

## INTRODUCED TROUT SEVER TROPHIC CONNECTIONS IN WATERSHEDS: CONSEQUENCES FOR A DECLINING AMPHIBIAN

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**Abstract.** Trophic linkages between terrestrial and aquatic ecosystems are increasingly recognized as important yet poorly known features of food webs. Here we describe research to understand the dynamics of lake food webs in relation to a native riparian amphibian and its interaction with introduced trout. The mountain yellow-legged frog *Rana muscosa* is endemic to alpine watersheds of the Sierra Nevada Mountains and the Transverse Ranges of California, but it has declined to a small fraction of its historical distribution and abundance. Although remaining frogs and introduced trout feed in different habitats of alpine lakes, our stable-isotope analyses clearly show that the same resource base of benthic invertebrates sustains their growth. During one period, insect emergence from naturally fishless lakes was nearly 20-fold higher compared to adjacent lakes with trout, showing that fish reduce availability of aquatic prey to amphibious and terrestrial consumers. Although trout cannot prey on adult frogs due to gape limitation, foraging post-metamorphic frogs are 10 times more abundant in the absence of trout, suggesting an important role for competition for prey by trout in highly unproductive alpine watersheds. Most Sierran lakes contain fish, and those that do not are usually small isolated ponds; in our study, these two lake types supported the lowest densities of post-metamorphic frogs, and these frogs were less reliant on local, benthic sources of productivity. Since *Rana muscosa* was formerly the most abundant vertebrate in the Sierra Nevada, the reduction in energy flow from lake benthos to this consumer due to fish introductions may have had negative consequences for its numerous terrestrial predators, many of which have also declined. We suggest that disruptions of trophic connections between aquatic and terrestrial food webs are an important but poorly understood consequence of fish introduction to many thousands of montane lakes and streams worldwide and may contribute to declines of native consumers in riparian habitats.

**Key words:** alpine ecosystems; amphibians; benthic; food webs; invasion; pelagic; *Rana muscosa*; riparian; spatial interactions.

### INTRODUCTION

The source of limiting resources for food webs is of fundamental importance to understanding of their productivity and dynamics. Empirical studies increasingly demonstrate diversity of energy and nutrient sources in ecosystems, and the complexity of their spatial and temporal provenance (reviewed in Polis et al. 1997). While an active area of research, information on sources and scales of energy supporting consumers is lacking for most ecosystems, limiting basic knowledge of food web dynamics as well as management and conservation of habitats that sustain native species.

Research in lakes has long fueled broader understanding of ecosystems. Despite this rich tradition, recent studies have exposed the limits of current knowledge and begun to substantially alter our understanding of lentic food webs. Previous research in lakes has emphasized resource- and consumer-driven dynam-

ics of phytoplankton-based pelagic food webs. Numerous papers published over the last decade show, however, that pelagic food webs are not isolated from other lake or terrestrial habitats, and in fact may be strongly linked by fluxes of organic matter, nutrients, and prey across habitat boundaries. For example, growth of many pelagic fishes in oligotrophic lakes is now known to be sustained by benthic as well as pelagic production (Vander Zanden and Vadeboncoeur 2002), with incompletely explored consequences for nutrient cycling, primary production, and species interactions (Vander Zanden et al. 2005). Another example of spatial interactions important to freshwater ecosystems is the role of terrestrial ecosystems in aquatic food webs. Inputs of terrestrial detritus commonly rival or exceed that of *in situ* primary production. The most well known influence of terrestrial detritus in aquatic ecosystems is its role in ecosystem metabolism. Most lakes and streams are heterotrophic, in that bacterial respiration exceeds autotrophic primary production on an annual basis (del Giorgio et al. 1997, Lamberti and Steinman 1997). Terrestrial organic carbon provides much of the

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energy base for consumers in small streams in forests (Wallace et al. 1997, Finlay 2001), and recent work also shows that terrestrial carbon enters lake food webs to a much greater extent than previously assumed (Pace et al. 2004).

While research that considers spatial interactions is providing new insights into energy flow within aquatic ecosystems, an overlooked aspect of lake food webs is their interaction with surrounding terrestrial ecosystems. The traditional emphasis of research on trophic interactions between terrestrial and aquatic ecosystems has been on flows of carbon and nutrients from terrestrial to aquatic environments (Polis et al. 1997). In streams and at ocean margins, however, there is increasing evidence of the importance of flows in the opposite direction. Here, many marginal terrestrial consumers have diets that are linked to aquatic organic matter or prey (e.g., Polis and Hurd 1996, Bastow et al. 2002, Paetzold et al. 2005). Trophic connections between lentic ecosystems and terrestrial, avian, and amphibious consumers have been less well-studied but are potentially important in oligotrophic lakes. As noted, benthic production dominates small lakes where the most abundant primary consumers are often insects. Virtually all aquatic insects have aerial adult stages, and many are weak fliers and thus highly susceptible to terrestrial predators. Predation by fish, however, strongly reduces the number, biomass, and size of benthic invertebrates (Shurin et al. 2002). Thus, fish may determine the strength of trophic interactions between lakes and surrounding terrestrial habitats, but this idea has received relatively little study.

Alpine watersheds are compelling systems to examine this hypothesis. Alpine lakes are often highly oligotrophic, and under nutrient-poor conditions, benthic algae and invertebrates dominate primary and secondary production. Further, many thousands of montane lakes are fish-free due to dispersal limitations following glacial retreat, and thousands more were fishless prior to the human introductions that occurred over the last century (Knapp et al. 2001a). The presence of fish in these lakes alters ecosystem processes such as nutrient cycling (e.g., Schindler et al. 2001) and strongly affects the composition, diversity, and size distribution of invertebrates (Knapp et al. 2001b). Fish introduction is negatively correlated with abundance of native vertebrates (Knapp 2005), but the mechanisms have not yet been thoroughly explored.

In this study, we examined food webs within and adjacent to fishless and previously stocked lakes in the Sierra Nevada Mountains of California. Much of the extensive aquatic habitat of the high Sierras was fish-free 100 years ago, but today the opposite is true as 70–90% of streams and lakes have fish (primarily trout) populations (Knapp 1996, Knapp and Matthews 2000). Given the high rates of endemism, the effects of fish on formerly fishless lakes have important considerations for management, yet there is limited understand-

ing of food web structure and energy flow in these ecosystems under both pristine and fish-influenced conditions. We hypothesized that, in addition to direct effects of predation, the presence of fish in historically fish-free montane lakes could negatively impact native vertebrates via reduction of aquatic insect prey for consumers that feed at lake margins on adult aquatic invertebrates.

We tested this hypothesis through a combination of natural experiments and stable-isotope analyses of food web structure. We first compared the abundance of a key native consumer, the mountain yellow-legged frog, *R. muscosa*, across a lake size gradient of 20 naturally fishless and 21 previously stocked lakes. We characterized the resource base and trophic structure of food webs supporting native consumers and introduced trout in nine fishless and three invaded lakes. We then examined the influence of trout on the flux of invertebrate prey from benthic habitats to the lake surface where they are available to native consumers including *R. muscosa*. This approach allowed us to examine effects of fish on food webs supporting *R. muscosa* relative to the influence of natural spatial variability in habitat quality in these ecosystems.

## METHODS

### *Field site and ecosystem context*

Our study area is the Sixty Lake Basin (36°49'7" N, 118°25'31" W), a 32-km<sup>2</sup> watershed located in the headwaters of the South Fork of the Kings River, Kings Canyon National Park, in the Sierra Nevada Mountains of California, USA. The watershed (3000–3500 m elevation) encompasses a habitat gradient typical of the high Sierra ranging from alpine tundra to warmer semi-forested valleys with numerous glacial lakes linked by streams. Both terrestrial and aquatic habitats have very low productivity due to short summers and low nutrient availability. Consumers are concentrated in aquatic ecosystems and riparian meadows since the uplands are largely barren granitic rock with little primary productivity.

Like many aquatic ecosystems, the lakes and streams of the Sierra Nevada have been severely altered by the introduction of nonnative species. Trout are the most important nonnative species in the Sierra due to their systematic introduction to every major watershed (Knapp 1996, Moyle and Randall 1998). Now introduced trout occupy up to 90% of aquatic habitat in a landscape that was historically almost entirely fishless above 1500 m (Knapp 1996, Moyle and Randall 1998). Research on the effects of trout introduction shows a negative relationship between trout presence and the abundance of native amphibians (Bradford 1989, Knapp and Matthews 2000, Matthews et al. 2001). Experiments show that this relationship is driven, at least in part, by predation on larval stages (Vredenburg 2004). However, alternate mechanisms and overall consequences of fish

introduction for energy flow through food webs remain largely unknown.

The Sixty Lake Basin is a suitable location to study food webs supporting native consumers and their interaction with introduced predators. Because of its remote setting, high elevation, and the presence of natural fish barriers, the watershed is among the least impacted by fish introductions in the Sierra Nevada. The watershed contains only 21 trout-occupied lakes and ponds out of total of 44 larger than 0.3 ha surface area. Approximately 40% of stream reaches contain trout, much lower than most watersheds (Knapp 1996). Perhaps as a result, some of the largest remaining populations of the frog *Rana muscosa* are present, and other native consumers are abundant. The Sixty Lakes Basin therefore has ecological features that are among the most analogous to the historically fishless state of Sierran ecosystems.

Of the many native consumer species present in the watershed, we focused our research on *R. muscosa* for several reasons. First, this frog was formerly the most abundant vertebrate in the Sierras with a wide historical distribution (Grinnell and Storer 1924). Second, its populations have undergone well-documented, severe declines throughout its range (Bradford et al. 1994, Vredenburg et al. 2005), such that the species is considered eligible for endangered status (Anonymous 2002). Thus basic research in support of recovery efforts is needed. Finally *R. muscosa* is a prey item for many native top predators including snakes, birds, and small mammals (Zweifel 1955, Vredenburg et al. 2005), and thus may play a role in transferring both aquatic and terrestrial productivity through food webs.

Under fishless conditions, *R. muscosa* metapopulations exist in a patchy environment with populations linked across individual lakes and streams by dispersal. Larval stages (i.e., tadpoles) are fully aquatic benthic grazers, and take up to 4 years to metamorphose (Camp 1917, Zweifel 1955, Vredenburg et al. 2005). Tadpoles reach very high densities in breeding lakes, and such lakes serve as source populations for nearby lakes with no breeding habitat (Vredenburg 2004). Adult and juvenile (hereafter "post-metamorphic") frogs may be long term residents of individual lakes, or may be highly mobile, moving up to 300 m to breeding and feeding locations during the summer (Pope and Matthews 2001). Post-metamorphic *R. muscosa* are visual predators that forage for invertebrate prey at the water surface and on land, and are not known to feed underwater (Zweifel 1955, Long 1970, Vredenburg et al. 2005).

#### *Distribution and abundance of R. muscosa*

We used diurnal visual encounter surveys (Vredenburg 2004) to assess natural patterns of abundance of *R. muscosa* across a gradient of lake size in fishless lakes, and to examine the influence of fish at stocked lakes. Over the study period (2000–2003), we surveyed all water bodies three times during the ice-free summer

period (June–September) when *R. muscosa* are most active. To understand the influence of trout on *R. muscosa* abundance, we compared the mean density (i.e., no. tadpoles/m shoreline, averaged for the three-year study period) of tadpoles, and post-metamorphic frogs in fish and fishless lakes using *t* tests.

We also assessed patterns of seasonal movements of frogs in our study lakes. Movement between lakes could influence stable-isotope analyses of diet sources, since isotopic signatures often vary between nearby lakes and streams. To determine the degree of lake fidelity for frogs throughout the summer, we compared abundance during the spring breeding period (early June) and during non-breeding, feeding period (August) during 2003.

Finally, we used abundance data to explore the role of interspecific competition (i.e., exploitation of aquatic insect prey by trout) and intraspecific competition (exploitation of benthic algae by tadpoles) in affecting abundance of post-metamorphic frogs. We compared the abundance of adults at four categories of lakes during late summer 2003: (1) lakes with trout, without tadpoles ( $n = 5$ ), (2) large lakes (perimeter > 300 m) without trout, with tadpoles ( $n = 5$ ), (3) small lakes (<300 m perimeter) without trout, with tadpoles ( $n = 5$ ), and (4) small lakes (<300 m perimeter) without trout or tadpoles ( $n = 9$ ). We compared densities across lake types with one-way ANOVA, with post hoc comparisons using Tukey-Kramer HSD.

#### *Trophic structure and energy sources*

We selected subset of the lakes described above for detailed food web analyses using stable carbon isotopes ( $\delta^{13}\text{C}$ ) to assess energy sources and stable nitrogen isotopes ( $\delta^{15}\text{N}$ ) to measure trophic position of native and introduced predators. Much less is known about the ecology of fishless lakes, and *R. muscosa* use habitats ranging from small ponds to large, deep lakes, so we selected nine fishless lakes along a size gradient for study, and three similar and adjacent trout-occupied lakes (Table 1, Fig. 1). We sampled primary consumers in the three important habitat types of the watershed (the littoral benthic and pelagic zones of lakes, and in meadows around lakes) as well as the two focal consumers (native frogs and introduced trout) of these prey during the summers of 2000 and 2003. We did not extensively sample basal organic resources (i.e. algae, detritus, and plant foliage), but rather focused on the contributions of primary consumers in the three habitats to predator diets (Vander Zanden and Rasmussen 1999, Vander Zanden and Vadeboncoeur 2002). Some sites were sampled during both years, and in such cases we used data from the year with the larger total sample size.

Terrestrial insects were collected with sweep nets in riparian shrubs and meadows, and three to 10 individuals were composited at each site for two herbivore groups: leafhoppers (Homoptera: Cicadellidae) and grasshoppers (Orthoptera: Acrididae). We assumed that

TABLE 1. Physical features of study sites and average densities for *Rana muscosa* at two time periods in 2003 (breeding season, June; and a feeding period, August).

Lake	Condition	Lake area (m <sup>2</sup> )	Lake perimeter (m)	Maximum depth (m)	Watershed area (km <sup>2</sup> )	June adults (no./m)	August adults (no./m)
H-G	-trout, -tadpoles	1100	49	1.9		0	0.57
8†	-trout, +tadpoles	1111	137	3.1	0.02	0.84	0.09
H-3	-trout, -tadpoles	1128	47	1.9		0	0.47
H-F	-trout, -tadpoles	1209	45	2.1		0	0.8
H-H	-trout, -tadpoles	1398	39	1.6		0	0.41
7	-trout, +tadpoles	1407	125	2		0.43	0.10
H-6	-trout, -tadpoles	1420	34	1.9		0	0.47
H-E	-trout, -tadpoles	1487	29	1.5		0	0.69
H-4	-trout, -tadpoles	1510	44	2.3		0	1.02
H-A	-trout, -tadpoles	1523	39	3.2		0	0.51
3	-trout, +tadpoles	1529	292	2.7		0.53	0.26
<b>29†</b>	<b>+trout, -tadpoles</b>	<b>1642</b>	<b>145</b>	<b>1.2</b>	<b>7.05</b>	<b>0.00</b>	<b>0.17</b>
31†	-trout, +tadpoles	2615	192	3.7	0.13	0.64	0.01
2†	-trout, +tadpoles	2815	278	5.1	0.38	0.47	0.04
11†	-trout, -tadpoles	3607	233	3.5	0.43	0.15	1.27
<b>100</b>	<b>+trout, -tadpoles</b>	<b>5466</b>	<b>424</b>	<b>5.2</b>	<b>~0.17</b>	<b>0</b>	<b>0.06</b>
13†	-trout, +tadpoles	7088	352	4.2	0.6	0.22	0.36
<b>9†</b>	<b>+trout, -tadpoles</b>	<b>8344</b>	<b>388</b>	<b>5.8</b>	<b>3.77</b>	<b>0.01</b>	<b>0.04</b>
51†	-trout, +tadpoles	8365	440	3.78	1.28	0.33	0.25
10†	-trout, +tadpoles	9816	516	5.7	0.58	0.49	0.52
<b>5†</b>	<b>+trout, -tadpoles</b>	<b>16 642</b>	<b>713</b>	<b>7.7</b>	<b>3.57</b>	<b>0.00</b>	<b>0.02</b>
48†	-trout, +tadpoles	18 615	545	18	0.17	0.52	0.64
<b>35</b>	<b>+trout, -tadpoles</b>	<b>54 878</b>	<b>1291</b>	<b>6.1</b>	<b>~5</b>	<b>0</b>	<b>0‡</b>
1†	-trout, +tadpoles	66 835	1863	12.7	0.36	0.32	0.35

Note: Lakes are arranged by increasing lake area, and lakes with trout are shown in boldface.

† Lakes where detailed food web analyses were conducted (see Table 2).

‡ Actual value = 0.002.

there were no between-site differences in terrestrial herbivore abundance and stable-isotope ratios because of similar environmental conditions and vegetation within the watershed. Therefore we used mean values for all samples collected during 2000 and 2003 for statistical comparisons.

Littoral benthic invertebrate larvae were composited by genus or family within two or three ~5–20 m long plots along the littoral zone (depths ranging from 0.1 to 1 m) for each lake. Two to 30 individuals of each taxon were collected for a sample at each plot. Benthic grazers were primarily ephemeroptera (*Ameletus* and *Callibaetis*) and trichoptera (*Desomna*, *Lepidostoma*). Invertebrate predators were primarily larval dytiscid beetles (Coleoptera: Dytiscidae) and corixids (Hemiptera: Corixidae). Samples for zooplankton were collected with plankton nets at one or two sites per lake. Zooplankton were separated into cladocerans (*Daphnia* spp.) and copepods (primarily *Hesperodiaptomus* and *Leptodiaptomus*) and 15–40 individuals were composited for each sample. No distinction was made between these two groups in subsequent analyses. For five lakes, zooplankton  $\delta^{13}\text{C}$  were estimated from the strong relationship between benthic grazer and zooplankton  $\delta^{13}\text{C}$  using a regression relationship derived from seven lakes where both groups were sampled (see *Results*).

Muscle tissue is most often used in stable-isotope food web studies but is lethal for small amphibians. Due to concern over low population sizes of *R. muscosa*, it was not possible to sample muscle tissue. Instead, we used

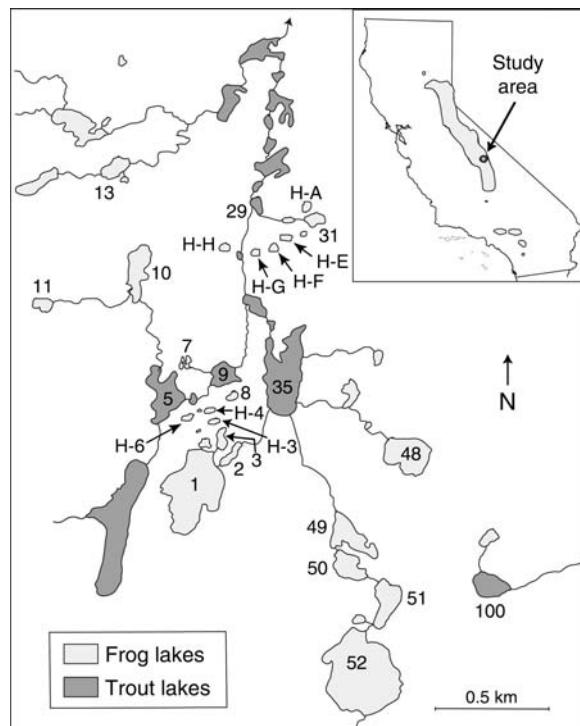


FIG. 1. Map showing general locations of study lakes and the presence or absence of introduced trout and *Rana muscosa* in the Sixty Lakes Basin, California, USA. Small ponds are scattered throughout the watershed but are not shown on the map. The inset map shows the historical range of *R. muscosa* in California and Nevada in gray.

tissue from toe clips, a standard technique for marking amphibians (Heyer et al. 1994), from frogs collected during midsummer population surveys. To test the assumption that muscle and toe tissues have similar isotope ratios, we examined the relationship between stable-isotope ratios of toe and muscle tissues of a closely related and very abundant species, bullfrogs (*Rana catesbeiana*). We obtained individuals from a natural area in northern California river where this species is not native (see Kupferberg 1997). Toes and muscle tissue were dissected from five individuals, rinsed in 0.1 mol/L HCl and deionized water, and dried for analysis. Rainbow and golden trout (*Oncorhynchus mykiss*, *O. m. aguabonita*) were collected by angling and by gill nets set for ~4 h during midsummer. Dorsal muscle was dissected from euthanized trout.

All stable-isotope samples were air dried in mesh bags or on tin foil within one to two days of collection. In the lab, samples were ground to a powder and analyzed for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  as described in Finlay et al. (1999). Approximately 20% of samples were run in duplicate, except for toe clips which did not contain enough mass for two analyses. Samples with standard deviations (SD) > 0.4‰ were rerun if adequate sample material remained. The average SD of analyses was <0.25‰ for both years for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Carbon source contributions to consumers were estimated with two-source mixing models that used the large differences in  $\delta^{13}\text{C}$  between benthos and other prey sources (i.e., zooplankton or terrestrial invertebrates) with error estimates calculated according to Phillips and Gregg (2001).

#### *Aquatic invertebrate flux*

To examine the potential influence of fish on energy flow to native frogs, we measured flux of benthic prey (as emergent adult insects) to the lake surface with standard emergence traps (i.e., floating 0.25-m<sup>2</sup> traps with mosquito netting mesh, anchored to the lake bottom). Three traps, spatially separated from each other by 10–30 m, were placed out for approximately two days at each lake over cobble and boulder substrata. Invertebrates were collected from emergence traps by aspiration into a small vial and immediately preserved with 70% EtOH. Samples were collected from four fishless lakes (i.e., lakes 1, 3, 48, and 52) and four trout-occupied lakes (5, 9, 49, and 50) in July and from two lakes of each type in August 2000. All of these lakes were sampled for frog abundance and half were also selected for food web analyses as described in *Trophic structure and energy sources*. Samples were sorted in the lab into broad taxonomic groups (i.e., chironomids, trichoptera, odonata, and ephemeroptera) and enumerated. For each taxon, body lengths were measured for at least 15 individuals, and biomass was estimated from length–mass relationships (Sabo et al. 2002). Data were analyzed with a two-way ANOVA to examine effects

of fish and season (early vs. late summer) on emergence biomass and abundance.

## RESULTS

### *Distribution and abundance of R. muscosa*

We surveyed 81 water bodies throughout the study. Of these, 31 lakes were excluded from further analysis because they were too high (>3400 m) and cold for frogs and trout. An additional eight lakes were either ephemeral or too isolated to contain frogs and trout and were also excluded. Of the remaining 41 lakes, 21 contained introduced trout and 20 did not. Adult frogs were present at 14 lakes with trout, and tadpoles were present at six lakes with trout. Densities of tadpoles were significantly higher in fishless lakes than those with trout (mean  $\pm$  SE, 2.056  $\pm$  3.306 tadpoles/m shoreline [ $n=20$ ], 0.0003  $\pm$  0.0001 tadpoles/m [ $n=21$ ], respectively;  $t$  test,  $P < 0.012$ ). Similarly, densities of post-metamorphic frogs were significantly higher in fishless lakes than in lakes containing trout (0.428  $\pm$  0.069 frogs/m [ $n=20$ ], 0.02  $\pm$  0.037 frogs/m [ $n=21$ ], respectively;  $t$  test,  $P < 0.0001$ ). Many of the fishless and trout-occupied lakes are in very close proximity (i.e., 5–100 m apart; Fig. 1) and all lakes containing both frogs and fish were within 500 m of a fishless lake.

Frog abundance in large (defined for this study as lakes > 5000 m<sup>2</sup> surface area) fishless lakes was more seasonally stable compared to small fishless lakes (Table 1). The seasonal patterns of movement at small lakes depended on the presence of tadpoles. Adult frog density at small breeding lakes declined following breeding, in contrast to small non-breeding lakes where adult density consistently increased. Surveys of alternate habitats surrounding small breeding lakes showed that adult frogs moved to nearby water bodies such as other lakes, ephemeral ponds and streams (V. T. Vredenburg, unpublished data).

Detailed examination of patterns of adult *R. muscosa* densities during a foraging period (August 2003) suggested an important role for competition in influencing populations of this species. Densities were significantly different between the four types of lakes compared (Fig. 2; one-way ANOVA,  $P < 0.001$ ). Large fishless lakes and small lakes and ponds that lacked tadpoles contained significantly higher densities of adults than the other two classes (post hoc comparisons;  $P < 0.05$ ). Trout-occupied lakes and small lakes with tadpoles had lower, statistically similar densities (Fig. 2).

### *Stable-isotope ratios*

Stable-isotope ratios of toe and muscle tissue of adult *Rana catesbeiana* were very similar. The average difference between toe and muscle tissue for five individuals analyzed was 0.1‰  $\pm$  0.5‰ (mean  $\pm$  SD) for  $\delta^{13}\text{C}$  and  $-0.2\text{‰} \pm 0.2\text{‰}$  for  $\delta^{15}\text{N}$ . This suggests that stable-isotope data for non-lethal toe clips yields identical information about diet and trophic position as muscle tissue for frogs.

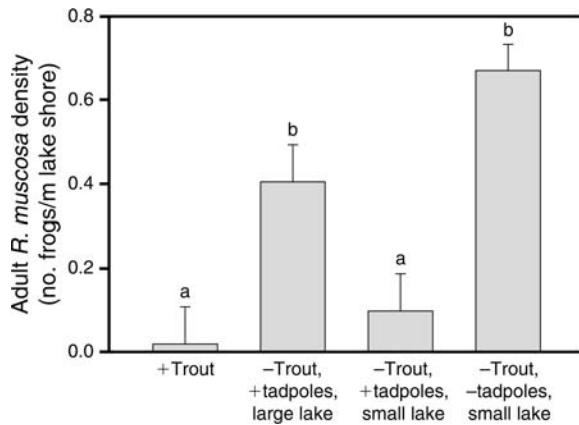


FIG. 2. Comparison of adult *R. muscosa* densities across common lake types occupied during late-summer foraging periods. Significant differences are indicated by different lowercase letters above each lake type. All lake sizes were considered for trout lakes where tadpoles were usually absent. For trout-free lakes, lakes with perimeter <300 m were considered "small" while lakes >300 m were considered "large." Lakes without tadpoles were small ponds and lakes (i.e., Lake 11) that do not provide suitable sites for oviposition or adequate environmental conditions for larval development.

Potential benthic and pelagic prey for frogs and trout often had distinct  $\delta^{13}\text{C}$  values (Table 2, Fig. 3a, b). As expected, primary consumers in benthic habitats (i.e., larval insects) were  $^{13}\text{C}$ -enriched (by an average of  $9.5\% \pm 1.6\%$  [mean  $\pm$  SD]) relative to zooplankton because of lower algal discrimination against  $^{13}\text{CO}_2$  in benthic habitats (France 1995, Hecky and Hesslein 1995).  $\delta^{13}\text{C}$  of primary consumers were variable across lakes, generally increasing with watershed area but not lake size (J. Finlay, *unpublished analyses*), probably due to greater contributions of respiratory  $\text{CO}_2$  to lake DIC used by algae in lakes with small watersheds compared to large ones (Finlay 2003).  $\delta^{13}\text{C}$  of benthic insects and zooplankton were tightly correlated across lakes (linear regression on data in Table 2; zooplankton  $\delta^{13}\text{C} = 1.31[\text{benthic herbivore } \delta^{13}\text{C}] - 3.7; r^2 = 0.85, P < 0.001, n = 7$ ). Terrestrial insect herbivores had  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of  $-27.3\% \pm 0.77\%$  (mean  $\pm$  SE,  $n = 6$ ) and  $0.54\% \pm 0.4\%$ , respectively. Terrestrial insect  $\delta^{13}\text{C}$  values were similar to those of zooplankton at large lakes.

Due to the similarity of zooplankton and terrestrial invertebrate  $\delta^{13}\text{C}$ , and the lack of another distinct isotope tracer, we could not distinguish between these two sources in consumers' diets. Instead, we used the most conservative end-member (i.e., the zooplankton or

TABLE 2. Mean values for consumer  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (‰) in the study lakes with trout-occupied lakes shown in boldface.

Isotope, by lake	Benthic grazers		Zooplankton		Invertebrate predators		<i>R. muscosa</i> tadpoles		<i>R. muscosa</i> adults		Trout	
	Mean	<i>n</i>	Mean	<i>n</i>	Mean	<i>n</i>	Mean	<i>n</i>	Mean	<i>n</i>	Mean	<i>n</i>
$\delta^{13}\text{C}$												
8	-23.0		-34.3		-30.1		-22.8 (0.2)	3	-21.1 (0.2)	4		
<b>29</b>	<b>-19.2 (1.6)</b>	<b>4</b>	<b>-28.8†</b>						<b>-20.4 (0.2)</b>	<b>3</b>	<b>-17.7 (0.4)</b>	<b>5</b>
31	-23.0 (0.6)	2	-33.8		-24.5 (0.9)	3	-23.3 (0.8)	8	-20.6 (0.3)	6		
2	-20.3 (0.9)	5	-30.2†		-23.6				-18.0 (0.6)	3		
11	-16.7 (1.5)	3	-26.8		-17.0				-16.3 (0.3)	2		
13	-18.1 (0.3)	2	-27.0†						-18.7 (0.6)	6		
<b>9</b>	<b>-17.0 (2.0)</b>	<b>3</b>	<b>-25.1</b>						<b>-19.4</b>		<b>-16.0 (0.3)</b>	<b>8</b>
51	-18.7 (1.0)	3	-27.8†		-20.7		-14.0 (0.1)	5	-17.7 (0.4)	8		
10	-17.4 (0.0)	1	-26.0†				-13.9 (0.1)	3	-17.5 (0.4)	8		
<b>5</b>	<b>-18.6 (0.5)</b>	<b>3</b>	<b>-25.6 (0.7)</b>	<b>2</b>					<b>-19.7 (0.1)</b>	<b>3</b>	<b>-17.5 (0.8)</b>	<b>9</b>
48	-20.0 (0.5)	3	-30.7 (0.7)	2	-26.3 (0.2)	2	-18.9 (0.3)	6	-20.4 (0.3)	8		
1	-19.2 (0.8)	7	-28.0 (0.6)	2	-23.2		-17.6 (0.5)	7	-18.5 (0.4)	6		
$\delta^{15}\text{N}$												
8	0		1.1		4.2		4.2 (0.3)	3	6.4 (0.3)	4		
<b>29</b>	<b>0.0 (0.4)</b>	<b>4</b>							<b>5.4 (0.4)</b>	<b>3</b>	<b>5.3 (0.2)</b>	<b>5</b>
31	-0.6 (0.9)	2	0.9		3.1 (0.6)	3	4.4 (0.1)	0.6	5.1 (0.1)	6		
2	0.7 (0.3)	5			2.9				5.8 (0.0)	3		
11	-0.5 (0.5)	3	-0.1		1.2				4.4 (0.1)	2		
13	-0.1 (0.4)	2							5.3 (0.2)	6		
<b>9</b>	<b>-0.3 (0.9)</b>	<b>3</b>	<b>-0.6</b>						<b>5.8</b>		<b>5.3 (0.4)</b>	<b>8</b>
51	0.1 (0.2)	3			2.6		3.0 (0.1)	6	4.9 (0.3)	8		
10	0.6						2.3 (0.5)	8	4.4 (0.2)	8		
<b>5</b>	<b>0.2 (1.6)</b>	<b>3</b>	<b>-0.6</b>						<b>6.0 (0.1)</b>	<b>3</b>	<b>5.1 (0.3)</b>	<b>9</b>
48	1.4 (0.4)	2	2.8 (0.1)	2	3.4 (0.6)	2	3.9 (0.1)	0.6	4.8 (0.2)	8		
1	1.3 (0.3)	7	2.1 (0.3)	2	3		3.8 (0.2)	7	5.9 (0.2)	6		

Notes: Numbers in parentheses indicate values of SE. For aquatic invertebrates, *n* indicates the number of samples analyzed per group; each sample is a composite of multiple individuals of a specific taxon as described in the text. We assumed that stable-isotope values for terrestrial invertebrate herbivores would not vary among sites, and mean values of  $-27\%$  for  $\delta^{13}\text{C}$  and  $0.54\%$  for  $\delta^{15}\text{N}$  were used in mixing-model analyses. Trout  $\delta^{15}\text{N}$  varied with size; a single mean value for each lake is shown for simplicity.

† Zooplankton  $\delta^{13}\text{C}$  calculated from the relationship between benthic grazer and zooplankton  $\delta^{13}\text{C}$ .

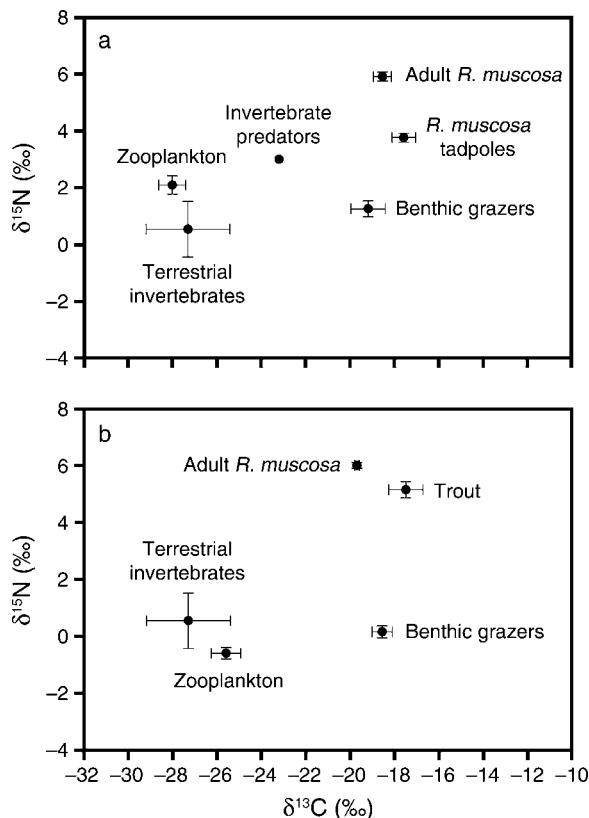


FIG. 3. Dual-isotope plots (i.e.,  $\delta^{13}\text{C}$  vs.  $\delta^{15}\text{N}$ ) for consumers in a typical (a) fishless and (b) invaded lake. These data, from summer 2003 for Lakes 1 and 5, respectively, are shown to illustrate relationships commonly observed in the study system (Table 2). For (b), trout  $\delta^{15}\text{N}$  ranged from 4‰ to 6.6‰ for the smallest to largest individuals collected, respectively; mean stable isotope values for all trout collected are shown for simplicity. Error bars show  $\pm\text{SE}$ .

terrestrial invertebrate  $\delta^{13}\text{C}$  that yielded the lowest estimate for benthic invertebrate contribution to consumer growth) in the two-source mixing model to estimate diet sources for *R. muscosa* at each lake. For trout, we considered only benthic invertebrates and zooplankton as prey for fish because there is very little riparian canopy cover over lakes and we thus expected terrestrial insect flux to lakes to be low.

The two-source mixing models showed that benthic prey sources dominate diets of both *R. muscosa* that fed at lake margins, and nonnative trout within lakes. Virtually all (i.e., 97%, as explained below) growth for frogs was derived from benthic food webs at fish-free lakes. At the three smallest fishless lakes, all which contained tadpoles, estimates for growth derived from benthic prey were significantly greater than 100%. This result may be explained by (1) movement to and feeding in other habitats with more  $^{13}\text{C}$ -enriched prey, (2) increase in  $\delta^{13}\text{C}$  of and substantial predation on benthic prey in these lakes late in the summer, or (3) higher trophic fractionation than the assumed value of 0.4‰

per trophic transfer (Vander Zanden and Rasmussen 2001). The first of these possibilities is supported by seasonal patterns of abundance (Table 1) and observations of movement of marked adult frogs away from small lakes during summertime (V. T. Vredenburg, unpublished data). This suggests that adults in small breeding lakes may frequently disperse to other habitats such as ephemeral ponds and streams to feed during the summer, as seen elsewhere (Pope and Matthews 2001). In any case, the overall results are consistent with heavy reliance on benthic food webs for growth. At lakes where our estimates exceeded 100% reliance on benthic prey, we assumed a value of 100% for calculation of the overall mean reliance on benthos.

Larval *R. muscosa* are benthic herbivores (Camp 1917, Zweifel 1955, Bradford 1983) but tadpole  $\delta^{15}\text{N}$  were higher than grazing benthic invertebrates at the same assumed trophic position in fish-free lakes (Table 2, Fig. 3a). Similarly, adult frog  $\delta^{15}\text{N}$  values were 5.1‰ greater than benthic insects, and thus higher than the assumed value of 3.4‰ for trophic enrichment. Such enrichment could arise from approximately seven months of winter hibernation (Bradford 1983, Gannes et al. 1997, Vredenburg et al. 2005), but could also result from omnivory by tadpoles (i.e., oophagy or predation on small aquatic insects), and cannibalism by adults (Vredenburg 2000, Vredenburg et al. 2005). Because post-metamorphic mass gain is substantial (i.e., average mass of 1.5 g as metamorphs and 8–12 g as adults [Vredenburg et al. 2005]), larval stable-isotope ratios would have little influence on those of adult frogs (Hesslein et al. 1993).

Invertebrate predators, common only in fishless lakes (Knapp et al. 2001b), had intermediate  $\delta^{13}\text{C}$  between benthic and pelagic prey (Table 2, Fig. 3a). This suggests substantial reliance on both benthos (40–80%; two-source mixing-model results not shown) and zooplankton (20–60%) prey by invertebrate predators in fishless lakes.

Mixing-model results also showed strong reliance (i.e., ~100%) on benthic production by introduced trout (Table 3). Planktonic and terrestrial food webs contribute little to growth of trout, consistent with results from other oligotrophic lakes (Vander Zanden and Vadeboncoeur 2002). Thus both native frogs and introduced trout rely on the same resource base in these Sierran lakes.

Adult frogs sampled at lakes occupied by trout showed a significantly lower contribution of local benthic prey to growth (i.e., mean of 74%;  $t$  test,  $P = 0.001$ ) than at fishless lakes (97%). The mixing model results suggest a higher contribution of terrestrial insects (26%) to frog diets at trout lakes than at trout-free lakes (3%). However, frogs at trout-occupied lakes may be transient and thus their stable-isotope ratios may reflect feeding in other habitats with more  $^{13}\text{C}$ -depleted insect prey, such as turbulent streams (Finlay et al. 1999) or small lakes (Table 1). In any case, our results collectively show that frogs avoid trout-occupied lakes, and the few

TABLE 3. Mixing-model results for mean proportion of diet sources contributing to predator growth in uninvaded and trout-occupied lakes.

Lake	<i>R. muscosa</i>			Trout		
	Benthic prey	Pelagic or terrestrial prey	SE	Benthic prey	Pelagic prey	SE
8	1.14	-0.14	0.18			
<b>29</b>	<b>0.80</b>	<b>0.20</b>	<b>0.16</b>	<b>1.09</b>	<b>-0.09</b>	<b>0.19</b>
31	1.18	-0.18	0.08			
2	1.20	-0.20	0.12			
11	1.00	0.00	0.15			
13	0.88	0.12	0.05			
<b>9</b>	<b>0.65</b>	<b>0.35</b>	<b>0.19</b>	<b>1.04</b>	<b>-0.04</b>	<b>0.26</b>
51	1.07	-0.07	0.12			
10	0.94	0.06	0.20			
<b>5</b>	<b>0.79</b>	<b>0.21</b>	<b>0.05</b>	<b>1.05</b>	<b>-0.05</b>	<b>0.13</b>
48	0.88	0.12	0.08			
1	1.03	-0.03	0.11			

Notes: The  $\delta^{13}\text{C}$  of pelagic and terrestrial prey overlapped so we could not distinguish their respective contributions to frog growth. We assumed only aquatic prey sources for trout in lakes, and thus only benthic and pelagic end-members were used. Results for trout-occupied lakes are shown in boldface. Contributions significantly above 1.0 for *R. muscosa* observed in the three smallest fishless lakes (i.e., 2, 8, and 31) are discussed in *Results: Stable-isotope ratios*.

frogs present at them rely less on local aquatic production than at fish-free lakes.

Temporal variation in stable-isotope ratios at the base of food webs can confound isotopic analyses of energy or nutrient sources (e.g., O'Reilly et al. 2002). Given a very short growing season, highly oligotrophic conditions, and observations of limited temporal variation in benthic consumers under similar conditions in lakes (Post 2002), we assumed minimal effects of temporal variation in stable-isotope ratios of consumers. We also examined stable-isotope ratios of adult *R. muscosa* in three lakes in late June and late August 2000 and found no differences over this period (unpublished data). Further, our food web sampling occurred over the period of peak productivity, suggesting that potential seasonal shifts in isotope ratios of basal consumers would have little effect on predators since prey availability is very low in early spring and late summer.

Trout  $\delta^{15}\text{N}$  increased with size ( $\delta^{15}\text{N} = 0.0121[\text{length, in mm}] + 3.44$ ,  $r^2 = 0.70$ ,  $P < 0.0001$ ,  $n = 21$ ; data not shown), ranging from 3.7‰ for the smallest individual sampled (68 mm total length) to 6.8‰ for the largest individual (245 mm). Assuming an increase in  $\delta^{15}\text{N}$  of 3.4‰ per trophic level, this represents an increase of nearly one trophic level. Size-related increases in trout  $\delta^{15}\text{N}$  indicate cannibalism, because trout do not prey on the only other abundant  $^{15}\text{N}$ -enriched prey item, larval and adult *R. muscosa*. In our study area, trout cannot prey on adult frogs because of gape limitation (Vredenburg 2002). Moreover, trout now rarely prey on tadpoles because they can no longer access them. When first introduced, trout extirpate tadpoles (Vredenburg 2004), and remaining adult frogs avoid breeding in lakes with fish (Vredenburg 2002).

#### *Trout effects on benthic prey flux*

Comparison of aquatic insect emergence from four natural and four invaded lakes showed a strong

influence of trout on prey fluxes to the watershed during a two-week period in July. Emergence at trout-occupied lakes was dominated by small-bodied diptera, and the overall number of invertebrates emerging from these lakes was slightly higher ( $P = 0.19$ ) than for fishless lakes (Fig. 4a). In contrast, the biomass flux was 19-fold higher ( $P = 0.03$ ) in trout-free lakes (Fig. 4b), primarily due the presence of two large-bodied ephemeroptera (*Ameletus* and *Callibaetis*), and, to a lesser degree, trichoptera.

The results from July demonstrate the role of trout in reducing availability of large, conspicuous aquatic prey to consumers that feed at or beyond the lake surface. We did not sample frequently enough to fully characterize seasonal patterns of emergence. Emergence before this period, however, is likely very low due to late ice cover in these lakes. Sampling during August showed low emergence rates from both fishless and fish lakes (Fig. 4). Although emergence can be temporally variable, we believe that the contrasts observed in July are indicative of the general nature of fish effects on insect emergence because they are consistent with studies showing strong, negative impacts of fish on benthic insect biomass in oligotrophic lakes (e.g., Knapp et al. 2001b).

#### DISCUSSION

Our work shows strong trophic connections between lake benthos and *Rana muscosa*, a key native species under the historical fish-free conditions common to thousands of lakes and streams in the high Sierra prior to fish stocking. *R. muscosa* is dependent on aquatic habitats for breeding (Zweifel 1955) but feeds along shorelines and on the lake surface (Zweifel 1955, Long 1970, Vredenburg et al. 2005) and is thus spatially isolated from aquatic prey (i.e., zooplankton and larval macroinvertebrates). However, the local dispersal of adult aerial stages of aquatic insects from lakes and streams appears to strongly link benthic production to

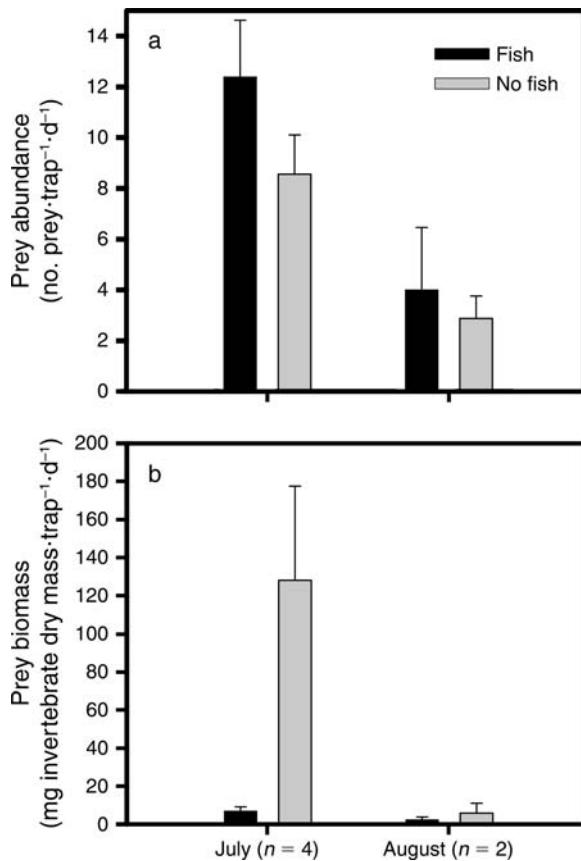


FIG. 4. Flux of aquatic prey to lake surfaces for fishless lakes (gray) and trout-occupied lakes (black) in 2000 expressed in (a) total numbers and (b) dry mass of invertebrates per 0.25-m<sup>2</sup> trap per day. The number of lakes sampled is indicated by *n*; error bars show +SE.

adult frog growth. As summarized in Fig. 5, the introduction of fish not only directly affects frogs by predation on tadpoles, but also greatly reduces the availability of prey to adult frogs, severing trophic

connections between water and land in a highly unproductive environment. Below we explore the implications of these results for our understanding of alpine food webs under natural, fish-free conditions and as well as under the influence of fish.

*Energy flow in fishless alpine food webs*

Our stable-isotope results suggest that the routing of benthic production from lakes to riparian zones provides the primary support for growth of post-metamorphic *Rana muscosa*. As an effective forager at the land-water margin, this species may have also played a key role in transferring energy from benthic production into terrestrial food webs. The frog is preyed upon by numerous native vertebrates including several bird and mammal species and a terrestrial snake (Vredenburg et al. 2005).

Montane lakes have features that may generally lead to strong trophic connections between aquatic production and terrestrial consumers in the absence of fish. First, these lakes are often nutrient poor, leading to dominance of benthic over planktonic algal production (Vadeboncoeur et al. 2003). Benthic insects with aerial adult stages dominate benthic grazer assemblages under such conditions. Second, montane lakes are often numerous and surrounded by unproductive terrestrial environments. The contrast in productivity between ecosystems may make aquatic production a particularly important resource for terrestrial consumers (Polis and Hurd 1996).

Although our results were generally consistent across a range of fishless lakes occupied by adult *R. muscosa*, we did find some evidence of variation in habitat quality associated with lake size and the presence of conspecific tadpoles. Small breeding lakes appear to provide poor conditions for adult frog growth, as suggested by low midsummer densities of frogs compared to similar, tadpole-free lakes, as well as larger fish-free lakes in the

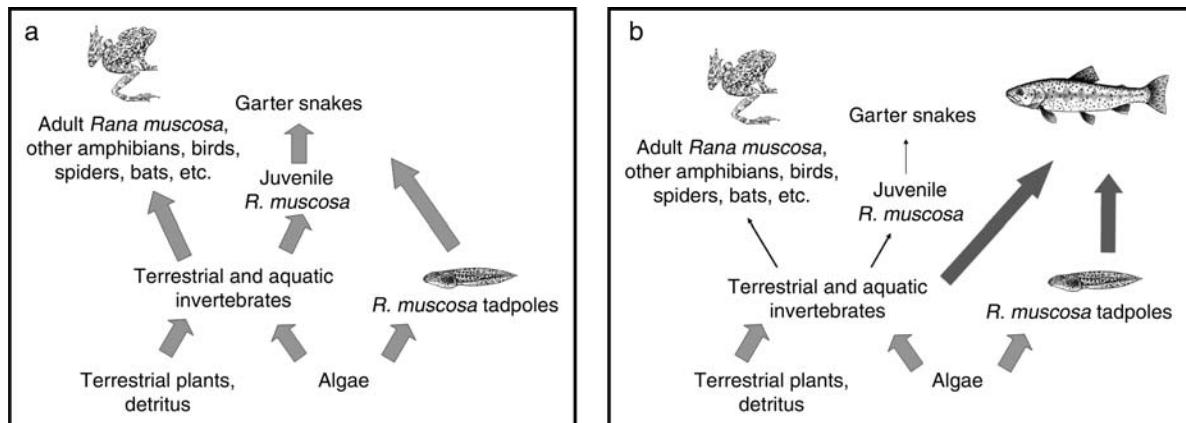


FIG. 5. Food web diagram contrasting energy flow pathways to consumers under (a) historical, fishless conditions and (b) as influenced by introduced trout. The size of arrows indicates the relative strength of trophic connections between food web components. Darker arrows indicate important changes in the flow of energy to fish in lakes where trout have been introduced compared to fishless lakes.

Sixty Lake Basin (Fig. 2). Further, frogs sampled at small breeding lakes had stable-carbon-isotope ratios that indicated diets linked to habitats other than local benthic production. Small breeding lakes thus appear to provide less prey for adult frogs than other fishless habitats. A possible mechanism to explain this pattern is that tadpoles reach greatest densities at small lakes (V. T. Vredenburg, unpublished data), and may compete with insect grazers for food, thereby reducing abundance of emergent insects. We did not measure insect emergence at enough lakes to test this hypothesis, but the lowest rates of emergence at fishless lakes were consistently observed at the smallest breeding lake sampled (unpublished data for Lake 31).

Benthic production was the primary resource exchanged across the water-land interface, and benthic prey were also dominant prey for introduced trout, as discussed in *Effect of trout on energy flow*. In contrast to these results, we found that invertebrate predators in fishless lakes preyed on both benthic invertebrates and pelagic zooplankton (Table 3). In other oligotrophic lakes, fish are also largely supported by benthos (Vander Zanden and Vadeboncoeur 2002) suggesting that predator identity plays an important role in determining energetic pathways within lake food webs.

#### *Effect of trout on energy flow*

The presence of introduced trout alters energy flow to native consumers in lakes and at lake margins. Within lakes, trout largely eliminate large invertebrate grazers and predators, leaving assemblages of inconspicuous or defended primary consumers (Northcote 1988, Knapp et al. 2001b). Suppression of invertebrate predators effectively severs trophic connections between benthic and pelagic habitats of lakes as indicated by the dominance of benthos in trout diets (Table 3).

Trout also had strong effects on energy flow from lakes to lake margins. Stable-isotope results indicate complete dietary overlap in use of benthic prey by *R. muscosa* and trout, even though these consumers feed in different areas of alpine lakes. Early in the short alpine summer, trout reduced the emergence of benthic insects by elimination of benthic grazers such as mayflies. Adult frogs are largely invulnerable to trout predation (Vredenburg 2002), but are 10-fold less abundant at stocked lakes compared to adjacent, trout-free lakes, suggesting the depression of densities around invaded lakes could be due to reduced prey availability.

Aquatic insect emergence can be highly pulsed in freshwater ecosystems, so our results do not adequately represent annual emergence from these lakes. Thus further work is necessary to fully quantify effects of trout on aquatic insect fluxes to lake surfaces. However, our results are consistent with similar reductions in biomass and abundance of larval stages of benthic insects by fish in montane lakes (Knapp et al. 2001b).

While trout have clear effects on food webs that support *R. muscosa* at individual lakes, the importance

of these effects in the dynamics of declining frog populations is complex and incompletely known. Decline of the mountain yellow-legged frog is clearly associated with the introduction of trout throughout most of its former range (Knapp and Matthews 2000). Experiments in our study system show that larval stages of amphibians are highly vulnerable to predation by trout (Vredenburg 2004). As a consequence, the introduction of fish eliminates frog reproduction at individual lakes, and this is often assumed to be the main impact of fish on *R. muscosa* populations. However, we suggest several factors that may make reduction of prey availability (i.e., exploitative competition) an important and overlooked negative influence of trout on *R. muscosa*. First, the productivity of terrestrial and aquatic ecosystems is very low due to cold temperatures and nutrient limitation in these glaciated, granitic watersheds (Knapp et al. 2001a). Resource exploitation by nonnative predators is expected to be most severe under these conditions, a situation where the effects of competition are expected to be greatest (Pimm 1988, Holt et al. 1994).

Second, *R. muscosa* populations exist in spatially complex metapopulations that may increase the influence of competition for prey. Small breeding ponds and lakes produce far more offspring than can be sustained locally (Briggs et al. 2005) leading to high rates of adult dispersal to nearby lakes and streams (Vredenburg 2002; this study). For example, when fish are experimentally removed from lakes, adult frogs immediately colonize them, although local reproduction cannot contribute to these populations for at least four years due to slow larval development (Vredenburg 2002). Thus, direct predatory influences of fish on larval frogs would limit *R. muscosa* populations when all habitats are occupied by fish, but exploitative competition for benthic invertebrate prey may limit metapopulation size when breeding but not alternate feeding habitats (i.e., large lakes, or lakes without tadpoles) are available within a watershed. Adequate breeding habitat for *R. muscosa* is common throughout its range because ponds are rarely stocked and are less likely to be colonized by fish via streams (Knapp 1996). However, populations limited to isolated ponds are small (<50 adults) and thus may be more vulnerable to extinction. Large populations of this amphibian only arise when a diversity of habitats are fishless, including productive, larger lakes and tadpole-free ponds. Such a situation exists in the Sixty Lake Basin where the highest adult frog densities are found in fishless lakes that lack breeding habitat. To improve metapopulation size and stability, restoration efforts may need to focus on removal of fish from a diversity of lakes (i.e., large lakes, and streams and small lakes that would not be used by tadpoles) in addition to provision of fish-free breeding habitat.

Competitive effects of trout on frogs may interact with other factors affecting *R. muscosa* populations. An aquatic fungal pathogen, *Batrachochytrium dendrobatidis*

*dis*, has been shown to negatively impact populations of *R. muscosa* (Briggs et al. 2005, Rachowicz et al. 2006) and air pollution is correlated with declines (Davidson 2004). Reductions in energy availability in fish-dominated watersheds may lead to higher susceptibility of frogs to these agents. In addition, frogs in habitats with less available productivity (due to fish) may be forced to move larger distances to forage, thus exposing them to higher rates of predation by terrestrial predators (Anholt et al. 2000) and conspecific or heterospecific disease carriers.

### Conclusions

Terrestrial contributions to aquatic food webs are the traditional focus of food web research at the land–water margin. However, there is a fast growing literature describing the importance of aquatic production to marginal and terrestrial food webs. In particular, recent work in streams shows that consumers at stream margins consume significant amounts of aquatic production, substantially altering the dynamics of consumer interactions (e.g., Henschel et al. 2001, Bastow et al. 2002, Murakami and Nakano 2002, Sabo and Power 2002). Given the well-documented influence of fish on benthic fauna in lakes and streams, it seems very likely that fish exert a primary yet little-studied control over trophic interactions between freshwater ecosystems and riparian zones. The rapid and thorough introduction of fish into streams and lakes has perhaps obscured this research question, but future efforts to restore ecosystems to better support native faunas must examine such effects closely.

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