

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/273319435>

Changes in fish diets and food web mercury bioaccumulation induced by an invasive planktivorous fish

Article in *Ecological Applications* · December 2008

DOI: 10.1890/06-1415.1

CITATIONS

52

READS

98

5 authors, including:



Collin Eagles-Smith
United States Geological Survey
112 PUBLICATIONS 2,710 CITATIONS

SEE PROFILE



Tom Suchanek
University of California, Davis
104 PUBLICATIONS 4,269 CITATIONS

SEE PROFILE



Peter B Moyle
University of California, Davis
402 PUBLICATIONS 19,183 CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:



Historical Salmon Fisheries [View project](#)



Mercury cycling in agricultural and managed wetlands, Yolo Bypass, California [View project](#)

December 2008



Volume 18 No. 8
Supplement

Ecological

APPLICATIONS

A PUBLICATION OF THE ECOLOGICAL SOCIETY OF AMERICA



Mercury Cycling and Bioaccumulation in Clear Lake

CHANGES IN FISH DIETS AND FOOD WEB MERCURY BIOACCUMULATION INDUCED BY AN INVASIVE PLANKTIVOROUS FISH

COLLIN A. EAGLES-SMITH,^{1,4} THOMAS H. SUCHANEK,^{1,2} ARTHUR E. COLWELL,³ NORMAN L. ANDERSON,³
AND PETER B. MOYLE¹

¹Department of Wildlife, Fish and Conservation Biology, University of California, Davis, California 95616 USA

²U.S. Geological Survey, Western Ecological Research Center, 3020 State University Drive East, Sacramento, California 95819 USA

³Lake County Vector Control District, P.O. Box 310, Lakeport, California 95453 USA

Abstract. The invasion, boom, collapse, and reestablishment of a population of the planktivorous threadfin shad in Clear Lake, California, USA, were documented over a 20-year period, as were the effects of changing shad populations on diet and mercury (Hg) bioaccumulation in nearshore fishes. Threadfin shad competitively displaced other planktivorous fish in the lake, such as inland silversides, young-of-year (YOY) largemouth bass, and YOY bluegill, by reducing zooplankton abundance. As a result, all three species shifted from a diet that was dominated by zooplankton to one that was almost entirely zoobenthos. Stable carbon isotopes corroborated this pattern with each species becoming enriched in $\delta^{13}\text{C}$, which is elevated in benthic vs. pelagic organisms. Concomitant with these changes, Hg concentrations increased by ~50% in all three species. In contrast, obligate benthivores such as prickly sculpin showed no relationship between diet or $\delta^{13}\text{C}$ and the presence of threadfin shad, suggesting that effects of the shad were not strongly linked to the benthic fish community. There were also no changes in Hg concentrations of prickly sculpin. The temporary extirpation of threadfin shad from the lake resulted in zooplankton densities, foraging patterns, isotope ratios, and Hg concentrations in pelagic fishes returning to pre-shad values. These results indicate that even transient perturbations of the structure of freshwater food webs can result in significant alterations in the bioaccumulation of Hg and that food webs in lakes can be highly resilient.

Key words: bioaccumulation; Clear Lake, California, USA; fish; inland silverside; invasions; invasive species; largemouth bass; mercury; nonnative fishes; stable isotopes; Sulphur Bank Mercury Mine; threadfin shad.

INTRODUCTION

Two major threats to freshwater ecosystems worldwide are invasions of alien species (Lodge 1993, Moyle and Light 1996) and contaminants (Colborn and Thayer 2000, Hammerschmidt et al. 2002, Relyea 2003). The two threats are particularly severe in California, USA, where freshwater systems are not only heavily invaded (Moyle and Marchetti 2006) but heavily contaminated, especially with mercury (Hg) (Macleod et al. 2005). Mercury is a problem in California because it became widely distributed in aquatic systems as the result of a long legacy of gold and Hg mining (Alpers et al. 2005, Wiener and Suchanek 2008). Widespread Hg contamination of fishes has been documented in the state, with consumption advisories currently issued for sportfish in 14 waterbodies (OEHHA 2006).

Manuscript received 22 August 2006; revised 15 May 2007; accepted 24 May 2007. Corresponding Editor (ad hoc): A. Fairbrother. For reprints of this Special Issue, see footnote 1, p. A1.

⁴ Present address: U.S. Geological Survey, Western Ecological Research Center, Davis Field Station, One Shields Avenue, Davis, California 95616 USA.
E-mail: ceagles-smith@usgs.gov

In aquatic environments, inorganic Hg (Hg^0 , Hg^{2+}) is converted to methylmercury (MeHg) by sulfate- and iron-reducing bacteria (Compeau and Bartha 1985, Fleming et al. 2006). Methylmercury, a potent neurotoxin, is a highly bioavailable form of Hg that readily passes through biological membranes and can accumulate to high concentrations in upper trophic level species (Mason et al. 2000). In fishes, the risk of exposure to Hg is directly related to the degree of contamination and methylating potential of their habitats. For example, the extent of wetland boundaries and wetting and drying cycles have been shown to be positively correlated with fish Hg contamination (Snodgrass et al. 2000, Greenfield et al. 2001, St. Louis et al. 2004, Hall et al. 2005). Independent of environmental factors, fish Hg accumulation is also strongly driven by the ecological attributes and life history of the fish (Wiener and Spry 1996). Moreover, because dietary exposure primarily dictates Hg accumulation (Rogers et al. 1987, Harris and Snodgrass 1993, Watras et al. 1998), upper trophic level species typically have greater Hg concentrations than those occupying lower trophic positions (Kidd et al. 1995).

Although both invasive species and Hg contamination are serious conservation threats to numerous (and often the same) ecosystems, little work has focused on how

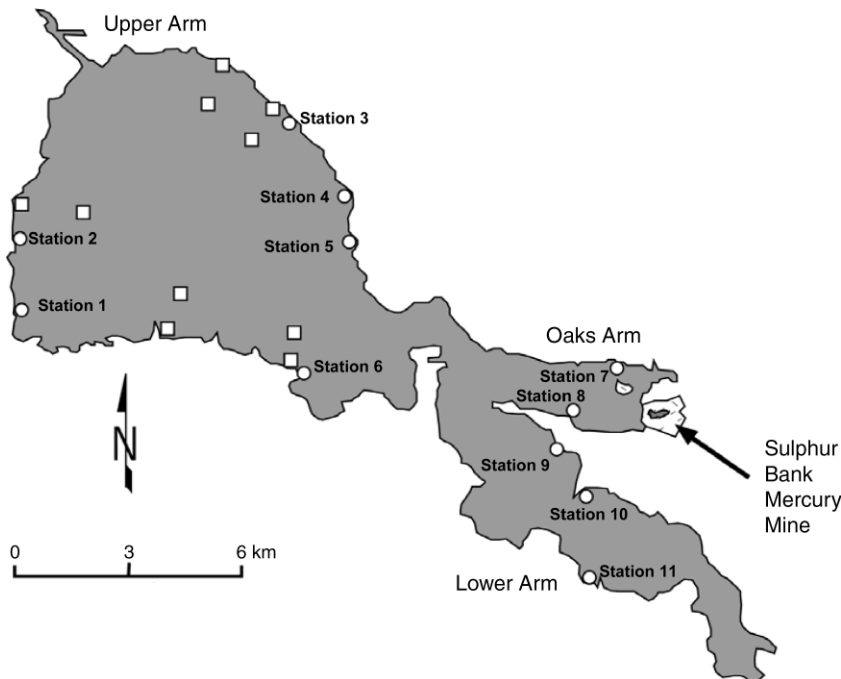


FIG. 1. Map of Clear Lake, California, USA, with fish (circles) and zooplankton (squares) sampling stations.

these two conservation threats interact with one another at population and community scales. This is presumably due to the shortage of direct measurements of community and trophic structure and of Hg concentrations in the environment before and after an invasion. The interactions between species invasions and Hg accumulation may become important when the trophic structure changes in the invaded habitat, resulting in alterations to dietary Hg exposure as a result of shifts in trophic position (Kidd et al. 1999), growth rate (Simoneau et al. 2005), or foraging habitat (Power et al. 2002).

This study is one component of a larger ecosystem-level study that traces the origin and pathways of Hg from the ore body at an abandoned mine, through the abiotic (sediment and water) matrices, and into the food web from primary producers to top predators. It integrates data from a holistic examination of the Hg sources and fate in a mine-impacted ecosystem with a long-term (~20-year) survey of fish and invertebrate population dynamics from Clear Lake, California, USA. Here we document the differences in food web structure associated with the boom, collapse, and reestablishment of an invading planktivore, the threadfin shad (*Dorosoma petenense*), and the concomitant changes in the diets and Hg bioaccumulation of some of the resident fish species. The following questions were asked in this study: (1) Did shifts in diets and foraging habitats of pelagic and benthic fishes correspond with shad abundance during the boom, collapse, and reestablishment of threadfin shad populations? (2) Did the

concentration of Hg in other fishes track the population fluctuations of the shad?

METHODS

Site description

Clear Lake is a eutrophic, polymictic lake located in the Coastal Range of northern California, USA (Suchanek et al. 2008e). At 17 670 ha, it is the largest lake fully contained within California (Fig. 1) and is a popular sportfishing location due to its trophy fishery for largemouth bass (*Micropterus salmoides*). Prior to the arrival of Euro-American settlers, it contained an abundant native fish fauna of 13 species, including several endemic to the lake (Moyle 2002). A well-documented history of invasions began in the late 19th century with the introduction of lake whitefish (*Coregonus clupeaformis*) and common carp (*Cyprinus carpio*). Today the fish community is dominated primarily by largemouth bass, bluegill (*Lepomis macrochirus*), common carp, and inland silverside (*Menidia beryllina*), with only four native species remaining (Moyle 2002).

On the northeastern shore of Clear Lake, in the Oaks Arm, lies the Sulphur Bank Mercury Mine (Fig. 1), an abandoned Hg mine that was responsible for ~100 Mg of Hg being deposited into the sediments between 1872 and 1957 (Suchanek et al. 2003, 2008e). Although the relative proportion of MeHg to total (primarily inorganic) Hg (TotHg) is low compared to other contaminated sites (Suchanek et al. 2008a), top predator fishes

in the lake are still commonly found with muscle tissue concentrations of 1.0–1.5 $\mu\text{g/g}$ (ppm) wet mass (WM), and a human consumption advisory based on Hg has been in effect since 1986 (Suchanek et al. 2008*d, e*).

Fish capture and collection

Relative abundance of nearshore fishes was monitored biannually (summer and fall) in Clear Lake from 1986 to 2004 as part of the Lake County Vector Control District's monitoring program. A seine (9.1 m long \times 1.2 m high) with an ace mesh (3.2 mm apertures) was used to sample an 83-m² area of the shoreline. On each sampling occasion three separate seine hauls were made at least 100 m apart at each of 11 fixed stations (Fig. 1). All captured fish were identified to species and counted, and standard lengths (SL) of up to 25 individuals of each species per capture event were measured. Additionally, five common species were selected for collection and subsequent biomass, diet, Hg, and stable isotope analyses. These species included: threadfin shad, inland silverside, largemouth bass, bluegill, and prickly sculpin (*Cottus asper*). Of these species, two subsets were selected. One subset was taken from all locations for stomach contents and biomass analyses between 1985 and 1997 and one from only the Oaks Arm (Stations 7 and 8) for mercury and stable isotope analyses. To reduce the effect of interannual carryover in isotope and Hg signatures, only young-of-year (YOY, <115 mm) bass and bluegill were collected. In the laboratory, each collected fish was measured for SL to the nearest 0.1 mm and weighed to the nearest 0.001 g. Additionally, each fish from the mercury and stable isotope subset was dried at 50°C for 48 h or until constant mass was achieved. Dry mass (DM) was then measured for each individual to the nearest 0.001 g. Mean relative biomass per unit area was estimated for each monitoring event by multiplying the number of fish captured with the estimated biomass of the mean fish size, determined using year and site-specific length–mass regressions (Eagles-Smith 2006). Biomass estimates are limited to years between 1986 and 2002 because representative size was not recorded for fish captured outside that time period.

Invertebrate abundance and biomass estimates

Zooplankton were sampled monthly between 1985 and 2003 from five onshore (2 m depth) and five offshore (7 m depth) stations (Fig. 1) using a 15-L Schindler trap (Schindler 1969) with an 80- μm mesh dolphin bucket. The zooplankton monitoring was a component of a vector control program focused on the Upper Arm of the lake. As a result there were no stations established in the Oaks or Lower Arms. Onshore stations were sampled by pooling surface, 1.0 m deep, and 1.5 m deep samples. Offshore stations were sampled by pooling surface, 1, 2, 3, 4, 5, and 6 m deep samples. Samples were preserved in 5% formalin and later identified and counted in the laboratory using keys by Edmondson

(1959), Pennak (1989), and Thorp and Covich (1991). Biomasses of dominant taxa were estimated using published length–mass regressions (Dumont et al. 1975, Pace and Orcutt 1981, Rosen 1981) and estimates of mean lengths for each zooplankton taxon (Eagles-Smith 2006).

Stomach content analysis

Fish were collected for diet analysis at least twice per annum (summer and fall) and occasionally more frequently between 1986 and 1997 (Eagles-Smith et al. 2008). Prey items were identified on a gridded Petri dish to the lowest identifiable taxon (generally genus or species). For each taxon a count and proportion of total contents was measured on a volumetric basis (Eagles-Smith et al. 2008). Fish with empty stomachs were excluded from the diet analysis. To facilitate interpretation of diet data, each food item was assigned to both a broad taxonomic classification (e.g., zooplankton, fish, benthic invertebrate) and primary habitat type (e.g., pelagic, benthic) based on published feeding information for each taxon (Eagles-Smith et al. 2008).

Stable isotope analysis

Although dietary studies using gut contents are valuable, this approach has drawbacks that limit applicability to understanding trophic dynamics. Gut content analyses are biased toward diet items recently consumed and provide only point-in-time analysis of prey consumed but not necessarily assimilated. Carbon and nitrogen stable isotopes provide a means for overcoming some of these limitations and have been used as a robust way to model complex trophic dynamics (Jeppesen and Winemiller 2002). Stable isotopes provide an integrated index of diet assimilated over a much longer time span (Maruyama et al. 2001), and each isotope offers different information regarding energy input. The stable isotope $\delta^{15}\text{N}$ increases from diet to consumer, providing an index of trophic position (Vander Zanden and Rasmussen 2001), whereas the $\delta^{13}\text{C}$ signature is relatively conserved with each trophic transfer, providing information on the basal energy sources assimilated in higher order consumers (Post 2002). The utility of $\delta^{13}\text{C}$ comes from differences in primary producer values at the base of the food web (France 1995) and can be used to indicate habitat-specific pathways of bioaccumulative contaminants.

Samples collected for stable isotope analyses were dried as indicated above. For fish >100 mm SL, skinless axial muscle tissue was dissected from behind the head, whereas fish <100 mm SL were decapitated, eviscerated, and skin and scales were removed. Dried tissue was ground to a fine powder, and ~0.80–1.60 mg of tissue were weighed into tin capsules and stored in a desiccator until analysis. Stable isotope analysis was performed on a continuous flow isotope ratio mass spectrometer (IRMS; dual-inlet Europa 20/20, PDZ Europa, Crewe, England) at the University of California, Davis Stable

Isotope Facility. Sample combustion to CO₂ and N₂ occurred at 1000°C in an inline elemental analyzer. A Carbosieve G column (Varian, Palo Alto, California, USA) separated the gas before introduction into the IRMS. Standards (PeeDee Belemnite for δ¹³C and N₂ gas for δ¹⁵N) were injected directly into the IRMS before and after sample peaks. Isotope ratios are expressed in per mil (‰) notation. Using δ¹³C as an example, ratios are defined by the following equation:

$$\delta^{13}\text{C} = \left\{ \left[\frac{(^{13}\text{C}/^{12}\text{C})_{\text{sample}}}{(^{13}\text{C}/^{12}\text{C})_{\text{standard}}} \right] - 1 \right\} \times 1000.$$

Replicates were measured every 10 samples and relative percentage of difference (RPD) averaged 0.51% for δ¹⁵N and 0.24% for δ¹³C ($N = 52$).

Total mercury analysis

Fish samples for TotHg analysis were processed as described in *Stable isotope analysis*. Muscle tissue was chosen for TotHg analysis because it has been identified as the primary repository of MeHg in fishes and serves as a strong proxy for whole-body concentrations (Goldstein et al. 1996, Suchanek et al. 2008d). All sampled fish were weighed before and after drying to determine moisture content. Fish were dried and powdered as described in the stable isotope analysis methods. Some archived frozen samples suffered moisture loss, thus all data are reported and analyzed on a dry-mass basis. Percentage of moisture in fresh samples averaged $75.7\% \pm 2.36\%$ (mean \pm SD) and did not differ among species (Eagles-Smith 2006), thus allowing for comparison with wet-mass concentrations from the literature. Fish were analyzed for TotHg on a Milestone DMA-80 Direct Mercury Analyzer (Milestone, Monroe, Connecticut, USA) using an integrated sequence of drying (160°C for 140 s), thermal decomposition (850°C for 240 s), catalytic conversion, and then amalgamation, followed by atomic absorption spectroscopy.

Quality assurance methods for mercury included analysis of at least two certified reference materials (dogfish muscle [DORM-2, National Research Council of Canada, Ottawa, Ontario, Canada], dogfish liver [DOLT-3, National Research Council of Canada], or lobster hepatopancreas [TORT-2, National Research Council of Canada]), two method blanks, two duplicates, two matrix spikes, and two matrix spike duplicates per batch of 20 samples. Reference material recoveries averaged $99.6\% \pm 2.4\%$ ($N = 67$), whereas recoveries for matrix spikes averaged $103.2\% \pm 2.4\%$ ($N = 61$). Absolute RPD averaged 2.9% for duplicates and 5.6% for matrix spike duplicates.

Statistical analyses

Statistical analyses included analysis of variance (ANOVA) and analysis of covariance (ANCOVA). All computations were conducted using Statistica 7.1 (StatSoft 2005) and/or JMP 5.0 (SAS Institute 2002). Residuals were assessed for normality during model

fitting, and data were assessed for homogeneity of variance. Density, biomass, and TotHg data were natural log-transformed to stabilize variance, and proportional diet data were arcsine square-root transformed to conform to model assumptions (Zar 1999).

Temporal variation in nearshore fish densities was assessed with respect to shad population fluctuations. Data were classified into three categories based upon threadfin shad abundance: (1) 1986–1989 during the initial shad invasion, when shad abundance was high (>10 fish/ha), (2) 1990–2001, when shad populations crashed and densities never exceeded 10 individuals/ha, (3) 2002–2004 when shad densities increased again above 10 individuals/ha. For each fish species a multiway nested ANOVA was conducted with either density or biomass as the dependent variable and shad abundance, season, station, and [seine haul (station)] as factors. Initially, the interaction term “shad abundance \times station” was included in all models and dropped if not significant ($P > 0.05$).

To assess the relationship between shad abundance and both δ¹³C values and TotHg concentrations, ANCOVA models were used with shad abundance and species as categorical factors and standard length as the covariate. The interaction terms “species \times shad abundance” and “species \times standard length” were also included in the model. Because of the significant interaction between species and shad abundance in the initial iteration, separate models were assessed for each of the four fish species, with shad abundance as the categorical factor and length as the covariate.

RESULTS

Fish abundance

Although they were only first detected in the lake in 1985 (A. E. Colwell, *unpublished data*), by 1988 threadfin shad were the dominant inshore fish species of Clear Lake, both numerically and on a biomass basis (Fig. 2E). Their population crashed in 1990, and threadfin shad were not detected in the lake again until 1997, when they made a brief reappearance followed by a major die-off the following winter. They reappeared again in 2001, and their density began to increase appreciably after 2002 (Fig. 2E). The abundance and biomass of five common nearshore fish species in Clear Lake, including threadfin shad, varied considerably over time (Fig. 2A–E). Changes in the annual abundance of threadfin shad and prickly sculpin tracked changes in their biomass, indicating that the size spectra of those species did not vary dramatically over time. However, in 1988 inland silverside biomass showed a greater relative decline than that seen in density (Fig. 2A), indicating a shift towards smaller individuals, a change concomitant with the peak of shad abundance. In contrast, YOY largemouth bass and bluegill numbers decreased relative to biomass during the initial threadfin shad invasion (Fig. 2B, C), suggesting that the average size of both species increased during the invasion period. During both time periods

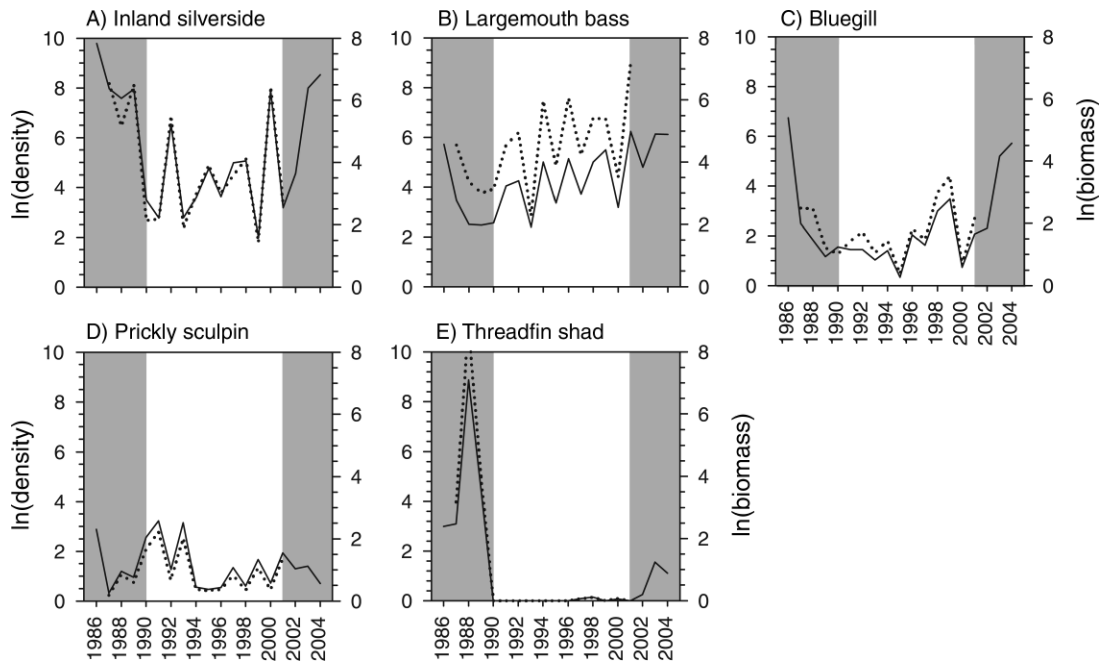


FIG. 2. Mean annual density (solid lines) and biomass (dashed lines) of five common nearshore fish species from Clear Lake between 1985 and 2004: (A) inland silverside (*Menidia beryllina*), (B) largemouth bass (*Micropterus salmoides*), (C) bluegill (*Lepomis macrochirus*), (D) prickly sculpin (*Cottus asper*), and (E) threadfin shad (*Dorosoma petenense*); density = $(n + 1)/\text{ha}$ where n = number of individuals; biomass = g dry mass/ha. The shaded regions represent years when threadfin shad abundance was elevated.

when shad abundance was elevated (1986–1989 and 2002–2004), inland silverside densities were significantly greater than when shad abundance was low (ANOVA, $F_{2,1055} = 76.64$, $P < 0.0001$; Fig. 3A). Silverside biomass was also higher during the years of elevated shad abundance relative to when shad were sparse (ANOVA, $F_{1,881} = 106.51$, $P < 0.0001$; Fig. 3B). Although silverside abundance varied among stations (ANOVA, $F_{10,1055} = 7.30$, $P < 0.0001$), there was no interaction between shad abundance and station ($P = 0.07$). However, for biomass there was a significant shad abundance \times station interaction ($P = 0.005$). Silverside biomass was greater in the shad-abundant years at all stations except 4 and 5, where there were no differences in silverside biomass between time periods. For largemouth bass, density was higher in each successive time period relative to the preceding one (ANOVA, $F_{2,1035} = 46.40$, $P < 0.0001$; Fig. 3A), and biomass was elevated in the shad-sparse years relative to those when shad first invaded Clear Lake (ANOVA, $F_{1,881} = 25.30$, $P < 0.0001$; Fig. 3B). Bluegill densities also differed among the shad abundance categories (ANOVA, $F_{2,1035} = 61.10$, $P < 0.0001$; Fig. 3A); however, only the second period of elevated shad abundance (2002–2004) was associated with elevated bluegill densities, whereas there were no differences between the initial shad invasion and subsequent decline (Fig. 3). Additionally, there was a significant interaction in bluegill densities between shad abundance and station ($P < 0.0001$). Bluegill densities

were higher in 2002–2004 than during the other two time periods at sites 1, 2, 7, 8, 10, and 11, whereas there were no differences among time periods at sites 3, 4, and 5. Moreover, bluegill densities did not differ between 1986–1989 and 1990–2001 at any station except 6, where density during the shad-sparse years was lower than either shad-abundant time period. Bluegill biomass did not differ between shad-abundant and shad-sparse years (ANOVA, $F_{1,891} = 0.18$, $P = 0.45$; Fig. 3B), and there were no interactions between station and shad abundance. The main effects of the relationship between prickly sculpin densities and shad abundance were difficult to assess because of the interaction between station and shad abundance ($P < 0.0001$). Overall, sculpin densities did not differ among time periods (ANOVA, $F_{2,1035} = 2.51$, $P = 0.08$; Fig. 3A), and the interactions indicate that differences only occurred at stations 2, 9, 10, and 11. Similarly, the interaction was also significant for sculpin biomass, and biomass did not differ between time periods (ANOVA, $F_{1,881} = 2.23$, $P = 0.34$; Fig. 3B).

Zooplankton abundance

When threadfin shad populations first proliferated in Clear Lake, zooplankton densities and biomass declined sharply. Both spiked soon after the shad disappeared, followed by a long period of low densities in the mid- to late 1990s (Fig. 4; see Suchanek et al. 2008c). Zooplankton began to increase again between 2000 and 2001, but

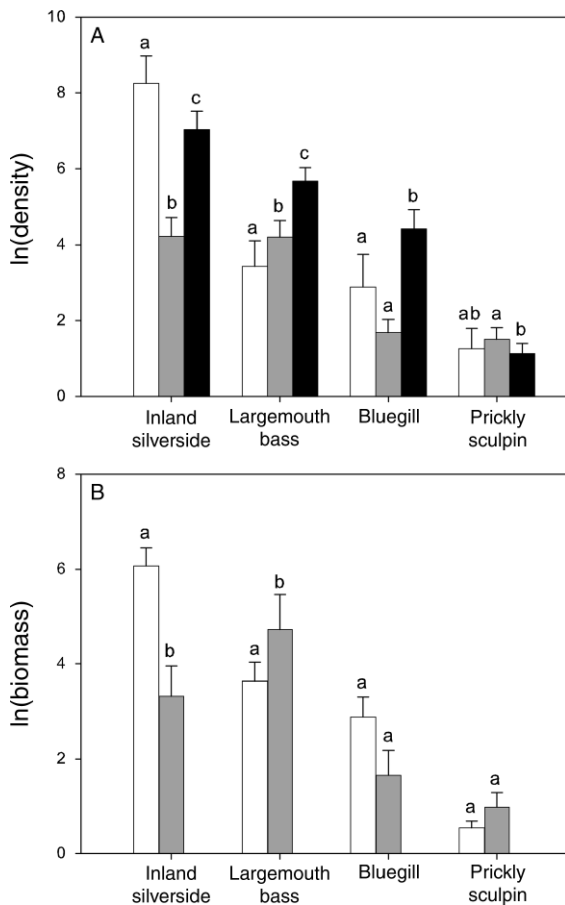


FIG. 3. Differences in (A) $\ln(\text{density})$ and (B) $\ln(\text{biomass})$ of four nearshore fish species (inland silverside [*Menidia beryllina*], largemouth bass [*Micropterus salmoides*], bluegill [*Lepomis macrochirus*], and prickly sculpin [*Cottus asper*]) from Clear Lake when threadfin shad (*Dorosoma petenense*) were abundant (white bars, 1986–1989; black bars, 2002–2004) vs. sparse or undetected (gray bars, 1990–2001); density = $(n + 1)/\text{ha}$, where n = number of individuals and biomass = g dry mass/ha. The error bars represent 95% confidence intervals. Different lowercase letters above bars indicate that values within a species are statistically different ($P < 0.05$).

densities underwent another decline in 2002 as shad abundance expanded. In addition to changes in overall abundance and biomass of zooplankton, the composition of individual taxa within this group varied greatly and corresponded to the shad dynamics (Fig. 5). Moreover, the overall composition and proportion of different zooplankton taxa differed dramatically when examined on an abundance or biomass basis (Fig. 5). Abundance and density data indicated that copepod nauplii and *Bosmina* sp. together generally composed the greatest proportion of total zooplankton, accounting for ~60% or more of the total number of individuals (Fig. 5A, C). *Daphnia pulex* and *D. galeata* also made up significant proportions of the zooplankton in the 1990s when shad were absent from the lake (Fig. 5E–F). The proportion of nearly all taxa changed dramatically

between the initial threadfin shad invasion and disappearance. Smaller and more evasive taxa, such as *Bosmina* sp. and copepods (e.g., Diptomus, cyclopoids, and nauplii) generally made up a greater proportion of the zooplankton assemblage when shad densities were high, whereas the large-bodied and less evasive taxa, such as *Daphnia* sp., seemed to dominate when shad densities were low (Fig. 5A–F). When examined on a biomass basis it is clear that the numerical trends were not completely indicative of the energy contribution of individual zooplankton taxa to food webs. Adult cyclopoid copepods are one of the most dominant taxa across years, and their proportion of the total biomass increased to around 70% between 1986 and 1990. During the same time period, biomass contribution of *Daphnia pulex* declined dramatically, with a rebound to roughly 40% of total mass after 1990.

Diet analysis

Stomach content analyses of nearshore fishes indicated a diet shift after the 1986–1989 threadfin shad invasion (Table 1). When shad were abundant, inland silverside, bluegill, and largemouth bass diets all contained considerably less zooplankton relative to years when shad were scarce. This difference was driven primarily by a reduction in the proportion of *Daphnia* sp. in the diets of all three species. The dietary proportion of *Daphnia* was more than twice as high during the shad-sparse time than during the years of high shad abundance (Table 1). The deficit left by the reduction in zooplankton prey was balanced by an equally dramatic increase in benthic invertebrates in fish diets, primarily chironomid larvae and, to a lesser extent, amphipods and ostracods (Table 1). This temporal trend in diet shifts was particularly evident for inland silverside, which underwent a striking reversal in pelagic vs. benthic foraging between 1985 and 1989 (Fig. 6). However, when examined by size classes, the effect of shad presence on silverside diets was not significant in silversides >60 mm (Table 2). Unlike the

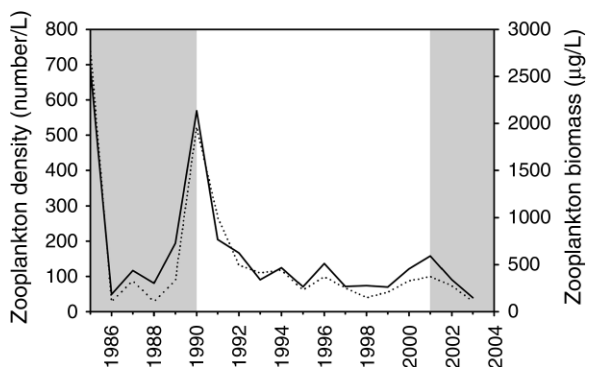


FIG. 4. Annual density (solid line) and estimated biomass (dotted line) of zooplankton collected from Clear Lake. The shaded regions indicate times when threadfin shad (*Dorosoma petenense*) abundance was high.

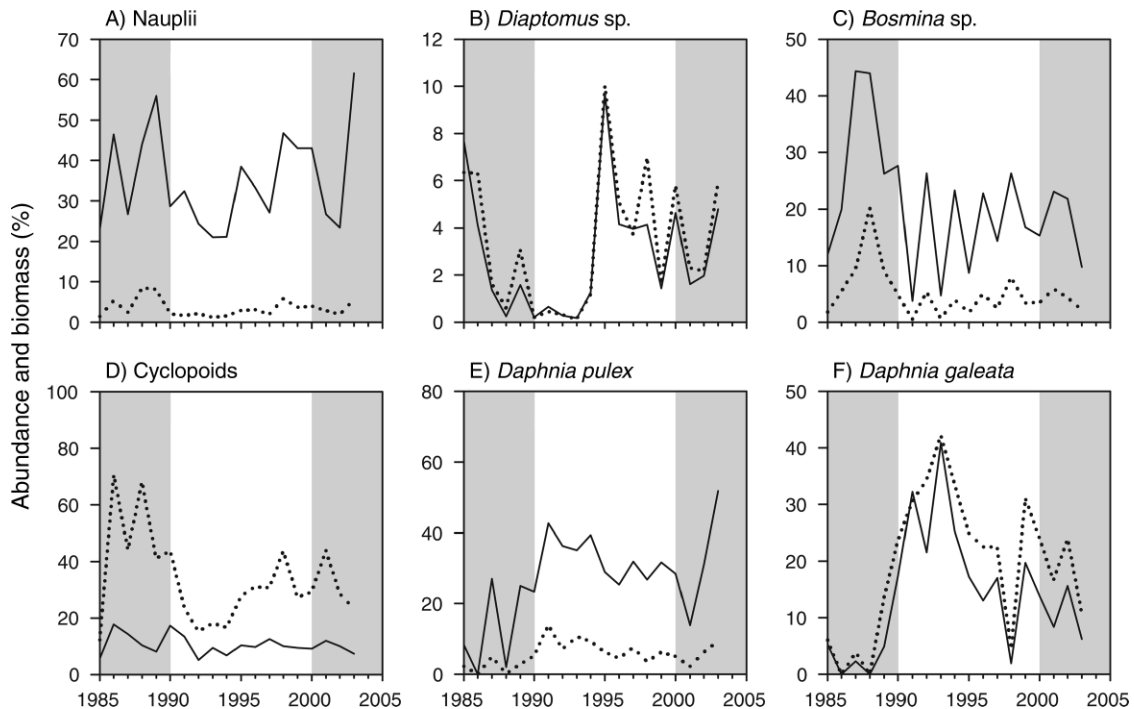


FIG. 5. Percentage of mean annual abundance (solid line) and biomass (dotted line) for major zooplankton taxa collected from Clear Lake: (A) copepod nauplii, (B) *Diaptomus* sp., (C) *Bosmina* sp., (D) cyclopoid copepods, (E) *Daphnia pulex*, and (F) *Daphnia galeata*. The shaded regions indicate time of high threadfin shad (*Dorosoma petenense*) abundance. Note the differences in y-axis scales among panels.

three species discussed above, prickly sculpin did not undergo a substantial diet shift corresponding with threadfin shad abundance (Tables 1 and 2).

Habitat-specific energy reliance also differed among species and shad abundance categories. For all species combined, $\delta^{13}\text{C}$, a proxy for benthic vs. pelagic energy reliance (France 1995), was significantly enriched during periods of elevated threadfin shad abundance (1986–1989, 2002–2004) relative to the shad-sparse time period (1990–2001) (ANCOVA, $F_{2,585} = 14.79$, $P < 0.0001$). However, there were significant interactions between species and both shad abundance ($P = 0.001$) and standard length ($P < 0.0001$). As a result, each species was assessed individually to better interpret the main effects. $\delta^{13}\text{C}$ was significantly enriched during both periods of high shad abundance relative to the shad-sparse years in inland silversides (ANCOVA, $F_{2,242} = 33.83$, $P < 0.0001$; Fig. 7A) and largemouth bass (ANCOVA, $F_{2,272} = 53.56$, $P < 0.0001$; Fig. 7A). In bluegill, $\delta^{13}\text{C}$ also differed among time periods (ANCOVA, $F_{2,50} = 5.35$, $P = 0.008$); however, only fish from 2002–2004 were enriched over those from the shad-sparse years, whereas there were no differences in bluegill $\delta^{13}\text{C}$ from the period 1986–1989 and those from either 1990–2001 or 2002–2004 (Fig. 7A). Finally, there were no differences in prickly sculpin $\delta^{13}\text{C}$ among time periods (ANCOVA, $F_{2,21} = 0.03$, $P = 0.97$), suggesting

that habitat-specific foraging did not differ in relation to shad abundance (Fig. 7A).

Total mercury also varied among species (ANCOVA, $F_{3,566} = 7.45$, $P < 0.0001$), and there was a significant effect of shad abundance (ANCOVA, $F_{2,566} = 5.17$, $P = 0.006$). However, similar to $\delta^{13}\text{C}$ there was also an interaction between shad abundance and species ($P < 0.0041$), thus each species was assessed independently. On a species-specific basis both silverside (ANCOVA, $F_{2,235} = 8.18$, $P = 0.0004$; Fig. 7B) and bass (ANCOVA, $F_{2,260} = 27.65$, $P < 0.0001$; Fig. 7B) TotHg concentrations were higher during the time periods when shad were abundant than when they were sparse. Moreover, there were no differences in TotHg concentrations between the two periods of high shad abundance for either species (Fig. 7B). However, there was a significant interaction between shad abundance and length for bass, which indicates that at smaller sizes (<70 mm) Hg concentrations were higher in 2002–2004 than in 1986–1989. Conversely, at bass lengths >70 mm Hg concentrations were higher in 1986–1989 than in 2002–2004. Bluegill Hg concentrations also varied among time periods (ANCOVA, $F_{2,49} = 13.01$, $P < 0.0001$); however, concentrations did not follow the same patterns as those for silverside and bass. Mercury was highest during the 2002–2004 time period, followed by the shad-sparse years (1990–2001), and then those during the initial shad invasion (1986–1989; Fig. 7B). Prickly sculpin Hg data

TABLE 1. Diet contents (percentage of volume, mean with SE in parentheses) of some nearshore fish species when threadfin shad were abundant vs. sparse in Clear Lake, California, USA.

Prey item	Bluegill		Inland silverside		Largemouth bass		Prickly sculpin	
	<i>N</i> = 276	<i>N</i> = 34	<i>N</i> = 682	<i>N</i> = 212	<i>N</i> = 416	<i>N</i> = 43	<i>N</i> = 81	<i>N</i> = 79
	Shad abundant (1986–1989)	Shad sparse (1990–2001)	Shad abundant (1986–1989)	Shad sparse (1990–2001)	Shad abundant (1986–1989)	Shad sparse (1990–2001)	Shad abundant (1986–1989)	Shad sparse (1990–2001)
Fish	0.00	0.00	0.00	0.00	25.80 (0.73)	34.14 (3.37)	0.00	0.00
Zooplankton								
<i>Daphnia</i> sp.	0.31 (0.16)	18.39 (9.43)	18.26 (1.86)	54.11 (4.89)	1.14 (0.72)	23.80 (3.37)	9.87 (5.50)	6.10 (4.74)
<i>Bosmina</i> sp.	6.63 (1.55)	6.02 (4.02)	10.62 (1.27)	9.43 (2.86)	0.00	0.12 (0.60)	3.41 (2.10)	14.02 (5.68)
<i>Chydorus</i> sp.	1.00 (0.44)	1.01 (2.01)	1.72 (0.41)	1.60 (0.97)	0.00	0.00	1.40 (1.42)	1.46 (1.74)
<i>Eurycerus</i> sp.	0.00	9.42 (4.51)	0.00	0.18 (0.44)	0.00	0.00	0.25 (0.38)	0.00
<i>Ceriodaphnia</i> sp.	0.00	0.07 (0.40)	0.00	0.12 (0.17)	0.00	0.00	0.00	0.00
<i>Cyclops</i> sp.	0.63 (0.24)	0.42 (1.08)	13.43 (1.67)	3.07 (1.61)	0.00	1.45 (2.97)	0.13 (0.24)	0.00
<i>Diaptomus</i> sp.	4.09 (0.64)	4.22 (3.62)	20.36 (2.09)	11.82 (2.70)	3.52 (1.30)	0.76 (1.22)	4.24 (2.86)	4.70 (3.69)
Benthic invertebrates								
Chironomidae	59.14 (2.81)	30.21 (6.07)	29.59 (1.20)	15.08 (1.79)	36.02 (1.79)	13.92 (0.97)	28.10 (3.22)	26.04 (4.18)
Ephemeroptera	6.40 (0.17)	12.30 (2.30)	0.56 (0.30)	0.22 (0.64)	9.66 (0.56)	3.32 (2.91)	4.13 (0.62)	6.54 (0.99)
Hemiptera	0.00	2.15 (1.03)	0.00	1.06 (0.17)	6.56 (0.08)	8.80 (1.00)	0.19 (0.37)	0.85 (0.93)
Odonata	0.00	0.28 (0.13)	0.00	0.10 (0.32)	0.00	4.35 (3.05)	3.63 (0.65)	2.56 (0.99)
Trichoptera	0.00	0.98 (0.15)	0.00	0.00	0.00	0.00	2.00 (0.58)	0.00
Amphipoda	0.94 (0.67)	9.47 (2.96)	0.66 (0.44)	0.51 (0.93)	8.05 (0.69)	3.51 (3.50)	24.66 (1.37)	18.29 (1.30)
Ostracoda	18.53 (0.70)	2.06 (2.80)	2.50 (0.41)	0.52 (0.78)	0.00	0.23 (3.29)	15.96 (1.34)	17.01 (1.36)
Unknown	2.76	3.57	2.30	2.18	9.26	5.61	2.04	2.43

Note: Species names are: bluegill, *Lepomis macrochirus*; inland silverside, *Menidia beryllina*; largemouth bass, *Micropterus salmoides*; prickly sculpin, *Cottus asper*; threadfin shad, *Dorosoma petenense*.

followed a similar pattern to the diet and $\delta^{13}\text{C}$ results, whereby TotHg did not vary among time categories (ANCOVA, $F_{2,23} = 1.58$, $P = 0.23$; Fig. 7B).

DISCUSSION

The threadfin shad invasions of Clear Lake were associated with considerable yet transient changes to the structure of the food web, resulting in elevated Hg concentrations in some small fish species during years of elevated shad abundance relative to those when shad were sparse. During times when large numbers of shad were present in the lake, two resident fish species that generally depend heavily on pelagic prey, the inland silverside and juvenile largemouth bass, had dramatically lower dependence upon pelagic resources and relied more on benthic prey. After shad populations crashed, the diets of both inland silverside and bass contained more zooplankton. Parallel to the shift in diet, Hg concentrations in both silversides and juvenile bass

were significantly higher during both time periods when shad were abundant relative to when they were scarce. These results suggest that dietary Hg exposure increased as a result of the shift to a more benthic foraging habit for both silversides and bass.

Further support of this interpretation comes from the prickly sculpin, an obligate benthic feeder (Moyle 2002). Neither the stomach contents nor their $\delta^{13}\text{C}$ signatures differed in relation to shad abundance, indicating that isotopic changes seen in silversides and bass likely resulted from an increase in benthic reliance and not a baseline shift in the lake's isotopic values at the primary producer level. Moreover, the absence of any change in TotHg in prickly sculpin further supports the argument that changes in TotHg in silversides and bass are related to foraging shifts and not system-wide alterations in Hg availability or methylation. Interestingly, the bluegill data are rather equivocal. Diet analysis indicates an increase in reliance on benthos during periods of high

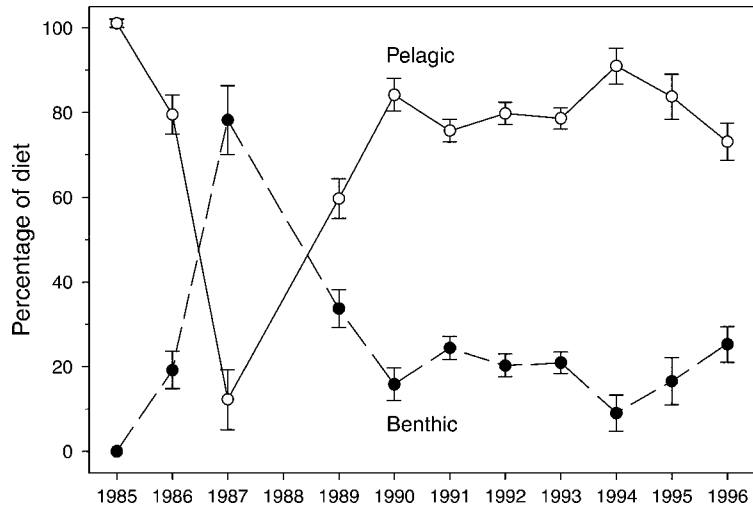


FIG. 6. Percentage of pelagic and benthic organisms in the diet of inland silversides (*Menidia beryllina*) between 1985 and 1996 (mean \pm SE).

shad abundance; however, $\delta^{13}\text{C}$ only differed between the second shad boom (2002–2004) and the shad-sparse years (1990–2001). Moreover, TotHg was lower during the first shad invasion (1986–1989) than the shad-sparse years, whereas it was higher during the 2002–2004 period. Other than prickly sculpin, bluegill was the most dependent upon benthic organisms when shad were rare. Thus the relative change in diet was not as dramatic as for silverside and bass, resulting in a less distinct change in both $\delta^{13}\text{C}$ signature and Hg concentrations. Additionally, the increase in bluegill benthic prey was driven by both chironomids and ostracods, as opposed to solely chironomids as noted in silverside and bass. Moreover, littoral invertebrates such as mayflies, hemipterans, and amphipods were less common in the bluegill diet during years of elevated shad densities, indicating that the greater reliance on profundal invertebrates may have dampened the benthic carbon isotope signal (Vander Zanden and Rasmussen 1999).

Threadfin shad are known for their ability to proliferate rapidly (Johnson 1970, Heidinger and Imboden 1974) and to reduce zooplankton abundance in lakes and ponds (DeVries et al. 1991). As shad grow, their foraging strategies change from visual feeding, focusing almost exclusively on zooplankton, to a more variable diet of zooplankton, phytoplankton, and detritus (Haskell 1959, Gerdes and McConnell 1963, Baker and Schmitz 1971). When targeting zooplankton, they particulate-feed on larger taxa and filter-feed on smaller species (Brooks 1968, Holanov and Tash 1978). This ability to use gill rakers to filter smaller plankton species is likely the principal mechanism by which shad decimate zooplankton communities. Bioenergetic studies on the ecologically similar gizzard shad *Dorosoma cepedianum* suggest that consumption rates of these clupeid species are more than sufficient to constrict zooplankton abundance in Clear Lake. Shepherd and

Mills (1996) estimated that during times of high zooplankton biomass (>100 mg/L DM), age 0 gizzard shad consumed ~ 50 mg DM of *Daphnia* per gram WM of shad per day. Using these figures, it is estimated that when threadfin shad biomass ranged from 2.11×10^6 to 6.62×10^7 g WM/ha in Clear Lake between 1987 and 1989, daily zooplankton consumption varied between 1.06×10^5 and 3.31×10^6 g DM/ha. Using a volume estimate for the entire lake of 1.43×10^7 m³ (Horne and Goldman 1972), the lake-wide mean zooplankton biomass (based on 1985 abundance data) was $\sim 4.00 \times 10^7$ g. These calculations overwhelmingly indicate that threadfin shad played a principal role in the change in zooplankton abundance and biomass in the lake, as well as the shift to smaller zooplankton species. In fact, at those consumption rates, the zooplankton resources alone should be unable to support the threadfin shad population. The fact that the shad remained in the lake continuously for at least four years suggests that they either had a lower consumption rate or that they subsidized their zooplankton consumption by feeding on phytoplankton and detritus. There is likely some validity to both explanations. Eagles-Smith et al. (2008) showed that shad in Clear Lake rely heavily on resources other than zooplankton, with both diet and stable isotope analyses indicating that phytoplankton and detritus make up a significant portion of their diet, particularly for larger fish (>70 mm).

Previous research on YOY largemouth bass in Clear Lake indicated a greater degree of piscivory (50–90%) than recent estimates of 17–60% (Eagles-Smith et al. 2008). When they examined bass foraging preferences by size class, Moyle and Holzhauser (1978) identified zooplankton (mainly *Daphnia* sp.) as the most important diet item for YOY largemouth bass. Diet from non-shad years in this study also indicate that zooplankton are of primary importance (Eagles-Smith et al. 2008), with

TABLE 2. ANCOVA models by fish species and size class: the effect of threadfin shad (*Dorosoma petenense*) abundance time periods on the pelagic and benthic energy reliance in inland silverside (*Menidia beryllina*), bluegill (*Lepomis macrochirus*), largemouth bass (*Micropterus salmoides*), and prickly sculpin (*Cottus asper*), using standard length as a covariate.

Species	Pelagic reliance				Benthic reliance			
	Effect of shad presence	F	df	P	Effect of shad presence	F	df	P
Silverside								
All sizes	decrease	25.16	1, 831	<0.0001	increase	12.41	1, 832	0.001
<36 mm	decrease	8.78	1, 194	0.003	increase	7.55	1, 198	0.007
37–60 mm	decrease	16.54	1, 424	<0.0001	increase	7.55	1, 425	0.007
>60 mm	no change	1.87	1, 204	0.173	no change	0.04	1, 204	0.85
Bluegill								
<75 mm	decrease	14.03	1, 212	<0.0001	increase	12.78	1, 212	<0.0001
Bass								
<115 mm	decrease	7.37	1, 346	0.007	no change	3.50	1, 346	0.06
Sculpin								
<48 mm	no change	0.74	1, 145	0.39	no change	0.32	1, 145	0.57

Notes: Benthic and pelagic reliance are the proportions of total diet classified as benthic or pelagic, derived from diet analyses. See Eagles-Smith et al. (2008) for classification details.

mainly chironomid larvae filling the void when shad were abundant.

Inland silversides are visual foragers, commonly preying upon on pelagic zooplankton species in Clear Lake (Wurtsbaugh and Li 1985). This general foraging strategy continued during this study, with *Bosmina* sp., *Daphnia pulex*, and various copepods as the major diet components (Eagles-Smith et al. 2008). Although benthic invertebrates such as chironomid midges are occasionally important prey items of silversides, most are consumed as emerging adults and not benthic larvae (Elston and Bachen 1976, Wurtsbaugh and Li 1985). In this study, when threadfin shad were absent from the lake 40% of the chironomids found in silverside stomachs were adults, whereas only 22% were adults when shad were present.

Although our results clearly show a strong relationship between threadfin shad abundance, benthic-pelagic energy reliance, and Hg bioaccumulation, it is notable that benthic chironomids actually had lower MeHg concentrations (0.044 ± 0.011 ppm DM) than zooplankton (0.059 ± 0.008 ppm DM) analyzed from the same times and locations (Suchanek et al. 2008c). It is intriguing that silverside and bass Hg concentrations increased in light of their dietary MeHg concentrations slightly decreasing. This discrepancy is likely the result of some combination of increased Hg exposure from sediment consumption and increased inorganic Hg (IoHg) exposure and assimilation associated with chironomid prey (Suchanek et al. 2008c). Other potential causal mechanisms such as reduced growth rate as well as cascading changes in zooplankton community structure and primary productivity do not appear to have occurred to an extent large enough to have driven these changes (C. A. Eagles-Smith, unpublished data).

Oaks Arm sediment MeHg concentrations range from ~ 0.002 to 0.020 ppm DM, whereas TotHg concentrations vary between ~ 10 and 400 ppm (Suchanek et al.

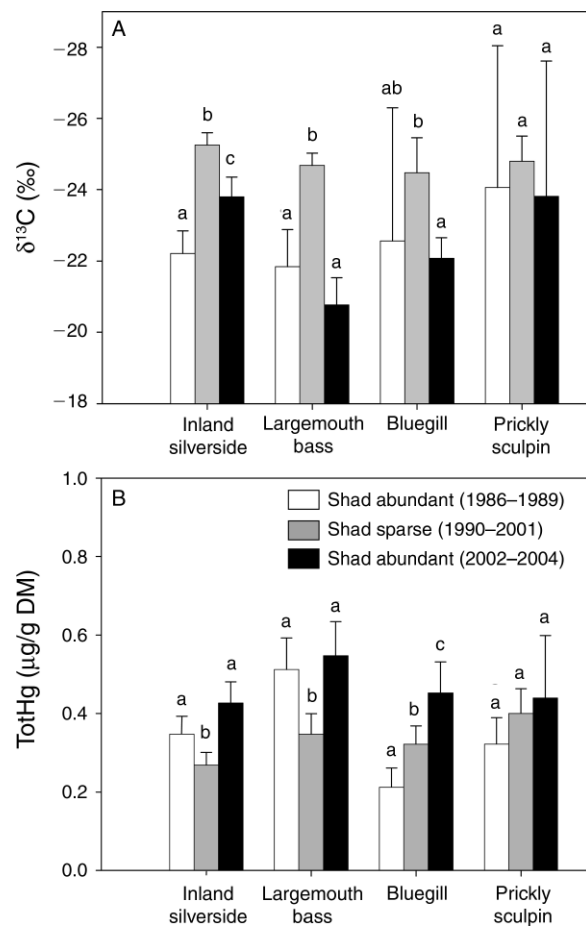


FIG. 7. (A) $\delta^{13}\text{C}$ and (B) total mercury (TotHg; DM, dry mass) concentrations in inland silversides (*Menidia beryllina*), largemouth bass (*Micropterus salmoides*), bluegill (*Lepomis macrochirus*), and prickly sculpin (*Cottus asper*) during periods when threadfin shad (*Dorosoma petenense*) were abundant vs. sparse or undetected. The error bars represent 95% confidence intervals. The lowercase letters above bars indicate statistical differences ($P < 0.05$) within species.

2008*b*). Moreover, TotHg concentrations in benthic prey from the Oaks Arm are one to two orders of magnitude greater than those in zooplankton (Suchanek et al. 2008*c*), indicating much higher IoHg burdens. The assimilation efficiency of MeHg from prey to predator ranges from 56% to 95%, whereas that of IoHg is ~10–27% (Wang and Wong 2003). Thus, a 10-fold increase in IoHg exposure, as is the case with a switch to benthic prey in Clear Lake, likely explains the elevated concentrations seen during the shad invasion. The rapid elimination of IoHg relative to MeHg (three to five times faster) is also consistent with the rapid reduction of concentrations upon resumption of zooplankton foraging (Trudel and Rasmussen 1997, Wang and Wong 2003). Limited data for silversides from Clear Lake indicate that the percentage of TotHg as MeHg is highly variable (20–60%) and the proportion of MeHg is relatively low in comparison to larger fish from the lake (Suchanek et al. 2008*d*).

Growth biodilution, the result of the biomass accretion increasing relative to Hg uptake (Stafford et al. 2004), is strongly related to growth rate in fishes regardless of the Hg species accumulated (Essington and Houser 2003, Simoneau et al. 2005). Foraging shifts commonly induce changes in fish growth rates with energy dynamics varying as a result of changes in either resource quality (Werner et al. 1983, Juanes and Conover 1994, Bowen et al. 1995) or energy use associated with seeking and handling alternate prey types (Mittelbach 1981). If the nutritional quality of alternative prey is lower, then to obtain equivalent caloric or nutritive intake the fish must increase their daily consumption rate or else exhibit a decrease in growth rate. Either mechanism could cause an increase in Hg concentrations in the fish. However, limited data suggest that the diet shifts in Clear Lake fishes accompanying the threadfin shad invasion did not appear to impact growth rates or body condition (C. A. Eagles-Smith, *unpublished data*). Caloric content of chironomids and zooplankton are likely not different enough (Wissing and Hasler 1971) to result in sufficiently drastic changes in fish growth rates such that Hg concentrations would fluctuate to the extent detected here. In addition, zoobenthos biomass is sufficiently high that it is unlikely there was a significant change in energy expended during foraging (Suchanek et al. 2008*c*).

Because Hg bioaccumulation ultimately originates at the basal trophic levels of a food web, variation in the standing biomass, productivity rate, or composition of lower trophic levels may cascade through the food web and result in alterations to the bioaccumulation rate in higher trophic level species (Allen et al. 2005). Algal bloom dilution is the negative correlation between phytoplankton density and mass-specific Hg burdens (Chen and Folt 2005). Phytoplankton can concentrate Hg to levels that are several orders of magnitude greater than in the surrounding water (Watras et al. 1998).

Assuming a finite supply of Hg, as cell density increases the total amount of Hg per cell will decrease (Pickhardt et al. 2002). This reduction in Hg concentration can then be propagated through the food web, as demonstrated by Chen and Folt (2005), who showed a clear link between chlorophyll concentrations and Hg concentrations in phytoplankton, zooplankton, and fish from 20 northeastern U.S. lakes. In the same study, Chen and Folt (2005) showed that zooplankton and fish Hg concentrations were also negatively correlated with zooplankton density, implicating zooplankton population growth rate and growth dilution as another potential driver. The structure of the zooplankton community may also significantly influence Hg bioaccumulation (Pickhardt et al. 2005). Many contaminant bioaccumulation studies lump zooplankton into a broad taxonomic grouping for analysis (Garcia and Carignan 1999) or merely analyze by size classes (Back et al. 2003). However, different zooplankton taxa may have variable Hg concentrations as a result of differences in foraging, growth rate, and ratios of surface area to volume (Kainz et al. 2002). Thus changes in zooplankton community structure may also explain some variability in fish Hg bioaccumulation.

The alkaline and highly eutrophic nature of Clear Lake, in addition to the chemical nature of the refractory cinnabar Hg source, is likely a major factor for the relatively low Hg concentrations seen in biota relative to other contaminated sites (Eagles-Smith et al. 2008, Suchanek et al. 2008*b, d*). Although the invasion of the threadfin shad significantly reduced zooplankton abundance and biomass, we did not see these effects cascade to the primary producers as indicated by algal cell densities (A. E. Colwell, *unpublished data*) or secchi depth (Suchanek et al. 2008*e*). Thus there is little indication that bloom dilution played a significant role in the variability of forage fish Hg concentrations between the shad and non-shad years. The shad invasion did, however, have a substantial impact on zooplankton community structure with relative increases in littoral (e.g., *Bosmina* sp.), small bodied (e.g., copepod nauplii), and evasive (e.g., cyclopoid copepods) species, whereas larger-bodied pelagic taxa such as *Daphnia* sp. decreased in abundance. Pickhardt et al. (2005) used mesocosm experiments to show that cladocerans such as *Daphnia* accumulated two to three times more MeHg than either calanoid or cyclopoid copepods in the same conditions, indicating that *Daphnia* may be a principal trophic conduit in pelagic Hg both because of their higher Hg concentrations and because of their susceptibility to fish predation. Assuming taxa-specific zooplankton Hg concentrations in Clear Lake followed this pattern, a reduction in pelagic Hg availability should have followed the shad invasion; thus it is unlikely that the shift in zooplankton species had much overall influence in the Hg concentrations in bluegill, largemouth bass, and silversides.

The effects of food web structure and foraging ecology on Hg bioaccumulation dynamics have been examined extensively (Wren and MacCrimmon 1986, Cabana and Rasmussen 1994, Vander Zanden and Rasmussen 1996, Doyon et al. 1998); however, we are aware of few instances in which this has been explicitly tied to food web changes resulting from nonnative species invasions (Kidd et al. 1999, Johnston et al. 2003, Swanson et al. 2003, 2006). Kidd et al. (1999) studied the introduction of piscivorous northern pike (*Esox lucius*) to two experimental lakes and found that while organochlorine contaminant concentrations in forage fish did not change between pre- and post-introduction levels in either lake, one of the lakes showed a significant decline in Hg concentrations in small fishes while stable isotope evidence pointed to a shift from pelagic zooplankton foraging to a heavy reliance on zoobenthos. A thorough treatment has also been given to the rainbow smelt (*Osmerus mordax*) invasion of the Hudson Bay drainage and its effects on Hg bioaccumulation in predatory (Vander Zanden and Rasmussen 1996, Johnston et al. 2003) and lower trophic level fish (Swanson et al. 2003, 2006). These studies found that, for the most part, the invasion caused very little change in fish Hg concentrations and suggested that compensation via changes in growth rate was the most probable reason.

Like these studies, our work provides a novel example of how invasion-induced shifts in food web structure can influence contaminant dynamics. However, the response in Clear Lake was notably different from those previously documented. Our data indicate that point source inorganic Hg loading and accumulation in benthic invertebrates drove an increase in TotHg concentrations of nearshore fishes that switched from pelagic to benthic diets, even though MeHg concentrations in zooplankton exceeded those of benthic prey items. Unlike the rainbow smelt studies, we did not detect any relationships between the shad invasion and shifts in either trophic position or growth rates of small fishes, which highlights the importance of understanding Hg loading and speciation dynamics in a system when examining bioaccumulation through trophic levels.

This study also provides a good example of resilience of food webs in lakes. After the shad population crashed, the food web structure quickly changed. This observation has implications for management and regulation of Hg in water bodies throughout the United States if the short-term plasticity of fish diets can result in dramatic fluctuations of fish Hg concentrations. These results suggest that regulations such as total maximum daily loads (TMDLs) for Hg should require a relatively robust characterization of trophic relationships of the taxa considered for regulation.

ACKNOWLEDGMENTS

We thank many colleagues for their dedicated field and laboratory assistance. We are especially grateful to Liz Vignola, Matt Fine, Rebekka Woodruff, Levi Lewis, Amanda Bern,

Patrick Crain, and Katie Small. Peter Green and Doug Nelson graciously provided access to analytical equipment and laboratory space. We thank Sudeep Chandra, Josh Ackerman, Dan Anderson, Patrick Crain, and Darell Slotton for many thoughtful discussions. We also thank Julie Yee, Karen Phillips, and two anonymous reviewers for suggestions that substantially improved the quality of the manuscript. This work was supported by the U.S. EPA-funded (R819658 and R825433) Center for Ecological Health Research at UC–Davis, U.S. EPA Region IX Superfund Program (68-S2-9005) to T. H. Suchanek, and UC Toxic Substances Research and Teaching Program (UC–Davis Lead Campus), UC–Davis block grant, and Jastro-Shields fellowships to C. A. Eagles-Smith. Although portions of this work have been funded fully or in part by the U.S. Environmental Protection Agency, it may not necessarily reflect the views of the Agency, and no official endorsement should be inferred. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. government.

LITERATURE CITED

- Allen, E. W., E. E. Prepas, S. Gabos, W. M. J. Strachan, and W. Zhang. 2005. Methyl mercury concentrations in macro-invertebrates and fish from burned and undisturbed lakes on the Boreal Plain. *Canadian Journal of Fisheries and Aquatic Sciences* 62:1963–1977.
- Alpers, C. N., M. P. Hunnerlach, J. T. May, and R. L. Hothem. 2005. Mercury contamination from historic gold mining in California. U.S. Geological Survey Fact Sheet 2005-3014. (<http://water.usgs.gov/pubs/fs/2005/3014/>)
- Back, R. C., P. R. Gorski, L. B. Cleckner, and J. P. Hurley. 2003. Mercury content and speciation in the plankton and benthos of Lake Superior. *Science of the Total Environment* 304:349–354.
- Baker, C. D., and E. H. Schmitz. 1971. Food habits of adult gizzard shad and threadfin shad in two Ozark reservoirs. *American Fisheries Society Special Publication* 8:3–11.
- Bowen, S. H., E. V. Lutz, and M. O. Ahlgren. 1995. Dietary protein and energy as determinants of food quality: trophic strategies compared. *Ecology* 76:899–907.
- Brooks, J. L. 1968. The effects of prey size selection by lake planktivores. *Systematic Zoology* 17:273–291.
- Cabana, G., and J. B. Rasmussen. 1994. Modeling food-chain structure and contaminant bioaccumulation using stable nitrogen isotopes. *Nature* 372:255–257.
- Chen, C. Y., and C. L. Folt. 2005. High plankton densities reduce mercury biomagnification. *Environmental Science and Technology* 39:115–121.
- Colborn, T., and K. Thayer. 2000. Aquatic ecosystems: harbingers of endocrine disruption. *Ecological Applications* 10:949–957.
- Compeau, G., and R. Bartha. 1985. Sulfate-reducing bacteria—principal methylators of mercury in anoxic estuarine sediment. *Applied Environmental Microbiology* 50:498–502.
- DeVries, D. R., R. A. Stein, J. G. Miner, and G. G. Mittelbach. 1991. Stocking threadfin shad: consequences for young-of-the-year fishes. *Transactions of the American Fisheries Society* 120:368–381.
- Doyon, J. F., R. Schetagne, and R. Verdon. 1998. Different mercury bioaccumulation rates between sympatric populations of dwarf and normal lake whitefish (*Coregonus clupeaformis*) in the La Grande complex watershed, James Bay, Quebec. *Biogeochemistry* 40:203–216.
- Dumont, H. J., I. Van de Velde, and S. Dumont. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia* 19:75–97.
- Eagles-Smith, C. A. 2006. Mercury in fish: food web structure, trophic transfer, and bioaccumulation in two California lakes. Dissertation. University of California, Davis, California, USA.

- Eagles-Smith, C. A., T. H. Suchanek, A. E. Colwell, and N. L. Anderson. 2008. Mercury trophic transfer in a eutrophic lake: the importance of habitat specific foraging. *Ecological Applications* 18(Supplement):A196–A212.
- Edmondson, W. T. 1959. *Fresh-water biology*. Second edition. John Wiley and Sons, New York, New York, USA.
- Elston, R. E., and B. Bachen. 1976. Diel feeding cycle and some effects of light on feeding intensity of the Mississippi silversides, *Menidia audens*, in Clear Lake, California. *Transactions of the American Fisheries Society* 105:84–88.
- Essington, T. E., and J. N. Houser. 2003. The effect of whole-lake nutrient enrichment on mercury concentration in age-1 yellow perch. *Transactions of the American Fisheries Society* 132:57–68.
- Fleming, E. J., E. Mack, P. G. Green, and D. C. Nelson. 2006. Mercury methylation from unexpected sources: molybdate-inhibited freshwater sediments and an iron-reducing bacterium. *Applied and Environmental Microbiology* 72:457–464.
- France, R. L. 1995. Differentiation between littoral and pelagic food webs in lakes using stable carbon isotopes. *Limnology and Oceanography* 40:1310–1313.
- Garcia, E., and R. Carignan. 1999. Impact of wildfire and clear-cutting in the boreal forest on methyl mercury in zooplankton. *Canadian Journal of Fisheries and Aquatic Sciences* 56:339–345.
- Gerdes, J. H., and W. J. McConnell. 1963. Food habits and spawning of the threadfin shad in a small desert impoundment. *Journal of the Arizona Academy of Science* 2:113–116.
- Goldstein, R. M., M. E. Brigham, and J. C. Stauffer. 1996. Comparison of mercury concentrations in liver, muscle, whole bodies, and composites of fish from the Red River of the North. *Canadian Journal of Fisheries and Aquatic Sciences* 53:244–252.
- Greenfield, B. K., T. R. Hrabik, C. J. Harvey, and S. R. Carpenter. 2001. Predicting mercury levels in yellow perch: use of water chemistry, trophic ecology, and spatial traits. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1419–1429.
- Hall, B. D., V. L. St. Louis, K. R. Rolfhus, R. A. Bodaly, K. G. Beaty, M. J. Paterson, and K. A. Peech Cherewyk. 2005. Impacts of reservoir creation on the biogeochemical cycling of methyl mercury and total mercury in boreal upland forests. *Ecosystems* 8:248–266.
- Hammerschmidt, C. R., M. R. Sandheinrich, J. G. Wiener, and R. G. Rada. 2002. Effects of dietary methylmercury on reproduction of fathead minnows. *Environmental Science and Technology* 36:877–883.
- Harris, R. C., and W. J. Snodgrass. 1993. Bioenergetic simulations of mercury uptake and retention in walleye and yellow perch. *Water Pollution Research Journal of Canada* 28:217–236.
- Haskell, W. L. 1959. Diet of the Mississippi threadfin shad, *Dorosoma petenense archafalayae*, in Arizona. *Copeia* 4:298–302.
- Heidinger, R., and F. Imboden. 1974. Reproductive potential of young-of-the-year threadfin shad (*Dorosoma petenense*) in southern Illinois lakes. *Transactions of the Illinois State Academy of Science* 67:397–401.
- Holanov, S. H., and J. C. Tash. 1978. Particulate and filter feeding in threadfin shad, *Dorosoma petenense*, at different light intensities. *Journal of Fish Biology* 13:619–625.
- Horne, A. J., and C. R. Goldman. 1972. Nitrogen fixation in Clear Lake, California. I. Seasonal variation and the role of heterocysts. *Limnology and Oceanography* 17:678–692.
- Jeppesen, D. B., and K. O. Winemiller. 2002. Structure of tropical food webs revealed by stable isotope ratios. *Oikos* 96:46–55.
- Johnson, J. E. 1970. Age, growth, and population dynamics of threadfin shad, *Dorosoma petenense*, in central Arizona reservoirs. *Transactions of the American Fisheries Society* 99:739–753.
- Johnston, T. A., W. C. Leggett, R. A. Bodaly, and H. K. Swanson. 2003. Temporal changes in mercury bioaccumulation by predatory fishes of boreal lakes following the invasion of an exotic forage fish. *Environmental Toxicology and Chemistry* 22:2057–2062.
- Juanes, F., and D. O. Conover. 1994. Rapid growth, high feeding rates, and early piscivory in young-of-the-year bluefish (*Pomatomus saltatrix*). *Canadian Journal of Fisheries and Aquatic Sciences* 51:1752–1761.
- Kainz, M., M. Lucotte, and C. C. Parrish. 2002. Methyl mercury in zooplankton—the role of size, habitat, and food quality. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1606–1615.
- Kidd, K. A., R. H. Hesslein, R. J. P. Fudge, and K. A. Hallard. 1995. The influence of trophic level as measured by delta-15N on mercury concentrations in freshwater organisms. *Water Air and Soil Pollution* 80:1011–1015.
- Kidd, K. A., M. J. Paterson, R. H. Hesslein, D. C. G. Muir, and R. E. Hecky. 1999. Effects of northern pike (*Esox lucius*) additions on pollutant accumulation and food web structure, as determined by $\delta^{13}C$ and $\delta^{15}N$, in a eutrophic and an oligotrophic lake. *Canadian Journal of Fisheries and Aquatic Sciences* 56:2193–2202.
- Lodge, D. M. 1993. Biological invasions: lessons for ecology. *Trends in Ecology and Evolution* 8:133–137.
- Macleod, M., T. E. McKone, and D. Mackay. 2005. Mass balance for mercury in the San Francisco Bay area. *Environmental Science and Technology* 39:6721–6729.
- Maruyama, A., Y. Yamada, B. Rusuwa, and M. Yuma. 2001. Change in stable nitrogen isotope ratio in the muscle tissue of a migratory goby, *Rhinogobius* sp., in a natural setting. *Canadian Journal of Fisheries and Aquatic Sciences* 58:2125–2128.
- Mason, R. P., J. M. Laporte, and S. Andres. 2000. Factors controlling bioaccumulation of mercury, methylmercury, arsenic, selenium, and cadmium by freshwater invertebrates and fish. *Archives of Environmental Contamination and Toxicology* 38:283–297.
- Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* 62:1370–1386.
- Moyle, P. B. 2002. *Inland fishes of California*. University of California Press, Berkeley, California, USA.
- Moyle, P. B., and N. Holzhauser. 1978. Effects of the introduction of the Mississippi silverside (*Menidia audens*) and Florida largemouth bass (*Micropterus salmoides floridanus*) on the feeding habits of young-of-year largemouth bass in Clear Lake, California. *Transactions of the American Fisheries Society* 107:574–582.
- Moyle, P. B., and T. Light. 1996. Fish invasions in California: Do abiotic factors determine success? *Ecology* 77:1666–1670.
- Moyle, P. B., and M. P. Marchetti. 2006. Predicting invasion success: freshwater fishes in California as a model. *BioScience* 56:515–524.
- OEHHA [California Office of Environmental Health Hazard Assessment]. 2006. Water bodies with fish consumption advisories. (www.oehha.ca.gov/fish/pdf/Adv_Map_2006.pdf)
- Pace, M. L., and J. D. Orcutt. 1981. The relative importance of protozoans, rotifers, and crustaceans in a freshwater zooplankton community. *Limnology and Oceanography* 26:822–830.
- Pennak, R. W. 1989. *Fresh-water invertebrates of the United States*. Third edition. John Wiley and Son, New York, New York, USA.
- Pickhardt, P. C., C. L. Folt, C. L. Chen, B. Klaue, and J. D. Blum. 2002. Algal blooms reduce the uptake of toxic methylmercury in freshwater food webs. *Proceeding of the National Academy of Sciences* 99:4419–4423.
- Pickhardt, P. C., C. L. Folt, C. Y. Chen, B. Klaue, and J. D. Blum. 2005. Impacts of zooplankton composition and algal enrichment on the accumulation of mercury in an experi-

- mental freshwater food web. *Science of the Total Environment* 339:89–101.
- Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83:703–718.
- Power, M., G. M. Klein, K. R. R. A. Guiguer, and M. K. H. Kwan. 2002. Mercury accumulation in the fish community of a sub-Arctic lake in relation to trophic position and carbon sources. *Journal of Applied Ecology* 39:819–830.
- Relyea, R. A. 2003. Predator cues and pesticides: a double dose of danger for amphibians. *Ecological Applications* 13:1515–1521.
- Rogers, D. W., T. A. Watson, J. S. Langan, and T. J. Wheaton. 1987. Effects of pH and feeding regime on methylmercury accumulation within aquatic microcosms. *Environmental Pollution* 45:261–274.
- Rosen, R. A. 1981. Length-dry weight relationships of some freshwater zooplankton. *Journal of Freshwater Ecology* 1:225–229.
- SAS Institute. 2002. JMP: the statistical discovery software. Version 5.0. SAS Institute, Cary, North Carolina, USA.
- Schindler, D. W. 1969. Two useful devices for vertical plankton and water sampling. *Journal of the Fisheries Research Board of Canada* 26:1948–1955.
- Shepherd, W. C., and E. L. Mills. 1996. Diel feeding, daily food intake, and *Daphnia* consumption by age-0 gizzard shad in Oneida Lake, New York. *Transactions of the American Fisheries Society* 125:411–421.
- Simoneau, M., M. Lucotte, S. Garceau, and D. Laliberte. 2005. Fish growth rates modulate mercury concentrations in walleye (*Sander vitreus*) from eastern Canadian lakes. *Environmental Research* 98:73–82.
- Snodgrass, J. W., C. H. Jago, A. L. Bryan, Jr., H. A. Brant, and J. Burger. 2000. Effects of trophic status and wetland morphology, hydroperiod, and water chemistry on mercury concentrations in fish. *Canadian Journal of Fisheries and Aquatic Sciences* 57:171–180.
- Stafford, C. P., B. Hanson, and J. A. Stanford. 2004. Mercury in fishes and their diet items from Flathead Lake, Montana. *Transactions of the American Fisheries Society* 133:349–357.
- StatSoft. 2005. STATISTICA. Version 7.1. StatSoft, Tulsa, Oklahoma, USA.
- St. Louis, V. L., J. W. M. Rudd, C. A. Kelly, R. A. Bodaly, M. J. Patterson, K. G. Beaty, R. H. Hesslein, A. Hayes, and A. R. Majewski. 2004. The rise and fall of mercury methylation in an experimental reservoir. *Environmental Science and Technology* 38:1348–1358.
- Suchanek, T. H., C. A. Eagles-Smith, and E. J. Harner. 2008a. Is Clear Lake methylmercury distribution decoupled from bulk mercury loading? *Ecological Applications* 18(Supplement):A107–A127.
- Suchanek, T. H., C. A. Eagles-Smith, D. G. Slotton, E. J. Harner, and D. P. Adam. 2008b. Mercury in abiotic matrices of Clear Lake, California: human health and ecotoxicological implications. *Ecological Applications* 18(Supplement):A128–A157.
- Suchanek, T. H., C. A. Eagles-Smith, D. G. Slotton, E. J. Harner, D. P. Adam, A. E. Colwell, N. L. Anderson, and D. L. Woodward. 2008c. Mine-derived mercury: effects on lower trophic species in Clear Lake, California. *Ecological Applications* 18(Supplement):A158–A176.
- Suchanek, T. H., C. A. Eagles-Smith, D. G. Slotton, E. J. Harner, A. E. Colwell, N. L. Anderson, L. H. Mullen, J. R. Flanders, D. P. Adam, and K. J. McElroy. 2008d. Spatiotemporal trends in fish mercury from a mine-dominated ecosystem: Clear Lake, California. *Ecological Applications* 18(Supplement):A177–A195.
- Suchanek, T. H., et al. 2003. Evaluating and managing a multiply stressed ecosystem at Clear Lake, California: a holistic ecosystem approach. Pages 1239–1271 in D. J. Rapport, W. L. Lasley, D. E. Rolston, N. O. Nielsen, C. O. Qualset, and A. B. Damania, editors. *Managing for healthy ecosystems*. Lewis, Boca Raton, Florida, USA.
- Suchanek, T. H., et al. 2008e. The legacy of mercury cycling from mining sources in an aquatic ecosystem: from ore to organism. *Ecological Applications* 18(Supplement):A12–A28.
- Swanson, H. K., T. A. Johnston, W. C. Leggett, R. A. Bodaly, R. R. Doucett, and R. A. Cunjak. 2003. Trophic positions and mercury bioaccumulation in rainbow smelt (*Osmerus mordax*) and native forage fishes in northwestern Ontario lakes. *Ecosystems* 6:289–299.
- Swanson, H. K., T. A. Johnston, D. W. Schindler, R. A. Bodaly, and D. M. Whittle. 2006. Mercury bioaccumulation in forage fish communities invaded by rainbow smelt (*Osmerus mordax*). *Environmental Science and Technology* 40:1439–1446.
- Thorpe, J. H., and A. P. Covich. 1991. *Ecology and classification of North American freshwater invertebrates*. Academic Press, New York, New York, USA.
- Trudel, M., and J. B. Rasmussen. 1997. Modeling the elimination of mercury by fish. *Environmental Science and Technology* 31:1716–1722.
- Vander Zanden, M. J., and J. B. Rasmussen. 1996. A trophic position model of pelagic food webs: impact on contaminant bioaccumulation in lake trout. *Ecological Monographs* 66:451–477.
- Vander Zanden, M. J., and J. B. Rasmussen. 1999. Primary consumer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and the trophic position of aquatic consumers. *Ecology* 80:1395–1404.
- Vander Zanden, M. J., and J. B. Rasmussen. 2001. Variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ trophic fractionation: implications for aquatic food web studies. *Limnology and Oceanography* 46:2061–2066.
- Wang, W., and R. S. K. Wong. 2003. Bioaccumulation kinetics and exposure pathways of inorganic mercury and methylmercury in a marine fish, the sweetlips *Plectorhinchus gibbosus*. *Marine Ecology Progress Series* 261:257–268.
- Watras, C. J., R. C. Back, S. Halvorsen, R. J. M. Hudson, K. A. Morrison, and S. P. Wentz. 1998. Bioaccumulation of mercury in pelagic freshwater food webs. *Science of the Total Environment* 219:183–208.
- Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540–1548.
- Wiener, J. G., and D. J. Spry. 1996. Toxicological significance of mercury in freshwater fish. Pages 297–339 in W. N. Beyer, G. H. Heinz, and A. W. Redmon-Norwood, editors. *Environmental contaminants in wildlife: interpreting tissue concentrations*. Lewis, Boca Raton, Florida, USA.
- Wiener, J. G., and T. H. Suchanek. 2008. The basis for ecotoxicological concern in aquatic ecosystems contaminated by historical mercury mining. *Ecological Applications* 18(Supplement):A3–A11.
- Wissing, T. E., and A. D. Hasler. 1971. Intraseasonal change in caloric content of some freshwater invertebrates. *Ecology* 52:371–373.
- Wren, C. D., and H. R. MacCrimmon. 1986. Comparative bioaccumulation of mercury in two adjacent freshwater ecosystems. *Water Research* 20:763–769.
- Wurtsbaugh, W., and H. Li. 1985. Diel migrations of a zooplanktivorous fish (*Menidia beryllina*) in relation to its prey in a large eutrophic lake. *Limnology and Oceanography* 30:565–576.
- Zar, J. H. 1999. *Biostatistical analysis*. Prentice-Hall, Upper Saddle River, New Jersey, USA.