NON-NATIVE FISH IN MOUNTAIN LAKES: EFFECTS ON A DECLINING AMPHIBIAN AND ECOSYSTEM SUBSIDY

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Abstract

Wilderness water resources often provide wildlife habitat and associated recreational opportunities, such as angling or birdwatching. Introduced trout in mountain lakes could affect terrestrial wildlife by changing ecosystem subsidy, which is the flow of nutrients and organisms from aquatic to terrestrial habitats. Trout prey upon larval amphibians and aquatic insects, and the adult stages of aquatic insects and amphibians are prey for bats, birds, snakes, and other terrestrial insectivores. The indirect effects of introduced fish on terrestrial wildlife have rarely been considered, and there have been no prior experiments testing effects of fish stocking on the Cascades frog (federal and California species of special concern). We conducted a four-year replicated whole-lake experiment to assess whether changes in fish abundance could aid frog recovery and whether trout predation of larval amphibians and aquatic invertebrates indirectly affects the density of terrestrial predators. Results show that non-native trout suppress the numbers of the declining Cascades frog and other amphibians, as well as large-bodied aquatic insects such as dragonflies and damselflies. After trout removals, these groups show a marked increase in abundance. We found differences in the species and abundance of garter snakes feeding at lakes with and without trout present. Over 100 species of birds and more than six species of bats use the lake basins during the snow-free season and we are currently assessing the data for patterns associated with trout abundances.

Introduction and Problem Statement

Ecologists are beginning to assess the importance of 'ecosystem subsidies', which are flows of nutrients and organisms across adjacent ecosystem borders. This is an important topic for water resource managers, because decisions about how public or private entities utilize water resources can have implications that stretch beyond the aquatic system. Introduced aquatic vertebrate predators could affect ecosystem subsidy because they have large impacts on local communities. Sport fish have been introduced to many formerly fishless lakes and streams in public lands throughout the USA. The resulting fisheries foster recreational use of wilderness and national forests, however, widespread fish introductions have also dramatically transformed the formerly fishless aquatic ecosystems in ways likely to affect ecosystem subsidy.

Several recent studies have documented strong negative effects of introduced fish on native aquatic fauna, usually using correlations, 'natural experiments', mesocosm studies and field cage studies (Lawler et al. 1999, Knapp et al. 2001, Matthews et al. 2001, Parker et al., 2001, Welsh et al. 2006). These impacts included strong effects on amphibians and emerging aquatic insects. Because these taxa are available as prey for terrestrial animals, their loss indicated that fisheries management may affect ecosystem subsidy of upland habitats by lake communities. We addressed this question by comparing subsidies from basins with and without introduced fish, and by quantifying abundances of terrestrial species likely to consume these subsidies.

In the wilderness areas of the Klamath-Siskiyou bioregion of northern California, no native fishes historically occurred in the high elevation lentic habitats. Over the past several decades, the California Department of Fish and Game (CDFG) has stocked the majority of large lakes in the wilderness areas of California to provide a statewide recreational fishery. Recent surveys by CDFG and the US Forest Service (USFS) found that fish now occur in about 90% of the lakes greater than 2 m deep in the Trinity Alps, Marble Mountains, and Russian wildernesses. Analysis of the survey data from 730 lakes in these wilderness areas also found a negative relationship between the occurrence of fish and the presence and abundance of the Cascades frog, long-toed salamander, and Pacific treefrog (Welsh et al. 2006). These landscape-scale correlations suggest the need to better understand the effects that introduced fish are having on the native fauna in wilderness areas. In September 2006 we completed a four-year replicated whole-lake experiment to study the disturbance of lake communities and their subsidy of adjacent uplands by introduced predatory trout in California.

Objectives

Our work had three primary goals: 1) to assess the spatial extent of terrestrial community subsidy by adjacent aquatic communities by quantifying trout impacts on aquatic insect emergences and amphibians; 2) to assess whether impacts of trout on aquatic insects and amphibians lead to fewer wildlife in the vicinity of wilderness lakes, and 3) to measure the resilience of lake and terrestrial communities following lake restoration to a trout-free condition. We quantified differences among lake basins that were stocked annually with trout, suspended from stocking, had fish removed after the first year of data collection, and were fish-free prior to the start of the project. We focused on the composition, quantity, and size of fauna with both aquatic and terrestrial stages (insects and amphibians), and on upland taxa that are known to feed on these vectors (birds, bats and snakes). Specific hypotheses are:

1. There is a significant difference in the amount and size of emerging aquatic insects among lakes with different quantities of introduced fish.
2. There is a significant difference in the abundance of flying aquatic insects along transects up to 40 m away from lakes with different quantities of introduced fish.
3. There are fewer amphibians in lakes with fish compared to lakes without fish.
4. There are fewer amphibian-specialist snakes around lakes with fish compared to lakes without fish.
5. There are fewer birds in the vicinities of lakes with fish compared to lakes without fish.
6. There is a different assemblage of bats and less large bat activity in the vicinity of lakes with fish compared to lakes without fish.

Procedure

We designed an ecosystem-scale, replicated manipulative experiment to be conducted in the Trinity Alps Wilderness in Trinity and Siskiyou counties, California. Based on prior extensive surveys in the wilderness (Welsh et al. 2006), we identified 16 study basins that were as similar as possible in terms of physical conditions such as elevation, water quality, and size. The basins were between

1920 to 2210 m in elevation, with water depths ranging from 2.7 - 11.2 m. All supported at least a few Cascades frogs or were within 1 km of breeding populations, ensuring that amphibian population recovery was possible within the project period. Twelve of the lakes supported introduced trout and four were fishless. For the study, we chose three fish manipulations (stock annually, suspend stocking, and fish removal via gill-netting) because they are the fisheries management options currently being considered by CDFG for maintaining both a recreational fishery and native biodiversity in wilderness lakes. Aside from the fish-free "reference" basins, the remaining 12 basins were blocked into four groups based on geographic location, and then lakes in each block were randomly chosen as continue to stock lakes, stocking suspension lakes, or fish removal lakes (Figure 1).

Field sampling

We collected pre-treatment data in 2003 at all basins and removed trout from the four fish removal basins in the fall of and winter of 2003. Through the following three summers we conducted repeat sampling of the 16 study basins. All faunal sampling was conducted using a temporal blocked design. Over the course of a field season (June – September), four crews of three people surveyed the 16 study basins in a nine-day period. Given five days off between trips, a total of six sampling trips were conducted during the summers of 2004 and 2005. In 2003, we conducted only five sampling trips to allow time for fish removals, and in 2006 heavy spring snow precluded us from conducting the first sampling trip. Field crews rotated randomly among blocks to reduce surveyor bias. Sampling methods are described below and timing and effort for the different faunal groups and techniques are summarized in Table 1.

Insect sampling techniques included setting three emergence traps in each lake on two consecutive nights per trip, area-constrained odonate exuvia sampling along the shoreline, and sticky trap sampling along four transects that extended10-40 m from shore with four traps set at 10 m intervals per transect. Samples were preserved in the field and brought back to the lab at UC Davis for identification and measurement.

To determine presence and relative numbers of amphibians and garter snakes, we used a shoreline visual encounter survey (VES, Crump & Scott, 1994) in which we searched the shoreline and littoral zone habitats looking under banks and logs and in the substrates. When amphibians or snakes were found, we documented which species were present and counted the number of animals by life stage. In addition, adult Cascades frogs and the two species of garter snakes (*T. atratus* and *T. sirtalis*) were sampled via mark-recapture. This technique provided additional information about habitat use, movement patterns, and survival in habitats with and without fish. During mark-recapture surveys, lake, pond, wet meadow and riparian margins up to 50 m upstream and downstream of lakes were systematically searched for Cascades frogs and garter snakes. Animals were captured by hand or net. Frogs > 40 mm snout-vent length (SVL) and snakes > 340 mm SVL were individually marked using passive integrated transponders (PIT-tags)(see Pope and Matthews 2001 for PIT-tagging methods). To differentiate prey preferences of the two garter snake species, all garter snakes caught in 2005 and 2006 were palpated to force regurgitation of any food in their digestive tracts. We recorded the species and life stage of stomach contents and measured the approximate length of fresh prey items.

To sample birds in the basins, we conducted double observer point-counts on two consecutive mornings at each study basin every two weeks. We used a double-observer approach to increase bird detection probability and reduce variation due to differences in surveyor ability (Nichols et al. 2000). We sampled at up to six survey points in each basin spaced at 100 m intervals to increase the power to detect annual population trends in the basins (Thompson et al. 2002). Starting in 2005, we incorporated an area- and time-constrained bird mapping technique to gain more detailed information about resident and migrant species, territories, breeding and feeding. We set up one 300 X 50 m plot paralleling the shoreline of each study lake. During the survey, one person spent one hour in the plot locating and mapping individual birds, bird interactions, breeding behavior, feeding behavior, and nest sites.

Bat activity was measured in the fish removal and continue stocking lakes using Anabat II ultrasonic acoustic detectors and zero-crossing analyzers (storage zcaims). Starting in 2004, we set up one permanent acoustic monitoring station at each of the eight lakes on the first trip of each season. The detectors were set up within 1 m of the shoreline of the primary lake in the basin with the transducer (microphone) directed over the water. We attached the detectors and recording devices to solar chargers to maintain power throughout the summer. Bat activity was recorded every night all night (unless we had mechanical failure) on data storage cards. Cards were switched out and downloaded every two weeks. Although one cannot estimate density using bat detectors, their use to investigate differential use of habitats by bats has proven effective in identifying differences in activity in relation to habitat (Seidman and Zabel 2001, Gehrt and Chelsvig 2004) and invertebrate activity (Hayes 1997, O'Donnell 2000).

In addition to faunal sampling, we also measured aquatic and terrestrial habitats. In each lake we recorded substrate, coarse woody debris, emergent vegetation, depth and temperature at three points along 50 littoral zone transects per lake. We also recorded pH and conductivity at each lake every trip in 2004 and 2005. We quantified terrestrial habitats within 50 m around each lake by using a stratified sampling grid to estimate slope, aspect, substrate, tree diameter-at-breast height, and tree, shrub, and forb cover in plots spaced 50 m apart around the lake. Distance from shore for plot center was selected using random numbers.

Analysis

Our analysis focuses on differences and changes over time in number of aquatic insects and amphibians for taxa expected to be vulnerable to trout predation. We have not completed analyses on the indirect effects of trout on birds and bats so results will not be presented here but we do present preliminary summary information. In addition, we are still processing the insect samples collected in summer 2006, so we only provide summary results for the first three sampling years. For the amphibian and reptile surveys (both VES and mark-recapture), we have complete results from the four years. We also provide four years of results assessing the indirect effects of trout stocking on garter snakes.

Trout

Each year of the project we set one gill net per lake for a minimum of four hours to obtain an estimate of trout density (catch per unit effort, CPUE) in the study lakes. We compared trout densities in the 12 treatment lakes in 2003 to ensure that pretreatment densities were not significantly different among treatments. We used repeated measures ANOVA to compare CPUE in stocked lakes versus suspend stocking lakes from 2004-2006 to see if differences occurred post-treatment. Removal lakes were not included in this analysis because, after 2003, we did not catch any trout in the removal lakes during the 4-hr gill-net samples.

Insects

Using the emergence trap data from the first three years of the study, we compared sizes of insects from trout-containing (stock and suspend stocking) and trout-free lakes (removal and control) to assess whether trout affect large-bodied insects ($\geq$ 3 mm) differently than small-bodied (< 3 mm). We used repeated measures split-plot ANOVA for the analysis with treatment as the main plot effect and year as the subplot effect.

We identified the odonate exuvia samples collected from 2003-2005 to genus. We compared the mean number of exuvia collected per year of the most frequently occurring genera of dragonflies (*Aeshna*) and damselflies (*Enallagma*) using a split plot ANOVA.

Amphibians

The Cascades frog has been negatively correlated with the presence of trout in water bodies in the Trinity Alps (Welsh et al. 2006). Our analyses focus on determining if there is a cause/effect relationship between trout and this sensitive species by comparing frog abundances before treatments and then for three years post-treatment to see if there is recovery in the fish removal lakes. Again we used repeated measures split plot ANOVA with treatment as the main plot effect and year as the subplot effect.

We used the *Rana cascadae* mark-recapture data to assess changes in adult recruitment among treatments within years. We focused on the mean number of untagged or new adults at each basin per year to provide an estimate of new reproductive animals in the basins. Again, we used repeated measures ANOVA for the analysis.

Garter Snakes

We found two species of garter snakes in our 16 study basins: the common aquatic garter snake (*Thamnophis atratus*) is a known fish specialist that also preys upon amphibians and the common garter snake (*T. sirtalis*) is a local amphibian specialist in the Trinity Alps. We compared the diet and distribution of these two garter snake species in relation to introduced trout and amphibians to assess whether introduced trout may act as a supplemental prey source that facilitates the population increase and spread of *T. atratus* at the possible detriment of *T. sirtalis*. The presence of a common, consistent introduced prey source (fish) in sub-alpine mountain lakes of northern California may have allowed *T. atratus* to move upstream from their more typical natural trout stream habitats (Lind and Welsh 1994) into these historically fishless habitats. With the presence of introduced trout, *T. atratus* may be able to reach high densities independent of native amphibian prey. Even moderate predation by *T. atratus* on native amphibians could cause significant declines, especially if the amphibian population numbers are already depressed by other causes such as introduced fish.

We summarized the diet of the two species by comparing the proportion of trout or amphibian prey in stomach contents, obtained by palpating snakes encountered in the field. For the distribution analysis, we combined three data sets all collected from the Klamath Mountains between 1999 and 2006: the first is a large-scale snapshot census of lentic habitats throughout three wilderness areas in the Klamath-Siskiyou (High Lakes Survey), the second is the study described above, and the third is a detailed case study in one sub-watershed sampled in detail for three years (Deep Creek Monitoring). The combination of data sets allows us to compare observed patterns across spatial scales and to incorporate both experimental and correlational analyses (Pope et al. in preparation). We used logistic regression to compare the occurrence of the two garter snake species with amphibians and trout while accounting for spatial autocorrelation and habitat variables. We modeled the probability (p) of finding each snake species at location i as

$$p_i = \frac{e^{\theta i}}{1 + e^{\theta i}}$$

where the linear predictor θ is a function of the covariates given by:

$$\theta = \text{FISH} + \text{AMPHIBIANS} + \text{FISH*AMPHIBIANS} + lo(\text{AREA}) + lo(\text{ELEVATION}) + lo(\text{LOCATION}). \quad (1)$$

FISH and AMPHIBIANS are categorical variables indicating presence/non-detection of fish and amphibians during VES. The two variables combined by an asterisk represent the interaction between the covariates. We included this interaction term because the presence of both salmonids and amphibians together may increase the likelihood of finding *T. atratus* given that the snake eats both prey groups. *Lo*(·) is a nonparametric smoothing function that characterizes the relationship of the continuous variables on p_i. The variable *lo*(LOCATION) was a smooth plane of UTM northing and easting.

Results

We completed 22 two-day sampling periods at the experimental lake basins over the four-year study (five sampling periods in 2003 and 2006 and six in 2004 and 2005). Insect sampling resulted in approximately 1,900 emergence trap samples, 384 benthic sweep samples, 1,042 exuvia samples and 3,570 sticky trap samples. We are currently processing all 2006 samples and sticky traps from 2005. During VES surveys, five species of amphibians were encountered fairly regularly including Cascades frog (*Rana cascadae*), Pacific chorus frog (*Pseudacris regilla*), western toad (*Bufo boreas*), long-toed salamander (*Ambystoma macrodactylum*) and rough-skinned newt (*Taricha granulosa*). An additional species, Pacific giant salamander (*Dicamptodon tenebrosus*) was found at one study lake. The aquatic garter snake (*Thamnophis atratus*) and common garter snake (*T. sirtalis*) were the only reptiles consistently found in association with lentic habitats. We identified 113 species of birds during point-count surveys at the 16 basins during the first three years of the study with 21 species observed over 100 times (Table 2). Eight bat detectors were set at the fish removal and stock lakes in summers 2004-2006. Approximately 249,315 files were recorded over 283 detector nights in 2004; 388,287 files over 294 detector nights in 2005; and 224,383 files over 246 detector nights in 2006. Currently, the 2004 data has been sorted into call frequency categories and the 2005 data is close to 50% reviewed.

Trout

In 2003, pretreatment densities of trout in the 12 lakes with trout were similar in the three treatment categories (df = 2, F = 0.25, P = 0.784) with an average CPUE of 3.57 trout per hour (95% confidence intervals 1.31-5.83). We removed 672 trout from the four fish removal lakes in the fall and winter of 2003 and did not catch trout again in the 2004-2006 four-hour gill net sets (Figure 2). In 2006, however, we observed fingerling brook trout in the fish removal lake in Block 4 suggesting that we missed at least two trout in that lake during fish removals. We used repeated measures ANOVA to compare 2004-2006 CPUE data from the stock and suspend lakes to see if a difference between treatments was observable in three years (Figure 2). We did not find any significant differences by treatment (df = 1, F = 2.03, P = 0.23) or treatment:year (df = 2, F = 0.63, P=0.13). In one of the suspend stocking lakes, however, CPUE dropped from 5.88 trout/hr in 2003 to 0 trout/hr in 2006.

Insects

We ran simple split plot ANOVAs on the mean number of all insects < 3 mm and $\geq$ 3 mm caught in emergence traps during 2003-2005 surveys. We only found a significant year effect for insects $\geq$ 3 mm (Table 3). Although we did not find significant treatment X year effects for either size group, we did see trends where insects $\geq$ 3 mm were increasing in removal lakes and insects < 3 mm were increasing in stocked lakes (Figure 3). In general the number of insects in the emergence trap samples were highly variable. With another year of data we hope to improve our analyses.

We found a significant treatment and treatment X year effect for *Aeshna* and a significant treatment effect for *Enallagma* (Table 4). Mean numbers of exuvia of these groups increased more in the trout removal lakes compared to the stock or suspend lakes over the two post-treatment years (Figure 4). An interesting note is that both *Aeshna* and *Enallagma* also increased in 2005 at Hidden Lake, the stocking suspension lake that was found fishless in 2006 (Figure 4).

Amphibians

We found significant year (df = 3, F-ratio = 9.52, P = 0.0002) and treatment X year (df = 3, F-ratio = 5.05, P = 0.0004) effects for *R. cascadae* frogs from repeated measures ANOVA on the 4-year VES data (Figure 5). Moreover, using repeated measures ANOVA on the mean number of adult *R. cascadae* (> 42 mm

SVL) caught during mark-recapture surveys per year at the treatment lakes, we found that recruitment dramatically increased in the trout removal basins compared to the stock and suspend stocking lakes (Treatment X Year df = 6, *F*-ratio = 2.56, *P* = 0.057; Figure 6).

Garter Snakes

We sampled stomachs from 458 snake captures: 155 T. *atratus* and 303 *T. sirtalis*. A total of 152 (33%) of the stomachs contained prey (57 *T. atratus* and 95 *T. sirtalis*), which produced 405 individual prey items. About half of the *T. atratus* with stomach contents had trout in their stomachs and the other half had amphibians with *R. cascadae* in 33% of the *T. atratus* with prey. We only found amphibians in the stomachs of *T. sirtalis. Five* amphibian species were represented including all life stages except eggs. *Rana cascadae* was found in 66% of the *T. sirtalis* with prey in their stomachs.

Details on the results of the logistic regression models to assess the distribution of *T. atratus* and *T. sirtalis* in relation to amphibians and fish are beyond the scope of this report. In summary, we found that *T. atratus* presence at a water body is positively associated with presence of trout and the presence of trout with amphibians but not amphibians alone. In contrast, *T. sirtalis* is only positively associated with the presence of amphibians (Pope et al. in prep.)

Conclusions

This study has yielded several significant findings to date, with more expected as data analysis proceeds. Most importantly, this carefully controlled, manipulative experiment provides conclusive proof that fish removals are effective in restoring local populations of amphibians, including *Rana cascadae*, a state and federal species of special concern. Although densities of adults in fish removal basins are still below those in some historically fishless basins, we have had excellent recruitment of frogs in all lakes where trout removal was successful.

Large bodied aquatic insects also increased in abundance following fish removals, especially dragonflies and damselflies. These taxa are important predators in both aquatic and terrestrial life stages; for example they provide natural mosquito control (e.g., Finke et al. 1997). Preserving populations of these insects is likely to enhance the wilderness experience for stakeholders, as evidenced by the frequency with which they are featured in the arts (paintings, jewelry, photography, poetry, and so forth). We note that our largest data set for insects is still being constructed via lab work (sticky traps) but observations thus far suggest that these data will serve to strengthen our hypothesis that trout decrease the emergence of large-bodied insects from lakes.

The research also showed that the presence of fish is strongly correlated with the distribution of garter snakes. In lakes with fish, *T. sirtalis* is largely replaced by the aquatic garter snake (*T. atratus*). Diet analysis strongly suggests that the lack of amphibian prey in lakes with fish causes the corresponding dearth of *T. sirtalis*. Approximately 100% of meals recovered from *T. sirtalis* were identified as amphibians. The diet of *T. atratus* was mixed; it contained an equal percentage of fish and amphibians. The presence of abundant alternative prey (fish) means that the density of *T. atratus* does not depend on amphibians, so it can drive amphibians to low levels without suffering a corresponding reduction in its population size. This food web configuration is known as apparent competition (Holt et al. 1994) or sometimes hyperpredation (Courchamp et al. 2000).

In addition to the results from our main experiment, the data we collected is some of the best natural history data available for the Trinity Alps. We have the first documented sighting of Pine Martin for this region, we have generated a list of 113 bird species complete with relative abundances and breeding activity data, and our extensive bat surveys are the first completed for the area. We plan to make the bird data available as a birder's checklist, to be distributed to area campsites, resorts and outfitters. The bat data will establish whether fisheries management of water resources affects the local abundances or taxonomic composition of the bat community. Bat activity over the water was often quite intense, as indicated by the number of call files logged.

Water resource managers are almost always required to balance the needs of various stakeholders, including environmentalists, anglers, and wildlife managers, among others. The wider effects of sport fish stocking have rarely been addressed, and never as comprehensively as in this study. The idea that sport fish might cause amphibian population declines has been controversial, because most studies to date have been correlational (but see Vredenburg 2004) and because amphibian decline may have a variety of causes. This project demonstrated conclusively that fisheries management decisions can have large effects on amphibians, on large-bodied insects, and on terrestrial predators that feed emerging aquatic animals.

Wildlife managers can use these results to preserve a diversity of wildlife viewing opportunities and to protect populations that are important to natural food webs (e.g. dragonflies). In particular we show that removal of fish from some lakes can reverse local amphibian declines. This is of increasing urgency in high mountain lakes, because an invasive fungal disease, chytridiomycosis, is currently decimating frog populations. In most diseases, a small percentage of individuals have some natural disease resistance, however if the population becomes too small, not enough resistant individuals will occur and the population will go extinct.

We hope the information provided by this study will enable wildlife managers to balancing angling opportunities with the need to maintain sizable amphibian populations. In addition to the usual scientific outlets, we plan to disseminate our results broadly to fisheries and wildlife managers, water resource managers, angling associations, and environmental groups.

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Table 1. Summary of faunal sampling techniques, timing of sampling and purpose of sampling during the four-year study.

Taxon	Technique	Years Implemented	Frequency	Purpose
Insects	Emergence traps	2003-2006	3 traps, 2 nights, every trip	Estimate of composition,number and size emerging from lakes
	Benthic sweeps	2003-2006	3 sweeps, 2 trips per year	Estimate of composition,number and size in benthos
	Odonate exuvia sampling	2003-2006	4 plots every trip	Identification and size at metamorphosis
	Sticky traps	2003-2005	16 traps set for 2 wks every trip	Abundance and proportion of aquatic vs. terrestrial insects up to 40 m from shore
Trout	Gill-netting	2003-2006	1 4-hr set per year	Density, size and species of trout
Amphibians	Visual encounter surveys	2003-2006	1 every trip	Presence and abundance of species by lifestage
	Mark-recapture (adult *Rana cascadae*)	2003-2006	1 every trip	Recruitment, movement, population size and growth
Reptiles	Visual encounter surveys	2003-2006	1 every trip	Presence and abundance of species by lifestage
	Mark-recapture (garter snakes)	2004-2006	whenever encountered	Recruitment, movement and growth
	stomach palpation	2005-2006	whenever encountered	Diet
Birds	Point count surveys	2003-2006	2 mornings every trip	Composition and relative abundance
	Bird mapping	2005-2006	2 mornings every trip	Composition and behavior
Bats	call recording	2004-2006	1 detector recording nightly all summer	Species group identification and index of activity

Table 2. Bird species recorded > 100 times during 2003-2005 point count surveys and number of times recorded at any of the 16 study basins.

Species	2003	2004	2005	Total
Dark-eyed Junco	814	1474	1565	3853
Mountain Chickadee	918	680	1080	2678
Red-breasted Nuthatch	771	608	857	2236
Yellow-rumped Warbler	622	390	615	1627
Steller's Jay	356	292	359	1007
American Robin	230	109	290	629
Golden-crowned Kinglet	121	132	289	542
Rufous Hummingbird	68	273	114	455
Pine Siskin	51	242	114	407
Brown Creeper	95	93	189	377
Clarck's Nutcracker	74	119	154	347
Townsend's Solitaire	106	56	162	324
Northern Flicker	58	137	116	311
Fox Sparrow	39	57	166	262
American Dipper	30	71	86	187
Green-tailed Towhee	47	43	77	167
Olive-sided Flycatcher	43	58	65	166
Hermit Warbler	52	35	76	163
Lincoln's Sparrow	5	49	96	150
Hermit Thrush	54	9	76	139
Nashville Warbler	56	60	17	133

Table 3. Repeated Measures ANOVA results for mean number of insects < 3 mm and ≥ 3 mm from 2003-2005 emergence trap samples for treatment lakes. All count data was log-transformed.

Source	df	ss	ms	*F*	
< 3 mm					
Treatment (*T*)	2	13785.92	6892.959	4.44	*P* = 0.066
Lake (*L*)	6	9322.239	1553.707		
Year (*Y*)	2	29412.96	14706.48	1.34	*P* = 0.299
T X *Y*	4	28109.83	7027.457	0.64	*P* = 0.645
L X *Y*	12	131978.7	10998.23		
≥ 3 mm					
Treatment (*T*)	2	1334.595	667.2973	3.8	*P* = 0.086
Lake (*L*)	6	1053.932	175.6553		
Year (*Y*)	2	562.2752	281.1376	4.79	*P* = 0.030
T X *Y*	4	369.3375	92.33437	1.57	*P* = 0.245
L X *Y*	12	704.9012	58.74177		

Table 4. Repeated Measures ANOVA results for the mean number of Aeshna and Enallagma found per year during exuvia surveys for 2003-2005 by treatment. All count data was log-transformed.

Source	df	ss	ms	*F*	
Aeshna					
Treatment (*T*)	3	2.27197	0.757323	3.28	*P* = 0.080
Lake (*L*)	8	1.849811	0.231226		
Year (*Y*)	2	0.571371	0.285686	6.99	*P* = 0.007*
T X *Y*	6	1.065358	0.17756	4.34	*P* = 0.009*
L X *Y*	16	0.653935	4.09E-02		
Enallagma					
Treatment (*T*)	3	1.189296	0.396432	0.79	*P* = 0.532
Lake (*L*)	8	4.008849	0.501106		
Year (*Y*)	2	1.773161	0.886581	7.11	*P* = 0.006*
T X *Y*	6	0.713276	0.118879	0.95	*P = 0.486*
L X *Y*	16	1.996369	0.124773		

List of Figures

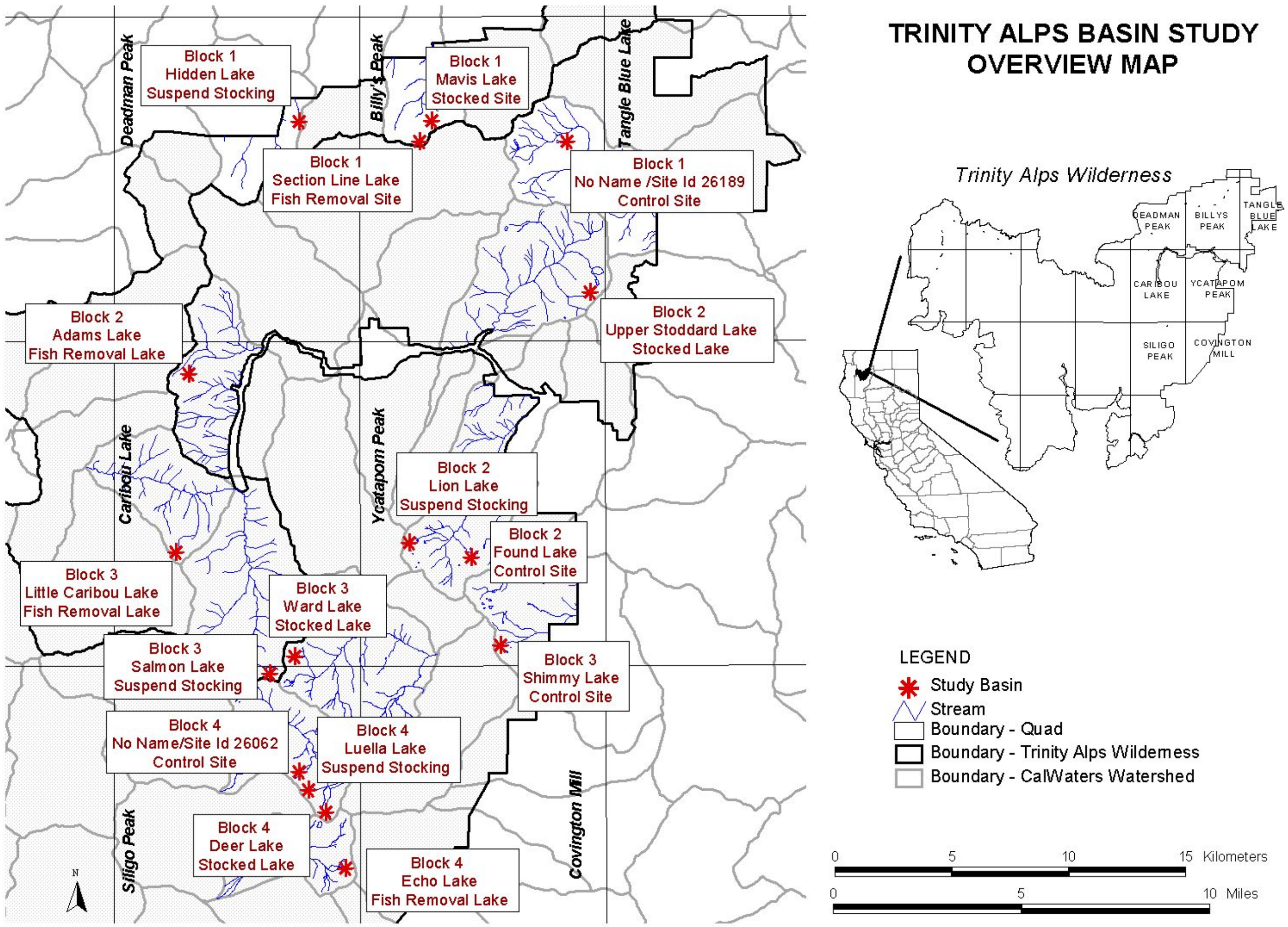

Figure 1. Map of study area including the 16 study lakes and their treatment categories.

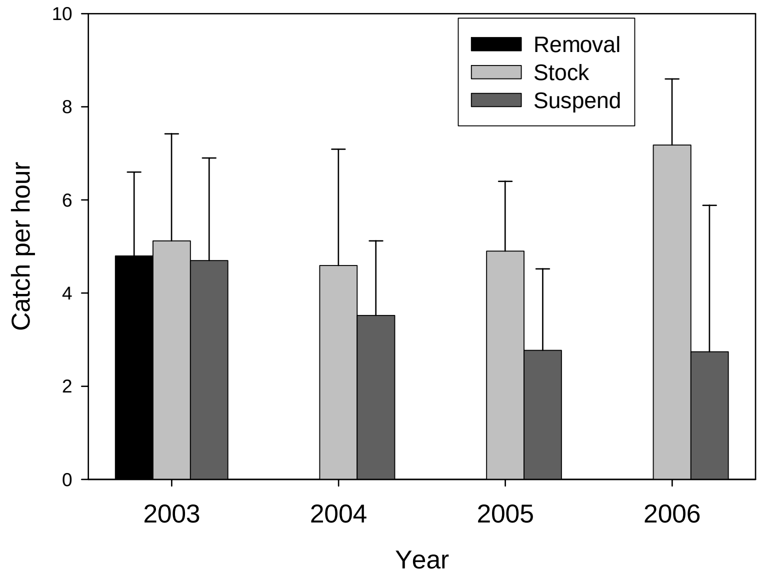

Figure 2. Mean number of trout caught per hour of gill net set for each treatment category over the four years of the study. 2003 was pre-treatment (before fish removals) and 2004-2006 were post-treatment. Error bars represent +1 SE.

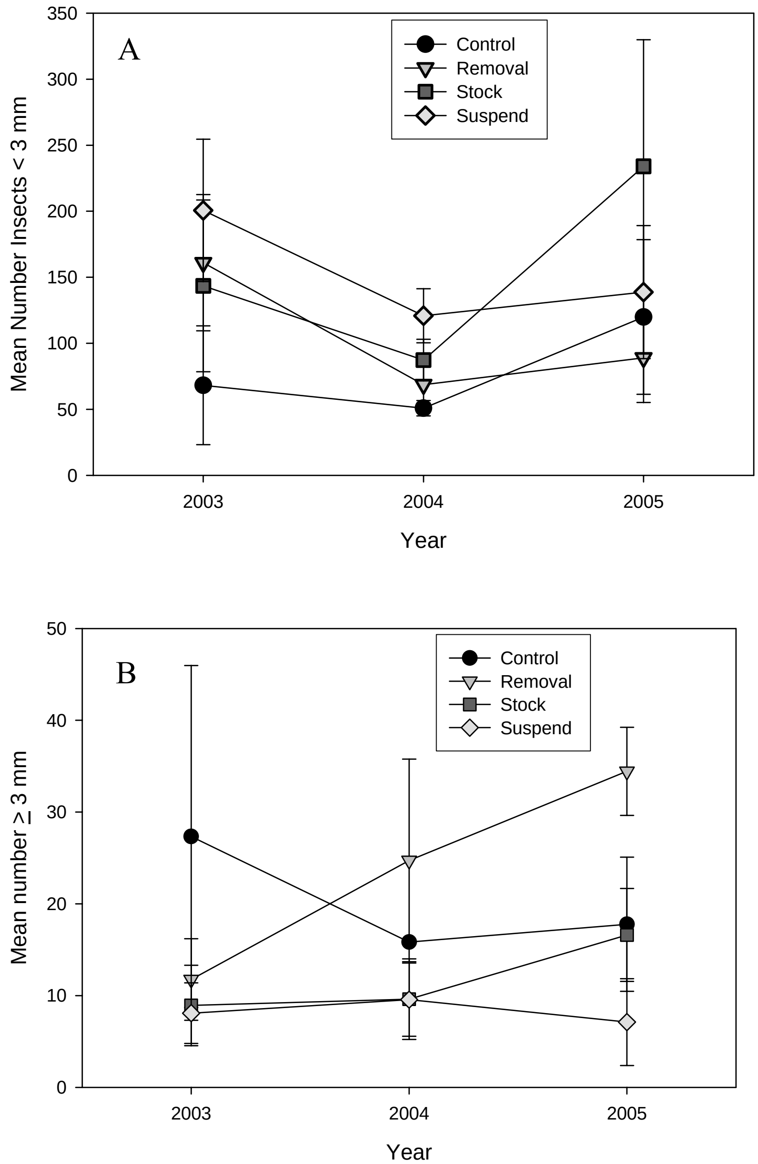

Figure 3. Summary of the mean number of insects caught in emergence traps by treatment per year separated by insects smaller than 3 mm (A), and insects equal or greater than 3 mm (B). 2003 was pre-treatment (before fish removals) and 2004-2006 were post-treatment. Error bars represent +/- 1 SE.

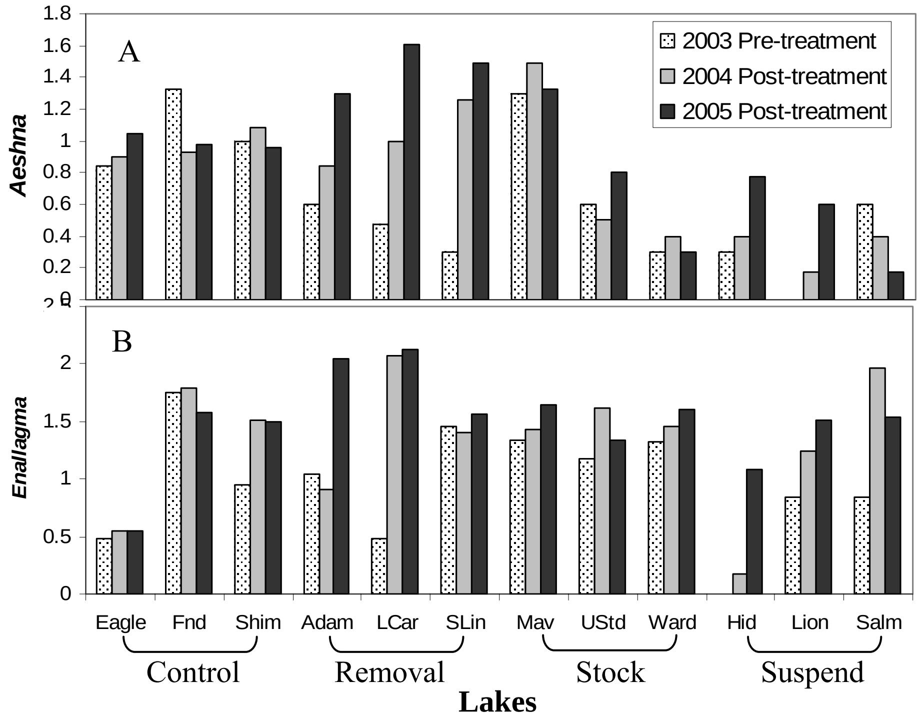

Figure 4. Mean number of *Aeshna* (A) or *Enallagma* (B) exuvia collected per year per lake. Lakes are grouped by treatment category or control. Block 4 lakes were not included because that group was at the elevational limit of odonates and very few (< 10) exuvia were collected in that block.

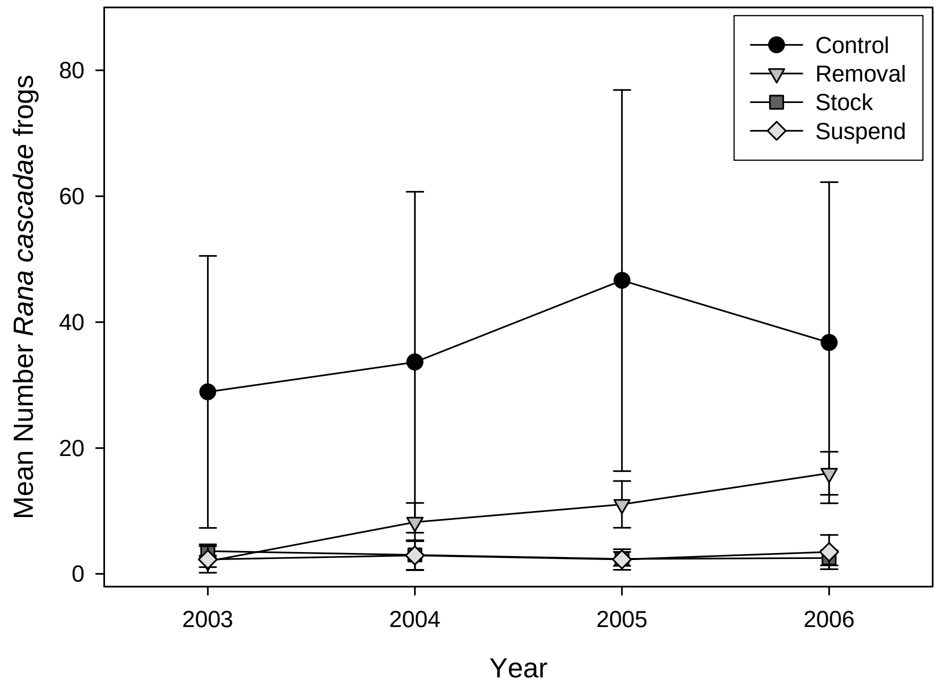

Figure 5. Summary of the mean number of *Rana cascadae* frogs observed in the treatment lakes from 2003-2006 by treatment category. 2003 was pre-treatment (before fish removals) and 2004-2006 were post-treatment. Error bars represent +/- 1 SE.

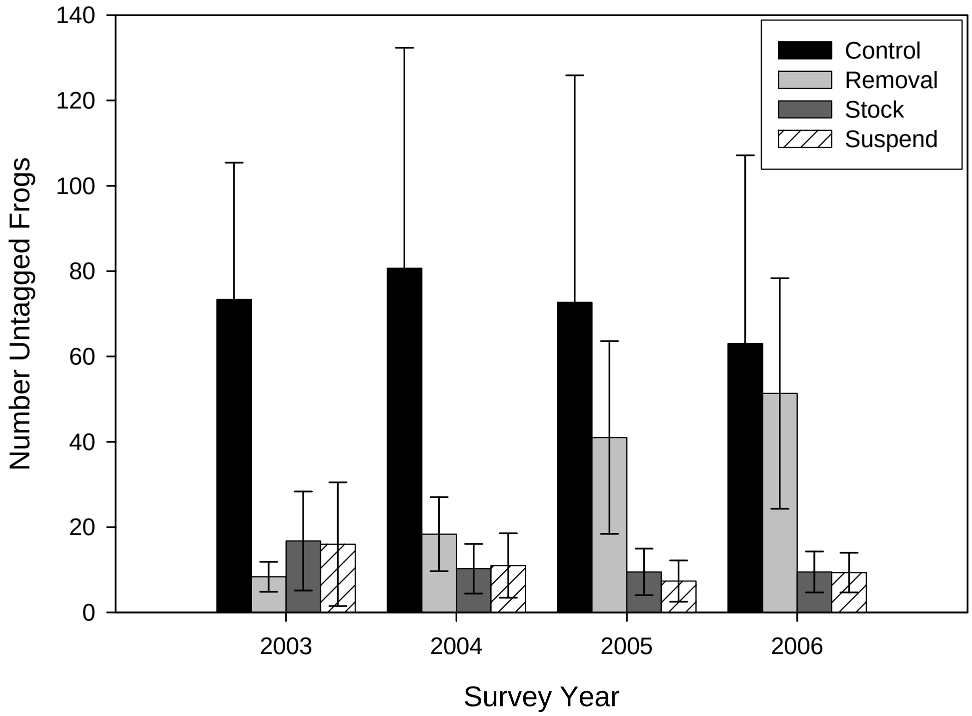

Figure 6. Summary of the mean number of untagged adult (>42 mm SVL) *Rana cascadae* frogs caught in the treatment basins from 2003-2006 by treatment category. 2003 was pre-treatment (before fish removals) and 2004-2006 were post-treatment. No frogs were tagged prior to 2003. Error bars represent +/- 1 SE.

List of publications

Welsh, H. H., K. L. Pope and D. Boiano. 2006. Sub-alpine amphibian distributions related to species palatability to non-native salmonids in the Klamath mountains of northern California. *Diversity and Distributions* 12: 298–309.