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Four decades of change: dramatic loss of zoobenthos in an oligotrophic lake exhibiting gradual eutrophication

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Abstract. Native species in lakes commonly are affected by cultural eutrophication and introductions of nonnative species. The effects of these disturbances on benthic communities in large lakes have been understudied, despite the integral role that benthos play in maintaining habitat complexity and ecosystem processes. Lake Tahoe has experienced progressive eutrophication and introductions of nonnative species over the past several decades, but how its unique benthic communities have been affected is unclear. The density of Lake Tahoe's benthic fauna was compared between 1960s surveys and our recent (2008–2009) survey, and the association of zoobenthos with macrophytes was examined for contemporary and historical samples. The density of benthic invertebrates and the occurrence of macrophytes in benthic samples have declined dramatically since collections made in the 1960s. Lakewide densities of benthic invertebrate taxa endemic to Lake Tahoe have declined by 80 to 100%, and the community structure of benthic invertebrate assemblages has changed considerably. Several native benthic invertebrate taxa were closely associated with deepwater macrophytes in the 1960s, but contemporary invertebrate association with macrophytes could not be evaluated reliably because of the scarcity of macrophytes in contemporary samples. Declines in native benthic invertebrate density could be related to the loss of habitat and food resources previously provided by abundant deepwater macrophyte assemblages. In addition, establishment and increases in density of nonnative species that occurred after the benthic surveys of the 1960s probably have affected native benthic invertebrate communities. The observed declines in Lake Tahoe's native benthic invertebrate and macrophyte communities suggest that they are severely threatened.

Key words: Lake Tahoe, benthic invertebrates, macrophytes, density decline, endemic species, introduced species.

Cultural eutrophication and introductions of nonnative species are among the most common anthropogenic causes of ecosystem change in lakes (Sala et al. 2000, Lodge 2001, Schindler 2006, Smith et al. 2006). Changes to lake condition usually are assessed with pelagic indicators, but benthic indicators are being used increasingly often in long-term monitoring efforts. For example, in Lake Ladoga, the shift from a sensitive benthic invertebrate assemblage to a relatively tolerant assemblage since the 1950s to 1960s has been attributed to the combined effects of eutrophication and pollution (Slepukhina et al. 1996, Rumyantsev et al. 1999). In the Great Lakes region, the relative abundance of benthic invertebrate taxa has fluctuated dramatically since the 1960s because of nutrient inputs, subsequent nutrient control, and the establishment of invasive dreissenid mussels (Nalepa

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1987, Schloesser et al. 1995, Nalepa et al. 2000, 2003, Lozano et al. 2001).

Eutrophication and introductions of nonnative species also can affect submerged macrophyte populations. Eutrophication causes decreased subsurface light availability via shading by phytoplankton. The first macrophytes to disappear from lakes as a result of eutrophication are small, slow growing taxa, such as mosses and characeans (Blindow 1992, Sand-Jensen et al. 2008). In some lakes, crayfish have been implicated in the further decline of macrophyte communities whose distribution has already been reduced by eutrophication (Schwarz et al. 2000). Introduced crayfish populations can cause extensive declines in macrophyte density, biomass, and richness through direct feeding and nonconsumptive damage (Chambers et al. 1990, Lodge 1991, Lodge et al. 1994, Wilson et al. 2004).

Benthic communities in oligotrophic lakes are particularly vulnerable to the introduction of nonnative species and cultural eutrophication. Oligotrophic systems often are characterized by low benthic taxon richness (Declerck et al. 2005), which makes these communities less resistant than more diverse communities to species invasions (Stachowicz et al. 2002). In addition, in oligotrophic lakes undergoing progressive eutrophication, the predominant primary producers may change from benthic to pelagic (Vadeboncoeur et al. 2003), thereby altering benthic community structure. Such effects on benthic communities in oligotrophic lakes have important implications for habitat complexity and ecosystem processes, such as sediment mixing, breakdown of organic matter, nutrient cycling, microbial and algal growth, and fisheries production (Covich et al. 1999, Palmer et al. 2000).

Lake Tahoe is a large lake that has experienced gradual eutrophication and introductions of nonnative species. Lake Tahoe's water clarity has declined by almost 10 m over the past 4 decades, but the lake has remained oligotrophic (Goldman 1988, Jassby et al. 2003). Over the same period, Lake Tahoe has seen the introduction and establishment of mysid shrimp (*Mysis relicta*) (Linn and Frantz 1965, Frantz and Cordone 1996), increased densities of nonnative signal crayfish (*Pacifastacus leniusculus*) (J. Umek, University of Nevada, Reno, unpublished data), and the recent establishment of nonnative Asian clams (*Corbicula fluminea*) (Wittmann et al. 2012). The effects of eutrophication and nonnative invertebrate introductions on benthic biotic assemblages in Lake Tahoe are unknown. Our goal was to replicate the spatial and vertical extent of historical benthic collections to elucidate potential changes to the benthos in response to recognized changes in the lake.

Methods

Study site and historical studies

Lake Tahoe is a subalpine, ultraoligotrophic lake in California and Nevada (USA). It has a maximum depth of 501 m, an average depth of 305 m, and a surface area of 495 km^2. Lake Tahoe's mixing depth is variable, but the entire water column is oxygenated throughout the year. Average Secchi depth has decreased steadily from 31 m to ~21 m, and pelagic primary production has increased 4.5× since the late 1960s (Chandra et al. 2005). The first extensive collection of benthic invertebrates and macrophytes from Lake Tahoe occurred in 1962–1963 and revealed the existence of 10 endemic benthic invertebrate species, including 2 species of blind amphipod (*Stygobromus tahoensis* and *Stygobromus lacicolus*), a deepwater stonefly (*Capnia lacustra*) that completes its life cycle underwater (Jewett 1963), 2 turbellarians (*Phagocata tahoena* and *Dendrocoelopsis hymanae*), and an ostracod (*Candona tahoensis*) (Frantz and Cordone 1966, 1996). This unique benthic invertebrate assemblage appeared to be associated with deepwater macrophyte beds found mainly between 50 and 110 m, including 10 species of moss (Bryophyta:Bryophytina), 2 species of stoneworts (Charophyta), and 2 species of liverworts (Bryophyta:Marchantiophytina) (Frantz and Cordone 1967, 1996). In 1968, Goldman (1974) conducted another benthic survey, in which benthic samples were collected primarily between 200 and 500 m. In this survey, endemic *Stygobromus* spp. and endemic ostracods (*C. tahoensis*) were the most commonly encountered organisms, and no macrophytes were noted in samples (Goldman 1974), perhaps because most samples were collected from the deepest depths of the lake. Other historical benthic collections in Lake Tahoe were not comprehensive and used variable sampling methods (see Frantz and Cordone 1996).

Sampling method

In an attempt to replicate the spatial extent and depth profiles of historical sample collections, benthic grab samples were collected in 2008 to 2009 from 4 transects that spanned littoral and profundal habitats (1–450 m). In each transect, triplicate samples were collected at 5-m depth intervals from 1 to 95 m, 10-m depth intervals from 100 to 130 m, and 50-m depth intervals from 150 to 450 m (Fig. 1). This sampling regime resulted in the collection of ~60 samples from 1 to 95 m, 12 samples from 100 to 130 m, and 25 samples from 150 to 450 m within each transect. We also collected triplicate samples in the littoral zone at

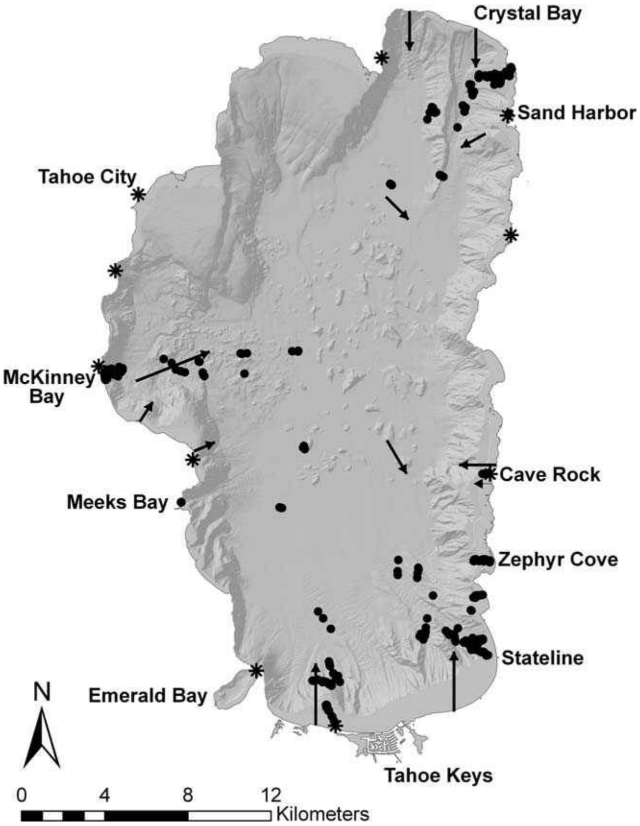

FIG. 1. Map of Lake Tahoe with sampling sites indicated. Circles represent samples taken along transects with a benthic dredge in 2008–2009, and asterisks represent samples collected from hard substrate with a modified lake vacuum in 2009. Arrows show transects from which benthic grabs were collected in 1962–1963 (Frantz and Cordone 1996).

6 additional locations from 5-, 10-, and 15-m depths, for a total of 9 samples at each location (Fig. 1). Each sample was collected with a Shipek grab and washed through a 500-µm-mesh bucket sieve. The presence or absence of macrophytes in each sample was noted. Collections also were made from hard substrate (cobble, boulders) in shallow (0.5 m) areas around the lake with a modified lake vacuum sampler, similar to that described by Vander Zanden et al. (2006). Hard substrate collections were used only to assess taxon presence/absence to develop a taxon list (Appendix S1; available online from: http://dx.doi.org/10.1899/12-064.1.s1), and were not included in quantitative comparisons to historical data. Collections occurred from June to September 2008 and March to July 2009 as weather permitted.

In the laboratory, samples were elutriated (if necessary), and a sugar flotation and visual inspection method was used to separate live organisms from other material (Anderson 1959). All invertebrates visible to the naked eye were handpicked from each sample on the same day of collection. Invertebrates were counted, identified to the lowest possible taxonomic level, and preserved in 70% ethanol. Head capsules of Chironomidae were separated from their bodies and slide mounted in Euparal® for identification. After final taxonomic determination, each invertebrate sample including chironomid bodies, was dried at 60°C for 48 h, and weighed to measure dry mass of the material and estimate biomass.

Data analysis

We obtained previously archived data from collections in 1962–1963 and 1968 to make direct comparisons of benthic invertebrate density, distribution, and macrophyte association between our surveys and those of Frantz and Cordone (1996) and Goldman (1974). Frantz and Cordone (1996) collected benthic samples from May to December 1962 and February to December 1963 as weather permitted. Collections were made along transects at 4 locations, with ~70 samples collected from 1 to 99 m, 10 samples from 100 to 149 m, and 15 samples from 150 to 501 m at each location (Fig. 1). Goldman (1974) conducted a benthic survey from August to October 1968 and collected a total of 6 samples from 1 to 99 m, 1 sample from 100 to 149 m, and 29 samples from 150 to 501 m at various locations around the lake. The 1962–1963 collections were made with standard and large Ekman grabs (area = 0.023 m^2 and 0.052 m^2, respectively), and 1968 and 2008–2009 collections were made with a Shipek grab (area = 0.039 m^2). Inherent differences in the collection efficiency of these samplers required us to multiply benthic invertebrate densities by conversion factors previously established in Lake Tahoe (Caires and Chandra 2012). Because the Shipek grab is generally less efficient than the Ekman grab used for collections in 1962–1963, densities derived from the 1968 and 2008–2009 collections were multiplied by substrate- and taxon-specific conversion factors ranging from 1.0 (no conversion) to 5.2 (Caires and Chandra 2012). For example, in silt substrate, a large Ekman grab is 5.2× more efficient for collecting chironomids than the Shipek grab (Caires and Chandra 2012), necessitating multiplication of Shipek-derived chironomid densities by 5.2 before comparing them to densities in silt-dominated samples collected with a large Ekman sampler in 1962–1963. In contrast, in sandy substrate, efficiency of chironomid collection did not differ between the Shipek and standard Ekman grabs (Caires and Chandra 2012). Thus, no conversion was applied when comparing Shipek-derived chironomid densities with standard Ekman-derived densities in sand-dominated substrate. Taxon-specific conversion factors were available for Oligochaeta, Chironomidae, and Bivalvia, and conversion factors generated from a collective invertebrate assemblage (total invertebrate density) were applied to all other taxa. Samples collected in 1962–1963 and 2008–2009 were sieved using the same mesh size (500-µm). However, the sieve mesh size used in 1968 is unknown and was described only as ‘‘fine enough to prevent the passage of even such small organisms as cladocerans and copepods’’ (Goldman 1974, p. 289). Wet masses of benthic invertebrates from the 1962–1963 collections were used for biomass comparisons. Dry mass of benthic invertebrates in lakes can range from 15 to 25% of wet mass (Wetzel 2001). Therefore, an intermediate value of 20% was used to convert historical wet mass to dry mass.

Lakewide-weighted benthic invertebrate density and biomass were used to estimate % change in density and biomass since the 1960s for each major benthic invertebrate taxon. Lakewide-weighted density was calculated by multiplying the mean of benthic invertebrate density at a given depth interval by the proportion of the lake represented by that depth interval, and summing the resulting weighted densities. Lakewide-weighted biomass was calculated in the same manner. Few benthic invertebrate samples were collected from depths <200 m in 1968, so lakewide comparisons could be made only between the 1962–1963 and 2008–2009 collections. Weighted densities and biomass were calculated for historical and contemporary collections using the same hypsographic curve.

Densities of benthic invertebrates also were compared between 1962–1963, 1968, and 2008–2009 collection periods at specific depth intervals: 1 to 30 m, 31 to 50 m, 51 to 110 m, 111 to 200 m, 201 to 300 m, and 301 to 500 m. The 1968 data were used only in comparisons between 201–300 m and 301–500 m because of the limited number of samples collected between 1 and 200 m in 1968. Differences in invertebrate density among collection periods were evaluated using a 2-tailed Student's *t*-test for depth intervals up to 200 m and a 1-way analysis of variance (ANOVA) for depth intervals beyond 201 m. Following 1-way ANOVA, Tukey's Honestly Significant Difference (HSD) post hoc tests were used to identify which collection periods differed.

Descriptions of sample content were used to compare macrophyte occurrence in samples and associations of benthic invertebrates with macrophytes in historical (1962–1963) and contemporary (2008–2009) collections. The 1968 collections were not included in these analyses because macrophyte occurrence was not indicated for these samples. A 2-tailed Student's *t*-test was used to compare benthic invertebrate density between samples that contained macrophytes and samples that did not. To avoid interaction effects between depth and macrophyte presence, invertebrate association with macrophytes was assessed only in samples collected between 50 and 110 m, the depth zone in which macrophytes were most concentrated in historical collections (Frantz and Cordone 1967). All benthic invertebrate densities were $\sqrt{(x + 0.5)}$-transformed to meet assumptions of normality and homogeneity of variance. Statistical tests were done with JMP (version 7.0; SAS Institute, Cary, North Carolina). Significance was judged at $p \leq 0.05$.

Results

Lakewide density and biomass of most taxa have declined since the 1960s (Table 1). Lakewide density of total benthic invertebrates decreased ~75%, and density of endemic taxa decreased 80 to 100% (Table 1). *Pisidium* spp. is the only taxon that showed increased lakewide density and biomass. Oligochaete densities declined, but the percentage of total invertebrate density made up of oligochaetes increased from 44% in historical collections to 75% in recent collections.

Depth-specific densities of most taxa also have declined (Table 2). In the nearshore (0–30 m), the density of several taxa decreased significantly, and only *Pisidium* spp. densities increased significantly (Table 2). Between 31 and 50 m, all taxa except Oligochaeta and *Pisidium* spp. decreased significantly (Table 2). Declines were most pervasive between 51 and 110 m, where all taxa except *Pisidium* spp. declined significantly (Table 2). Between 111 and 200 m, taxa that were collected in 1962–1963 were largely absent from samples collected in 2008–2009, with the exception of Oligochaeta, which was found in similar abundance during the 2 periods (Table 2).

Some significant differences in invertebrate density were observed between the 1962–1963 and 1968 collection periods. However, the most striking differences remained between collections in the 1960s and 2008–2009. Many of the taxa that were dominant and abundant in deep (201–500 m) samples during both collection periods in the 1960s were absent or scarce in 2008–2009 collections at these depths (Table 2). Overall, the endemic taxa *Stygobromus* spp., Turbellaria (*P. tahoena* and *D. hymanae*), and *C. lacustra* underwent the largest density declines in deepwater (50–500 m) areas of Lake Tahoe.

Table 1. Mean (±1 SE) lakewide-weighted densities (no./m^2) and dry mass (mg/m^2) of benthic invertebrate taxa collected in historical and contemporary collections in Lake Tahoe. Percent change in density and biomass since the 1962–1963 collections is given for each taxon.

Taxon	1962–1963	2008–2009	% change
Density	(n = 389)	(n = 420)	
Stygobromus spp.	762.0 ± 179.5	0.1 ± 0.1	<−99.9
Turbellaria	164.3 ± 46.6	0.02 ± 0.02	<−99.9
Candona tahoensis	131.8 ± 57.2	21.9 ± 12.2	−83.4
Capnia lacustra	3.1 ± 1.7	0.2 ± 0.1	−93.5
Oligochaeta	938.8 ± 191.0	402.2 ± 79.4	−57.2
Gastropoda	6.2 ± 4.1	2.8 ± 1.9	−54.8
Chironomidae	68.1 ± 21.5	44.8 ± 11.0	−34.2
Pisidium spp.	3.3 ± 1.9	10.9 ± 2.9	230.3
All invertebrates	2134.9 ± 401.9	534.8 ± 103.5	−74.9
Biomass	(n = 389)	(n = 420)	
Stygobromus spp.	231.3 ± 56.2	0.01 ± 0.01	<−99.9
Turbellaria	36.7 ± 12.5	0.03 ± 0.03	−99.9
Candona tahoensis	11.8 ± 4.2	1.0 ± 0.4	−92.0
Capnia lacustra	1.5 ± 0.9	0.04 ± 0.03	−97.4
Oligochaeta	651.6 ± 165.4	121.7 ± 23.5	−81.3
Gastropoda	28.6 ± 19.9	14.6 ± 8.0	−48.9
Chironomidae	23.0 ± 8.5	4.2 ± 1.2	−82.2
Pisidium spp.	2.8 ± 1.7	17.7 ± 4.6	540.8

Several of Lake Tahoe's endemic benthic invertebrate species were encountered in the 2008–2009 survey. However, most endemics were poorly represented in our samples relative to their representation in 1962–1963, despite a similar sampling effort. The endemic oligochaete *Spirosperma beetoni* was found at several locations around the lake in 2008–2009, whereas the other endemic oligochaetes (*Varichaetadrilus minutus* and *Rhyacodrilus brevidentatus*) may have been found, but were too damaged for identification to species level. Endemic turbellarians were not encountered in our collections. Only 1 turbellarian was found at a depth of 18 m in 2009. It was too small for identification, but did not conform well to descriptions of the 2 endemic Tahoe flatworm species (Kenk 1970, 1973). In the 1962–1963 collections, 797 specimens of endemic turbellarians were found in all locations sampled at an average depth of 97 m. Turbellarians also were found in all areas of the lake in the 1968 collections. Ten specimens of the endemic deepwater stonefly *C. lacustra* were found in 2008–2009 at an average depth of 74 m. All *C. lacustra* specimens were collected from McKinney Bay in gravel substrate containing no macrophytes. In contrast, 98 specimens of *C. lacustra* were found in the 1962–1963 collections in all locations sampled at an average depth of 94 m, mostly in samples containing macrophytes. *Capnia lacustra* also was widespread in collections in 1968. In our 2009 lake vacuum collections from hard substrate, 21 individuals of another endemic stonefly, *Utacapnia tahoensis*, probably were found. However, the identification of *U. tahoensis* could not be confirmed because of the immaturity of the specimens. Only 6 specimens of *Stygobromus* spp. were collected in 2008–2009 at an average depth of 81 m in McKinney Bay in gravel substrate containing no macrophytes. Of the 6 specimens, 3 were positively identified as *S. tahoensis*, 2 were identified as potential, but damaged, *S. lacicolus*, and 1 was unidentifiable because of damage. In contrast, 2373 specimens of *Stygobromus* spp. were found in the 1962–1963 collections in all locations sampled at an average depth of 166 m. Peak average densities of *Stygobromus* spp. occurred around a 250-m depth in samples collected during 1962–1963. The maximum number of *Stygobromus* spp. individuals collected in a single sample was 281 in 1962 and 235 in 1963. Densities of each *Stygobromus* species were not quantified in 1962–1963 samples, but researchers noted that *S. tahoensis* was substantially more abundant than *S. lacicolus* in a subset of samples from which identifications were made (Frantz and Cordone 1996). In 1968, *Stygobromus* spp. were found in 83% of all samples collected and were widespread throughout the lake. The 2 species of *Stygobromus* were not distinguished in collections from 1968. The endemic ostracod, *C. tahoensis*, was present and relatively abundant in all transects that were sampled in 2008–2009, similar to its distribution in the 1960s collections.

Comparisons of species and genus richness within the Chironomidae and Oligochaeta suggest that Lake Tahoe's benthic community structure has changed

TABLE 2. Mean (±1 SE) densities (no./m^2) of benthic invertebrate taxa collected in Lake Tahoe during 3 periods: 1962–1963, 1968, and 2008–2009 at 6 depth intervals. Collection periods sharing the same letter for a given taxon within each depth interval are not significantly different. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, NA = not applicable, ND = no data, ANOVA = analysis of variance.

	1962–1963	1968	2008–2009	*F*
Depth: 0–30 m	(n = 189)	(n = 0)	(n = 148)	*t*-test
Stygobromus spp.	0.0 ± 0.0	ND	0.0 ± 0.0	NA
Turbellaria	38.7 ± 6.1	ND	0.3 ± 0.3	56.71***
Candona tahoensis	210.5 ± 24.8	ND	72.1 ± 13.9	36.85***
Capnia lacustra	0.0 ± 0.0	ND	0.0 ± 0.0	NA
Oligochaeta	1452.3 ± 70.2	ND	928.6 ± 74.2	29.38***
Gastropoda	43.5 ± 27.6	ND	32.3 ± 14.3	0.08
Chironomidae	409.4 ± 41.9	ND	543.6 ± 65.0	2.32
Pisidium spp.	12.8 ± 2.7	ND	111.5 ± 14.1	94.28***
All invertebrates	2552.1 ± 122.5	ND	1980.5 ± 146.4	12.28***
Depth: 31–50 m	(n = 10)	(n = 0)	(n = 48)	*t*-test
Stygobromus spp.	4.3 ± 4.3	ND	0.0 ± 0.0	5.15*
Turbellaria	318.6 ± 91.0	ND	0.0 ± 0.0	199.01***
Candona tahoensis	503.7 ± 115.5	ND	133.9 ± 49.9	17.24***
Capnia lacustra	0.0 ± 0.0	ND	0.0 ± 0.0	NA
Oligochaeta	2927.7 ± 570.2	ND	1931.7 ± 243.9	4.00
Gastropoda	47.4 ± 26.8	ND	0.0 ± 0.0	23.98***
Chironomidae	180.8 ± 56.2	ND	86.0 ± 45.6	5.16*
Pisidium spp.	21.5 ± 14.7	ND	56.1 ± 14.2	1.44
All invertebrates	4383.0 ± 753.3	ND	2382.8 ± 306.0	9.37**
Depth: 51–110 m	(n = 93)	(n = 0)	(n = 106)	*t*-test
Stygobromus spp.	321.3 ± 72.4	ND	2.9 ± 1.3	42.65***
Turbellaria	187.0 ± 29.0	ND	0.0 ± 0.0	111.25***
Candona tahoensis	912.5 ± 104.8	ND	37.3 ± 7.9	170.75***
Capnia lacustra	56.5 ± 13.0	ND	4.1 ± 2.6	31.22***
Oligochaeta	1622.2 ± 106.6	ND	521.2 ± 43.7	107.82***
Gastropoda	42.6 ± 9.0	ND	0.0 ± 0.0	38.64***
Chironomidae	214.8 ± 33.6	ND	12.5 ± 4.1	98.87***
Pisidium spp.	40.3 ± 10.7	ND	19.1 ± 5.1	2.64
All invertebrates	3545.8 ± 238.6	ND	696.0 ± 54.6	212.02***
Depth: 111–200 m	(n = 69)	(n = 0)	(n = 35)	*t*-test
Stygobromus spp.	372.3 ± 61.8	ND	0.0 ± 0.0	47.20***
Turbellaria	106.4 ± 17.3	ND	0.0 ± 0.0	35.79***
Candona tahoensis	165.3 ± 29.6	ND	28.4 ± 12.4	21.11***
Capnia lacustra	5.6 ± 2.2	ND	0.0 ± 0.0	3.74
Oligochaeta	454.6 ± 47.1	ND	487.7 ± 68.2	0.49
Gastropoda	0.6 ± 0.6	ND	0.0 ± 0.0	0.51
Chironomidae	104.8 ± 22.9	ND	0.0 ± 0.0	28.43***
Pisidium spp.	2.6 ± 1.2	ND	0.0 ± 0.0	2.50
All invertebrates	1245.1 ± 130.7	ND	561.7 ± 74.9	11.34**
Depth: 201–300 m	(n = 10)	(n = 6)	(n = 25)	1-way ANOVA
Stygobromus spp.	2247.3 ± 514.2^{a}	680.8 ± 271.6^{b}	0.0 ± 0.0^{c}	45.30***
Turbellaria	90.0 ± 29.8^{a}	140.6 ± 46.6^{a}	0.0 ± 0.0^{b}	21.68***
Candona tahoensis	119.6 ± 39.3^{a}	89.3 ± 64.7^{ab}	14.7 ± 7.2^{b}	10.17***
Capnia lacustra	1.9 ± 1.9^{a}	0 ± 0^{a}	0.0 ± 0.0^{a}	1.60
Oligochaeta	839.1 ± 192.8^{a}	248.3 ± 121.6^{a}	460.1 ± 115.6^{a}	3.13
Gastropoda	0.0 ± 0.0	0 ± 0	0.0 ± 0.0	NA
Chironomidae	14.4 ± 3.8^{a}	57.7 ± 25.8^{a}	0.0 ± 0.0^{b}	14.63***
Pisidium spp.	0.0 ± 0.0	0 ± 0	0.0 ± 0.0	NA
All invertebrates	3333.2 ± 660.7^{a}	1775.6 ± 574.4^{a}	492.7 ± 116.0^{b}	21.44***
Depth: 301–500 m	(n = 15)	(n = 22)	(n = 58)	1-way ANOVA
Stygobromus spp.	682.5 ± 128.3^{a}	511.9 ± 89.5^{a}	0 ± 0^{b}	128.49***
Turbellaria	207.9 ± 50.0^{a}	87.0 ± 23.0^{b}	0 ± 0^{c}	44.02***
Candona tahoensis	26.8 ± 10.0^{a}	423.8 ± 103.9^{b}	7.5 ± 3.7^{a}	39.53***
Capnia lacustra	0 ± 0^{a}	3.7 ± 3.7^{a}	0 ± 0^{a}	1.68
Oligochaeta	881.5 ± 160.5^{a}	292.8 ± 70.5^{b}	259.8 ± 41.1^{b}	11.20***
Gastropoda	0 ± 0	0 ± 0	0 ± 0	NA

TABLE 2. Continued.

	1962–1963	1968	2008–2009	*F*
Chironomidae	23.0 ± 8.4[a]	18.2 ± 10.0[a]	0 ± 0[b]	10.85***
Pisidium spp.	0 ± 0	0 ± 0	0 ± 0	NA
All invertebrates	1833.2 ± 293.9[a]	1628.2 ± 232.5[a]	288.5 ± 42.6[b]	54.85***

considerably. For example, in the family Chironomidae, 20 genera were found in 1962–1963, and 46 genera were found in 2008–2009. Four genera found in the 1960s were not found in contemporary collections, and many contemporary taxa were not found in historical collections (Appendix S1), a result indicating a shift in chironomid assemblage structure. Within the subclass Oligochaeta, 11 species were found in the 1960s, 9 species were found in recent collections, and only 5 species were common to both collection periods (Appendix S1).

Macrophyte occurrence in samples was higher in 1962–1963 than in 2008–2009, particularly in the 50- to 110-m depth interval (Fig. 2). Macrophytes were found in deeper water in 1962–1963 than in 2008–2009 (Fig. 2). Overall, macrophytes were encountered in 20% of all samples collected in 1962–1963, whereas macrophytes were found in 3% of all samples collected in 2008–2009. The average depth of samples from which macrophytes were collected was 77 m in 1962–1963 and 53 m in 2008–2009. Macrophytes were found in all areas of the lake that were sampled in 1962–1963, but were found only in the Stateline, Camp Richardson, and Crystal Bay transects in 2008–2009.

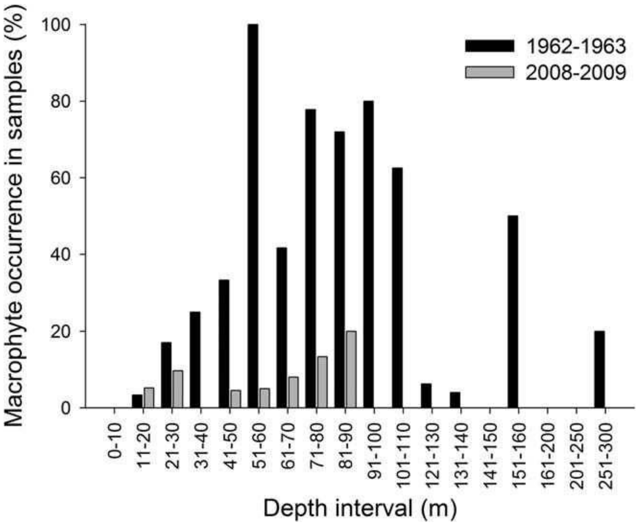

FIG. 2. Percent occurrence of macrophytes in historical and contemporary benthic samples collected from Lake Tahoe. Occurrence is defined as the presence of macrophyte material in a sample.

Between 50 and 110 m in 1962–1963, Turbellaria, *C. lacustra*, Gastropoda, and *Pisidium* spp. were significantly more abundant in samples that contained macrophytes than in those that did not (Table 3). In 2008–2009, benthic invertebrate densities did not differ significantly between samples containing macrophytes and those that did not for any of the taxa evaluated. However, the large difference in sample size between groups limited the power of the test (Table 3). Peaks in density of most taxa collected in 1962–1963 were within or near the zone of peak macrophyte occurrence during that time period, with the exception of *Stygobromus* spp., whose densities peaked at depths deeper than most macrophyte occurrence (Fig. 3A). Except for *Pisidium* spp., benthic invertebrate densities from collections in 2008–2009 were very low compared to densities in 1962–1963 in the zone of historical peak macrophyte occurrence, making this the zone in which the greatest invertebrate density declines were observed (Fig. 3A–H).

Discussion

Changes in benthic invertebrate communities

Comparisons of our data to historical data suggest that the unique benthic invertebrate assemblage of Lake Tahoe has changed considerably since the 1960s, with most taxa experiencing a severe reduction in density. Taxa endemic to Lake Tahoe showed the largest declines. Collectively, 2 endemic blind amphipods (*S. lacicolus* and *S. tahoensis*) have declined 99.9% in lakewide density since 1962–1963. Two endemic turbellarians (*P. tahoena* and *D. hymanae*) were abundant and widespread in samples in the 1960s, but no endemic turbellarians were collected in 2008–2009. The lakewide density of the endemic stonefly, *C. lacustra*, has decreased 93.5% since 1962–1963. Although still widespread in Lake Tahoe, the lakewide density of endemic ostracods (*C. tahoensis*) decreased 83.4% since 1962–1963.

It is unlikely that such large declines in density reflect sampling differences between the 1960s collections and our recent collections. Ekman dredges were used in 1962–1963 and a Shipek dredge was used in 1968 and 2008–2009, but conversion factors based on sampler efficiency were applied to density data prior

TABLE 3. Mean (±1 SE) densities (no./m^2) of benthic invertebrate taxa in samples with and without macrophytes during 1962–1963 and 2008–2009 in the 50- to 110-m depth zone. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, NA = not applicable.

Taxon	Macrophytes	No macrophytes	*F*
1962–1963	(n = 62)	(n = 31)	*t*-test
Stygobromus spp.	398.6 ± 102.7	166.7 ± 64.8	3.64
Turbellaria	238.2 ± 40.1	84.7 ± 25.9	7.89**
Candona tahoensis	1022.2 ± 140.6	693.0 ± 135.2	2.22
Capnia lacustra	77.8 ± 18.7	13.9 ± 6.7	8.17**
Oligochaeta	1645.1 ± 121.4	1576.4 ± 211.1	0.49
Gastropoda	63.2 ± 12.7	1.4 ± 1.4	17.71***
Chironomidae	190.3 ± 35.5	263.9 ± 71.8	0.99
Pisidium spp.	57.0 ± 15.5	6.9 ± 3.5	6.67*
All invertebrates	3884.0 ± 304.2	2869.4 ± 352.6	4.84*
2008–2009	(n = 9)	(n = 97)	*t*-test
Stygobromus spp.	0.0 ± 0.0	3.1 ± 1.4	0.47
Turbellaria	0.0 ± 0.0	0.0 ± 0.0	NA
Candona tahoensis	63.0 ± 23.4	35.0 ± 8.3	3.12
Capnia lacustra	0.0 ± 0.0	4.5 ± 2.9	0.26
Oligochaeta	478.6 ± 162.6	525.1 ± 45.6	0.41
Gastropoda	0.0 ± 0.0	0.0 ± 0.0	NA
Chironomidae	12.8 ± 12.8	12.4 ± 4.3	0.01
Pisidium spp.	5.7 ± 5.7	20.4 ± 5.6	0.79
All invertebrates	781.5 ± 145.4	688.1 ± 58.3	0.54

to comparisons. The same mesh size was used to sieve samples in 1962–1963 and 2008–2009. Goldman (1974) did not specify the mesh size of the sieve used to wash samples in 1968, so comparisons of 1968 benthic invertebrate densities with 1962–1963 and 2008–2009 densities (Table 2) should be interpreted with caution. Regardless, the magnitude of the observed density declines since the 1960s cannot be attributed solely to differences in sampling protocol. Despite inevitable differences in sampling locations, overall sampling effort was similar in historical and contemporary collections and most of our collections occurred in the same general areas that were sampled in the 1960s. Endemic species that were absent or rare and limited to a single location in 2008–2009 were present and abundant in all areas of the lake in 1962–1963 and 1968, results showing the impressive spatial scale over which these declines have occurred.

Substantial changes also have occurred in benthic invertebrate community structure. For example, Lake Tahoe's chironomid assemblage is now more taxon-rich than it was in the 1960s. The chironomid assemblage has shifted from few genera, of which nearly 25% indicated oligotrophic conditions, to many genera, of which only ~10% indicate oligotrophic conditions according to trophic ranges developed for chironomid taxa by Saether (1979). The assemblage of chironomids collected during our 2008–2009 survey was composed of more cosmopolitan genera, such as *Tanypus* and *Chironomus* (Cranston et al. 1989, Murray and Fittkau 1989); more warm-adapted genera, such as *Clinotanypus* (Murray and Fittkau 1989); and more pollution-tolerant taxa, such as *Cricotopus bicinctus* (Huggins and Moffett 1988), when compared to chironomid taxa collected in 1962–1963. Despite small differences in oligochaete densities between 1962–1963 and 2008–2009, the assemblage structure of oligochaetes in Lake Tahoe appears to have changed. At least 3 of the species that were collected in 1962–1963 were not encountered in 2008–2009, and 4 species that were collected in 2008–2009 were not found in 1962–1963. Two of the oligochaete species that were present in the 1960s and were not encountered in recent collections were *Arcteonais lomondi* and *Uncinais uncinata*. *Arcteonais lomondi* and *U. uncinata* have similar diets composed mainly of diatoms that are sometimes found in association with aquatic vegetation (Brinkhurst and Jamieson 1971, Moore 1981). A reduction in the extent of Lake Tahoe's deepwater macrophyte and algal communities may have reduced habitat and food sources for such taxa.

Implications of decline in macrophyte distribution

Benthic invertebrate density declines were most striking at depths in which declines in deepwater macrophyte occurrence were greatest, suggesting that the reductions in invertebrate and macrophyte communities in Lake Tahoe are closely tied. In the 1962–1963 collections, several native invertebrate taxa were significantly more abundant in samples that

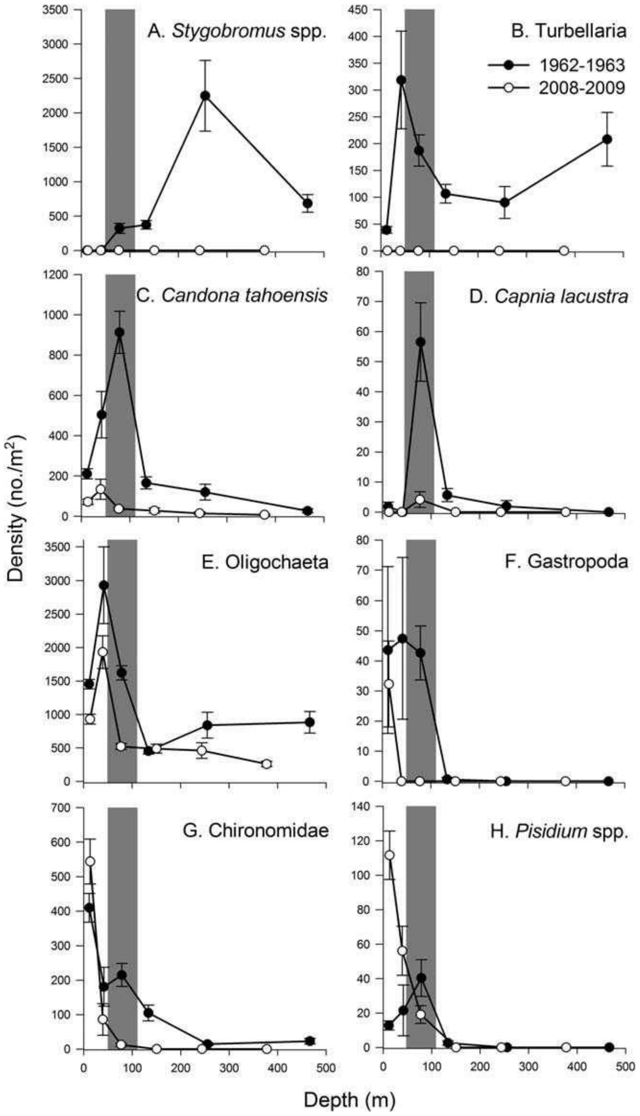

FIG. 3. Mean (±1 SE) density by depth for *Stygobromus* spp. (A), Turbellaria (B), *Candona tahoensis* (C), *Capnia lacustra* (D), Oligochaeta (E), Gastropoda (F), Chironomidae (G), and *Pisidium* spp. (H) taxa that dominated benthic invertebrate assemblages in 1962–1963 collections. The grey area from 50–110 m indicates the area in which macrophyte beds were concentrated in the 1960s.

contained macrophytes than in samples that did not. Two benthic invertebrate taxa endemic to Lake Tahoe (*Stygobromus* spp. and *C. lacustra*) showed a preference for gravel substrate in 2008–2009, in the apparent absence of macrophytes in McKinney Bay. These now-rare endemics could be choosing gravel substrate because it provides some of the same habitat characteristics (e.g., surface for periphyton growth, refuge from predators) that macrophytes provide when present. Since the time of our 2008–2009 survey, several *C. lacustra* specimens were collected in samples that contained a large amount of macrophyte material in southern Lake Tahoe at a depth of 40 m (M. Denton, University of Nevada, Reno, unpublished data). This finding suggests that macrophyte beds still exist in the southern part of the lake, and that *C. lacustra* may be abundant in these areas. Benthic invertebrate associations with deepwater macrophyte assemblages in Lake Tahoe have been documented previously (Frantz and Cordone 1996), and submerged macrophytes in lakes have long been known to support a greater abundance and biomass of aquatic invertebrates than sediments without macrophytes (Krecker 1939, Dvořak and Best 1982, Brown et al. 1988, Newman 1991). The macroalga *Chara* spp., which was common in benthic samples from Lake Tahoe in the 1960s, can support an even greater biomass of invertebrates than rooted macrophyte communities (Hanson 1990).

In the 1962–1963 survey, several taxa (ostracods, oligochaetes, and chironomids) were not significantly more abundant in samples containing macrophytes, although their densities were highest at or near the depth of peak macrophyte occurrence (Fig. 3C, E, G). These taxa might not have been directly dependent on macrophytes, but could have benefited from greater food availability and habitat quality near macrophytes than in areas devoid of vegetation. Macrophytes, including beds of *Chara* spp., increase nutrient cycling rates, increase sediment oxygenation, and decrease effects of wave action, thereby increasing sediment stabilization (Carpenter and Lodge 1986, Barko et al. 1991, Kufel and Kufel 2002). Decomposing macrophyte tissue and associated microbial communities also provide an important food source for many benthic invertebrates (Smock and Stoneburner 1980, Suren and Lake 1989, Newman 1991, Kornijów et al. 1995).

Macrophyte-derived organic matter in Lake Tahoe may have provided a food source for deepwater *Stygobromus* spp. populations historically if detritus was transported to deep areas of the lake. Lake Tahoe supported an extremely large population of *Stygobromus* spp. between 60 and 500 m in the 1960s, despite low pelagic primary productivity. Such high densities of a benthic invertebrate taxon are rare in the profundal zones of deep lakes, which are generally thought of as depauperate and dependent on phytodetritus inputs from pelagic production (Goedkoop and Johnson 1996, Vadeboncoeur et al. 2003). The contribution of detrital material from macrophyte beds to profundal zones of deep lakes has not been examined, but such macrophyte food falls have been documented in marine systems, in which populations of deepwater amphipods are attracted to the resulting detritus as a food source (Lawson et al. 1993, Vetter 1995, 1998).

Potential drivers of change

The observed declines in the density and distribution of benthic invertebrates and deepwater macrophytes in Lake Tahoe coincide with changes to the lake's pelagic condition. Lake Tahoe's decrease in clarity over the past 4 decades has been associated with a shift in the bottom of the euphotic zone (1% light penetration) from 80 to 57 m (Chandra et al. 2005). Progressive eutrophication since the 1960s probably has caused increased shading to areas of the lake bottom that previously supported widespread benthic macrophyte and algal growth. Decreased macrophyte and periphyton abundance because of reduced transparency has been well documented in other oligotrophic systems (Hansson 1992, Schwarz and Hawes 1997, Schwarz et al. 1999, Jeppesen et al. 2000). Present-day food webs in Lake Tahoe are supported predominantly by pelagic production, whereas benthic production was dominant historically (Chandra et al. 2005). Such a shift would be expected to cause a decline in specialist invertebrate taxa and a change in feeding habits of generalist invertebrates to reflect changes in food availability (Vadeboncoeur et al. 2003). Sphaeriid clams and many chironomid species are fast-growing, generalist herbivores that can rapidly take advantage of increased primary productivity, as has been found in fertilized lake systems (Smith 1969, Clarke et al. 1997). Densities of *Pisidium* spp. and generalist chironomid taxa have increased in nearshore areas of Lake Tahoe since the 1960s, whereas specialist taxa have declined.

Nonnative species also could have contributed to the observed decline in benthic invertebrate density in Lake Tahoe. In 1963–1965, shortly after the 1962–1963 benthic invertebrate survey, 333,000 mysid shrimp (*M. relicta*) were introduced to Lake Tahoe as a food source for lake trout (*Salvelinus namaycush*) (Linn and Frantz 1965, Frantz and Cordone 1996). The introduced mysids established a large population in Lake Tahoe (~300 individuals/m^2) by 1971 and subsequently caused the disappearance of 2 cladoceran species (Richards et al. 1975, Goldman et al. 1979, Threlkeld 1981). *Mysis relicta* feeds at night in the water column and returns to the bottom of Lake Tahoe during the day to avoid fish predation, for a total daily vertical migration of up to 1000 m (Rybock 1978). *Mysis relicta* is omnivorous and consumes a variety of benthic and pelagic food items, including zooplankton, larval amphipods, and even small fish larvae (Parker 1980, Sealer and Binowski 1988, Johannsson et al. 2001, Bailey et al. 2006). *Mysis relicta* might have taken advantage of native benthic invertebrates in Lake Tahoe as a food source, especially exposed *Stygobromus* spp. in profundal areas too deep for macrophyte growth. *Mysis relicta* were collected in benthic samples at all transects during 2008–2009, but accurate densities could not be estimated because planktonic sampling methods were not used. In the McKinney Bay transect, several specimens of *M. relicta* were found in grabs that also contained *C. lacustra* and *Stygobromus* spp. No recent collections of mysids have been made in Lake Tahoe, but quantitative sampling in 1991 indicated that mysids occurred at densities of ~63 individuals/m^2 (SC, unpublished data).

Another nonnative invertebrate that could be affecting native benthic invertebrate and macrophyte assemblages in Lake Tahoe is the signal crayfish (*P. leniusculus*). *Pacifastacus leniusculus* has been present in the lake since 1895, but crayfish catch per unit effort (CPUE) has nearly doubled since the 1960s (J. Umek, University of Nevada, Reno, unpublished data). Adult crayfish in Lake Tahoe target benthic periphyton and macrophytes for food, whereas juveniles consume mainly small benthic invertebrates (Flint 1975). In other lake systems, crayfish are notorious for causing severe gastropod declines and negatively affecting macrophyte populations (Chambers et al. 1990, Lodge 1991, Lodge et al. 1994, 1998, Wilson et al. 2004, McCarthy et al. 2006). Crayfish in Lake Tahoe migrate to ≥50 m in the winter (J. Umek, unpublished data). Thus, they potentially could affect deepwater macrophyte assemblages and their associated fauna. The specific effects of nonnative species on benthic invertebrate and macrophyte populations in Lake Tahoe are not well understood, but they probably have contributed to the declines observed in our study.

Implications for lake management and conservation

Benthic and pelagic environments are linked in lakes, where factors, such as light availability, detrital fallout, and pelagic biota, dictate benthic community structure. In many oligotrophic lakes, eutrophication has been associated with increased benthic invertebrate densities through increased pelagic primary production and subsequent fallout to the benthos (Robertson and Alley 1966, Nalepa 1987, Clarke et al. 1997, Nalepa et al. 2000). Our data suggest that the opposite has occurred in Lake Tahoe. Increased eutrophication appears to have increased shading of the benthos, contributing to declines in macrophyte

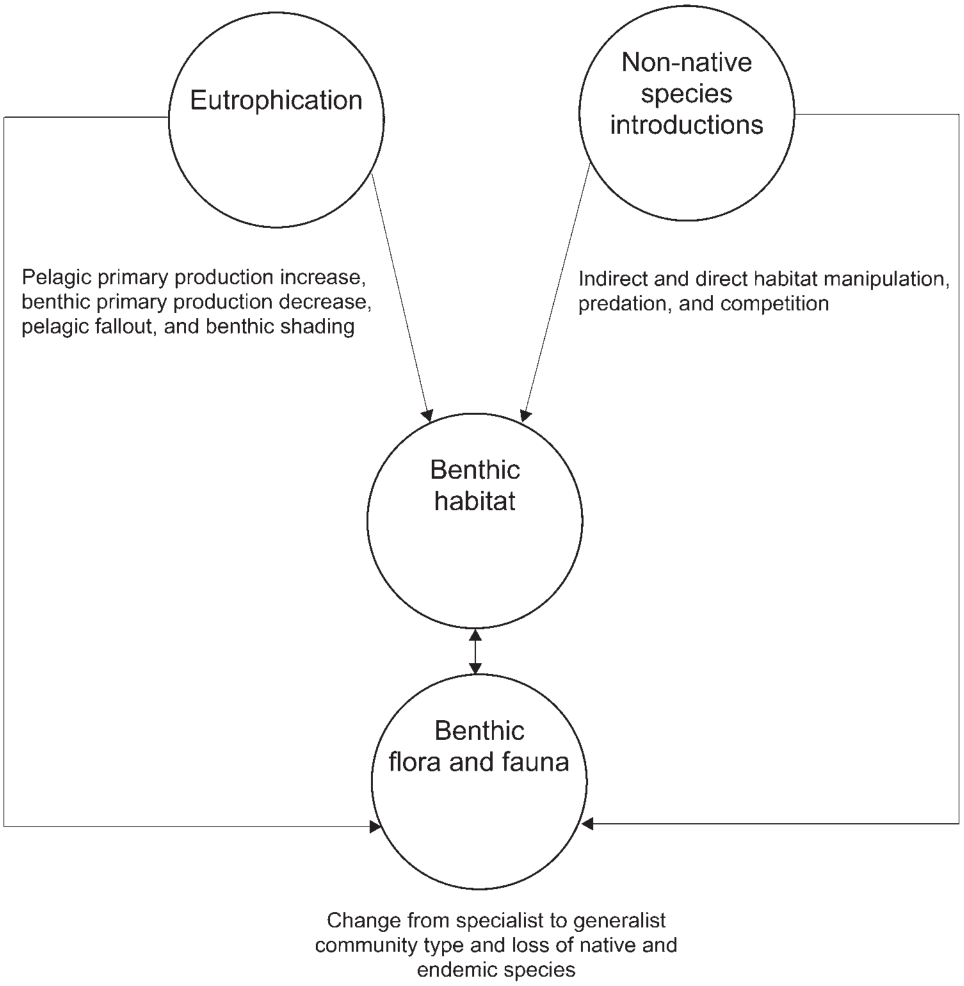

FIG. 4. Conceptual model of the effects over the past 4 decades of eutrophication and nonnative species introductions on Lake Tahoe's benthic floral and faunal communities.

abundance. This decline in preferred habitat for native benthic invertebrates and an increase in the abundance of nonnative invertebrate taxa probably have led to the dramatic benthic invertebrate declines and community changes observed in our study (Fig. 4). Another possibility is that the increase in benthic invertebrate density associated with eutrophication in other lakes has not occurred in Lake Tahoe because it remains oligotrophic. Continued cultural eutrophication could further increase the density of generalist taxa, thereby increasing overall benthic invertebrate density. The long period between sampling events makes it difficult to determine whether the declines observed in our study are solely a function of changes that have occurred to the lake over the past 4 decades, or if the declines also reflect temporal variation in benthic invertebrate populations. However, the absence or extreme scarcity of several endemic taxa (*P. tahoena*, *D. hymanae*, *S. lacicolus*, *S. tahoensis*, and *C. lacustra*) in our collections indicates that these taxa are at risk of extinction. Research is needed to examine seasonal variation in the abundance and distribution of endemic taxa, the association between endemic taxa and native macrophytes, and mechanisms contributing to the observed declines in native macrophyte and invertebrate communities.

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