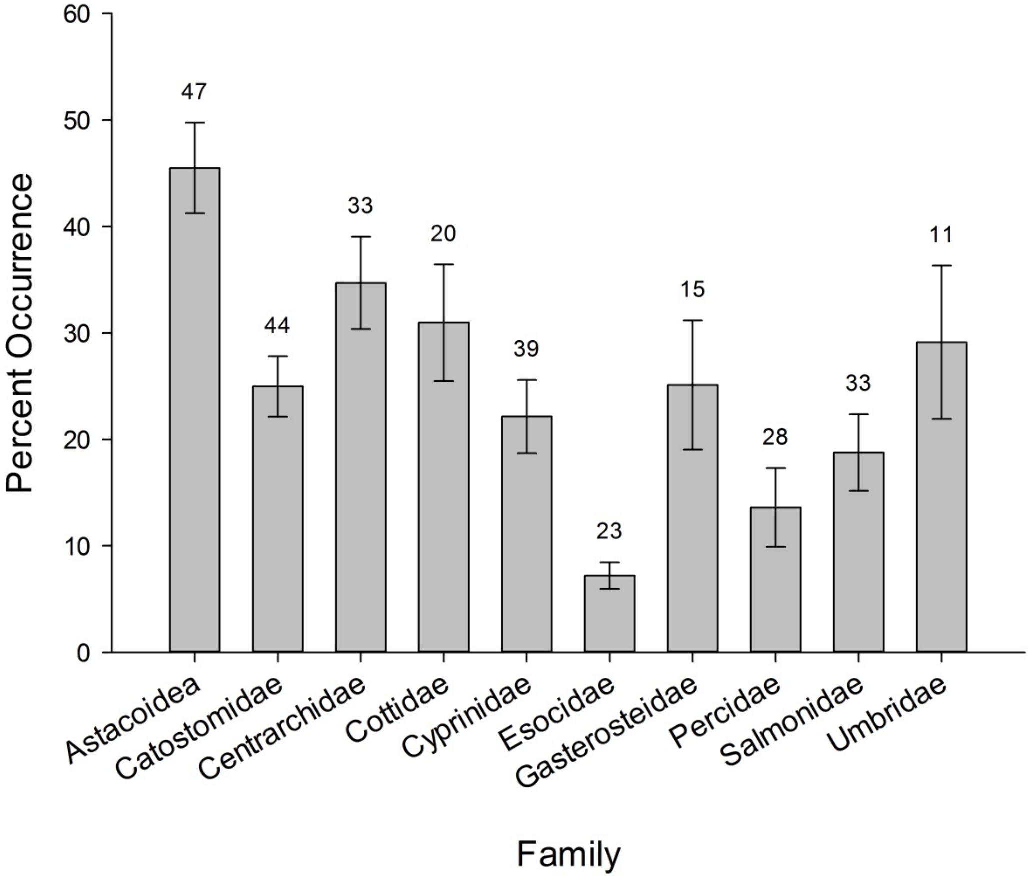
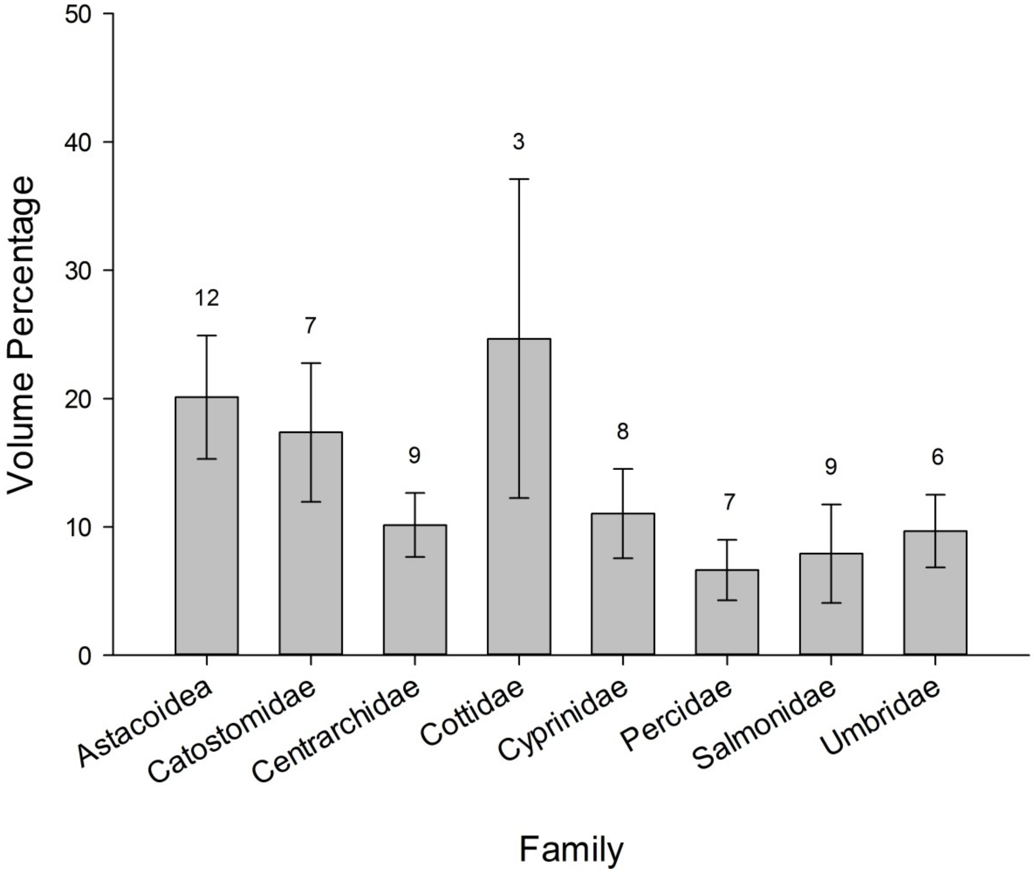
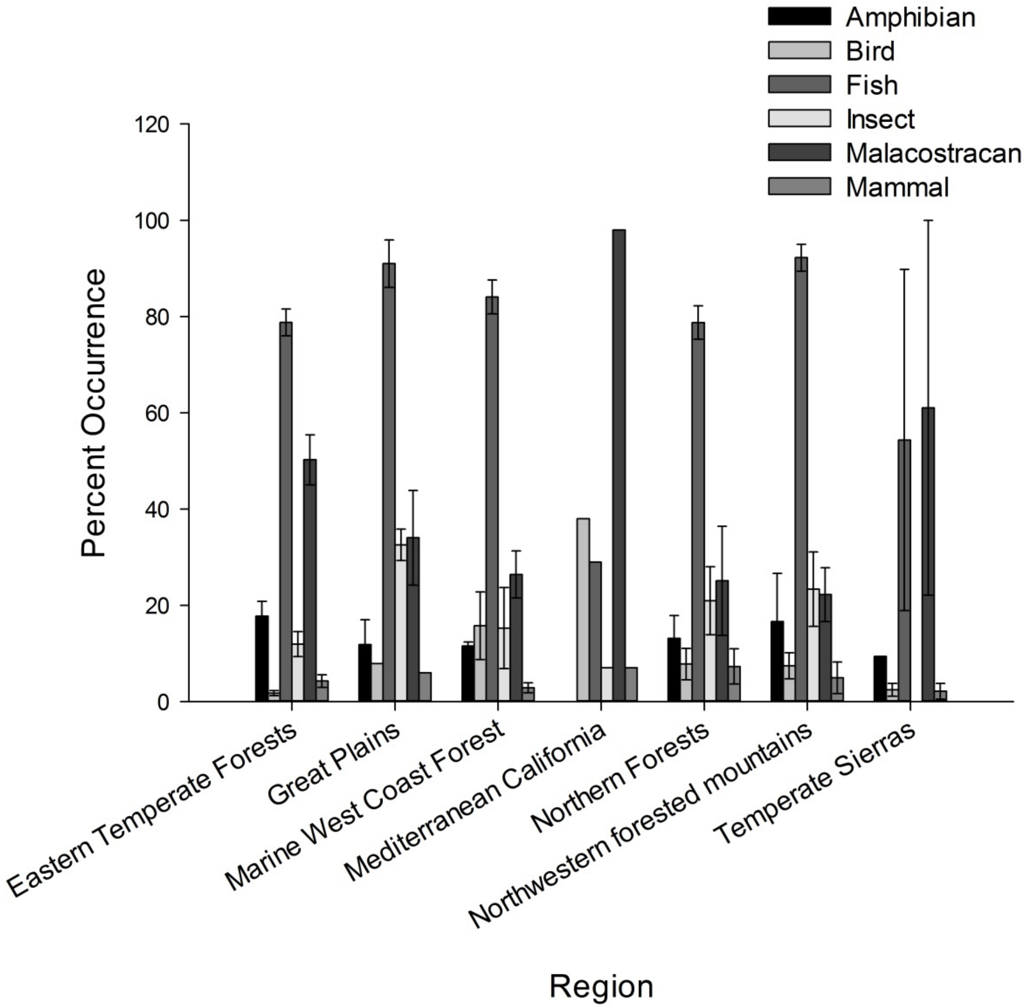

60
50
40
30
20
10
0
Percent Occurrence
47
44
33
20
39
23
15
28
33
11
Astacoidea
Catostomidae
Centrarchidae
Cottidae
Cyprinidae
Esocidae
Gasterosteidae
Percidae
Salmonidae
Umbridae
Family

Fig. 8



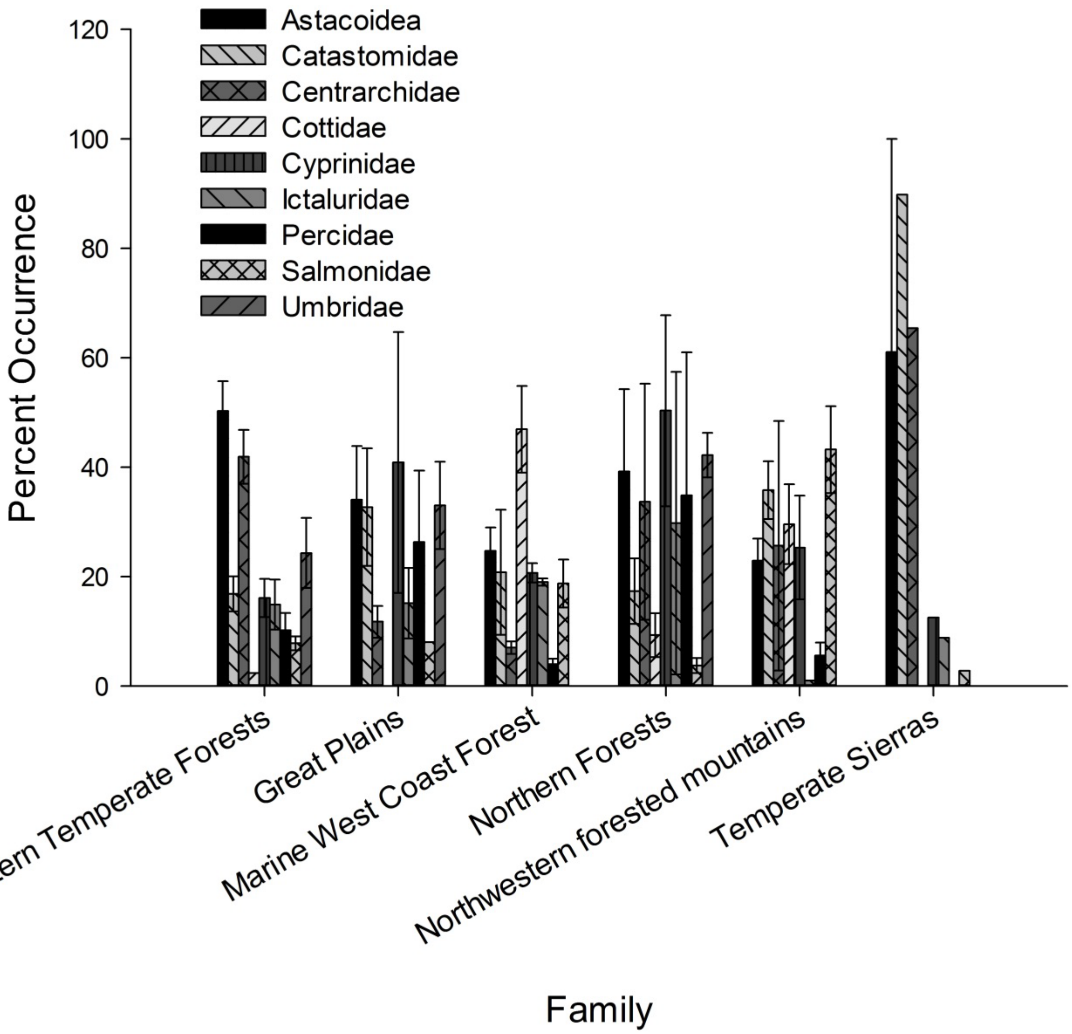
50
40
30
20
10
0
Volume Percentage
12
7
9
3
8
7
9
6
Astacoidea
Catostomidae
Centrarchidae
Cottidae
Cyprinidae
Percidae
Salmonidae
Umbridae
Family

Fig. 9



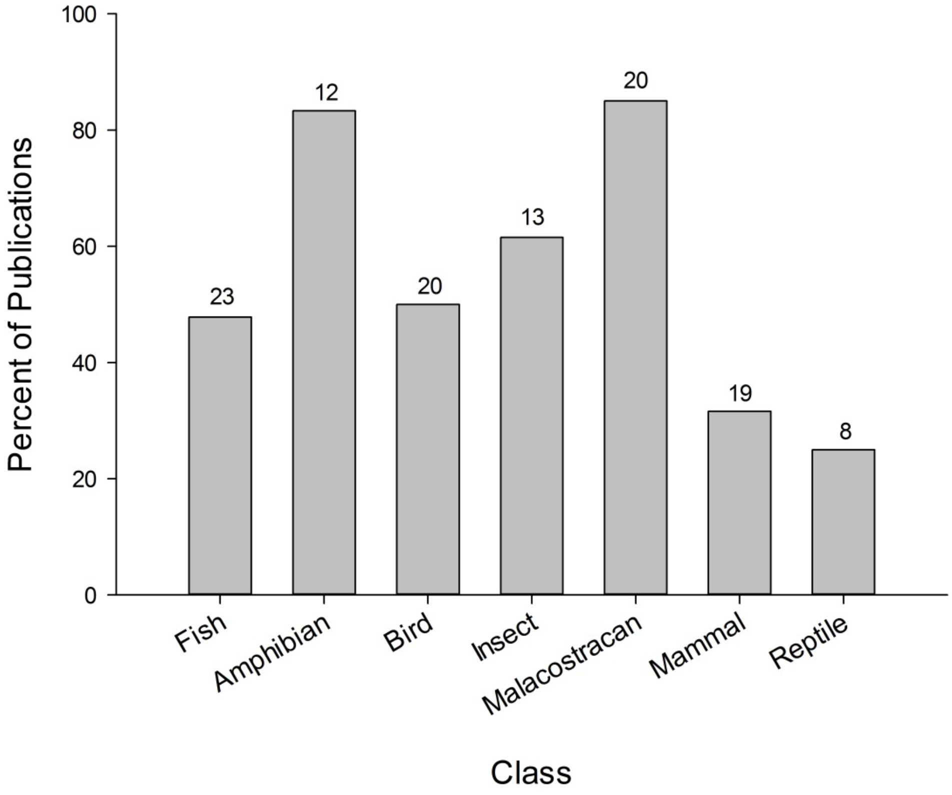
Amphibian
Bird
Fish
Insect
Malacostracan
Mammal
Percent Occurrence
0
20
40
60
80
100
120
Eastern Temperate Forests
Great Plains
Marine West Coast Forest
Mediterranean California
Northern Forests
Northwestern forested mountains
Temperate Sierras
Region

Fig. 10



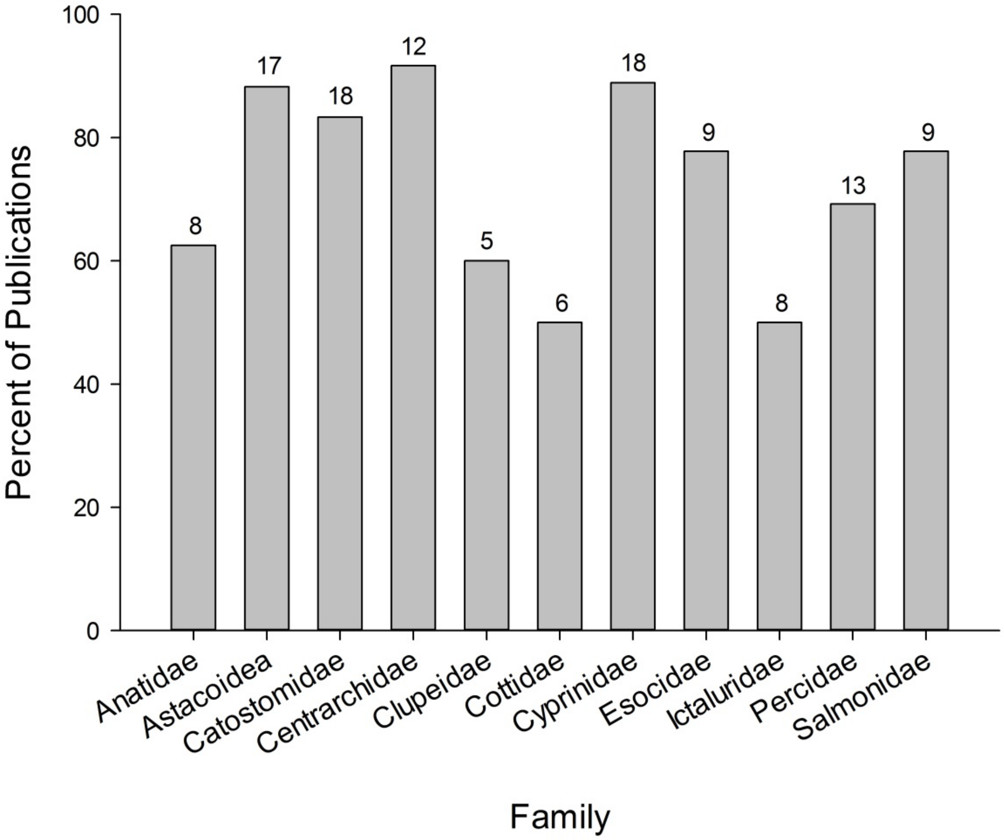
Astacoidea
Catastomidae
Centrarchidae
Cottidae
Cyprinidae
Ictaluridae
Percidae
Salmonidae
Umbridae
Percent Occurrence
0
20
40
60
80
100
120
Eastern Temperate Forests
Great Plains
Marine West Coast Forest
Northern Forests
Northwestern forested mountains
Temperate Sierras
Family

Fig. 11



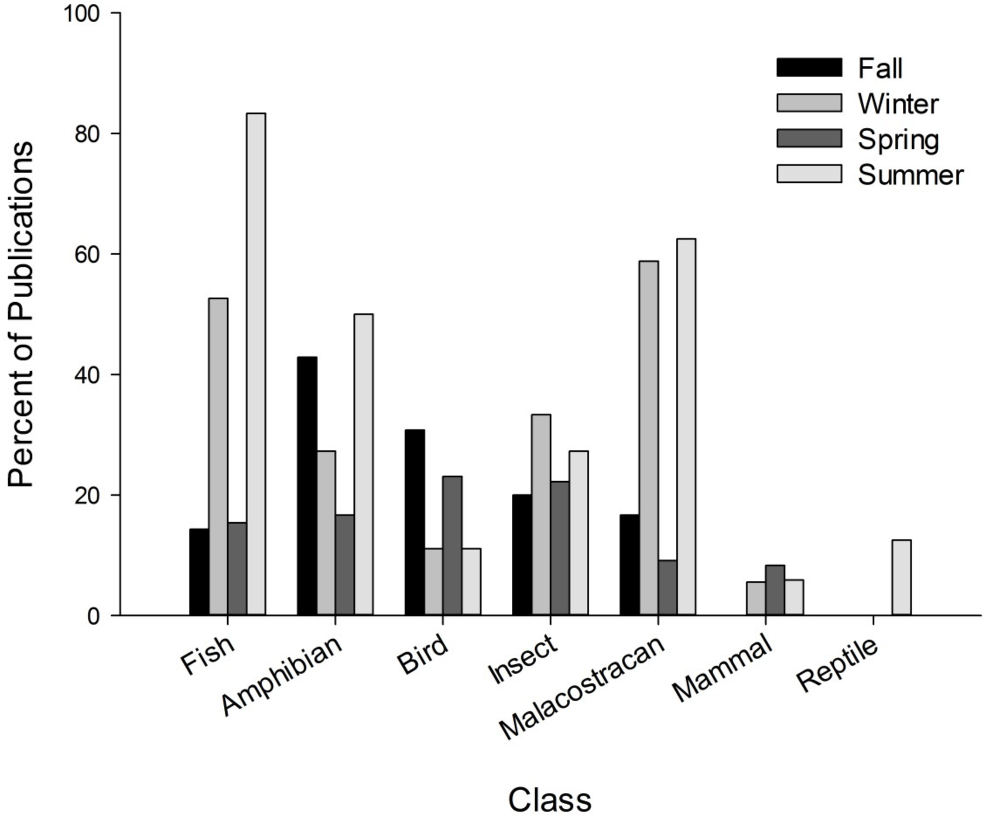
100
80
60
40
20
0
Percent of Publications
23
12
20
13
20
19
8
Fish
Amphibian
Bird
Insect
Malacostracan
Mammal
Reptile
Class

Fig. 12



100
80
60
40
20
0
Percent of Publications
8
17
18
12
5
6
18
9
8
13
9
Anatidae
Astacoidea
Catostomidae
Centrarchidae
Clupeidae
Cottidae
Cyprinidae
Esocidae
Ictaluridae
Percidae
Salmonidae
Family

Fig. 13



Percent of Publications
100
80
60
40
20
0
Fall
Winter
Spring
Summer
Fish
Amphibian
Bird
Insect
Malacostracan
Mammal
Reptile
Class

Fig. 14

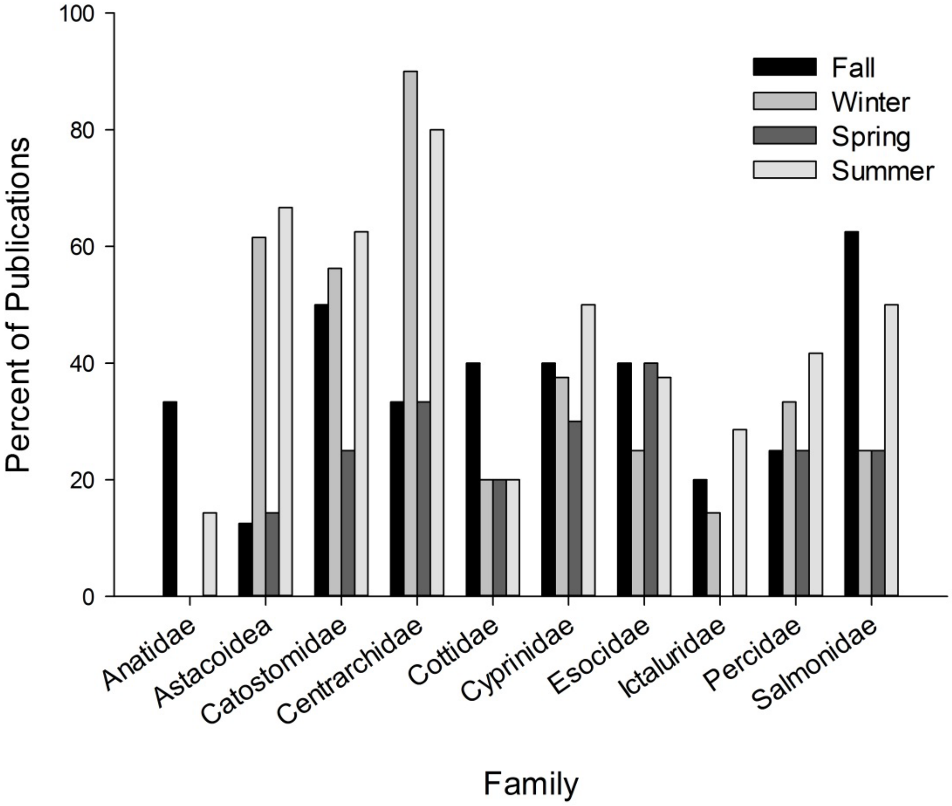
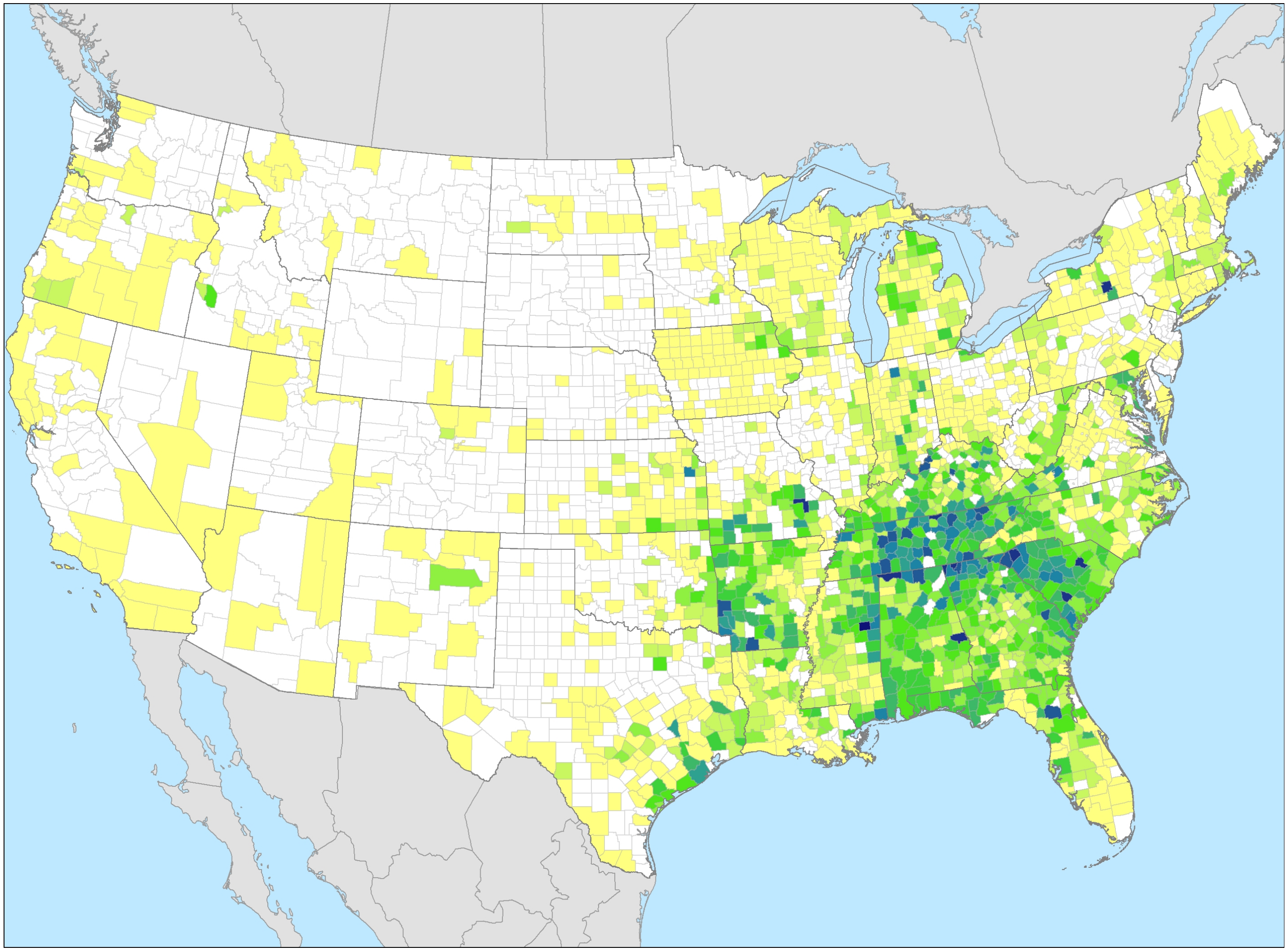

Fall
Winter
Spring
Summer
Percent of Publications
100
80
60
40
20
0
Anatidae
Astacoidea
Catostomidae
Centrarchidae
Cottidae
Cyprinidae
Esocidae
Ictaluridae
Percidae
Salmonidae
Family

Fig. 15



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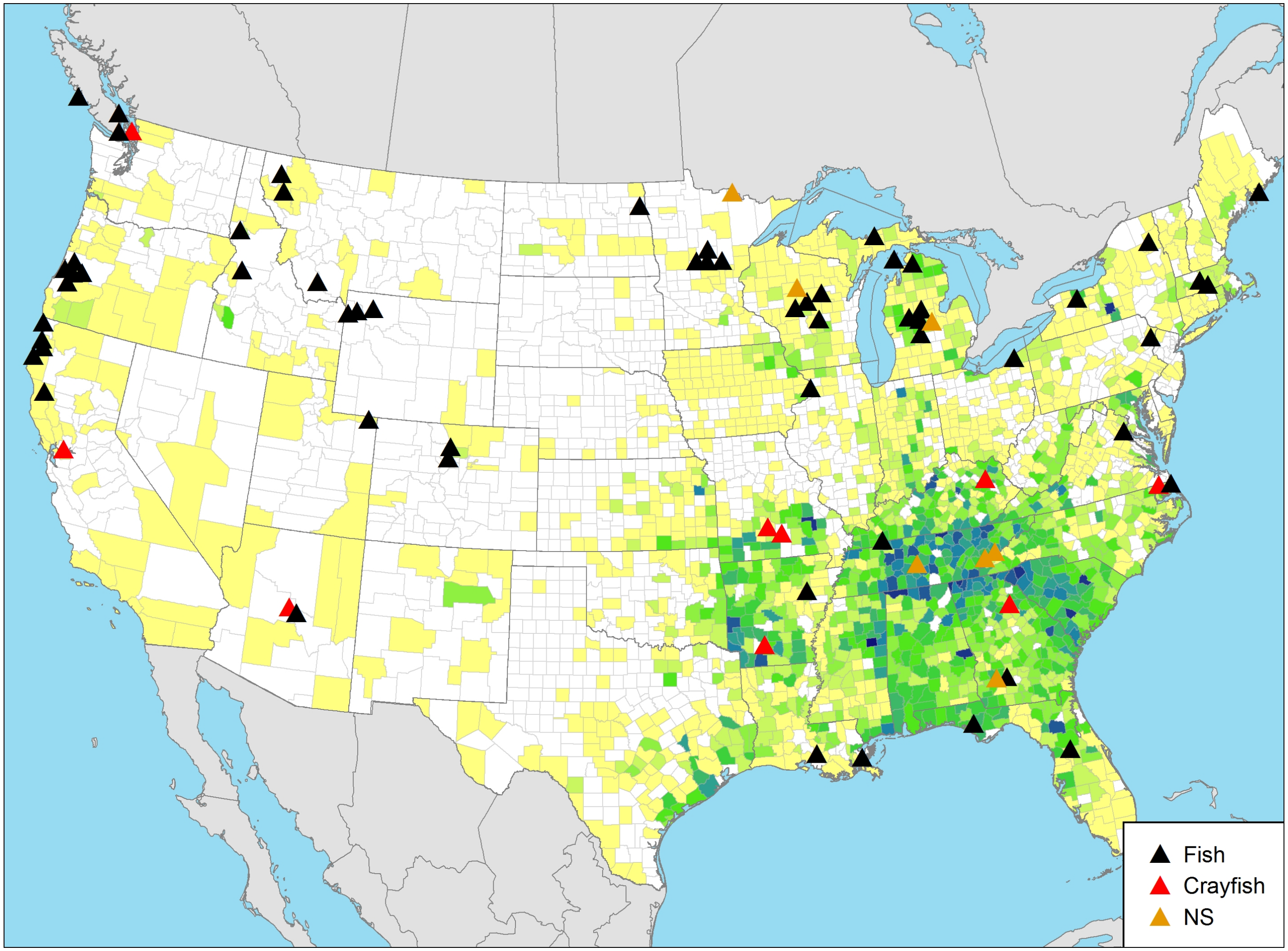

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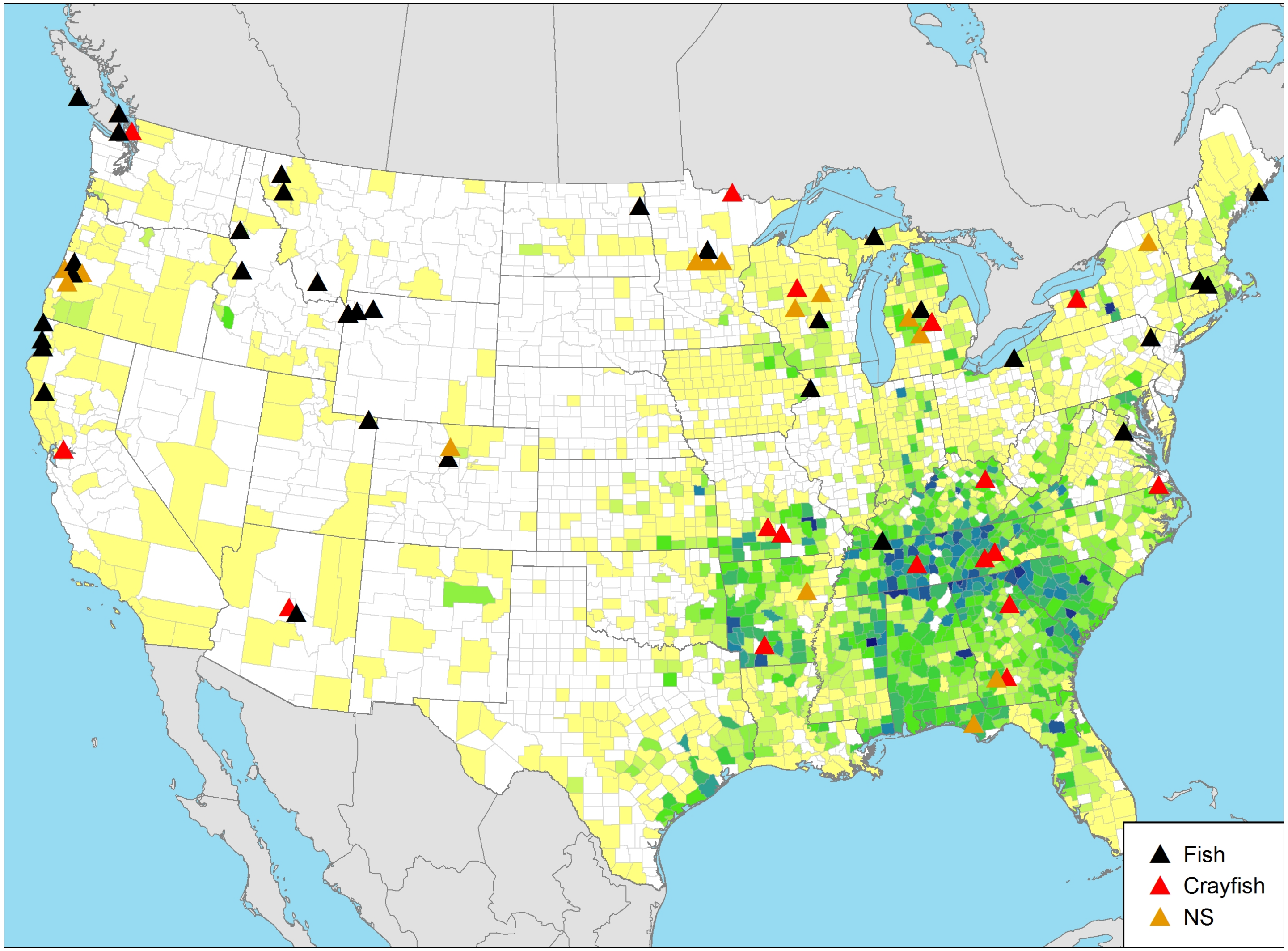

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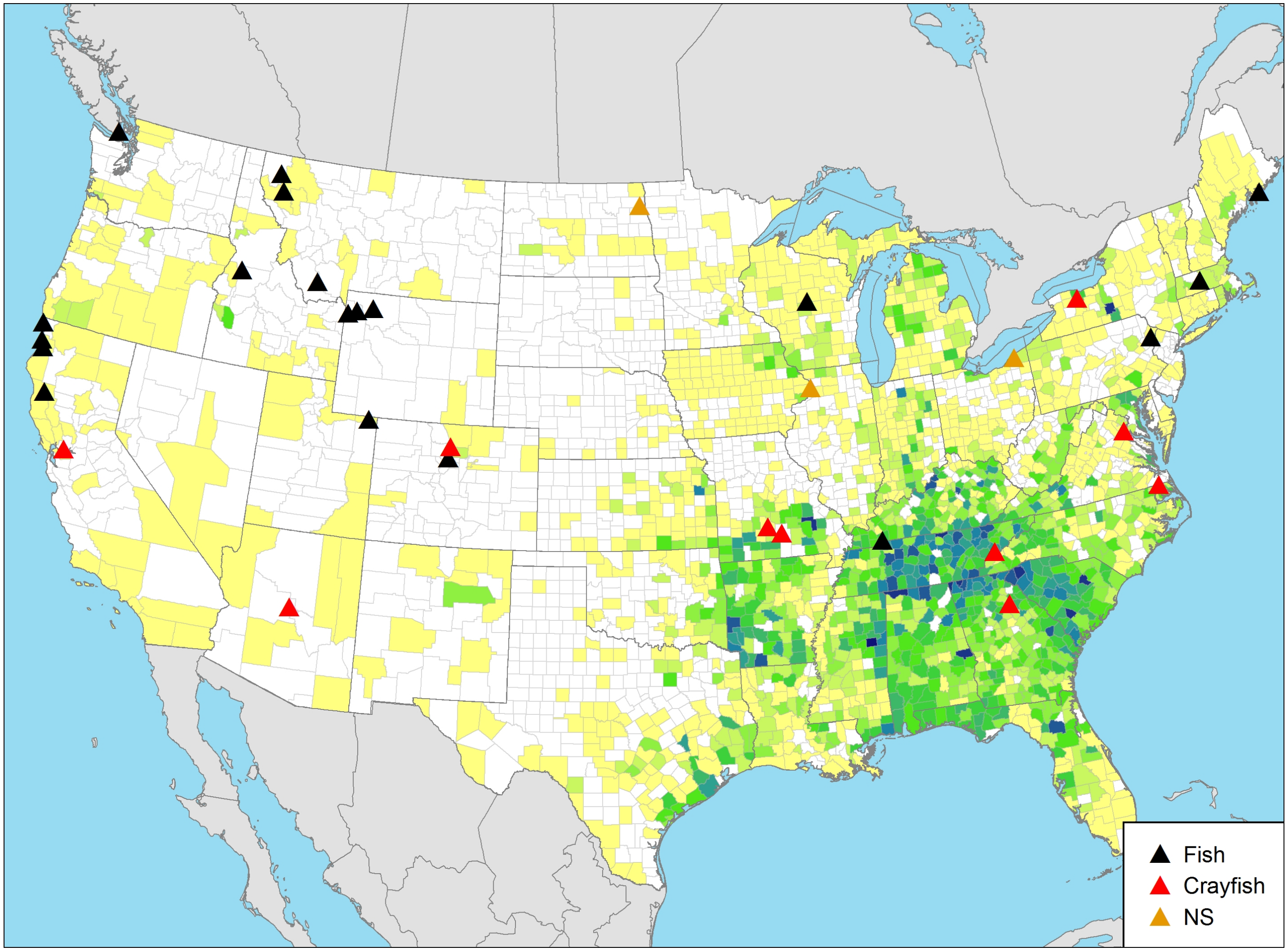


Fig. 19

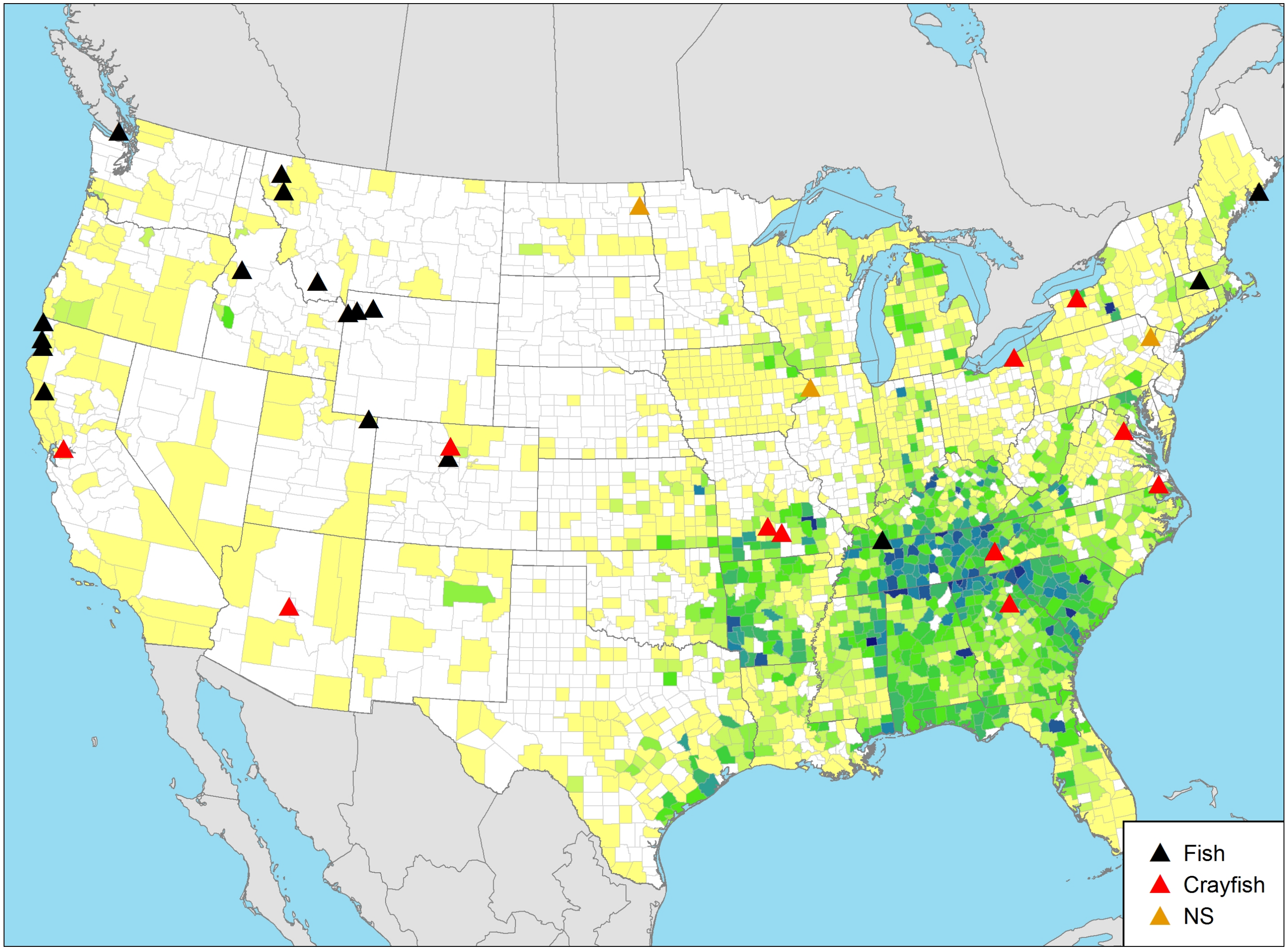


Fig. 20

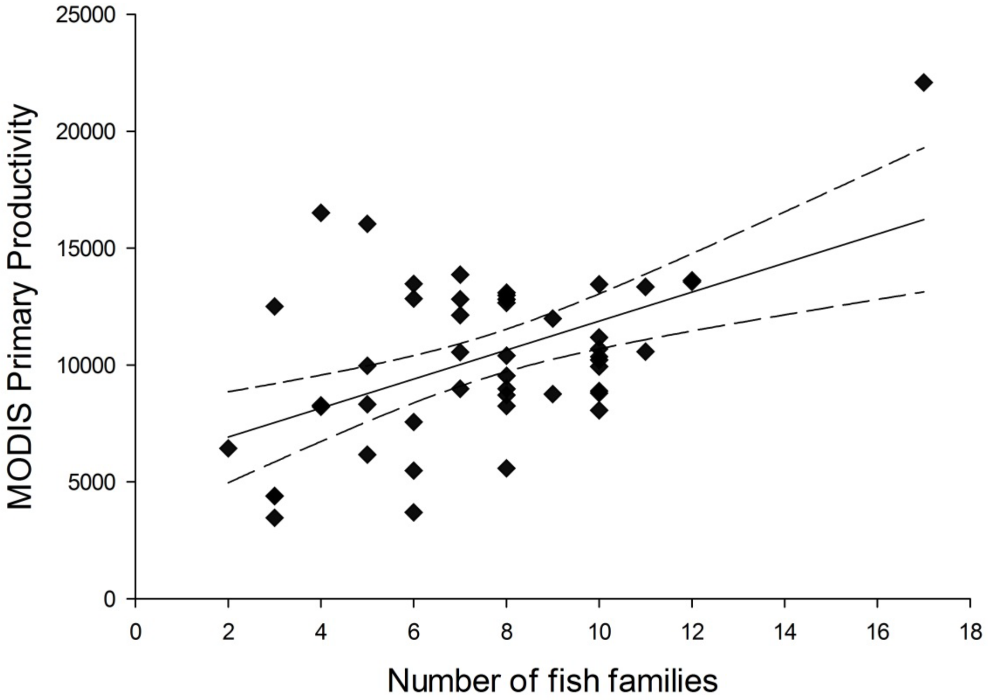
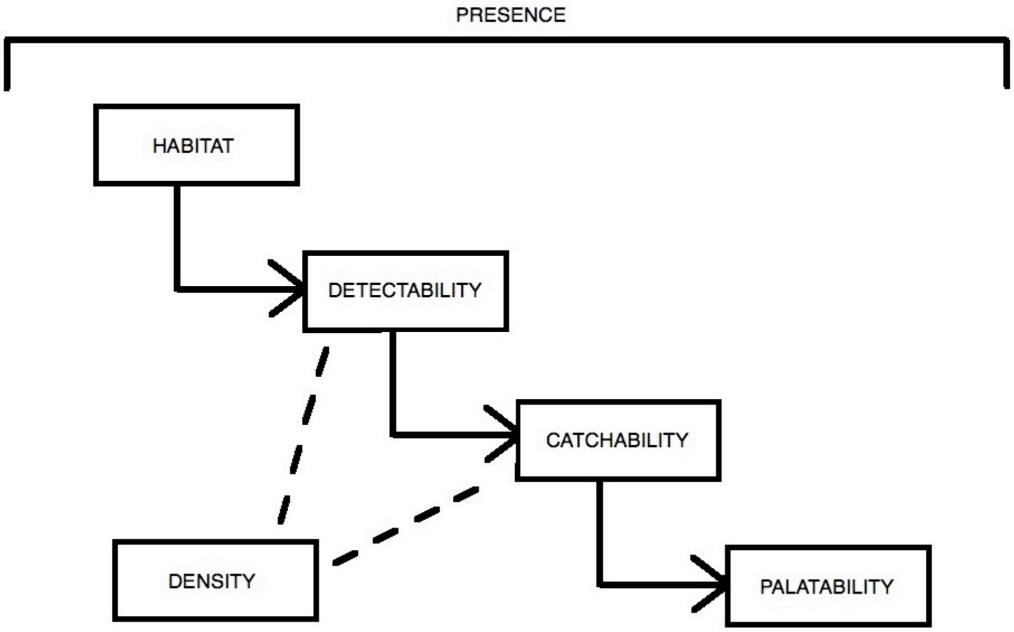

25000
20000
15000
10000
5000
0
MODIS Primary Productivity
0
2
4
6
8
10
12
14
16
18
Number of fish families

Fig. 21


PRESENCE
HABITAT
DETECTABILITY
CATCHABILITY
DENSITY
PALATABILITY