

---

Alteration of Nutrient Cycles and Algal Production Resulting from Fish Introductions into Mountain Lakes

Author(s): Daniel E. Schindler, Roland A. Knapp, Peter R. Leavitt

Source: *Ecosystems*, Vol. 4, No. 4 (Jun., 2001), pp. 308-321

Published by: Springer

Stable URL: <http://www.jstor.org/stable/3658928>

Accessed: 16/04/2010 17:23

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=springer>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).



Springer is collaborating with JSTOR to digitize, preserve and extend access to *Ecosystems*.

# Alteration of Nutrient Cycles and Algal Production Resulting from Fish Introductions into Mountain Lakes

Daniel E. Schindler,<sup>1\*</sup> Roland A. Knapp,<sup>2</sup> and Peter R. Leavitt<sup>3</sup>

<sup>1</sup>Department of Zoology, University of Washington, Box 351800, Seattle, Washington 98195-1800, USA; <sup>2</sup>Sierra Nevada Aquatic Research Laboratory, University of California, Star Route 1, Box 198, Mammoth Lakes, California 93546, USA; and <sup>3</sup>Limnology Laboratory, Department of Biology, University of Regina, Saskatchewan Canada, S4S 0A2

## ABSTRACT

The introduction of salmonid fishes into naturally fishless lakes represents one of the most prevalent environmental modifications of aquatic ecosystems in western North America. Introduced fish may alter lake nutrient cycles and primary production, but the magnitude and variation of these effects have not been fully explored. We used bioenergetics modeling to estimate the contributions of stocked trout to phosphorus (P) cycles across a wide range of fish densities in lakes of the Sierra Nevada, California. We also assessed the larger effects of fish-induced changes in phosphorus cycling on primary production using paleolimnological analyses from lakes in the southern Canadian Rockies. Our analyses showed that total P recycling by fish was independent of fish density but positively related to fish biomass in the Sierra Nevada. In lakes with fish populations maintained by continued stocking, fish recycled P at over twice the rate of those in lakes where introduced fish populations are maintained by natural reproduction and stocking has been dis-

continued. We estimate that P regeneration by introduced fishes is approximately equivalent to atmospheric P deposition to these lakes. Paleolimnological analyses indicated that algal production increased substantially following trout introductions to Rocky Mountain lakes and was maintained for the duration of fish presence. The results of our modeling and paleolimnological analyses indicate that introduced trout fundamentally alter nutrient cycles and stimulate primary production by accessing benthic P sources that are not normally available to pelagic communities in oligotrophic mountain lakes. These effects pose a difficult challenge for managers charged with balancing the demand for recreational fisheries with the need to maintain natural ecosystem processes.

**Key words:** algal production; exotic species; introduced species; fishless lakes; nutrient cycles; paleolimnology; phosphorus; Rocky Mountains; Sierra Nevada; fish stocking.

## INTRODUCTION

Fish introductions and translocations are one of the most widespread anthropogenic threats to aquatic ecosystems (Allan and Flecker 1993; Lodge and others 1998). Intentional stocking by fisheries man-

agers and inadvertent introductions through vectors such as bait buckets have resulted in the dispersal of fish species far beyond their natural geographic ranges and in the homogenization of species among ecosystems within their natural geographic ranges (Radomski and Goeman 1995; Lodge and others 1998; Rahel 2000). Although some species introductions appear to have subtle effects on native communities (Moyle and Light

Received 28 March 2000; accepted 4 January 2001.

\*Corresponding author; e-mail: deschind@u.washington.edu

1996), others have caused local extirpation of native fauna and substantial changes to the structure of the ecosystem (for example, see Anderson 1980; Herbold and Moyle 1986; Hrabik and others 1998).

In western North America, approximately 95% of mountain lakes were historically fishless (Bahls 1992). In the United States, intensive stocking of sport fishes into these lakes, which began in the mid-1800s, has resulted in the introduction of exotic fishes to more than 60% of all western mountain lakes and more than 95% of sites deeper than 3 m and larger than 2 ha (Bahls 1992). In the Canadian Rocky Mountains, at least 20% of all lakes have been stocked with nonnative trout (Donald 1987). Trout introduced into mountain lakes have dramatically altered native faunal assemblages, often extirpating amphibians and large-bodied zooplankton and benthic macroinvertebrate species (Anderson 1972, 1980; Bradford and others 1998; Carlisle and Hawkins 1998; Knapp and Matthews 2000).

Introduced trout can also alter nutrient cycling, as well as algal production and standing crop in previously fishless lakes (Leavitt and others 1994). Primary production can increase when size-selective predation by fish on large herbivorous zooplankton reduces grazing on phytoplankton communities (Carpenter and Kitchell 1993). However, several studies have shown that overall lake production may be more strongly limited by nutrient supply than by the intensity of herbivory, particularly in oligotrophic systems (Neill and Peacock 1980; Elser and others 1990). In these systems, introduced trout may stimulate algal production by regenerating benthic and terrestrial nutrients, thereby increasing pelagic nutrient supply necessary for phytoplankton growth.

The magnitude of the response by lake primary producers to introduced fish depends on the source of nutrients that fish regenerate. Predation by fish on zooplankton regenerates pelagic nutrients (for example, phosphorus [P] and nitrogen [N]) within the water column, but pelagic regeneration does not constitute a new source of nutrients for phytoplankton. In contrast, fish predation on benthic and terrestrial prey regenerates nutrients that would not otherwise be readily available to pelagic algae (Schindler and others 1993; Vanni 1996; Schaus and others 1997). Thus, the excretion of benthic-derived P by fishes can increase the supply of new P to phytoplankton (Carpenter and others 1992; Schindler and others 1993; Vanni 1996; Schaus and others 1997). Despite the pervasive nature of fish

introductions, little is known of the magnitude or significance of nutrient cycle disruption when fish are stocked into naturally fishless lakes.

Here we use a bioenergetics model (Hanson and others 1997) to analyze patterns of fish growth, diet, and P regeneration by introduced trout in mountain lakes in the Sierra Nevada of California. Total P regeneration was partitioned into contributions from benthic and pelagic sources in lakes with different food webs, trout densities, and stocking histories. In addition, we used new and previously published paleolimnological data (Leavitt and others 1994) from three similar lakes in the Canadian Rocky Mountains to evaluate the potential magnitude of changes in algal production rates that can result from high-density fish introductions. We expected that P regeneration by stocked trout would be directly related to trout density and biomass and that this nutrient regeneration would enhance algal accumulation in historically fishless mountain lakes.

## STUDY AREAS

### Sierra Nevada

The Sierra Nevada of California is a 5 million-ha mountain range composed mainly of national parks and forests (SNEP 1996). Most Sierra Nevada lakes lie in granitic, sparsely vegetated basins, and are generally small (less than 10 ha), oligotrophic (average,  $1 \mu\text{g chl. a L}^{-1}$ ), and depauperate (Stoddard 1987; Melack and Stoddard 1991; Bradford and others 1998). More than 99% of these lakes were historically fishless (Moyle and others 1996). Starting in the mid-1800s, trout were introduced into 80%–95% of these fishless lakes to provide opportunities for recreational fishing (Bahls 1992; Moyle and others 1996). The most commonly introduced species were rainbow trout (*Oncorhynchus mykiss*), golden trout (*O. m. aguabonita*), brook trout (*Salvelinus fontinalis*), and brown trout (*Salmo trutta*).

Trout introductions to Sierra Nevada lakes have dramatically altered the composition of amphibian, benthic macroinvertebrate, and zooplankton communities. Fishless lakes are characterized by mountain yellow-legged frogs (*Rana muscosa*), large crustacean zooplankton (*Daphnia middendorffiana*, *Hesperodiaptomus shoshone*), few rotifers, and large benthic macroinvertebrates (families Baetidae, Limnephilidae, Dytiscidae, Corixidae). In contrast, lakes with introduced trout populations are dominated by small crustacean zooplankton (*Daphnia rosea*, *Leptodiaptomus signicauda*, Cyclopoda), abundant ro-

**Table 1.** Characteristics of Study Lakes from the Sierra Nevada, California

Lake Name	Lake ID	Maximum Depth (m)	Surface Area (ha)	Elevation (m)	Current Stocking Practice	Trout CPUE (fish/h)	No. Fish	No. Age Classes
Negit Lake	40192	4.2	1.3	3395	N	4.9	18	8
10210	10210	4.9	1.7	3292	N	5.0	19	8
Mesa Lake	50185	5.8	11.9	3437	S	4.8	10	3
Forsaken Lake	50143	6.3	2.7	3523	S	7.2	12	6
Council Lake	40058	7.4	1.7	3419	N	10.4	20	6
Upper Lobe Lake	50176	8.5	2.2	3291	N	1.8	19	3
Packsaddle Lake	50189	8.6	12.7	3249	N	6.5	20	6
10308	10308	11	4.0	3478	N	0.8	9	3
Ramona Lake	40222	11.3	12.5	3290	S	3.0	25	7
Paine Lake	50190	16	12.3	3418	S	3.0	21	4
10254	10254	16.5	11.2	3254	N	4.6	10	2
Upper Goethe Lake	50154	30	23.1	3514	S	2.7	23	7

The column for Current Stocking Practice refers to whether the lakes are still actively stocked (S) or were stocked historically and now only contain fish that are produced through natural reproduction (N). The last two columns denote the number of trout sampled from each lake and the number of age classes determined from otolith analysis that were used to derive the growth rate models.

**Table 2.** Mean Time-Weighted Limnological Conditions for the Epilimnion of Three Alpine Lakes in the Southern Canadian Rocky Mountains during the 1991 Ice-free Season

Variable	Snowflake Lake	Bighorn Lake	Harrison Lake
Elevation (m)	2320	2347	2243
Surface area (ha)	7.1	2.2	8.4
Maximum depth (m)	13.0	9.2	8.4
TDN ( $\mu\text{g} \cdot \text{L}^{-1}$ )	107	no data	52
TP ( $\mu\text{g} \cdot \text{L}^{-1}$ )	4	no data	6
Chl a ( $\mu\text{g} \cdot \text{L}^{-1}$ )	0.63	no data	0.82
Conductivity ( $\mu\text{S} \cdot \text{cm}^{-2}$ )	204	150	244
pH	8.07	no data	8.09
Alkalinity ( $\text{mg HCO}_3 \cdot \text{L}^{-1}$ )	201.7	no data	198.0
Secchi depth (m)	5–8	no data	4–8

tifers (*Conochilus unicornis*, *Keratella* spp., *Polyarthra* spp.), small or burrowing benthic macroinvertebrate taxa (orders Acari, Oligochaeta), and lack amphibians (Stoddard 1987; Rowan 1996; Bradford and others 1998; Knapp and Matthews 2000).

Diets, growth rates, and P regeneration rates by introduced trout were characterized for 12 lakes located in the John Muir Wilderness and Kings Canyon National Park (37°07'N, 118°45'W; Knapp and Matthews 2000). All 12 lakes were in the alpine zone (3249–3537 m) and varied widely in surface area (1–24 ha) and maximum depth (3.3–33 m) (Table 1). All lakes contained introduced populations of golden trout, rainbow trout, or rainbow/golden trout hybrids. Seven of the 12 lakes were no longer stocked and contained trout populations maintained by natural reproduction.

Five lakes had little or no spawning habitat and contained trout populations maintained by regular stocking of age-0 fish.

### Canadian Rocky Mountains

Paleolimnological analyses were performed in Snowflake, Bighorn, and Harrison lakes. These lakes are located in unproductive headwater drainages (Table 2) in the eastern Front Ranges of the Canadian Rocky Mountains in Banff National Park, Alberta (51°36'N, 115°50' W). All lakes lie at or above permanent treeline (approximately 2130 m) in limestone basins (Anderson and Donald 1978). The watersheds of these lakes have been undisturbed by fire for at least 100 yrs (Leavitt and others 1994). These lakes are clear (Secchi depth, 5–10 m), cold ( $T_{\text{max}}$  less than 14°C; 9–10 months ice cover),

and weakly stratified. Algal abundance is limited by low nutrient concentrations (less than  $6 \mu\text{g}$  total  $\text{P L}^{-1}$ ) and by short water residence time (Anderson and Donald 1978; Paul and others 1995).

Snowflake and Bighorn lakes were originally fishless and had food webs dominated by large zooplankton species. In Snowflake Lake, the zooplankton included *Hesperodiaptomus arcticus*, large cladocerans (*Daphnia pulex*, *D. middendorffiana*), and *Gammarus lacustris* (Anderson and Raasveldt 1974; Wilhelm and others 1999). Although Bighorn Lake originally had *Hesperodiaptomus*, there are no data to confirm whether large daphnids were present before fish stocking (B. Parker personal communication). In contrast, Harrison Lake contains a naturally reproducing population of bull trout (*Salvelinus confluentus*). The zooplankton community is dominated by *D. pulex*, *G. lacustris*, and cyclopoid copepods (*Diacyclops bicuspidatus thomasi*), and *Hesperodiaptomus* is absent.

Snowflake and Bighorn lakes were stocked during the 1960s to create trout fisheries (Mayhood 1992). Snowflake Lake received rainbow trout (1960, 1963–65), eastern brook trout (1960, 1963–64), and cutthroat trout (*Oncorhynchus clarki*) (1966) (Anderson 1975; Anderson and Donald 1978). Bighorn Lake was stocked with eastern brook trout from 1965 to 1966 (Anderson and Donald 1978) and occasionally with rainbow trout in subsequent years (B. Parker personal communication). According to Banff Park records, Harrison Lake was never stocked (Leavitt and others 1994).

In Snowflake Lake, introduced trout eliminated *Hesperodiaptomus arcticus*, *Daphnia pulex*, and *Gammarus lacustris* by 1968 and allowed populations of small-bodied copepods (*Diaptomus tyrelli*, *Acanthocyclops vernalis*, *Diacyclops bicuspidatus thomasi*) and rotifers (*Kellicota longispina*, *Synchaeta oblongata*) to flourish (Anderson 1972; Anderson and Donald 1978). However, these fish did not reproduce and populations disappeared by 1984 (Anderson and Donald 1978). Although *Daphnia pulex* and *Gammarus* had recolonized by 1975, *H. arcticus* remained absent until its experimental reintroduction in 1992 (McNaught and others 1999). Brook trout established a self-sustaining population in Bighorn Lake, but their effects on the zooplankton community are less well documented than those for Snowflake Lake. Unpublished surveys have indicated the presence of an age-structured population of brook trout, abundant small Cladocera and rotifers, and an absence of *Hesperodiaptomus*, *Daphnia middendorffiana*, and *D. pulex*.

## METHODS

### Fish Sampling—Sierra Nevada Lakes

Data on fish growth rates, diets, and population densities were collected during the summers of 1995–97 as part of a larger study investigating the effects of fish introductions on lake faunal assemblages (Matthews and Knapp 1999; Knapp and Matthews 2000). For the present study, we selected lakes from this larger data set based on having collections of fish that contained a minimum of two age classes (range, 2–8; average, 5) and in which at least five fish had prey in their stomachs (range, 5–18; average, 10) (Table 1).

Fish densities were estimated in each lake as catch-per-unit-effort (CPUE: number of fish captured  $\cdot \text{h}^{-1}$ ) using a single gill net set for 8–12 h. CPUE ranged from 0.8 to 10.4 (average, 4.1). Gill nets do not effectively capture trout less than 100 mm in length (less than 2 years old) (Hall 1991b). Therefore, our estimated fish densities apply only to fish 2 years old and older. The monofilament sinking gill nets were 36 m long and 1.8 m high, and each net had six 6-m panels with bar mesh sizes of 10, 12.5, 18.5, 25, 33, and 38 mm. Nets were set perpendicular to the lake shoreline with one end attached to the shore. All captured fish were measured to the nearest mm (fork length) and weighed to the nearest gram. Contents of the foregut were categorized as (a) large zooplankton (*Daphnia middendorffiana*, *Hesperodiaptomus shoshone*), (b) chironomid (family Chironomidae) larvae, pupae, or adults, (c) terrestrial insects, and (d) other taxa. For fish stomachs dominated by large zooplankton, we assumed zooplankton to be 20% *D. middendorffiana* and 80% *H. shoshone* (Needham and Vestal 1938). Based on a visual examination, the dominant food category (by volume) was recorded for each fish.

Fish from 12 lakes representing the range of population densities were aged using otoliths. Otoliths were prepared by mounting one specimen on a glass microscope slide scullus-side up, grinding to the sagittal midplane using 800-grit abrasive paper, and then polishing with aluminum oxide powder (Hall 1991a). Annuli were counted using a compound microscope at 100–200  $\times$  magnification.

To allow extrapolation of CPUE data to the actual population density of trout at least 2 years old, we followed the 8–12 h gill net sets in three lakes (1.6–3.4 ha, 3.5–8 m deep) with removal of the entire population of trout 2 years old or older. We set three to 12 gill nets in each lake and cleaned them of fish approximately every 24 h (Knapp and Matthews 1998). Nets were fished until no individ-



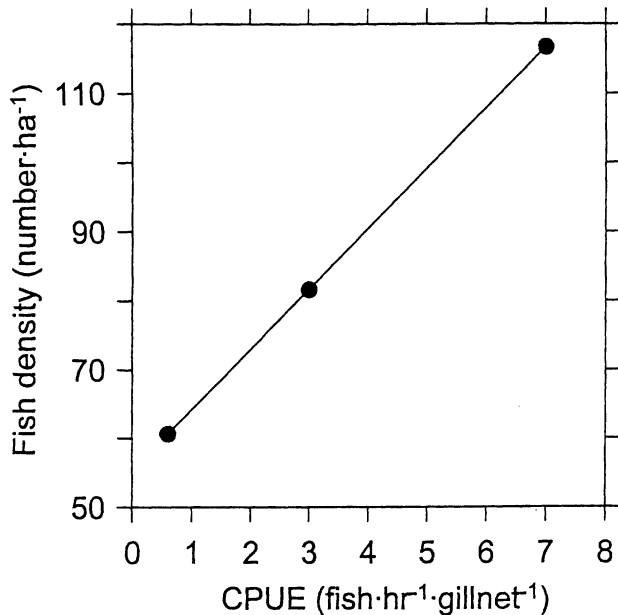


Figure 1. Relationship between catch-per-unit-effort (CPUE) estimates of relative trout density with variable mesh gill nets and the total fish density as determined by removal of the entire trout population with repeated gill netting. Each data point corresponds to an individual experimental lake. The linear regression that describes this relationship is: Fish density = 55+8.8·CPUE ( $P < 0.001$ ,  $n = 3$ ,  $r^2 = 0.999$ ). The units of CPUE are the number of trout per gillnet hour.

uals more than 100 mm in length were captured (2–4 weeks). Gill net sets conducted in subsequent years indicated that more than 99% of the adult population had been successfully removed. Trout densities in each of the 12 lakes for which we calculated P regeneration rates by fish were estimated from the relationship between the initial CPUE and the total number of fish removed from each of the three lakes in the eradication study (Figure 1), (Knapp and Matthews 1998).

#### Estimation of Phosphorus Regeneration by Trout

Phosphorus regeneration rates by trout in Sierra Nevada lakes were estimated with a phosphorus (P) mass balance model coupled to a bioenergetics model (Kraft 1992; Schindler and Eby 1997; Hanson and others 1997). The P mass balance takes the form  $E_p = C_p - F_p$ , where  $E_p$  is the mass of P excreted per day,  $C_p$  is the mass of P consumed by trout per day,  $G_p$  is the mass of P allocated to growth per day, and  $F_p$  is the mass of P released in feces per day. For all results presented in this paper, we report only the rates of P excretion by trout

because P in feces is relatively unusable by phytoplankton.

The mass of P consumed by trout per unit time ( $C_p$ ) was calculated according to  $C_p = \sum C_i \cdot P_i$ , where  $C_i$  is the wet mass of prey type- $i$  consumed per day and  $P_i$  is the P concentration in prey- $i$ .  $P_i$  was assumed to equal 0.0017 for *Daphnia*, 0.00072 for copepods, and 0.0015 for all other invertebrates (Schindler and Eby 1997). Vertebrates were never found in trout stomachs, and their contribution to P regeneration was assumed to be negligible. The wet mass of each prey category consumed by trout ( $C_i$ ) was estimated with a fish bioenergetics model (Hanson and others 1997) using physiological parameters for rainbow trout (Rand and others 1993).

The thermal environment experienced by trout was assumed to be invariant among lakes. Epilimnetic temperatures were recorded continuously in two lakes from 1996 to 1999. Temperature data were then averaged by date, across lakes and years, to produce the thermal regime used in our bioenergetics model runs. Energy densities of trout were assumed to vary with mass of fish according to Rand and others (1993), and invertebrate energy densities were assumed to be 2400 J/g for zooplankton and 4000 J/g wet mass for all other invertebrates (Schindler and Eby 1997). Mass lost to spawning was assumed to average 9% of wet mass for reproductive fish (Hall 1991b), and gonads were assumed to have the same energy density as somatic tissue.

Mass of P allocated to growth ( $G_p$ ) was calculated as  $P_{\text{fish}} \cdot \Delta B_{\text{fish}}$ , where  $P_{\text{fish}}$  is the P concentration in fish tissue (assumed to be 0.5% of wet mass) (Davis and Boyd 1978), and  $\Delta B_{\text{fish}}$  is the daily growth increment, as wet mass. Lake-specific growth rates for trout aged 2–11 years were determined by fitting von Bertalanffy growth curves to size-at-age data from each study lake. Length-at-age estimates were converted to mass-at-age estimates with lake-specific mass–length regressions (R. A. Knapp unpublished). Phosphorus lost in feces ( $F_p$ ) was calculated as a constant proportion (0.28) of consumed P ( $C_p$ ) (Nakashima and Leggett 1980).

To calculate total P recycling, we assumed that each of the stocked populations was characterized by the same stable-age distribution of trout. The age structure was calculated according to the age-specific survivorship schedules given by Hall (1991b) for individuals between 2 and 11 years old (Table 3). The total P recycled by each trout population was calculated as the product of P recycled by a standard age distribution of fish and the population density. Total population density for each lake was

**Table 3.** Survivorship Schedule Used to Calculate Stable Age Distribution of Trout in the Sierra Nevada Lakes

Age (y)	Annual Survivorship
2	0.89
3	0.85
4	0.82
5	0.77
6	0.73
7	0.73
8	0.7
9	0.67
10	0.64

*Data from Hall (1991b)*

calculated by converting standardized gill net CPUE to absolute density as described above (Figure 1).

Individuals less than 2 years old were not included in the analyses due to our inability to sample them effectively. However, we used the bioenergetics models to estimate the potential magnitude of P regeneration by these young fishes. We estimated the P excretion rates of fish less than 2 years old by assuming that age-0 and age-1 fish had annual survival rates of 0.3 and 0.92, respectively (Hall 1991b). We assumed that the energy and P content in the diets of young fish was identical to older fish. We then applied these mortality rates to both a high-growth scenario that matched the growth rates of trout in the fastest growing population, and a low-growth scenario from the lake with the slowest growing population. Given these assumptions, our estimates of the contributions to P recycling by fishes less than 2 years old range from 0.4% to 4.4% of the total P regenerated by the entire population fish population in these lakes. The highest contribution of young fish to total P regeneration by the population was produced in the simulation with the slow-growing trout. The small contributions of P regeneration by small trout differs substantially from other studies that have shown that young-of-year fishes can dominate the predation and nutrient regeneration rates by fish populations (Schindler and others 1993; Helminen and Sarvala 1997). However, the difference between this study and previous studies is that the number of juvenile trout comprises a much smaller fraction of the total population than in the small-bodied, short-lived species studied by other investigators.

### Paleolimnological Methods—Canadian Rocky Mountain Lakes

Paleolimnology was used to estimate the changes in algal production that resulted from trout stocking in Canadian Rocky Mountain lakes. Protocols for analysis of sedimentary pigments are detailed in Leavitt and others (1994). Briefly, sediments were collected using a freeze-corer, sectioned in 5-mm intervals, freeze-dried, and stored under an inert N<sub>2</sub> atmosphere. Fossil pigments were extracted, filtered, and dried under nitrogen gas before quantification using a Waters high-performance liquid chromatography (HPLC) system calibrated with authentic standards and pigments from unialgal isolates. Here we restrict our analyses to undegraded  $\beta$ -carotene, a reliable index of total algal abundance (Leavitt and Findlay 1994), and the chlorophyte indicator, lutein-zeaxanthin (Leavitt and others 1994). Similar patterns were recorded with other biomarker compounds (pheophytin a, chl a, alloxanthin, diatoxanthin). Pigment concentrations were expressed as nmol pigment  $\cdot$  g<sup>-1</sup> organic matter, following recommendations of Leavitt and Findlay (1994). Zooplankton fossils were too rare (<1 fossil  $\cdot$  g<sup>-1</sup> dry wt) to be accurately quantified. Bulk sediment accumulation rates (mg dry weight  $\cdot$  cm<sup>-2</sup>  $\cdot$  y<sup>-1</sup>) were estimated for Snowflake, Harrison and Bighorn lakes from activity profiles of <sup>210</sup>Pb and <sup>137</sup>Cs (Snowflake Lake only). As detailed in Leavitt and others (1994), sediment activities and ages were estimated using the distillation technique of Eakins and Morrison (1978) and the constant rate of supply model (Oldfield and Appleby 1984).

## RESULTS

### Trout Diets and Growth Rates

Trout diets varied widely among the 12 Sierra Nevada lakes. Contributions of large zooplankton to the diets of trout declined abruptly at fish densities greater than 90 fish  $\cdot$  ha<sup>-1</sup> (Figure 2A). At densities greater than 90 fish  $\cdot$  ha<sup>-1</sup>, diets were composed exclusively of terrestrial and benthic taxa, with chironomids dominant in approximately 70% of fish stomachs. Trout diets were composed exclusively of benthic and terrestrial prey in lakes with trout biomass less than about 12 kg ha<sup>-1</sup>. Diets in lakes with higher trout biomass were much more variable but generally included substantial contributions from zooplankton (Figure 2B). Zooplankton were found in diets of trout only from lakes that were at least 8.5 m deep.

Fish growth rates varied considerably among the 12 lakes for which we had fish age data. Much of

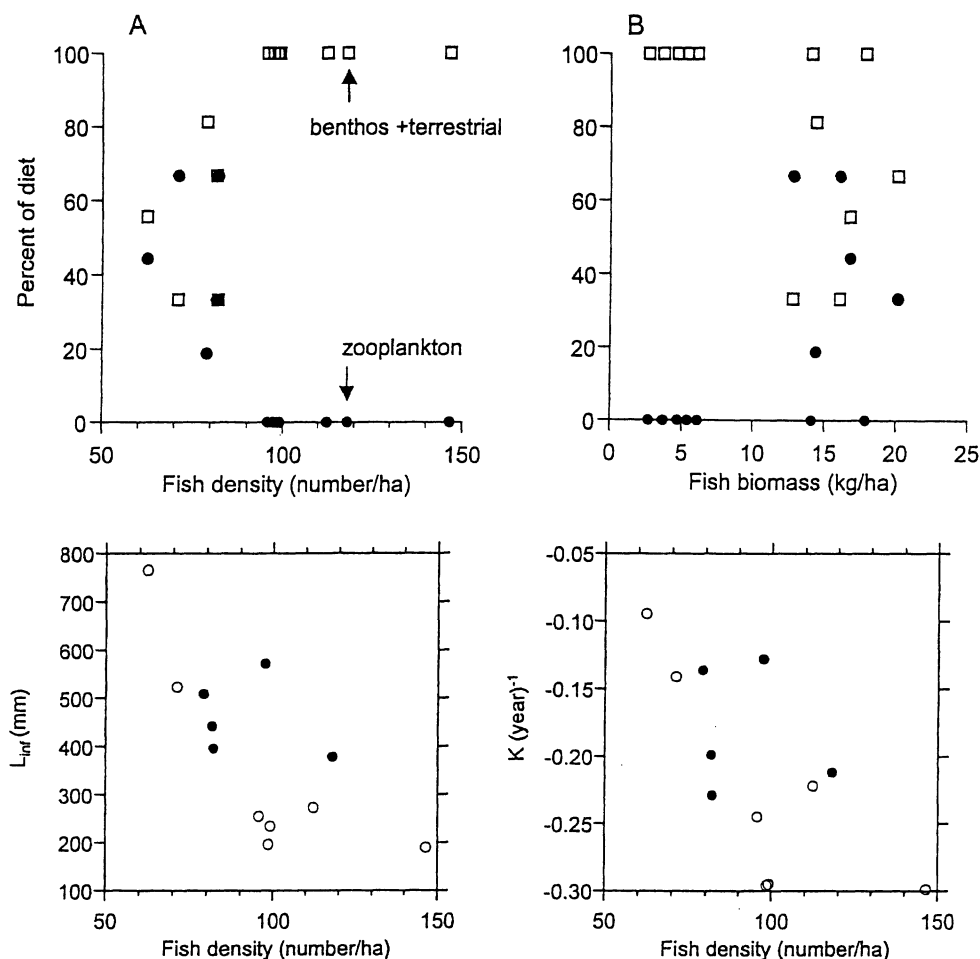


Figure 2. Trout diets as a function of fish density (A) and biomass (B) for 12 alpine lakes in the Sierra Nevada, California. Diet categories are collapsed into two classes that represent two distinct sources of phosphorus to pelagic nutrient cycles. Predation on benthic and terrestrial prey by fishes results in excretion of new phosphorus for phytoplankton, whereas predation on zooplankton results in excretion of recycled phosphorus within the water column.

Figure 3. The relationships between the von Bertalanffy growth parameters ( $L_{inf}$ , maximum projected size of fish and  $k$ , age-dependent growth coefficient) and trout density for the 12 Sierra Nevada lakes used in the P regeneration analyses.

the variation in growth rates was explained by fish density (Figure 3). Both the maximum projected size of fish in each lake ( $L_{inf}$ ) and the age-dependent growth coefficient ( $K$ ) were strongly negatively correlated with fish density ( $r = -0.72$  and  $-0.67$ , respectively). As an example of how variable trout growth was among the 12 study lakes, the average mass of a 10-year-old trout in a lake with a density of 60 fish  $\cdot$  ha $^{-1}$  was 960 g, whereas a 10-year-old fish from a lake with a density of 150 fish  $\cdot$  ha $^{-1}$  weighed about 50 g.

### P Regeneration by Trout Populations

Total annual P regeneration rates by trout populations averaged 2.3 mg P  $\cdot$  m $^{-3}$   $\cdot$  y $^{-1}$  across all lakes; it averaged 3.3 and 1.7 mg P  $\cdot$  m $^{-3}$   $\cdot$  y $^{-1}$  for currently stocked and unstocked lakes, respectively. Phosphorus regeneration rates varied considerably over the course of an annual temperature cycle that reflected the metabolic responses to changes in thermal conditions.

Here we present P regeneration estimates for trout in midsummer when lake temperatures, and

therefore P regeneration estimates, are highest. The rate of total P regeneration by trout populations was independent of fish density (Figure 4A) (linear regression,  $P > 0.7$ ) but positively related to fish biomass (Figure 4B) (linear regression,  $P < 0.001$ ). This difference in the relationship between P regeneration and trout density and biomass derived from the inverse relationship between trout density and biomass (Figure 5). Rates of P regeneration by fishes in currently stocked lakes (17  $\mu$ g P  $\cdot$  m $^{-3}$   $\cdot$  d $^{-1}$ ) were significantly different ( $t$  test,  $P < 0.005$ ) than in lakes with naturally reproducing populations of introduced trout (8.6  $\mu$ g P  $\cdot$  m $^{-3}$   $\cdot$  d $^{-1}$ ).

Trout density had a substantial effect on the proportion of P regenerated from planktonic vs benthic sources. In lakes with trout densities less than 90 fish  $\cdot$  ha $^{-1}$ , regeneration of plankton-derived P contributed an average of 5  $\mu$ g P  $\cdot$  m $^{-3}$   $\cdot$  d $^{-1}$  to the water column at the peak of the growing season (that is, at maximum water temperature) and was unrelated to current stocking status (Figure 6A). No plankton-derived P was regenerated at trout densities greater than 90 fish  $\cdot$  ha $^{-1}$ . Regeneration of



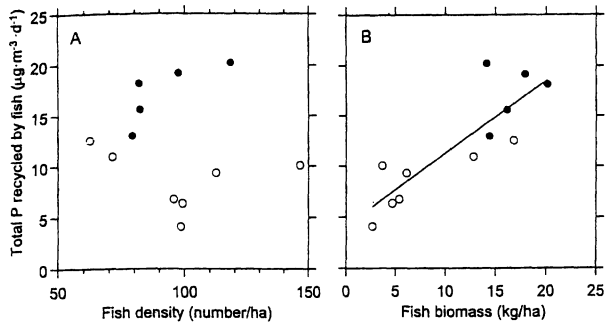


Figure 4. Regeneration rates of P by trout as a function of trout density (A) and trout biomass (B) in 12 historically fishless Sierra Nevada lakes. The line in B is the least-squares fit of total P regeneration as a function of trout biomass ( $P_{regen} = 4.08 + 0.72 \cdot Biomass$ ;  $n = 12$ ,  $P < 0.001$ ,  $r^2 = 0.74$ , standard error of estimate, 2.8). Solid symbols represent lakes that have been continuously stocked for several decades; open symbols represent lakes where stocking has not occurred for several decades and fish reproduce naturally.

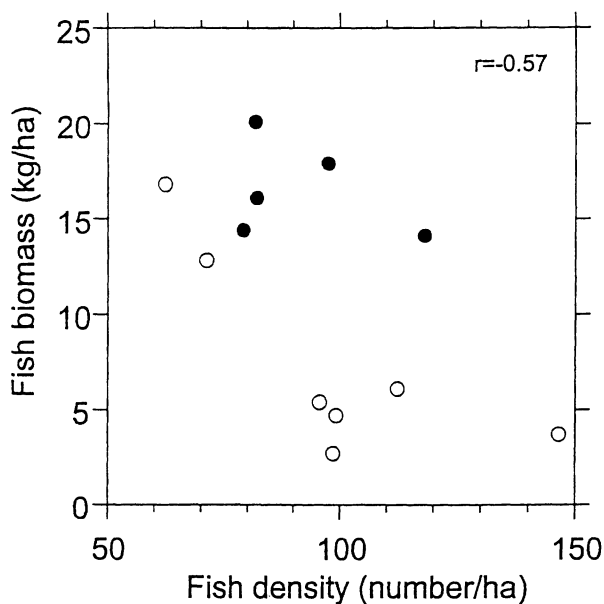


Figure 5. Relationship between trout density and trout biomass in 12 Sierra Nevada lakes. Solid symbols represent lakes that are continuously stocked; open symbols represent lakes that were stocked historically and now have naturally reproducing trout populations.

plankton-derived P was negligible in lakes with low fish biomass; it was higher but extremely variable in lakes with high fish biomass (Figure 6B). Phosphorus regenerated from benthic and terrestrial sources (that is, new P) contributed, on average,  $10.9 \mu\text{g P} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$ , and the regeneration rate was affected by the stocking regime (Figure 7). P regeneration in currently stocked lakes was twice as high as that in

lakes with self-sustaining fish populations; and this effect of stocking regime was driven by the high growth rates of trout in currently stocked lakes. A multiple regression model that included terms for both trout density and stocking regime explained 70% of the variance in new P regeneration rates among the study lakes (Figure 7A). Regeneration of new P by fish was weakly but positively related to fish biomass (Figure 7B).

### Paleolimnological Analyses—Canadian Rocky Mountains

Analysis of fossil pigment stratigraphies indicated that total algal abundance was low and constant in Bighorn and Snowflake lakes prior to trout introductions and constant but higher in Harrison Lake (Figure 8). In Bighorn Lake, a lake in which trout were introduced in the mid-1960s and have established a self-sustaining population, concentrations of  $\beta$ -carotene were relatively stable until approximately 4 cm burial depth (circa 1965), then they increased 10-fold in the more recent deposits. This change in fossil algal pigments is roughly coincident with the introduction of trout to Bighorn Lake, given the errors associated with  $^{210}\text{Pb}$ -dating of sediment age in these systems ( $\pm 4$  years). Similar patterns were also recorded for lutein-zeaxanthin produced from green algae. In Snowflake Lake, where trout were introduced but failed to reproduce and eventually disappeared, algal abundance also increased above the approximate 7-cm burial depth, reaching a historical maximum near 1965 ( $\pm 4$  years). Algal abundance declined to near-baseline values in the youngest sediments. The rate of P recycling by introduced trout, as determined using historical censuses of fish populations and bioenergetics modeling (Leavitt and others 1994), was a highly significant predictor of these patterns of change in algal biomass ( $r^2 = 0.76$ ,  $P < 0.0001$ ). As in Bighorn Lake, changes in total algal abundance in Snowflake Lake were inferred to result mainly from 10-fold increases in chlorophytes (lutein-zeaxanthin) rather than other algal taxa (less than a 5-fold change). In Harrison Lake, the only site with a natural fish population, concentrations of fossil  $\beta$ -carotene and lutein-zeaxanthin were consistently high and varied little within this same time period, except for 100% increases in the uppermost 1 cm of the core (Figure 8).

### DISCUSSION

During the past century, trout have been stocked into at least 80% of Sierra Nevada lakes and 20% of

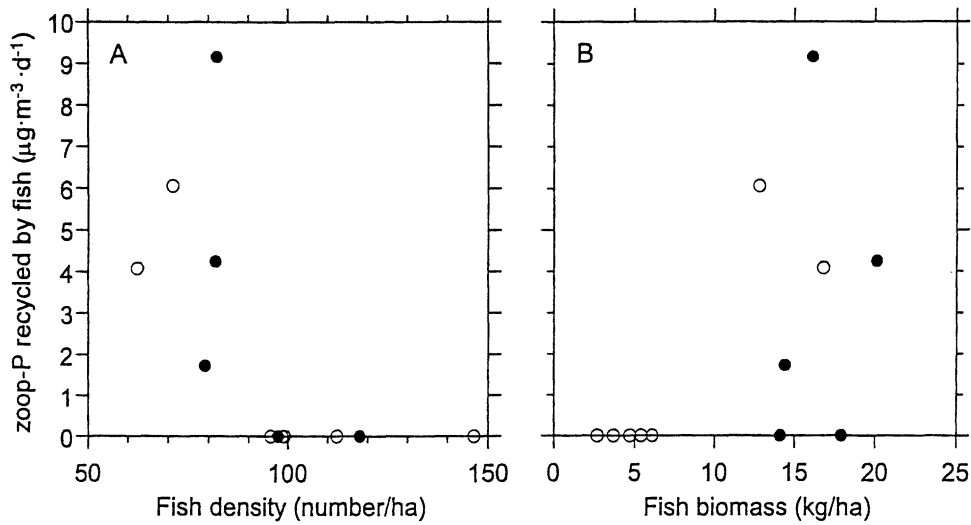


Figure 6. Regeneration rates of P derived from predation on zooplankton as a function of trout density (A) and trout biomass (B) in 12 historically fishless Sierra Nevada lakes. Solid symbols represent lakes that have been continuously stocked for several decades; open symbols represent lakes where stocking has not occurred for several decades.

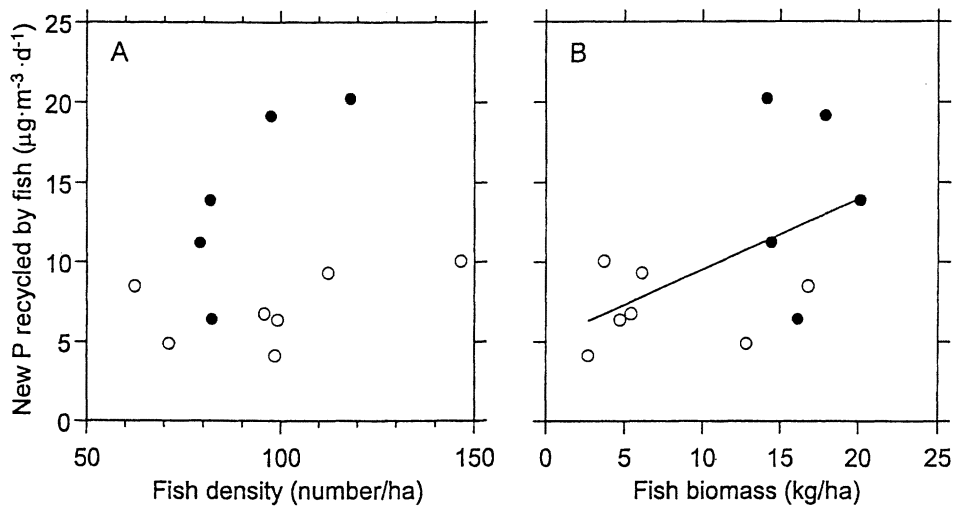


Figure 7. Regeneration rates of new P by trout as a function of trout density (A) and trout biomass (B) in 12 historically fishless Sierra Nevada lakes. New P is derived from predation on benthos and terrestrial prey; therefore, it represents an external source of P to pelagic nutrient cycles. Solid symbols represent lakes that have been continuously stocked for several decades; open symbols represent lakes where stocking has not occurred for several decades. A multiple regression of the form:  $\text{new P} = -1.21 + 0.085 \text{ fish} \cdot \text{stock}$ , where *fish* is the areal density of trout and *stock* is a dummy variable that describes the trout stocking history (1 for lakes that are not continuously stocked, 2 for continuously stocked lakes) explains 70% of the variation in the regeneration rate of new P ( $n = 12$ ,  $P < 0.0007$ ,  $R^2 = 0.70$ , standard error of estimate, 3.0). Fish biomass had a nearly significant effect on new P regeneration ( $\text{new P} = 5.09 + 0.443 \text{ biomass}$ ,  $n = 12$ ,  $P < 0.08$ ,  $r^2 = 0.28$ ).

Canadian Rocky Mountain lakes. Our analyses suggest that these introductions of trout into naturally fishless lakes routinely increase nutrient regeneration and that these increases are likely to be most marked in lakes that are currently being stocked (Figures 4–6). Comparisons of paleoecological reconstructions among lakes with varying stocking histories demonstrate that algal pigment concentrations in sediments increased by as much as 10-fold following fish introductions, but they returned to historical levels when the fish failed to establish

self-sustaining populations. Together, these results demonstrate that fish introductions may constitute a substantial biogeochemical perturbation to thousands of formerly fishless mountain lakes throughout western North America.

One mechanism by which introduced trout may stimulate algal production is via the transfer of nutrients to algae from previously inaccessible benthic and terrestrial sources (Carpenter and others 1992; Schindler and others 1993; Leavitt and others 1994). Our bioenergetics analyses of Sierra Nevada

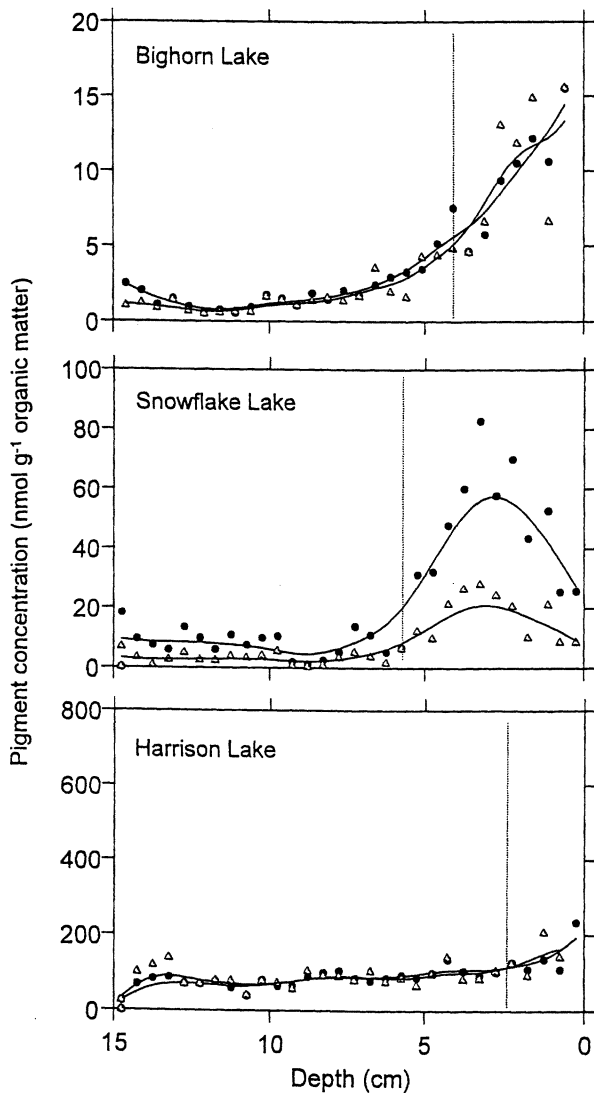


Figure 8. Concentration ( $\text{nmol pigment} \cdot \text{g}^{-1}$  organic matter) profiles of carotenoids from all algae ( $\beta$ -carotene) (closed circles) and chlorophytes alone (lutein-zeaxanthin); (open triangles) in sediments of Bighorn, Snowflake, and Harrison lakes in the Canadian Rocky Mountains. Dashed lines represent the date that trout were first introduced (around 1965) to Bighorn and Snowflake lakes. The dotted line in the Harrison Lake panel also shows 1965 for reference. Regressions were fit using distance-weighted least squares (Wilkinson 1989).

lakes indicate that introduced trout contribute between  $4$  and  $20 \mu\text{g}$  of new  $\text{P} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$  to the water column of lakes during peak summer temperatures and between  $0.8$  and  $3.9 \text{mg P} \cdot \text{m}^{-3} \cdot \text{y}^{-1}$  on an annual basis. Although these nutrient regeneration rates are low relative to estimates for invertebrates and plankton (compare Hudson and others 1999; Wilhelm and others 1999), they are important because they represent a new source of P for plank-

ton. Unfortunately, we currently lack the data necessary to directly estimate the relative magnitude of new P from fish regeneration vs loading from all other allochthonous sources (for example, atmospheric deposition, external loading from the watershed) (Caraco and others 1992). However, to benchmark our estimates of P regeneration by stocked trout, we compared estimates of P loading from fish and atmospheric deposition of P in the Sierra Nevada (Williams and Melack 1997) (Table 4). This comparison showed that P regeneration by trout in currently stocked lakes is about twice that arising from atmospheric P deposition. In lakes that have naturally sustaining trout stocks, P regeneration by fishes is equivalent to atmospheric P loading (Table 4). At the scale of entire catchments, P regeneration by trout is equivalent to 13% and 1% of total atmospheric P loading, for stocked and unstocked lakes respectively, assuming that all catchment P is transferred to the lake.

Leavitt and others (1994) showed that dramatic increases in algal production coincided with fish introductions to lakes in the Canadian Rocky Mountains. These changes in sediment pigment concentrations reflect changes in both planktonic and benthic algal production in response to changes in nutrient regimes and grazing intensity in pelagic and benthic habitats. Presently, it is unclear how much of the algal changes following trout stocking, as indicated by fossil pigments in the sediments, is attributable to alterations in nutrient cycling and to changes in herbivory. However, given the magnitude of P regeneration by fishes in the Canadian Rocky Mountain lakes, and the sensitivity of planktonic algae to small increases in allochthonous nutrient supply (Paul and Schindler 1994; Paul and others 1995), we inferred that a substantial component of algal response to trout stocking was a direct result of changes in nutrient cycles of these systems. Given that trout stocking rates in Sierra Nevada lakes were an order of magnitude lower than stocking rates in the Canadian Rockies, we expect that the effects of trout on P cycles will be more subtle in the Sierra Nevada than in the lakes of the Canadian Rocky Mountains.

Hudson and others (1999) reported that the amount of P recycled by the entire plankton community is much higher than that typically recycled by fish and suggested that fish made little contribution to the P cycles of lakes. However, unlike plankton, P regenerated by fish feeding on benthic and terrestrial prey represents a source of new nutrients that are unavailable when fish are absent (Brabrand and others 1990; Carpenter and others 1992; Schindler and others 1993; Vanni 1996; Schaus and oth-

**Table 4.** Comparison of P Regenerated by Trout ( $P_{\text{fish}}$ ) with P Loading from Precipitation for 12 lakes in the Sierra Nevada.

Parameter	Stocked Lakes ( $n = 5$ )	Unstocked Lakes ( $n = 7$ )
$P_{\text{fish}}$ (kg P/ha/y)	0.074	0.036
Proportion of $P_{\text{fish}}$ that is new	0.81	0.87
New- $P_{\text{fish}}$ (kg P/ha/y)	0.060	0.031
$P_{\text{rain}}$ (kg P/ha/y)	0.035	0.035
Ratio of $P_{\text{fish}} : P_{\text{rain}}$	2.1	1.0
Ratio of $P_{\text{fish}} : P_{\text{catchment}}$	0.16	0.012
Ratio of new- $P_{\text{fish}} : P_{\text{rain}}$	1.7	0.89
Ratio of new- $P_{\text{fish}} : P_{\text{catchment}}$	0.13	0.010

*P* loading from precipitation is presented in two ways.  $P_{\text{rain}}$  is an estimate of *P* loading directly onto the lake surface;  $P_{\text{catchment}}$  is the estimate of *P* loading onto the entire catchment of each of the lakes.

*P*-loading estimates from precipitation represent the median values presented in Table 2 of Williams and Melack (1997), who estimated annual atmospheric nutrient loads to a nearby site in the Sierra Nevada from 1984 to 1993.

ers 1997). This subsidy, although small, may be particularly important in dilute alpine lakes ( $\text{TP} \sim 1 \mu\text{g L}^{-1}$ ) where other allochthonous inputs are extremely low (Williams and Melack 1997). Prior to fish introductions to our study lakes, it is possible that benthic amphibian larvae and large benthic invertebrates provided some benthic nutrient subsidy (Seale 1980; Wilhelm and others 1999) to the pelagic zone. However, it is uncertain whether such benthic taxa actually cause nutrient translocation between benthic and pelagic pools, or whether they simply recycle nutrients within benthic habitats.

In mountain lakes that are relatively deep and have low fish densities, large zooplankton coexist with fish and can make up a substantial fraction of trout diets (Donald and others 1994). These zooplankton-dominated diets should result in relatively low amounts of new *P* regeneration compared with diets dominated by benthic and terrestrial sources (Schindler and others 1993; Vanni 1996; Schaus and others 1997). In combination with the fact that low-density fish populations should excrete lower amounts of *P* than high-density fish populations regardless of diet (Schindler and Eby 1997), we expected that total *P* regeneration would increase with density. Unexpectedly, our analyses demonstrated that total *P* regeneration was independent of fish density over the range of population densities modeled (Figures 4 and 7). A comparison of trout growth rates among lakes (Figures 3 and 5) suggests that this result derives from the strong density-dependent diet and growth responses of trout. As a result, *P* regeneration by fish was related better to fish biomass than density. In lakes with low fish density, trout growth and predation rates were high and resulted in per capita *P*

excretion rates that greatly exceeded those seen in lakes with high-density trout populations. As a result, the high predation and growth rates of trout in low-density populations compensated for the low trout density and low *P* prey, making total regeneration independent of trout density. We interpret this result as a reflection of the fact that these alpine lakes may have a fairly constant production capacity for introduced trout.

Trout grew substantially faster and therefore excreted significantly more *P* in currently stocked lakes than in lakes containing self-sustaining trout populations. One possible explanation for this pattern is that resident fish prey on stocked fingerlings and grow faster as a result. This seems unlikely, given that stocked fingerlings are small (around 3 g each) and are stocked at an average density of 680  $\text{ha}^{-1}$  once every other year. We used the bioenergetics model to estimate the potential contribution of stocked fingerlings to the diets of trout in the continuously stocked lakes. We estimate that fingerling trout are equivalent to about 1% of the total prey consumed by the resident fish populations and that such densities are insufficient to account for the increased trout growth rates. Similarly, it is unlikely that decades of continued stocking have added enough extra nutrients to these lakes to make them more productive because we estimate that stocking adds only  $0.16 \text{ mg P} \cdot \text{m}^{-3} \cdot \text{y}^{-1}$ , or less than 5% of the annual *P* regeneration rates by trout populations.

Other possibilities to explain the fast growth rates of fish in currently stocked lakes include: (a) that the strains of trout that are currently stocked grow more vigorously than those used to establish the original populations, (b) that fish in these lakes do



not reproduce (R. A. Knapp unpublished) and therefore shunt more energy into somatic rather than gonad growth and the associated energetic costs of engaging in reproductive behavior, and (c) that fish managers only stock lakes that they know can support high trout production. Finally, it is also possible that trout in stocked lakes have higher activity rates than trout in unstocked lakes, thus biasing our estimates of fish densities in the actively stocked systems.

### Implications for Current Stocking Practices in Mountain Wilderness Areas

Although the largest perturbations to lake communities and ecosystem processes probably occur soon after fishless lakes are stocked for the first time, our analyses show that continued stocking only serves to exacerbate the original effects. For example, some large invertebrate species (for example, *Hesperodiaptomus* spp.) may coexist with low densities of introduced trout, especially in large and deep lakes (Donald and others 1994). However, many Sierra Nevada lakes with self-sustaining trout populations are still being stocked (R. A. Knapp unpublished), thereby increasing populations above densities that would normally result from natural reproduction. Such increased densities can increase predation intensity and further reduce the number of lakes in which *Hesperodiaptomus* occur. In addition, our analyses of fish nutrient regeneration rates suggest that the contributions of introduced trout to nutrient cycles are approximately double the level estimated for lakes that have not been stocked for several decades (Figure 7).

Therefore, to truly minimize effects of introduced fish on mountain lake ecosystems, all stocking should be halted. This would allow the lakes that lack sufficient spawning habitat to revert to a fishless condition, while reducing the density of fish in lakes with self-sustaining trout populations. Because many currently stocked lakes are likely to harbor self-sustaining trout populations (Bahls 1992; R. A. Knapp unpublished), a moratorium on trout stocking in all lakes would provide fisheries managers a simple means by which to reduce the effects of introduced fish on native invertebrate communities and ecosystem processes while still providing ample recreational fishing opportunities. It remains to be seen whether native faunal assemblages and ecosystem processes in mountain lakes can be restored simply by eliminating fish populations (Funk and Dunlap 1999; McNaught and others 1999). This question is the focus of current whole-lake fish removal experiments in the Sierra Nevada (R. A. Knapp and O. Sarnelle unpublished).

### ACKNOWLEDGMENTS

This research was supported by grants from the Pacific Southwest Research Station to R.A.K. (Challenge Cost-Share Agreement PSW-95-001-CCS, Cooperative Agreements PSW-96-0007CA and PSW-98-0009CA), from the National Science Foundation (NSF) (DEB-9629473) to R.A.K. and O. Sarnelle, and from the National Sciences and Engineering Research Council of Canada to P.R.L. We thank Steve Corn, Jennifer Ruesink, Erik Jeppesen, Mark Scheuerell, and two anonymous reviewers for helpful comments on this manuscript. We are also grateful to Dave Schindler and Brian Parker from the University of Alberta for providing background information on Bighorn Lake.

### REFERENCES

- Allan JD, Flecker AS. 1993. Biodiversity conservation in running waters: identifying the major factors that threaten destruction of riverine species and ecosystems. *BioScience* 43:32-43.
- Anderson RS. 1975. An assessment of sport-fish production potential in two small alpine waters in Alberta, Canada. *Symposia Biologica Hungarica* 15:205-14.
- Anderson RS. 1980. Relationships between trout and invertebrate species as predators and the structure of the crustacean and rotiferan plankton in mountain lakes. In: Kerfoot WC, editor. *Evolution and ecology of zooplankton communities*. Hanover (NH): University Press of New England. p 635-41.
- Anderson RS. 1972. Zooplankton composition and change in an alpine lake. *Verhandlung Internationale Vereinigung für Theoretische und Angewandte Limnologie* 18:264-8.
- Anderson RS, Donald DB. 1978. Limnological survey of some small lakes in the vicinity of the Cascade Trail, Banff National Park. Miscellaneous report. Ottawa: Canadian Wildlife Service. 162 p.
- Anderson RS, Raasveldt LG. 1974. *Gammarus* predation and the possible effects of *Gammarus* and *Chaoborus* feeding on the zooplankton composition in some small lakes and ponds in western Canada. Occasional paper no. 18. Ottawa: Canadian Wildlife Service. 24 p.
- Bahls PF. 1992. The status of fish populations and management of high mountain lakes in the western United States. *Northwest Sci* 66:183-93.
- Brabrand A, Faafeng BA, Nilssen JPM. 1990. Relative importance of phosphorus supply to phytoplankton production: fish excretion versus external loading. *Can J Fish Aqua Sci* 47: 364-72.
- Bradford DF, Cooper SD, Jenkins TM Jr, Kratz K, Sarnelle O, Brown AD. 1998. Influences of natural acidity and introduced fish on faunal assemblages in California alpine lakes. *Can J Fish Aqua Sci* 55:2478-91.
- Caraco NF, Cole JJ, Likens GE. 1992. New and recycled primary production in an oligotrophic lake: insights for summer phosphorus dynamics. *Limnol Oceanogr* 37:590-602.
- Carlisle DM, Hawkins CP. 1998. Relationships between invertebrate assemblage structure, 2 trout species, and habitat structure in Utah mountain lakes. *J North Ame Benthol Soc* 17: 286-300.



- Carpenter SR, Cottingham KL, Schindler DE. 1992. Biotic feedbacks in lake phosphorus cycles. *Trends Ecol Evol* 17:332–6.
- Carpenter SR, Kitchell JF. 1993. *The trophic cascade in lakes*. Cambridge: Cambridge University Press.
- Davis JA, Boyd CE. 1978. Concentration of selected elements and ash in bluegill (*Lepomis macrochirus*) and certain other freshwater fish. *Trans Am Fish Soci* 107:862–7.
- Donald DB. 1987. Assessment of the outcome of eight decades of trout stocking in the mountain national parks, Canada. *North Am J Fish Manage* 7:545–53.
- Donald DB, Anderson RS, Mayhood DW. 1994. Coexistence of fish and large *Hesperodiaptomus* (Crustacea: Calanoida) species in subalpine and alpine lakes. *Can J Zool* 72:259–61.
- Eakins JD, Morrison RT. 1978. A new procedure for the determination of  $^{210}\text{Pb}$  in lake and marine sediments. *Int J Appl Radiation Isotopes* 29:531–6.
- Elser JJ, Carney HJ, Goldman CR. 1990. The zooplankton–phytoplankton interface in lakes of contrasting trophic status—an experimental comparison. *Hydrobiologia* 200:69–82.
- Funk WC, Dunlap WW. 1999. Colonization of high-elevation lakes by long-toed salamanders (*Ambystoma macrodactylum*) after the extinction of introduced trout populations. *Can J Zool* 77:1759–67.
- Hall DL. 1991a. Age validation and aging methods for stunted brook trout. *Trans Am Fish Soc* 120:644–9.
- Hall DL. 1991b. Growth, fecundity, and recruitment responses of stunted brook trout populations to density reduction [dissertation]. Vancouver: University of British Columbia. 210 p.
- Hanson PC, Johnson TB, Schindler DE, Kitchell JF. 1997. Fish bioenergetics 3.0 for Windows. University of Wisconsin Sea Grant Program. Madison.
- Helminen H, Sarvala J. 1997. Responses of Lake Pyhajarvi (southwestern Finland) to variable recruitment of the major planktivorous fish, vendace (*Coregonus albula*). *Can J Fish Aquat Sci* 54:32–40.
- Herbold B, Moyle PB. 1986. Introduced species and vacant niches. *Am Nat* 128:751–60.
- Hrabik TR, Magnuson JJ, McLain AS. 1998. Predicting the effects of rainbow smelt on native fishes in small lakes: evidence from long-term research on two lakes. *Can J Fish Aquat Sci* 55: 1364–1371.
- Hudson JJ, Taylor WD, Schindler DW. 1999. Planktonic nutrient regeneration and cycling efficiency in temperate lakes. *Nature (London)* 400:659–61.
- Knapp RA, Matthews KR. 1998. Eradication of non-native fish by gill-netting from a small mountain lake in California. *Restor Ecol* 6:207–13.
- Knapp RA, Matthews KR. 2000. Nonnative fish introductions and the decline of the mountain yellow-legged frog (*Rana muscosa*) from within protected areas. *Conserv Biol* 14:1–12.
- Kraft CE. 1992. Estimates of phosphorus and nitrogen cycling by fish using a bioenergetics approach. *Can J Fish Aquat Sci* 49:2596–604.
- Leavitt PR, Findlay DL. 1994. Calibration of fossil pigments with 20 years of phytoplankton data from eutrophic Lake 227, Experimental Lakes Area, Ontario. *Can J Fish Aquat Sci* 51: 2286–99.
- Leavitt PR, Schindler DE, Paul AJ, Hardie AK, Schindler DW. 1994. Fossil pigment records of phytoplankton in trout-stocked alpine lakes. *Can J Fish Aquat Sci* 51:2411–23.
- Lodge DM, Stein RA, Brown KM, Covich AP, Bronmark C, Garvey JE, Klosiewski SP. 1998. Predicting impact of freshwater exotic species on native biodiversity: challenges in spatial scaling. *Austr J Eco* 23:53–67.
- McNaught AJ, Schindler DW, Parker BR, Paul AJ, Anderson RS, Donald DB, Agbeti M. 1999. Restoration of the food web of an alpine lake following trout stocking. *Limnol Oceanog* 44:127–36.
- Matthews KR, Knapp RA. 1999. A study of high mountain lake fish stocking effects on the U.S. Sierra Nevada wilderness. *Int J Wilderness* 5:24–6.
- Mayhood DW. 1992. Approaches to managing freshwater fishes in North American parks and reserves. Prepared for Canadian Parks Service, Jasper National Park. Calgary (Alberta): Freshwater Research Ltd. 296 p.
- Melack JM, Stoddard JL. 1991. Sierra Nevada, California. In: Charles DF, editor. *Acidic deposition and aquatic ecosystems: regional case studies*. New York: Springer-Verlag. p 503–30.
- Moyle PB, Light T. 1996. Biological invasions of fresh water: empirical rules and assembly theory. *Biol Conserv* 78:149–61.
- Moyle PB, Yoshiyama RM, Knapp RA. 1996. Status of fish and fisheries. In: *Sierra Nevada Ecosystem Project. Final report to Congress. Volume 2, Assessments and scientific basis for management options*. Davis (CA): University of California, Centers for Water and Wildland Resources. Available online at <http://ceres.ca.gov/snep/pubs/v2.html>.
- Nakashima BS, Leggett WC. 1980. Natural sources and requirements of phosphorus for fishes. *Can J Fish Aquat Sci* 37:679–86.
- Needham PR, Vestal EH. 1938. Notes on growth of golden trout (*Salmo aqua-bonita*) in two High Sierra lakes. *California Fish Game* 24:273–9.
- Neill WE, Peacock A. 1980. Breaking the bottleneck: interactions of invertebrate predators and nutrients in oligotrophic lakes. In: Kerfoot WC, editor. *Evolution and ecology of zooplankton communities*. Hanover (NH): University Press of New England. p 715–25.
- Oldfield F, Appleby PG. 1984. Empirical testing  $^{210}\text{Pb}$ -dating models for lake sediments. In: Haworth EY, Lund JWG, editors. *Lake sediments and environmental history*. Leicester (UK): Leicester University Press. p 93–124.
- Paul AJ, Leavitt PR, Schindler DW, Hardie AK. 1995. Direct and indirect effects of predation by a calanoid copepod (subgenus: *Hesperodiaptomus*) and nutrients in a fishless alpine lake. *Can J Fish Aquat Sci* 52:2628–38.
- Paul AJ, Schindler DW. 1994. Regulation of rotifers by predatory calanoid copepods (subgenus: *Hesperodiaptomus*) in lakes of the Canadian Rocky Mountains. *Can J Fish Aquat Sci* 51:2520–28.
- Radomski PJ, Goeman TJ. 1995. The homogenization of Minnesota lake fish assemblages. *Fisheries* 20:20–3.
- Rahel FJ. 2000. Homogenization of fish faunas across the United States. *Science* 288:854–6.
- Rand PS, Stewart DJ, Seelbach PW, Jones ML, Wedge LR. 1993. Modeling steelhead population energetics in lakes Michigan and Ontario. *Trans Am Fish Soc* 122:977–1001.
- Rowan DE. 1996. Effect of fish and habitat factors on benthic invertebrate communities in high-elevation lakes [thesis]. Las Cruces, NM: New Mexico State University. 187 pp.
- Schaus MH, Vanni MJ, Wissing TE, Bremigan MT, Garvey JE, Stein RA. 1997. Nitrogen and phosphorus excretion by detritivorous gizzard shad in a reservoir ecosystem. *Limnol Oceanogr* 42:1386–97.
- Schindler DE, Eby LA. 1997. Stoichiometry of fishes and their prey: implications for nutrient recycling. *Ecology* 78:1816–31.
- Schindler DE, Kitchell JF, He X, Carpenter SR, Hodgson JR,

- Cottingham KL. 1993. Food web structure and phosphorus cycling in lakes. *Trans Ame Fish Soc* 122:756-72.
- Seale DB. 1980. Influence of amphibian larvae on primary production, nutrient flux, and competition in a pond ecosystem. *Ecology* 61:1531-50.
- [SNEP] Sierra Nevada Ecosystem Project. 1996. Sierra Nevada ecosystems. In: Sierra Nevada Ecosystem Project. Final report to Congress. Volume 1, Assessment summaries and management strategies. Davis (CA): University of California, Centers for Water and Wildland Resources. Available online at <http://ceres.ca.gov/snep/pubs/v1.html>.
- Stoddard JL. 1987. Microcrustacean communities of high-elevation lakes in the Sierra Nevada, California. *J Plankton Res* 9:631-50.
- Vanni MJ. 1996. Nutrient transport and recycling by consumers in lake food webs: implications for algal communities. In: Polis GA, Winemiller KO, editors. *Food webs: integration of patterns & dynamics*. New York; Chapman & Hall. p 81-95.
- Wilhelm FM, Hudson JJ, Schindler DW. 1999. Contributions of *Gammarus lacustris* to phosphorus recycling in a fishless alpine lake. *Can J Fish Aquat Sci* 56:1679-86.
- Wilkinson L. 1989. SYSTAT: the system for statistics. Evanston (IL): SYSTAT Inc., 882 p.
- Williams MR, Melack JM. 1997. Atmospheric deposition, mass balances, and processes regulating streamwater solute concentrations in mixed-conifer catchments of the Sierra Nevada, California. *Biogeochemistry* 37:111-44.