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Author(s): Sudeep Chandra, M. Jake Vander Zanden, Alan C. Heyvaert, Bob C. Richards, Brant C. Allen, Charles R. Goldman

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## The effects of cultural eutrophication on the coupling between pelagic primary producers and benthic consumers

Sudeep Chandra,<sup>1,2</sup> M. Jake Vander Zanden,<sup>3</sup> Alan C. Heyvaert, Bob C. Richards, Brant C. Allen, and Charles R. Goldman

Tahoe Research Group, Department of Environmental Science and Policy, University of California-Davis, Davis, California 95617

### Abstract

We investigated the effects of cultural eutrophication on the coupling between pelagic primary producers and benthic consumers in Lake Tahoe. Spatial and temporal changes in zoobenthos energetics were documented by measuring >40 yr of change in pelagic primary production through <sup>14</sup>C incubations, reduction in clarity by Secchi and light measurements, and sedimentation rates. Effects on zoobenthic primary consumers (oligochaete and chironomid) and an obligate benthic secondary consumer (*Catostomus tahoensis*) were determined by comparing  $\delta^{13}\text{C}$  values of historical and contemporary samples. A model that considers primary production (benthic or pelagic) contributions and their respective  $\delta^{13}\text{C}$  signals was used to examine the factors contributing to zoobenthic energy shifts. Spatially, zoobenthos exhibited a strong positive relationship between lake depth and pelagic isotopic signals. For depths at which ambient 1% light levels have shifted with time (50–85 m), pelagic primary producer and zoobenthic consumer coupling was positive. Historically, zoobenthos from this depth zone obtained 27% of their energy from phytoplankton sources. After 43 yr of eutrophication, they obtained 62% from pelagic sources. A simple model indicated that increased pelagic production and resultant export of matter combined with the loss of benthic primary production contributed to the change in zoobenthos energetics. This change was passed on to higher consumers, with the benthic fish Tahoe sucker (*Catostomus tahoensis*) now deriving ~21% of its energy from pelagic primary production sources. This study demonstrates how lake eutrophication increases the coupling between pelagic and benthic habitats.

Cultural eutrophication ranks among the major threats to freshwater ecosystems (Edmondson 1991, 1994; Carpenter et al. 1998, 1999). Often human-induced eutrophication results in large changes in lake ecosystems, including noxious algal blooms, anoxia, and changes to species assemblages (Britt 1955; Krieger 1984; Horne and Goldman 1994). These changes produce losses to ecosystem services, resulting in

large costs to lake managers and the public (Wilson and Carpenter 1999). Eutrophication and its costs are generally viewed as a pelagic problem, even though benthic habitats also provide valuable ecosystem services, including nutrient recycling, the control of algal biomass, the support of fisheries, and the regulation of energy flow through freshwater food webs (Covich et al. 1999; Palmer et al. 2000; Schindler and Scheuerell 2002). Recent studies emphasize the effects of eutrophication across habitat boundaries, focusing on changes to benthic littoral and profundal habitats (Vadeboncoeur et al. 2002).

Benthic primary production can be substantial and even dominate whole-lake primary production under low nutrient and productivity conditions (Vadeboncoeur et al. 2001, 2002). With increasing trophic status, whole ecosystem primary production shifts toward phytoplankton dominance. This results from increases in nutrient availability that increases pelagic production and shades benthic substrates (Sand-Jensen and Borum 1991). The shift in the amount and distribution of whole-lake primary production with lake eutrophication should have implications for benthic primary consumer energetics.

Studies have examined the effect of eutrophication on benthic invertebrate communities at varying natural and experimental timescales. For example, Blumenshine et al. (1997) varied nutrient inputs into the water column of large mesocosms, which shifted benthic primary consumer size structure, community composition, and density. Furthermore, zoobenthos that filter feed on newly sedimented phytoplankton respond positively in lakes undergoing eutrophication or nutrient additions (Jónasson 1972; Welch et al. 1988). Responses also vary temporally with primary con-

<sup>1</sup> Corresponding author (sudeep@cabnr.unr.edu).

<sup>2</sup> Present address: Department of Natural Resources and Environmental Science/MS 186, 1000 Valley Road, University of Nevada-Reno, Reno, Nevada 89512.

<sup>3</sup> Present address: Center for Limnology, 680 N Park Street, University of Wisconsin-Madison, Madison, Wisconsin 53706.

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sumers feeding on sedimented production immediately after spring and fall algal blooms (Ahlgren et al. 1997; Goedkoop et al. 1998, 2000). Thus changes in the amount, distribution, and timing of primary production should affect benthic primary consumers (Covich et al. 1999). Because lacustrine consumers can rely heavily on direct and indirect benthic energy pathways (Vander Zanden and Vadeboncoeur 2002), shifts toward greater dominance of pelagic primary production associated with eutrophication should be reflected in higher trophic levels of lake food webs (Vadeboncoeur et al. 2002).

In ultraoligotrophic lakes, we hypothesize that changes in energy sources supporting zoobenthos should occur before alterations in community composition. Lake Tahoe has undergone progressive cultural eutrophication in the last four decades and provides a valuable ecosystem for examining changes to the coupling between pelagic and benthic habitats. In this study, we use long-term measurements spanning greater than 40 yr to document the effects of eutrophication on pelagic primary production. We also quantified sedimentation rates and use stable isotopes from two extreme time periods to examine how eutrophication has affected the contribution of benthic and pelagic primary production to primary and secondary consumers. We used a simple model to determine the mechanisms that shift benthic primary consumer energetics in lakes undergoing progressive eutrophication. The observed shifts in energy source supporting zoobenthos were consistent with model predictions on the basis of the changes in relative contributions of benthic and pelagic primary production and their respective isotope signals.

## Methods

Lake Tahoe is an ultraoligotrophic, subalpine lake in the Sierra Nevada mountain range of California and Nevada in the United States. It has a maximum depth of 501 m, a mean depth of 305 m, and a surface area of 495 km<sup>2</sup>. For a thorough description of the study site, see Goldman (1981). The first measurements of pelagic primary production in the lake occurred in 1959 and continuously since 1967 (Goldman 2000). Annual estimates were based on an average of measurements from the <sup>14</sup>C tracer method. They were taken at 13 depths (0–105 m) on ~35 dates throughout the year from one location (Fig. 1). We determined the decline in transparency from both Secchi disk and light photometer (Rigosha RT-2051 and LI-COR 192) measurements taken on the same dates and location. Yearly averages of 1% light levels were calculated from extinction coefficients determined by the light photometer readings.

Historical mass sedimentation rates were calculated with <sup>210</sup>Pb results from samples recovered from a box core taken at 420 m lake depth (Heyvaert 1998). The segmented constant flux constant sedimentation rate model was used to calculate interval changes in sedimentation rates over the last 43 yr in the lake (Robbins 1978). The average carbon to dry weight matter (5.65% ± 0.48%) during this period was applied to dry weight estimates for each time interval to determine the carbon sedimentation rate (Heyvaert unpubl.

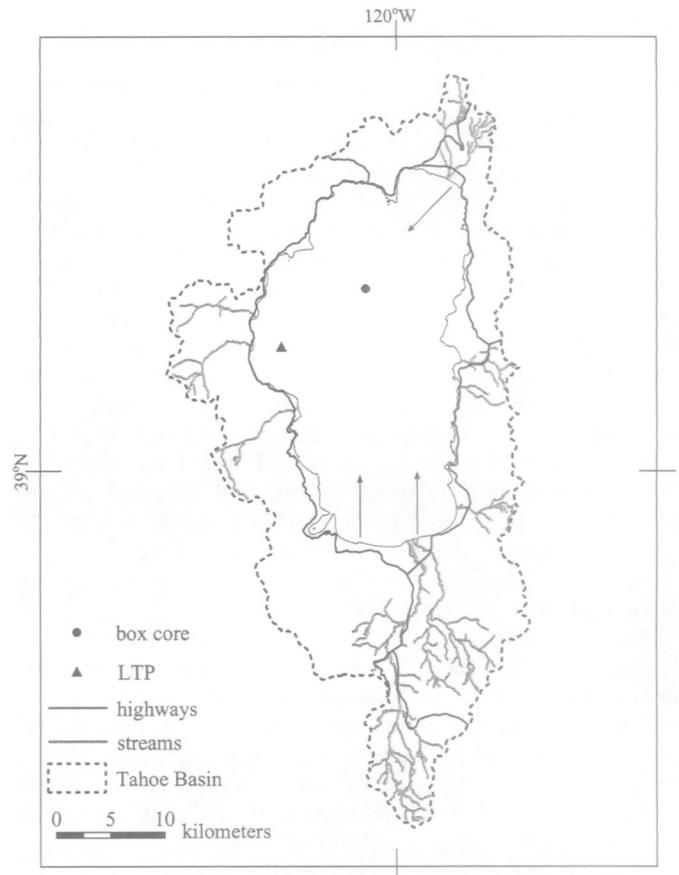


Fig. 1. Map of the Lake Tahoe watershed and the locations of pelagic sampling from the midlake station (LTP), box core station, and zoobenthos transects (indicated by arrows).

data). Sediments were dried to constant weight at 60°C, ground to a fine powder by mortar and pestle, and sent for <sup>210</sup>Pb and <sup>13</sup>C analyses. The methods for <sup>210</sup>Pb analysis are thoroughly outlined in Heyvaert (1998). The analyses for <sup>13</sup>C content were conducted as described later for biotic tissue samples. Isotopic analysis of sediment samples was used to determine whether increasing pelagic primary production signatures shift  $\delta^{13}\text{C}$  during this time period.

Isotopic  $\delta^{13}\text{C}$  was used to determine the flow of organic matter through food webs (Gu et al. 1994; Vander Zanden et al. 1999). The minimal enrichment ( $\pm 0.47\text{‰}$ ) from lower to high trophic levels allowed for the differentiation of littoral and pelagic primary production sources (Hecky and Hesslein 1995; Vander Zanden and Rasmussen 2001). Benthic invertebrates were collected from the same location and depths during the summer of 1963 (May–October) and 2001 (May–July; Fig. 1). Information on the sample sizes collected in 1963 were not available; however, over 360 grab samples were collected in 2001 and sieved through a 60- $\mu\text{m}$  mesh bucket. From each grab, zoobenthos were identified to Family (oligochaete and chironomid) and identified as primary consumers. Multiple individuals from each family were pooled for  $\delta^{13}\text{C}$  analysis. Thus, up to two samples (one from each Family) of  $\delta^{13}\text{C}$  was measured for each depth. Dorsal muscles from archived and contemporary specimens

of Tahoe suckers (*Catostomus tahoensis*), ranging from 13 to 33.6 cm total length, were also collected for  $\delta^{13}\text{C}$ .

Fish and invertebrate samples were dried at 60°C for at least 24 h then ground into a fine powder by mortar and pestle. The samples were packed into tin capsules (8 × 5 mm) and analyzed for carbon with continuous flow isotope ratio mass spectrometry (IRMS; 20-20 mass spectrometer, PDZEuropa Scientific). Sample combustion to CO<sub>2</sub> occurred at 1,000°C in an inline elemental analyzer (PDZEuropa Scientific, ANCA-GSL). The gases were separated on a Carbosieve G column (Supelco) before introduction to the IRMS. These gases were compared with a standard gas (Pee Dee Belemnite) injected directly into the IRMS before and after the sample peaks. Carbon isotopic ratio was expressed as a per mil (‰) deviation defined by the equation  $\delta^{13}\text{C} = [(^{13}\text{C}/^{12}\text{C})_{\text{sample}} / (^{13}\text{C}/^{12}\text{C})_{\text{standard}} - 1] \times 1,000$ . Thus, more positive  $\delta^{13}\text{C}$  was more isotopically enriched, or contained proportionally higher concentrations of heavier <sup>13</sup>C isotope. After ~20 samples, a replicate and a standard were added to the analysis. Replicate variation was <3%, and machine analytical error is within 0.2‰.

Archived fish and invertebrates were originally fixed in formalin and transferred to alcohol. The investigation of Sarakinos et al. (2002) and Edwards et al. (2002) on the effects of formalin and formalin/ethanol preservation on both fish muscle tissue and invertebrates showed a decrease in  $\delta^{13}\text{C}$  resulting from preservation (mean ± SE; -1.12‰ ± 0.23‰ and -1.77‰ ± 0.52‰, respectively). This difference was not statistically significant (Student's *t*-test,  $t_{10} = 1.295$ ,  $p = 0.224$ ). Thus, the mean effect for all taxa (fish and invertebrates; -1.28‰ ± 0.22‰) was used as the  $\delta^{13}\text{C}$  correction factor (Vander Zanden et al. 2003). The 2001 zoobenthos were stored in isopropyl alcohol, and the Tahoe suckers were processed immediately after collection. Because isopropyl alcohol preservation does not affect  $\delta^{13}\text{C}$  signatures (Sarakinos et al. 2002; Edwards et al. 2002), no correction factor was applied to these samples.

The archived and contemporary  $\delta^{13}\text{C}$  values were compared to determine the effects of cultural eutrophication on the primary production sources supporting zoobenthos. To facilitate their comparison, archived signatures were adjusted for changes in atmospheric isotopic levels that have occurred in the past century (Suess effect). Archived concentrations were normalized to present day by calculating the time-dependent depletion value with Eq. 1 (Schelske and Hodell 1995),

$$\delta^{13}\text{C} = -4.5778 + 7.3430t - 3.9213 \times 10^{-3}t^2 + 6.9812 \times 10^{-7}t^3 \quad (1)$$

where  $t$  is time (yr). This depletion value was subtracted from the archived signatures to adjust for the Suess effect.

Because primary consumers have different feeding strategies (oligochaetes are subsurface deposit feeders, chironomids are filter feeders of recently deposited matter), potentially affecting their  $\delta^{13}\text{C}$  signals, we compared taxa-specific signals for each time period within two habitats: the euphotic and aphotic zones. The photic habitats for each time period were differentiated by their respective 1% light level thresholds. Assumed to be the lower limit for primary production,

1% light levels were thought to differentiate sources of primary production (benthic and pelagic) due to changes in light condition. The pooled primary consumer  $\delta^{13}\text{C}$  concentrations were compared to see whether eutrophication affected the zoobenthos (across all depths and between years). Zoobenthos  $\delta^{13}\text{C}$  from depths approximately to where 1% light levels shifted over this time period (50–85 m) were evaluated. To aid in interpretation, the energetics dependency of zoobenthos and fish were quantified with a two-end member mixing model of the  $\delta^{13}\text{C}$  data (Vander Zanden and Vadboncoeur 2002). Percent pelagic reliance was estimated as

$$\% \text{Pelagic} = \left( \frac{\delta^{13}\text{C}_{\text{consumer}} - \delta^{13}\text{C}_{\text{littoral}}}{\delta^{13}\text{C}_{\text{pelagic}} - \delta^{13}\text{C}_{\text{littoral}}} \right) \times 100 \quad (2)$$

where  $\delta^{13}\text{C}_{\text{consumer}}$  was the individual  $\delta^{13}\text{C}$  value for a primary consumer at a given depth. The littoral endpoint is the mean  $\delta^{13}\text{C}$  of zoobenthos at <10 m for each year and represents the benthic primary production signal. The pelagic endpoint (mean  $\delta^{13}\text{C}$  of zoobenthos >241 m deep) represented the pelagic primary production signal. These values correspond to phytoplankton/zooplankton (range -25.32 to -26.99) and periphyton (range -11.01 to -13.26) signals from the lake (Chandra unpubl. data).

Taxa-specific means of  $\delta^{13}\text{C}$  for each time period between photic habitats were compared with a Student's *t*-test (euphotic: 1963 oligochaete  $n = 20$ , chironomid  $n = 20$ ; 2001 oligochaete  $n = 12$ , chironomid  $n = 14$ ; aphotic: 1963 oligochaete  $n = 5$ , chironomid  $n = 4$ ; 2001 oligochaete  $n = 17$ , chironomid  $n = 7$ ). Primary consumer  $\delta^{13}\text{C}$  between years over all depths were compared with logarithmic curves and 95% confidence intervals. A linear fit was used because the data were log transformed to normalize the  $\delta^{13}\text{C}$  values for both years. An analysis of covariance (ANCOVA) was used to test for differences between years in  $\delta^{13}\text{C}$  for zoobenthos collected between 50 and 85 m ( $n = 13$  for 1963,  $n = 17$  for 2001). All statistical analyses were conducted on the nontransformed  $\delta^{13}\text{C}$  data with the two-end member mixing model used for interpretive purposes. A Student's *t*-test was used to compare Tahoe sucker  $\delta^{13}\text{C}$  values collected for two time periods ( $n = 3$  for 1964,  $n = 12$  for 1998). Analyses were conducted with JMP 4.0.3 (SAS Institute Inc., academic version).

A simple model was created to predict zoobenthic  $\delta^{13}\text{C}$  values as the lake has undergone eutrophication and to examine the mechanisms changing zoobenthic energy uptake. It was calculated as in Eq. 3,

$$\delta^{13}\text{C}_{\text{zoobenthos predicted}} = \left\{ \frac{\text{PPr}_{\text{benthic}(z)}}{\text{PPr}_{\text{benthic}(z)} + [\text{PPr}_{\text{pelagic}(z)} \times 0.07]} \right\} \times \delta^{13}\text{C}_{\text{littoral}} + 1 - \left\{ \frac{\text{PPr}_{\text{benthic}(z)}}{\text{PPr}_{\text{benthic}(z)} + [\text{PPr}_{\text{pelagic}(z)} \times 0.07]} \right\} \times \delta^{13}\text{C}_{\text{pelagic}} \quad (3)$$

where  $\text{PPr}_{\text{benthic}(z)}$  was benthic primary production at a given depth  $z$ . Benthic primary production was calculated from a benthic photosynthesis irradiance curve developed from benthic primary production estimates from 1980 (Loeb 1980). A conservative estimate of benthic production was used be-

cause we only measured epilithic production.  $PP_{\text{pelagic}(z)}$  was the total annual pelagic production exported to a given depth  $z$ . Pelagic primary production was based on the integration from 0 to 90 m depth calculated in 1967 and 2000 with  $^{14}\text{C}$  incubations. The constant 0.07 was the export ratio for the lake. This ratio was determined from pelagic production estimates and sedimentation trap measurements taken down to 94 m in 1994 (Heyvaert unpubl. data) and is consistent with values reported in Baines and Pace (1994). No other measurements were made for Lake Tahoe; thus, there is no variability associated with this export value, and this value was assumed to be constant over the time periods evaluated. The  $\delta^{13}\text{C}_{\text{littoral}}$  and  $\delta^{13}\text{C}_{\text{pelagic}}$  endpoints were the same used for the two time periods compared in the two–end member mixing model (Eq. 2). James et al. (2000) found no significant alterations of periphyton  $\delta^{13}\text{C}$  as a function of depth; thus, none was incorporated into the model.

## Results

The average annual pelagic primary production in Lake Tahoe has increased exponentially since initial measurements in 1959, with a >4.5-fold increase over this time pe-

riod ( $y = 21.04e^{0.043x}$ ,  $R^2 = 0.96$ ; Fig. 2a). Concurrent with this production increase, a marked decline in water clarity measured both by Secchi and light photometer readings occurred (Fig. 2b). The Secchi steadily declined from 31.2 to 22.4 m ( $y = 35.05 - 0.28x$ ,  $R^2 = 0.84$ ). Estimated 1% light penetration to the lake bottom shifted from 79.5 m in 1967 to 57.2 m in 2001 ( $y = 93.70 - 0.73x$ ,  $R^2 = 0.77$ ; Fig. 2c). Both methods of measuring clarity indicated a 28% decline since initial measurements. The carbon sedimentation rate estimated from the deep-water core showed an almost two-fold increase from 1948 to 1991, increasing from 5.30 to 10.20  $\text{g m}^{-2} \text{yr}^{-1}$  (Fig. 2d). Sediment  $\delta^{13}\text{C}$ , used to determine whether planktonic matter has changed its isotopic value as the lake has undergone increased pelagic production, remained constant over this time period (range  $-26.29\text{‰}$  to  $-26.56\text{‰}$ ,  $y = 0.0007x - 27.83$ ,  $R^2 = 0.001$ ; Fig. 2d) and is similar to phytoplankton/zooplankton collected from the lake (see Methods).

Taxa-specific (oligochaete vs. chironomid)  $\delta^{13}\text{C}$  signals for each time period showed no significant difference within habitats (Table 1). As a result, taxa  $\delta^{13}\text{C}$  were pooled, and differences were analyzed across depths. Lake Tahoe primary consumers collected in 1963 and 2001 showed no sig-

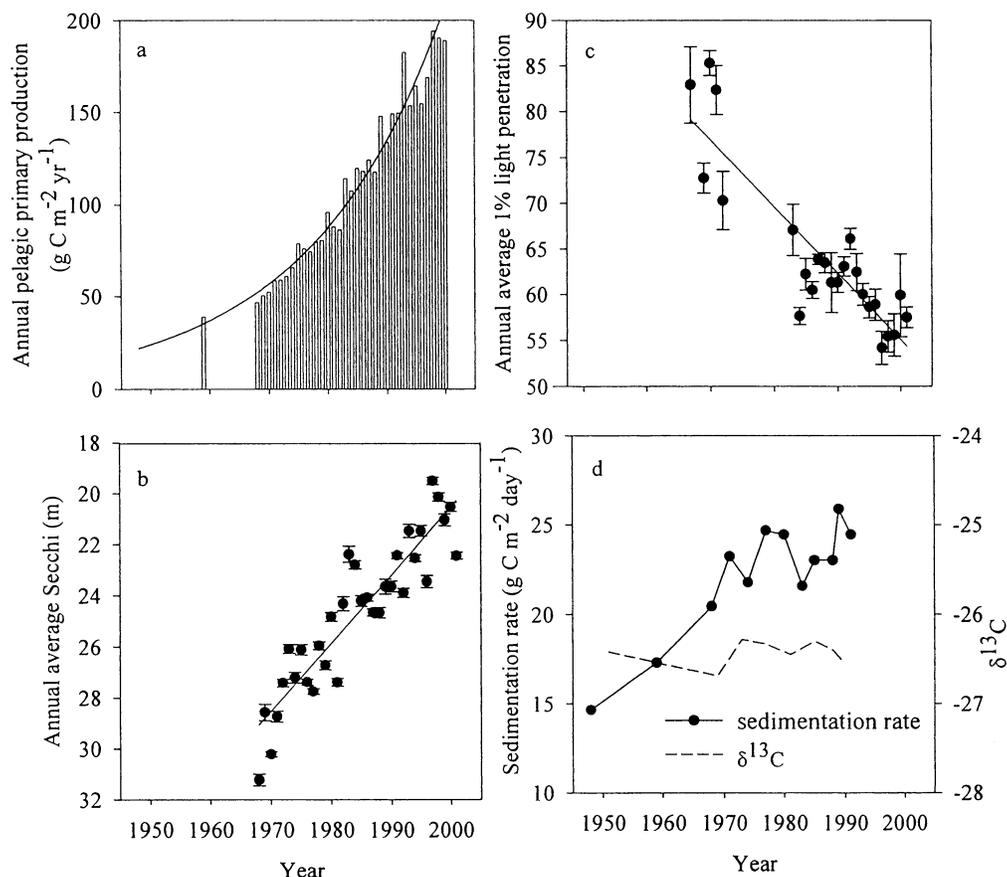


Fig. 2. Long-term (>40 yr) responses in Lake Tahoe from cultural eutrophication. The long-term trends observed in Lake Tahoe over time. Annual averages for (a) pelagic primary production, (b) Secchi, and (c) 1% light levels from the pelagic sampling station. Statistics for curves are presented in the text. (d) Estimated sedimentation rate and  $\delta^{13}\text{C}$  to the lake bottom calculated from the box core station.

Table 1. Taxa comparison of mean  $\delta^{13}\text{C}$  signals for each sampled time period within euphotic and aphotic habitats.

Year	Habitat	Family	Mean $\pm$ SE	<i>p</i> value
1963	Aphotic	Oligochaete	$-22.13 \pm 0.23$	0.307
		Chironomidae	$-22.30 \pm 0.46$	
	Euphotic	Oligochaete	$-16.10 \pm 0.65$	
		Chironomidae	$-16.45 \pm 0.52$	
2001	Aphotic	Oligochaete	$-23.29 \pm 0.27$	1.054
		Chironomidae	$-22.77 \pm 0.42$	
	Euphotic	Oligochaete	$-18.06 \pm 0.91$	
		Chironomidae	$-16.43 \pm 0.83$	

nificant difference in  $\delta^{13}\text{C}$  across all depths and exhibited an overlapping range of values (for 1963,  $y = -10.76x - 4.62$ ,  $R^2 = 0.74$ ; for 2001,  $y = -9.75x - 6.16$ ,  $R^2 = 0.70$ ; Fig. 3). At shallow depths (0–92 m), primary consumers had more positive  $\delta^{13}\text{C}$  values, indicative of predominantly periphyton consumption ( $-16.28\text{‰} \pm 0.43\text{‰}$  for 1963,  $-18.93\text{‰} \pm 0.61\text{‰}$  for 2001; mixing model range = 0–100% pelagic sources).  $\delta^{13}\text{C}$  values from 100 m or deeper were more negative and less variable relative to shallower waters ( $-22.22\text{‰} \pm 0.26\text{‰}$  for 1963,  $-23.55\text{‰} \pm 0.32\text{‰}$  for 2001), indicative of pelagic reliance (mixing model range = 77–100% pelagic sources).

When restricted to depths at which 1% light shifted (between 50 and 85 m), ANCOVA analysis, including year and depth as covariates, showed no significant interaction (Table 2). This allowed for the comparison of year effects (*y* intercepts) for the two time periods. The difference between 1963 and 2001 was highly significant, demonstrating a shift to more negative  $\delta^{13}\text{C}$  ( $-16.56\text{‰}$  in 1963,  $20.81\text{‰}$  in 2001 at 50 m; Fig. 4a; Table 2). The two-end member mixing model indicates a resource shift for these consumers from 27% to 62% reliance on pelagic carbon (Fig. 4b). The simple model of primary consumer  $\delta^{13}\text{C}$  shifts over this time period predicted similar responses to eutrophication (Fig. 4a,b; Table 2). A comparison between the 1963 and 2001 predicted compared with observed regressions showed similar slopes but dissimilar *y* intercepts (Table 2). The model predicts relative decreases in zoobenthos reliance on benthic production over time resulting from the decrease in benthic primary production and increase in pelagic primary production (Fig. 5a,b).

Tahoe sucker  $\delta^{13}\text{C}$  values from 1964 and 1998 were compared to determine whether these observed zoobenthic energy changes were passed to higher trophic levels. Student's *t*-test showed a highly significant ( $p = 0.003$ ) decrease in  $\delta^{13}\text{C}$  from  $-10.64\text{‰}$  to  $-15.99\text{‰}$ . The mixing model demonstrated no pelagic energy contribution for this fish in 1964 and ~21% pelagic carbon in 1998.

## Discussion

**Basic effects.**—Lake Tahoe is responding to eutrophication by increasing pelagic primary production (Fig. 2a), which results in decreased light penetration into the lake (Fig. 2b,c). Concurrent with the increase in pelagic production, organic matter sedimentation also increases to the lake bottom (Fig. 2d). Heyvaert (1998) found a threefold increase

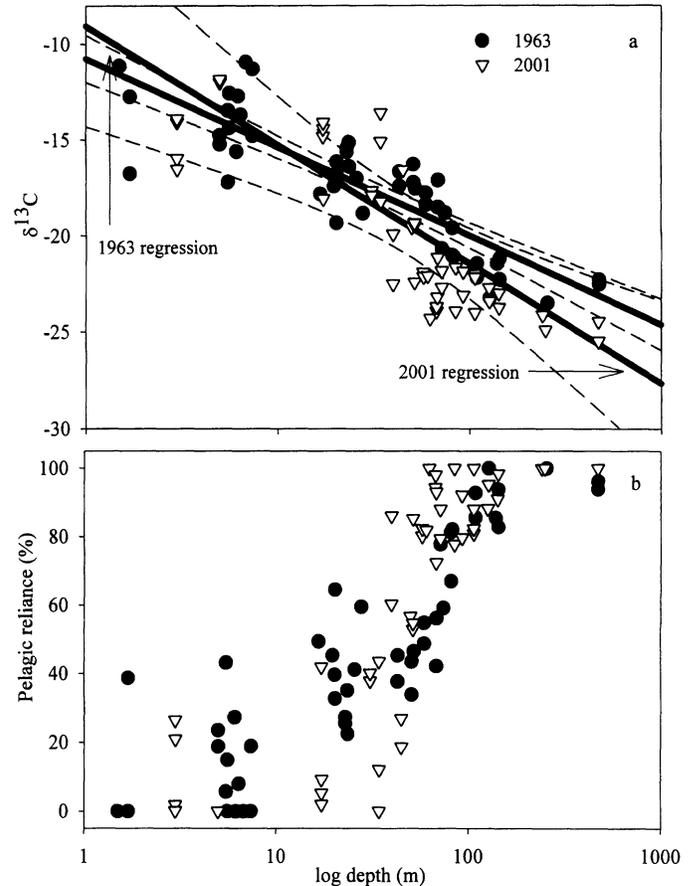


Fig. 3. Spatial measurements of the energetic reliance for all zoobenthic primary consumers for 2 yr (1963 and 2001) by depth gradient. (a)  $\delta^{13}\text{C}$ . More negative signatures indicate pelagic primary production sources. There is no significant difference between years (linear regression: log scale  $\pm$  95% confidence intervals), but changes by depth are significant. (b) Percent pelagic reliance is calculated from the two-end member mixing model, indicating a strong spatial coupling of pelagic primary production to benthic primary consumers with depth.

Table 2. Statistical coefficient summaries of logarithmic curves for  $\delta^{13}\text{C}$  values by depth, ANCOVA analysis from 50 to 85 m and model predicted and observed regressions for  $\delta^{13}\text{C}$  versus depth.

	df	Sum of squares	<i>F</i> ratio	<i>p</i>
ANCOVA analysis from 50–85 m				
Depth (m)	1	35.91	24.12	<.0001
Year	1	44.16	26.66	<.0001
Year $\times$ depth	1	0.5	0.33	0.57
	<i>y</i> intercept	Slope		
Model predictions versus observed $\delta^{13}\text{C}$ values				
1963 Predicted	-9.11	-0.11		
Observed	-11.05	-0.11		
2001 Predicted	-15.49	-0.10		
Observed	-16.78	-0.09		

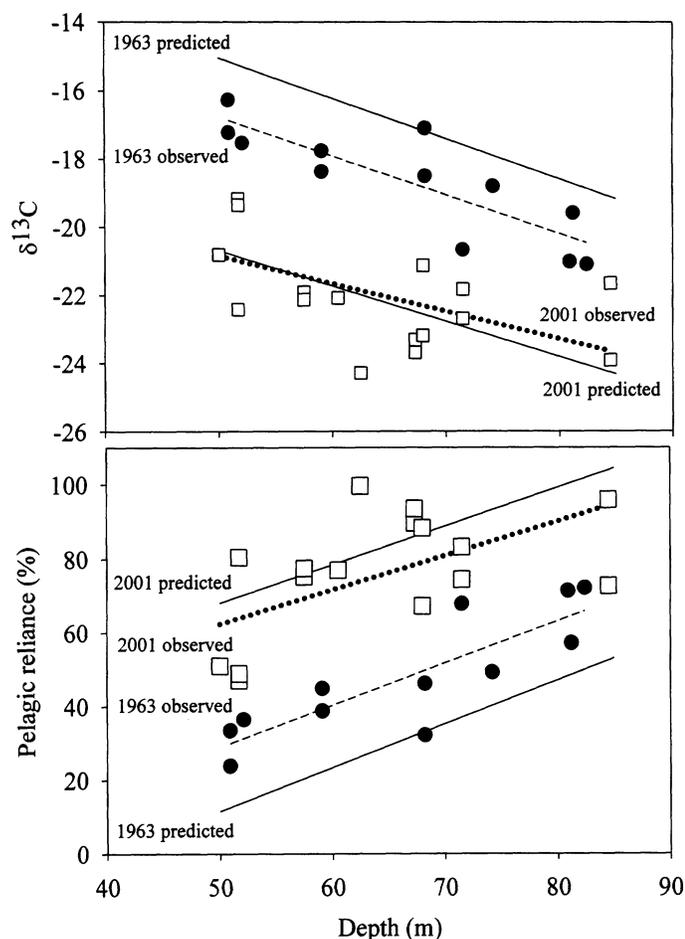


Fig. 4. Long-term temporal energetic shifts for zoobenthic primary consumers between depths of present day and historical (1963) 1% light levels (50–85 m). Data points and linear regressions from ANCOVA analysis are presented for observed values. Predicted regression curves from the model are presented without data points. (a)  $\delta^{13}\text{C}$  changes by depth indicate a significant shift in zoobenthic reliance on pelagic primary production sources over time. (b) Percent pelagic reliance by depth calculated from the two-end member mixing model indicates a shift from 32% to 62% in pelagic primary production sources over time at 50 m.

in the flux of biogenic silica between two time periods of major watershed development (1900–1970 and 1971–1996), indicating that organic matter derived from the pelagic zone is transported to the lake bottom. Previous experimental and monitoring studies show similar responses to eutrophication (Edmondson and Lehman 1981; Anneville and Pelletier 2000; Ostojic 2000). As nutrient loading increases, pelagic primary production is stimulated, resulting in organic matter sedimentation to the lake bottom (Hodell and Schelske 1998). The export of organic matter should strengthen the coupling between pelagic to benthic habitats (Vadeboncoeur et al. 2003), particularly in large lakes in which the coupling is already strong (Schindler and Scheuerell 2002).

**Sediment  $\delta^{13}\text{C}$  variability**—Sediment  $\delta^{13}\text{C}$  from Lake Tahoe, representing recently deposited pelagic material and the food source to zoobenthos, had a similar signal over time

(Fig. 2d). This is contrary to what might be expected by the Suess effect, in which the  $\delta^{13}\text{C}$  signature should decrease over time (Schelske and Hodell 1995). The increase in pelagic primary production, which should increase the  $\delta^{13}\text{C}$  of this matter, could also be acting in concert, however, keeping the  $\delta^{13}\text{C}$  signals stable over time. Although the  $\delta^{13}\text{C}$  of organic matter and primary production is not exactly the same as profundal zoobenthos, the organic matter might be fractionating as phytoplankton decomposition occurs as it settles to the lake bottom. In Lake Tahoe, Pearl (1973) demonstrated that microbial activity plays an important role in the aggregation and potential remineralization of settling particulate organic carbon.

**Pelagic primary producer to zoobenthic primary consumer coupling**—Intertaxa variability of  $\delta^{13}\text{C}$ : The primary consumers measured have different feeding strategies (surface and subsurface), potentially influencing their  $\delta^{13}\text{C}$  signals because feeding on a refractory food source or recently settle particles should result in different isotopic fractionations. Intertaxa  $\delta^{13}\text{C}$  signals for each time period within different photic habitats were similar (Table 1). Similar food and taxa signals suggest that fractionation differences were not a major influence in this study; thus, we pooled the  $\delta^{13}\text{C}$  values from both Families to determine the effect of eutrophication on primary consumers in Lake Tahoe.

**A spatial perspective:** This study demonstrates the strength of pelagic primary production to zoobenthic primary consumer coupling along a spatial gradient. A mix of benthic and pelagic primary production supports benthic littoral (0–20 m) consumers, whereas profundal ( $\geq 150$  m) consumers are supported by sedimented phytoplankton production (77–100%). A study of zoobenthos energy sources from Lake Baikal show similar results (Yoshii 1999). In Baikal, shallower zoobenthos also obtain their energy from a complex mix of primary production sources. At greater depths, zoobenthos have more negative and less variable  $\delta^{13}\text{C}$  values, representing pelagic energy sources. Thus, the pelagic to benthic coupling changes along a spatial gradient becoming stronger with depth.

**A long-term temporal perspective:** The coupling between pelagic primary production and zoobenthic consumers can also change temporally. In this study, cultural eutrophication resulted in significant effects on zoobenthos energy between the depths of historical and present day 1% light levels. Historically, zoobenthos from this depth range received 27% of their energy from sedimenting phytoplankton production. This has more than doubled, with 62% of energy uptake now coming from pelagic sources. Thus, the increase in Lake Tahoe's pelagic production and the resulting sedimentation has changed zoobenthos energy uptake. This study, however, compared two extreme time periods after the lake had undergone progressive eutrophication. Because pelagic production follows an interannual pattern (Jassby et al. 1992), the degree of pelagic–benthic coupling will depend on the amount of pelagic production for a given year. Thus, energetic shifts in zoobenthos are likely variable over time. In Lake Tahoe, however, there has been a strong increase over

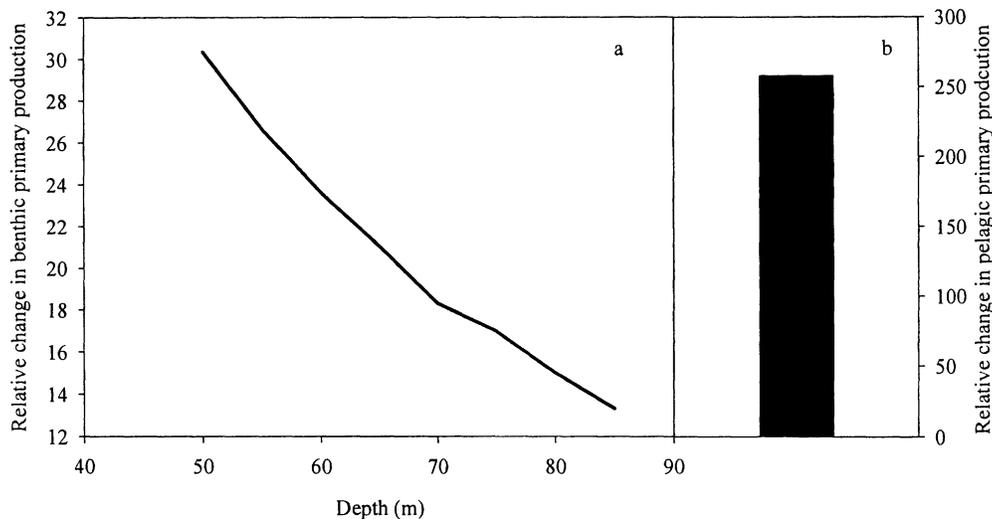


Fig. 5. Model output showing the response primary production (benthic and pelagic) resulting from cultural eutrophication between depths of present day and historical (1963) 1% light levels (50–85 m). Relative change in (a) benthic primary production, estimated from photosynthesis irradiance curves, shows a strong decline in production with depth over time. (b) Assuming a constant export factor, pelagic phytoplankton export has increased 257% to these depths over time.

time in pelagic primary production despite the interannual variation (Jassby et al. 1992), indicating that a comparison of two extreme time periods can demonstrate the effect of eutrophication to zoobenthos energetics.

Studies evaluating eutrophication effects on whole-ecosystem primary production (benthic and pelagic) show that increases in pelagic production cause a decline in light penetration and a compensatory decline in periphyton production. Using  $\delta^{13}\text{C}$  tracers, Vadeboncoeur et al. (2003) found that benthic littoral consumers increased their pelagic reliance along a lake trophic gradient. Thus, it is probable that the strengthening of coupling of pelagic primary production to benthic consumers that we observe results not only from increased export of pelagic production but also from the decline in benthic primary production (Vadeboncoeur et al. 2003).

Our model predictions were consistent with the observed trend of zoobenthos shifting to pelagic primary production between historical and present day 1% light levels. Predicted and observed changes in  $\delta^{13}\text{C}$  with depth had similar slopes; however, the model predicted more positive  $\delta^{13}\text{C}$  values than were observed for both years. This probably results in part from a variety of estimations and assumptions placed into the model. For example, we assumed a constant export ratio during the period of eutrophication because of a lack of regular samplings from the lake. This ratio however is likely variable over time because of the interannual variation in pelagic primary production (Jassby et al. 1992), which is one factor that determines the amount of matter exported to the lake bottom. This ratio is also mediated by complex processes, such as microbial remineralization and zooplankton species composition (Elser et al. 1995), which has been altered in Lake Tahoe (Richards et al. 1975). Thus, the variation in the export ratio should affect the model calculations for primary production contributions to zoobenthos. Second, benthic primary production was measured only on epilithic

surfaces in 1980, ignoring sediment surfaces in Lake Tahoe. Sediment primary production, however, can be a significant component of benthic production. Thus the model underestimated benthic contributions to the zoobenthos at discrete depths. Therefore, the predicted shift of zoobenthos toward pelagic primary production as a result of eutrophication should be interpreted with caution. With similar slopes, however, the mechanisms changing zoobenthic  $\delta^{13}\text{C}$  can be determined. The model suggests that not only are increases in pelagic production and its export important contributors for zoobenthos energy but that the decline in periphyton production is also an important factor in changing zoobenthos  $\delta^{13}\text{C}$  values. Thus, cultural eutrophication affects the distribution of whole-lake algal primary production by shifting it from benthic to pelagic habitats. The synergistic effects of benthic algal declines and increased export of pelagic production alter zoobenthic primary consumer energetics.

**A short-term temporal perspective:** This study demonstrates the importance of pelagic primary production as an energy source for benthic communities and the increased positive coupling between these habitats as eutrophication persists over decadal timescales. Previous research demonstrates the coupling between pelagic primary production and zoobenthic primary consumers at shorter temporal scales. For example, seasonal inputs from spring and fall phytoplankton blooms are important drivers for zoobenthos growth and biomass, as well as sediment microbial activity (Goedkoop and Johnson 1996; Gullberg et al. 1997; Goedkoop et al. 1998). In particular, sedimenting phytoplankton to the profundal zone have been shown to be important for different zoobenthos taxa and cohorts (Ahlgren et al. 1997; Goedkoop et al. 1998). Thus, changes in coupling between pelagic primary production and zoobenthic primary consumers can occur at both annual and decadal timescales. Changes

in habitat coupling should also be passed on to fish that feed on zoobenthos.

**Effects on secondary consumers:** The effect of eutrophication on energy sources of Tahoe suckers was examined with  $\delta^{13}\text{C}$  signatures. The Tahoe sucker is a deep-water fish that is morphologically constrained as an obligate bottom feeder (Moyle 2002), making it ideal for assessing whether changes to primary consumer energetics are passed on to higher consumers. Suckers collected in 1963 and 2000 shift  $-5.35\%$  over this period, indicating a shift ( $\sim 21\%$ ) toward pelagic energy sources. Because fish undergo changes in diet with increase in size, it is possible that this study overestimated the shift for the suckers. Unfortunately, specimens from 1963 were limited; thus, it is not possible to measure changes to specific size classes of fish over time. The broad size range of fish compared, however, represents inhabitants from the deeper waters of the lake who are thought to be highly omnivorous, feeding on chironomids and oligochaetes as major food sources (Moyle 2002). Although no evidence exists in the literature that the shifts in carbon sources to suckers adversely affect these fish, there has been a decline in the abundance of minnows in the lake since the 1960s (Thiede 1997). Reports from long-time local residents describe similar population and size declines in the Tahoe sucker (Chandra unpubl. data), perhaps because of a decrease in benthic consumer biomass or community composition shifts that result from eutrophication.

Other studies show changes to zoobenthic community composition and biomass resulting from cultural eutrophication (Britt 1955; Nalepa 1987; Krieger and Ross 1993). This in turn results in the decline of fish growth rates for consumers that relied on zoobenthos (Schaeffer et al. 2000). Unfortunately, we were not able to compare our invertebrate biomass results with historical values because of a lack of raw data from historical samplings. Thus, future studies should focus on comparing changes in benthic invertebrate composition and biomass as the lake continues to undergo cultural eutrophication. Regardless, energetics changes to zoobenthic primary consumers resulting from cultural eutrophication appear to be passed on to higher consumers.

The effect and cost of eutrophication is often focused on pelagic habitats. Recent studies refocus attention across traditional habitat boundaries and assess the effects on whole ecosystems. These studies examine shifts in primary production from benthic to pelagic habitats and the effect on zoobenthos energetics, community composition, and biomass. Although pelagic export along a seasonal gradient is an important contributor for zoobenthic energy sources, this study demonstrates the strong positive coupling of pelagic to benthic habitats along spatial and decadal temporal scales. In particular, cultural eutrophication leads to increases in pelagic and reduction in benthic primary production. The resulting export of phytoplankton to the lake bottom and loss of periphyton alter zoobenthic primary consumer energy uptake. These energetic changes are passed on to higher consumers that rely on benthic resources. These shifts will alter benthic community composition, size structure, and biomass, which could substantially affect fisheries because lake food

webs are highly dependent on benthic primary production and zoobenthos for their energy.

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