

MERCURY TROPHIC TRANSFER IN A EUTROPHIC LAKE: THE IMPORTANCE OF HABITAT-SPECIFIC FORAGING

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Abstract. Mercury (Hg) trophic transfer and bioaccumulation in fish from a mine-impacted, eutrophic lake were examined in relation to foraging habitat, trophic position, and size. Diet analysis indicated that there were clear ontogenetic shifts in foraging habitats and trophic position. Pelagic diet decreased and benthic diet increased with increasing fish length in bluegill, black crappie, inland silverside, and largemouth bass, whereas there was no shift for prickly sculpin or threadfin shad. Stable carbon isotope values ($\delta^{13}\text{C}$) were inversely related to the proportion of pelagic prey items in the diet, but there was no clear relationship with benthic foraging. There were distinct differences between pelagic and benthic prey basal $\delta^{13}\text{C}$ values, with a range of approximately -28% in pelagic zooplankton to approximately -20% in benthic caddisflies. Profundal prey such as chironomid larvae had intermediate $\delta^{13}\text{C}$ values of approximately -24% , reflecting the influence of pelagic detrital subsidies and suppressing the propagation of the benthic carbon isotope signal up the food chain. Fish total mercury (TotHg) concentrations varied with habitat-specific foraging, trophic position, and size; however, the relationships differed among species and ages. When controlling for the effects of species, length, and trophic position, TotHg and $\delta^{13}\text{C}$ were positively correlated, indicating that Hg trophic transfer is linked to benthic foraging. When examined on a species-specific basis, TotHg was positively correlated with $\delta^{13}\text{C}$ only for bluegill, largemouth bass, and threadfin shad. However, diet-based multiple regression analyses suggested that TotHg also increased with benthic foraging for inland silverside and black crappie. In both species, benthic prey items were dominated by chironomid larvae, explaining the discrepancy with $\delta^{13}\text{C}$. These results illustrate the importance of foraging habitat to Hg bioaccumulation and indicate that pelagic carbon can strongly subsidize the basal energy sources of benthic organisms.

Key words: bioaccumulation; Clear Lake, California, USA; diet analysis; fish; food webs; foraging habitat; mercury; stable isotopes; Sulphur Bank Mercury Mine; trophic transfer.

INTRODUCTION

Over the last century there have been widespread increases in environmental mercury (Hg) contamination (Evans et al. 1972, Appelquist et al. 1985, Hakanson et al. 1988, UNEP 2003). In addition, recent studies have shown elevated Hg concentrations in fish from areas with low background levels and source inputs (Watras et al. 1995, Bodaly and Fudge 1999). These findings have generated significant concern regarding Hg risks to humans and wildlife (U.S. EPA 1997). In response, a relatively large body of literature has developed examining environmental, physiological, and ecological factors that drive Hg accumulation through food webs (Wiener and Spry 1996, Gorski et al. 1999, Allen et al.

2005). Methylmercury (MeHg) is generally acknowledged as the form of Hg that is of most concern due to its toxicity and propensity to biomagnify in food webs (Kidd et al. 1999). Thus there has been a strong focus on the limnological factors such as pH (Cope et al. 1990), hydroperiod (Bodaly and Fudge 1999, Snodgrass et al. 2000), dissolved organic carbon concentrations (Watras et al. 1998), degree of wetlands (Greenfield et al. 2001), and primary productivity rate (Pickhardt et al. 2002) that regulate MeHg production and entry into the food web. By controlling the input of MeHg to food webs, these variables play a strong role in determining Hg concentrations in fish; however, attributes of fish such as growth rate (Swanson et al. 2006) and age (Evans et al. 2005) are also influencing factors. Moreover, ecological properties such as trophic position of fish species and food web structure can dictate the degree of contamination (Cabana and Rasmussen 1994).

Once Hg enters a food web concentrations generally increase with trophic position, with top predators and older fish having the highest concentrations. Thus, the number of trophic levels in a system can be a strong

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indicator of bioaccumulation potential (Cabana and Rasmussen 1994). However, both within and among systems there can be considerable variation in the transfer of Hg from one trophic level to another. This suggests that there are inherent properties of food webs that affect Hg transfer. Food webs are extremely complex with extensive omnivory and a great deal of spatial and temporal variability (Winemiller 1990, Polis 1991, Lawler and Morin 1993, Dunne et al. 2002). They consist of a network of weak and strong trophic interactions (linkages) that vary both temporally and spatially (Dunne et al. 2002). The strength, density, and habitat specificity of linkages are factors likely to confound interpretations of Hg bioaccumulation because the magnitude of trophic transfer is in part dictated by source Hg concentrations and energetic strength of the trophic interaction. For example, habitat-specific foraging can expose various consumers to differential levels of contamination, particularly if one taxon has a strong linkage with prey that are more highly contaminated, resulting in a disparity in Hg concentrations in consumers occupying similar trophic positions (Power et al. 2002). This has been demonstrated with other contaminants (Stewart et al. 2004) and is likely an important mechanism for determining species- and habitat-specific accumulation risk.

The advent of stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes as tracers of energy flow in food webs has significantly improved our ability to understand ecosystem trophic dynamics (Petersen and Fry 1987, Cabana and Rasmussen 1996, Vander Zanden and Rasmussen 1999). Classic approaches using gut contents are valuable for providing taxonomic diet information or insight regarding diel feeding cycles. However, these approaches are limited in their applicability to understanding energy flow. Gut content analyses are biased towards recent prey, and unless a population is sampled extensively, they may reflect transient trends in prey abundance. They also provide only an analysis of prey consumed, but not necessarily assimilated. Moreover, there is substantial variability in the integrity of prey items in digestive tracts, and as a result, there can be a strong bias towards prey that decompose slowly or contain hard parts.

Carbon and nitrogen stable isotopes overcome some of these limitations and have been used as a robust way to model complex trophic dynamics (Jepesen and Winemiller 2002). Stable isotopes, however, rarely provide taxon-specific information about prey items. In addition, their proper use requires some general assumptions about tissue-specific and diet-consumer fractionation factors, which may not be as generally applicable as originally proposed (Goedkoop et al. 2006). Moreover, to detect differences in habitat-specific foraging, there must be a consistent disparity in the baseline carbon isotope signatures of the habitats (Vander Zanden and Rasmussen 1999). Because of weaknesses inherent in both diet and stable-isotope

studies, the two methods complement one another and when used together can provide a robust assessment of foraging relationships, trophic dynamics, and contaminant bioaccumulation.

This study examines Hg contamination in the food web of a eutrophic California lake, Clear Lake. The diet and isotope signatures of six abundant fish species were quantified, and their Hg concentrations were assessed relative to trophic position, foraging habitat, and size. Diet data were compared with isotope ratios to assess comparability between methods, with the a priori hypothesis that diet would better describe foraging habitat because benthic energy pathways are confounded by the Clear Lake's trophic status. Mercury concentrations were compared among fish species and size classes, and the following questions were asked: (1) Does Hg vary among fish species? (2) Are Hg concentrations related to foraging habitats? (3) How important is foraging habitat relative to fish size and trophic position in determining Hg concentrations in Clear Lake?

The results of this study are integrated with a larger ecosystem-based assessment of Hg loading, movement, and fate through Clear Lake's abiotic and biotic matrices. This study provides the linkage between MeHg entry at the base of the food web, through accumulation in higher trophic level fishes and piscivorous birds (Anderson et al. 2008). It also provides a foundation for understanding the relative importance of both foraging habitat and trophic position in the transfer of Hg through successive trophic levels. Moreover, the simultaneous use of two complementary methods (diet and stable isotopes) show that in eutrophic systems with strong benthic-pelagic coupling, benthic prey of fishes can be tightly linked to pelagic primary productivity.

METHODS

Site description

Clear Lake (39°00' N, 122°45' W) is a large (17 670 ha), shallow (6.5 m mean depth) lake located in the Coast Range of northern California, USA (Fig. 1). The lake is moderately alkaline (pH 7.5–8.5) and, despite its name, has likely been eutrophic to hyper-eutrophic since long before European settlers arrived (Osleger et al. 2008, Richerson et al. 2008). The lake is composed of three basins, each with its own distinct hydrological and limnological characteristics (Horne and Goldman 1972). Along the eastern shoreline of one of those basins, the Oaks Arm, resides the Sulphur Bank Mercury Mine, a large open-pit mine that was designated a U.S. Environmental Protection Agency (U.S. EPA) Superfund Site in 1990 and represents a significant point source for inorganic Hg input to the lake (Suchanek et al. 2008b).

Sample collections

Biannual (early summer and late fall) beach seines were conducted at two sites in the Oaks Arm (Fig. 1) from 1985 to 2004 using a 9.1 × 1.2 m beach seine with a 3.2-mm ace mesh. To increase the size range of some

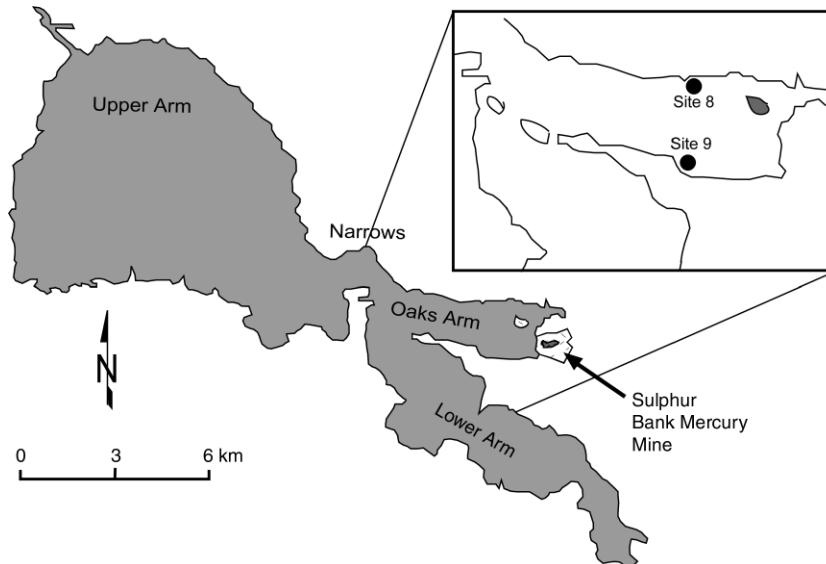


FIG. 1. Map of Clear Lake, California, USA. Solid circles in inset represent monitoring collection sites.

species collected, additional fish were taken in the same vicinity as the monitoring stations in 2000, 2001, and 2004 using a boat-mounted electroshocker. Standard length (SL) was measured to the nearest 1 mm on all captured fish. Fish collected for TotHg and stable-isotope analyses were immediately placed in polyethylene bags and frozen at -20°C until they were processed. Fish collected for diet analysis were immediately fixed in 10% formalin and later transferred to 70% ethanol until stomach contents were analyzed. An incision was made in the peritoneum of fish >100 mm SL to ensure rapid fixation of stomach contents. Phytoplankton, periphyton, benthic invertebrates, and zooplankton were collected for TotHg, MeHg, and stable-isotope analyses using methods outlined in detail in Suchanek et al. (2008c). Briefly, phytoplankton and zooplankton were collected with a Van Dorn water sampler (phytoplankton) and Nitex plankton net ($80\ \mu\text{m}$) at 18 locations in the Oaks Arm between 1992 and 2001. Periphyton was haphazardly scraped from the surfaces of rocks and tule stems (*Scirpus californicus*) along the shoreline in the Oaks Arm. Periphyton collections were from depths of <1 m and occurred on several occasions between 1997 and 2000. Littoral invertebrates were collected by hand from six sites in the Oaks Arm in 1993, 2000, and 2004. Chironomids were collected with a 15-cm Eckman dredge from 18 sites in the Oaks Arm between 1992 and 2004. Previous chironomid transect monitoring in Clear Lake indicated that chironomid densities peaked (10980 individuals/ m^2) near the shore in waters 2–3 m deep (A. E. Colwell, unpublished data). Moreover, the taxa were dominated almost entirely by those associated with profundal habitats, *Chironomus plumosus* and *Procladius* sp. (Merritt and Cummins 1996). As a result, chironomids in this study were classified as profundal unless they were identified as littoral species.

Gut content analysis

Dissected stomachs were opened and all contents washed into a gridded Petri dish. Each diet item was identified to the lowest possible taxon (family, genus, or species) using taxonomic keys (Edmondson 1959, Pennak 1989, Thorp and Covich 1991, Moyle 2002). Each prey item was enumerated, and for each taxon the proportion of total stomach content was determined on a volumetric basis. Prior to statistical analyses, all diet proportion data were arcsine square-root transformed (Zar 1999), and fish with empty stomachs were noted but excluded from analysis.

Each prey item was assigned to both a broad taxonomic classification (e.g., zooplankton, fish, benthic invertebrate, etc.), and primary habitat type based on published information for each taxa and/or observations in Clear Lake (Appendix A). Pelagic taxa were those residing in the water column, which forage on phytoplankton or planktivorous herbivores. Littoral taxa included those associated with shoreline substrate shallow enough for light penetration to support substantial benthic primary productivity. Profundal taxa were considered to inhabit the substrate at depths at which light penetration was not adequate to support primary productivity and basal energy sources are primarily derived from sedimentary detritus. Digestive processes often prevented identification of chironomids to resolutions lower than order or family. Thus, based on their abundance throughout the lake, most unidentifiable chironomids in fish guts were assumed to be profundal. When identification to lower resolutions was possible, chironomids were almost always profundal taxa. To estimate fish trophic position using diet data, each prey item was assigned a trophic position using literature-based trophic designations (Appendix A).

Trophic position of each fish was calculated using the following equation (Winemiller 1990):

$$TP_i = 1 + \sum_{j=1}^G DC_{ij} \times TP_j \quad (1)$$

where TP_i is the trophic position of the i th consumer, DC_{ij} is the proportion of prey j in the diet of consumer i , TP_j is the trophic position of prey j , and G is the number of diet groups for consumer i .

To facilitate interpretation of diet data and to account for ontogenetic changes in diet, length–frequency distributions were examined and each species was divided into size classes based on interpretation of those distributions (Eagles-Smith 2006). Linear regression was used to examine changes in diet proportion within size classes, and ANOVA was used to test differences between size classes.

Interpretations of proportional diet data are often heavily biased when simple means are examined (Bowen 1996), thus modified Costello diagrams (Amundsen et al. 1996) were developed for each species and size class. The Costello diagrams incorporate two key descriptive diet statistics, percentage of occurrence (number of stomachs containing diet item $j \div$ total number of stomachs $\times 100$) and prey-specific abundance (mean percentage of volume of diet item j for those individuals with diet item j in stomachs). The graphical representation of these two metrics indicates degree of specialization and prey item importance.

Stable-isotope analysis

Prior to stable-isotope analysis, skinless axial muscle samples were dissected from all fish >100 mm SL, and smaller fish were decapitated, eviscerated, and their skin and scales removed. Invertebrates were separated from detritus and sorted to the lowest identifiable taxon. All samples were rinsed in deionized water, blotted dry, and weighed to the nearest 0.001 g. Samples were dried at 60°C for 48 h or until a constant mass was achieved. Each sample was then reweighed, ground to a fine powder, 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, UK) at the University of California, Davis Stable Isotope Facility. Approximately 0.80–1.60 mg of tissue were weighed and sealed into tin capsules. Sample combustion to CO_2 and N_2 occurred at 1000°C in an inline elemental analyzer. A Carbosieve G column separated the gas before introduction into the IRMS. Standards (PeeDee Belemnite for $\delta^{13}C$ and N_2 gas for $\delta^{15}N$) were injected directly into the IRMS before and after sample peaks. Isotope ratios are expressed in per mil (‰) notation. Using $\delta^{13}C$ as an example, ratios are defined by the following equation:

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

Evaluation of stable-isotope signatures in food webs

can be confounded by variability in signatures at the base of the food webs (Vander Zanden and Rasmussen 1999, Post 2002), resulting in difficulty comparing values (particularly $\delta^{15}N$) across habitats. Because there were no differences in primary consumer $\delta^{15}N$ values among habitats in Clear Lake, we used the trophic position model below, developed by Cabana and Rasmussen (1996) to estimate trophic position with $\delta^{15}N$:

$$TP = (\delta^{15}N_{\text{fish}} - \delta^{15}N_{\text{pc}}) / 3.4 + 2$$

where TP is the trophic position, $\delta^{15}N_{\text{fish}}$ is the nitrogen isotope ratio in fish, $\delta^{15}N_{\text{pc}}$ is the nitrogen isotope ratio in primary consumers (snails, clams, zooplankton), and 3.4 represents the stepwise trophic fractionation of $\delta^{15}N$.

Mercury determination

Total Hg concentrations were determined on dried samples prepared as above via cold-vapor atomic absorption spectroscopy (CV-AAS) using either a CETAC M-6100 analyzer (CETAC Technologies, Omaha, Nebraska, USA) or a Milestone DMA-80 analyzer (Milestone, Monroe, Connecticut, USA). For the CETAC analyzer, ~ 0.050 g of sample was weighed into a borosilicate glass culture tube followed by the addition of a 2:1 solution of concentrated sulfuric and nitric acids. Samples were then digested at 95°C under pressure for 1 h, followed by 2 h of oxidation via the addition of a 5% $KMnO_4$ and 5% K_2SO_8 solution. Upon cooling, a 10% hydroxylamine hydrochloride, 10% sodium chloride solution was added and the samples were brought to volume with Milli-Q deionized water (Millipore, Billerica, Massachusetts, USA). The samples were then analyzed by CV-AAS using stannous chloride as the reductant. For the Milestone DMA-80, ~ 0.05 g of ground sample was weighed into a nickel boat, and the sample was analyzed following U.S. EPA method 7470, decomposition via combustion followed by gold amalgamation coupled with CV-AAS.

For both methods quality assurance methods included analysis of 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 $99.2\% \pm 1.8\%$ (mean \pm SE; $N = 106$), whereas recoveries for matrix spikes averaged $101.7\% \pm 3.2\%$ ($N = 89$). Relative percentage of deviation (RPD) averaged 3.2% for duplicates and 5.2% for matrix spike duplicates. Analysis of MeHg was conducted by Battelle Marine Science Laboratory (Sequim, Washington, USA) using gas chromatography and cold-vapor atomic fluorescence detection as described in Suchanek et al. (2008c).

Statistical analyses

Prior to analysis, data were examined to ensure the underlying distributions met the assumptions of the

TABLE 1. Slope direction, correlation, and P value for linear regression models examining the relationship between fish length and habitat-specific prey for six species in Clear Lake, California, USA.

Variable (%)	Slope direction	R^2	P
Bluegill			
Pelagic diet	negative	0.13	<0.0001
Littoral diet	positive	0.32	<0.0001
Profundal diet	none	0.01	0.07
Black crappie			
Pelagic diet	negative	0.49	<0.0001
Littoral diet	positive	0.07	0.03
Profundal diet	positive	0.06	0.03
Fish	positive	0.27	<0.0001
Inland silverside			
Pelagic diet	negative	0.07	<0.0001
Littoral diet	positive	0.03	<0.0001
Profundal diet	positive	0.08	<0.0001
Largemouth bass			
Pelagic diet	negative	0.08	<0.0001
Littoral diet	negative	0.09	<0.0001
Profundal diet	Positive	0.0002	0.75
Fish	None	0.09	<0.0001
Prickly sculpin			
Pelagic diet	none	0.005	0.39
Littoral diet	none	0.02	0.07
Profundal diet	none	0.006	0.36
Threadfin shad			
Pelagic diet	none	0.07	0.0009
Littoral diet	negative	0.002	0.61
Profundal diet	none	0.003	0.52

parametric models. Mercury data were natural-log transformed, and diet proportions were arcsine square-root transformed. Analysis of variance (ANOVA), analysis of covariance (ANCOVA), and linear regression were used to examine the influence of species and size on diet composition. The ANCOVA and multiple regression analyses were used to examine the effects of species, size, trophic position, and habitat-specific diet on Hg concentrations. An information theoretic approach, Akaike's Information Criterion (AIC), was used to select the most parsimonious model from an a priori candidate set for explaining Hg concentrations in Clear Lake fish. This method seeks parsimony between the variation explained and the complexity of the various models such that spurious results may be minimized (Burnham and Anderson 2002).

A systematic, stepwise AIC approach was used whereby the first step consisted of comparing 34 candidate models. These models included all possible main-effects combinations of species, trophic position, habitat-specific foraging (percentage of pelagic reliance), and standard length, as well as interactions between species and each covariate, and a null model (intercept and variance only; Appendix D). The AIC values were calculated using ANCOVA and multiple regression in JMP version 5.01 (SAS Institute 2002). The importance of all interactions in the top model complicated

interpretations of main effects; therefore, a second step included separate AIC analyses for each species. In this step, only main effects were assessed since species was no longer a factor, resulting in eight candidate models per species containing all possible combinations of trophic position, pelagic reliance, and length, and the null model (Appendix E). Finally, because of the nonlinear responses in diet with age, each species was evaluated separately by life stage (juvenile and adult) using the same candidate models described above (Appendix E).

The AIC_c was used as a sample size corrected AIC value, and the model with the lowest AIC_c value was considered the most parsimonious (Burnham and Anderson 2002). The difference between each model's AIC_c and that of the best model, ΔAIC_c , was calculated for model ranking, and models were considered for biological importance when $\Delta\text{AIC}_c \leq 2$ (Anderson et al. 2001). Akaike weights were used to assess each model's probability of being the Kullback-Leibler best model in the set of models considered (Burnham and Anderson 2002). Variable importance was assessed using variable weights, which were determined by summing Akaike weights across all models incorporating the same variable (Ackerman et al. 2007).

RESULTS

Gut contents

Bluegill.—Bluegill ranged in size from 11 to 130 mm SL (mean = 56 mm; $n = 274$). The importance of pelagic organisms decreased and littoral organisms increased in the diet with fish size, and there was no relationship between profundal prey and fish size (Table 1). When corrected for year, size class had a significant effect on pelagic (ANOVA, $F_{2,262} = 24.78$; $P < 0.001$), littoral (ANOVA, $F_{2,262} = 33.70$; $P < 0.001$), and profundal (ANOVA, $F_{2,262} = 4.94$; $P = 0.007$) diet. Fish <45 mm SL consumed a roughly equal mix of pelagic and benthic prey, with profundal taxa (primarily Chironomidae), accounting for nearly all zoobenthos. Fish >45 mm switched to a more benthos-dominated diet (Fig. 2). The proportion of *Daphnia* sp. in bluegill diets did not change with size, thus the reduction in pelagic diet items was driven mainly by diminished selection of smaller zooplankton, such as *Bosmina* sp., *Eurycercus* sp., and Cylcopoida (Appendix B, Fig. 3). The benthic diet for the larger bluegill size classes shifted from profundal to littoral dominance (Fig. 2), with amphipods (*Hyallela azteca*) becoming the dominant prey item (Appendix B, Fig. 3). The Costello diagrams (Fig. 3) agreed closely with the mean proportion data (Appendix B, Fig. 3) and indicated a progressive increase in littoral prey as fish grow, although prey-specific abundance changed little. Except for the littoral prey of <45 mm bluegill, relationships between diet and length within size class were fairly weak or nonsignificant ($P > 0.05$) for all prey and size class combinations (Table 2), suggesting that in general, ontogenetic diet shifts occur between and not within size classes.

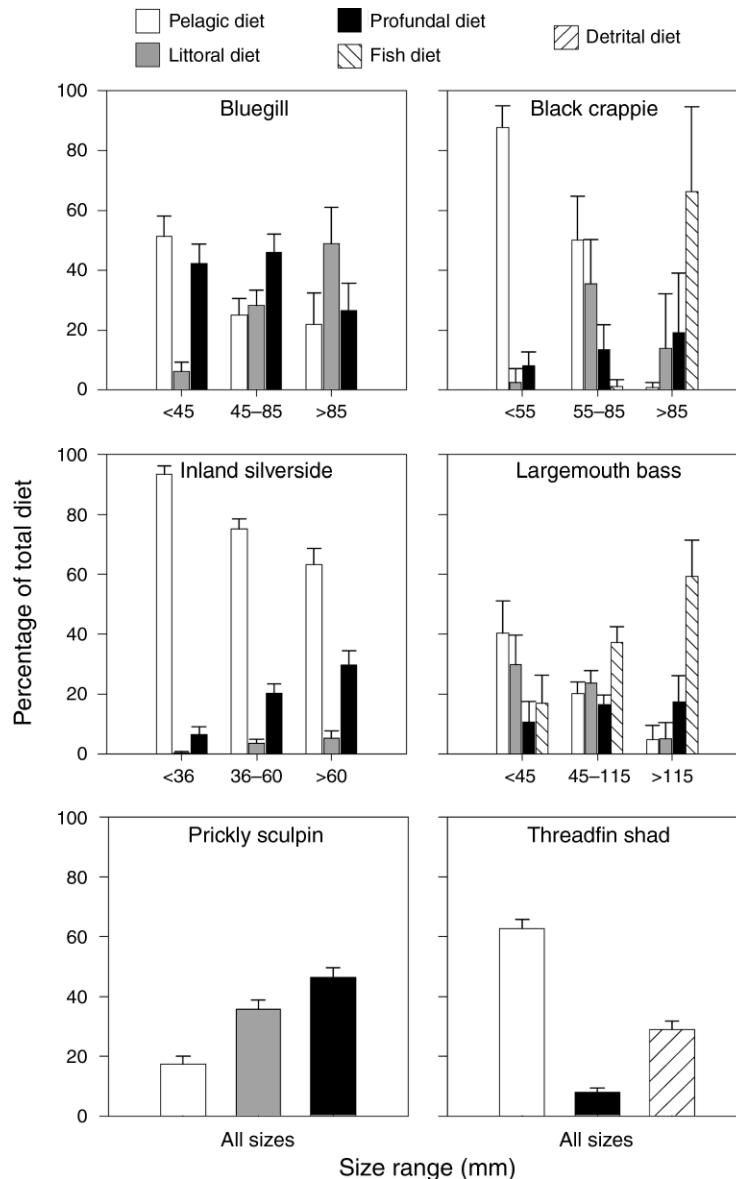


FIG. 2. Mean habitat-specific diet by size class in six fish species from Clear Lake derived from stomach content analysis. Error bars represent 95% confidence intervals.

Black crappie.—Black crappie ranged in size from 17 to 195 mm SL (mean = 64 mm; $n = 72$). Foraging patterns shifted significantly with length, particularly for pelagic and fish prey (Table 1). Black crappie <55 mm were almost solely pelagic foragers (Fig. 2), with *Daphnia* sp. and *Bosmina* sp. representing the majority of the diet (Appendix B, Fig. 3). Fish 55–85 mm consumed nearly equal proportions of pelagic and benthic prey (Fig. 2). For these intermediate-sized fish, benthic prey were mostly littoral invertebrates, including Baetidae, Corixidae, and amphipods, whereas profundal diet items were almost exclusively Chironomidae (Appendix B, Fig. 3). Other fish, mainly inland silverside,

were important prey for crappie >85 mm (Figs. 2 and 3). There were no relationships between fish prey and length within any size classes. However, pelagic foraging was negatively correlated with size within the small and intermediate size classes, and profundal and littoral foraging reliance increased within the small and intermediate size classes, respectively (Table 2).

Inland silverside.—Inland silversides ranged in size from 18 to 84 mm SL (mean = 49 mm; $n = 839$). Although linear regression models explained <10% of the variance in diet, there was a significant negative correlation between length and proportion of pelagic prey and significant positive correlations between length

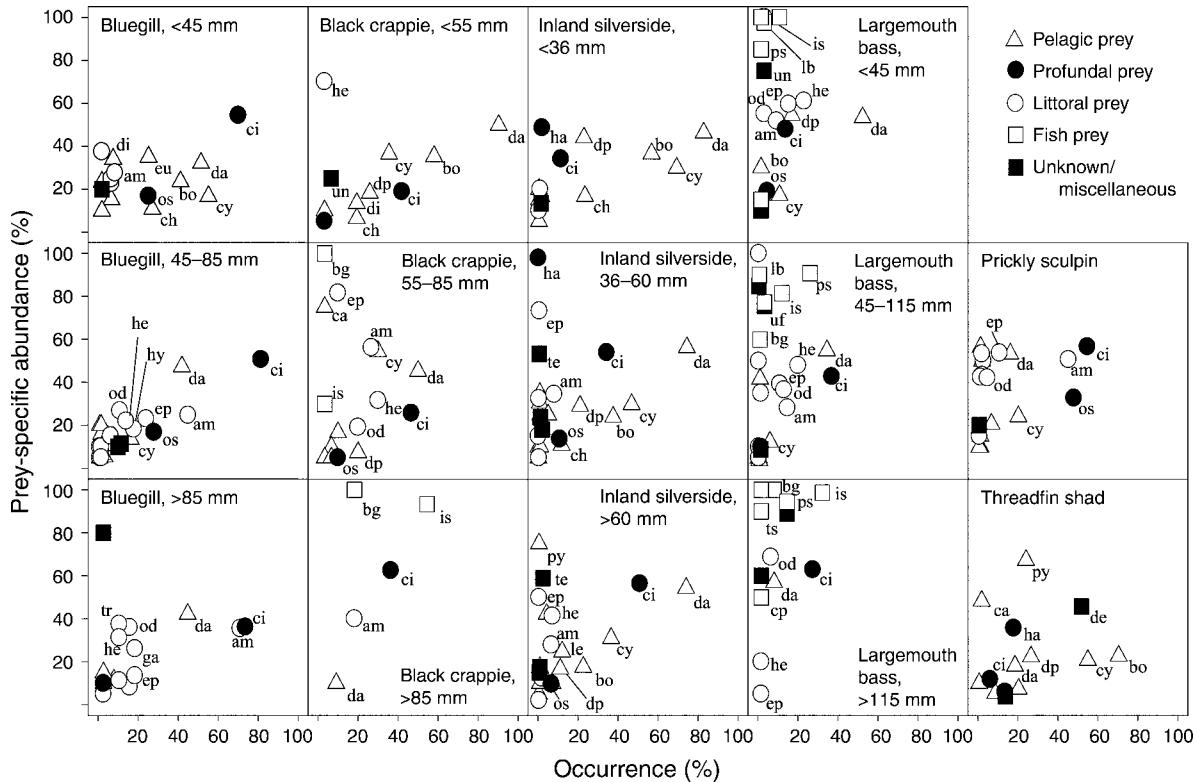


FIG. 3. Modified Costello diagrams for six fish species from Clear Lake. Specific diet items are represented with the following codes: am, amphipod; bg, bluegill; bo, *Bosmina*; ca, *Chaoborus*; ch, Chydoridae; ci, chironomids; cp, common carp; cy, cyclopid; da, *Daphnia*; de, detritus; di, *Diacyclops*; dp, *Diaptomus*; ep, Ephemeroptera; eu, *Eurycercus*; ga, gastropods; ha, Harpacticoida; he, Hemiptera; hy, Hydracarina; is, inland silverside; lb, largemouth bass; le, Leptodora; od, Odonata; os, ostracod; ps, prickly sculpin; py, phytoplankton; te, terrestrial; ts, threadfin shad; tr, Trichoptera; uf, unidentified fish; un, unknown.

TABLE 2. Regression of relationship between standard length and habitat-specific prey for four species of fish, within size classes.

Size class	Bluegill			Black crappie			Inland silverside			Largemouth bass		
	Slope	R^2	P	Slope	R^2	P	Slope	R^2	P	Slope	R^2	P
Pelagic												
Small	+	0.06	0.01	-	0.15	0.03	-	0.04	0.004	-	0.27	< 0.0001
Medium	0	0.0004	0.82	-	0.23	0.01	0	0.002	0.35	0	0.0001	0.87
Large	0	0.0061	0.64	0	0.16	0.17	0	0.001	0.67	0	0.05	0.08
Littoral												
Small	+	0.18	< 0.0001	0	0.01	0.65	0	0.01	0.25	+	0.21	< 0.0001
Medium	+	0.07	0.004	+	0.23	0.01	0	0.01	0.07	-	0.1	< 0.0001
Large	0	0	0.98	0	0.02	0.64	0	0.001	0.67	0	0.06	0.14
Profundal												
Small	0	0.01	0.27	+	0.26	0.003	+	0.08	< 0.001	0	0.02	0.22
Medium	+	0.04	0.02	0	0.01	0.57	0	0.001	0.51	0	0.01	0.16
Large	0	0.01	0.57	0	0.15	0.19	0	0.001	0.59	-	0.1	0.01
Fish												
Small	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0	0.005	0.55
Medium	N/A	N/A	N/A	0	0.01	0.65	N/A	N/A	N/A	+	0.04	0.002
Large	N/A	N/A	N/A	0	0.04	0.49	N/A	N/A	N/A	0	0.05	0.09

Notes: The abbreviation "N/A" means that data were not available. Values in boldface correspond to slopes that are significantly different from zero.

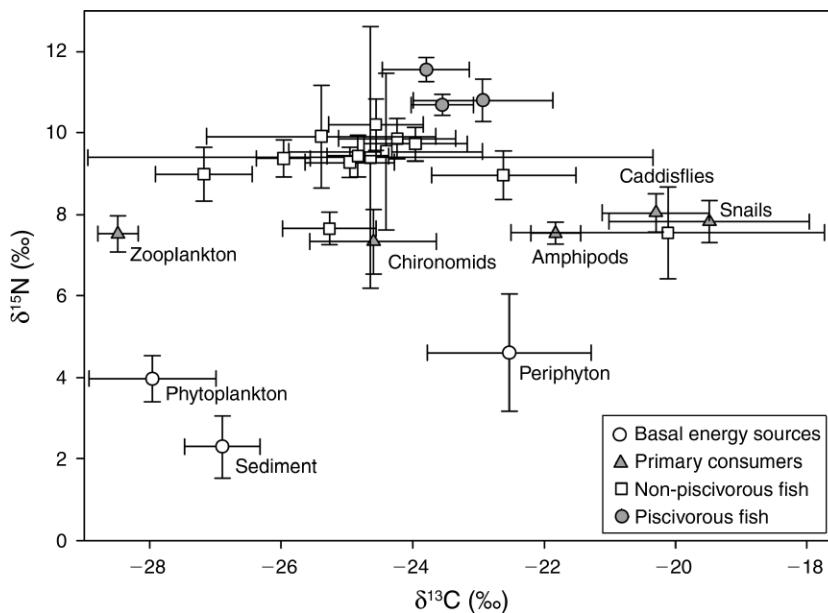


FIG. 4. Stable-isotope biplot of Clear Lake food web. Error bars represent 95% confidence intervals.

and proportions of both littoral and profundal diet items (Table 1). Pelagic prey items made up the majority of silverside diets regardless of size class. However, each successive size class consumed less pelagic prey and more profundal prey, mainly chironomid larvae (Fig. 2). As with bluegill, the proportion of *Daphnia* sp. in silverside diets was not related to size, and the primary reason reliance on pelagic prey declined was a reduction of small-bodied zooplankton prey (Fig. 3). There were no strong relationships between diet and length within size classes (Table 2).

Largemouth bass.—Largemouth bass ranged in size from 17 to 303 mm SL (mean = 80 mm; $n = 411$). Pelagic and littoral prey decreased and fish prey increased with bass size; however, length explained <10% of the variability in diet (Appendix B, Fig. 3). Diet of bass <45 mm contained a roughly equal proportion of pelagic and benthic prey items, with most of the benthic prey littoral in origin (Fig. 2, Appendix B). Substantial piscivory (mean ~ 40%) first occurred in the 45–115 mm size class; however, even fish <45 mm consumed some fish (Fig. 2). Regardless of size class, fish exhibiting piscivory generally did so to the exclusion of all other prey types (Fig. 3). Correlations within size class between SL and diet were substantial for the young-of-year (YOY) fish (<115 mm). Bass <45 mm rapidly increased their littoral forage while decreasing pelagic diet, and 45–115 mm bass substituted fish for littoral prey (Table 2).

Prickly sculpin.—Prickly sculpin ranged in size from 19 to 48 mm SL (mean = 30 mm; $n = 148$). Diet was not correlated with length for any habitat-specific prey classification (Table 1), and sculpin diets were dominat-

ed by benthic prey, composed of nearly equal proportions littoral and profundal taxa (Fig. 2). Profundal diet was dominated by chironomids and ostracods, and littoral diet was almost completely composed of amphipods (Appendix B, Fig. 3).

Threadfin shad.—Threadfin shad ranged in size from 21 to 105 mm SL (mean = 44 mm; $n = 162$). Shad were primarily pelagic foragers on small zooplankton (*Bosmina* sp. and *Cyclops* sp.). Phytoplankton also contributed a considerable proportion to the total diet (Fig. 3).

Stable isotopes

The δ¹³C ratios of basal energy sources in the Clear Lake food web diverged significantly between pelagic and littoral habitats, with a mean value of -22‰ in periphyton and -28‰ in phytoplankton (Fig. 4). Representative primary consumers from each habitat type (zooplankton, pelagic; amphipods, snails, and caddisflies, littoral) reflected the δ¹³C signature of their assumed diet; however, profundal invertebrates (chironomids) occupied an intermediate position between pelagic and benthic δ¹³C values (Fig. 4). The δ¹³C values of secondary and tertiary consumers were not well differentiated from one another, indicating either a fairly high degree of overlap in habitat-specific prey or a heavy reliance on profundal resources. The δ¹⁵N values ranged from a mean of 0.5‰ in *Gleotrichia* sp. to nearly 12.0‰ in piscivores, and baseline values (habitat-specific primary consumers) did not differ among habitats (ANOVA, $F_{2,63} = 0.82$; $P = 0.44$).

The stable-isotope ratios in fish agreed relatively well with the diet data for pelagic foragers. The δ¹³C values decreased with increasing percentage of pelagic diet (R^2

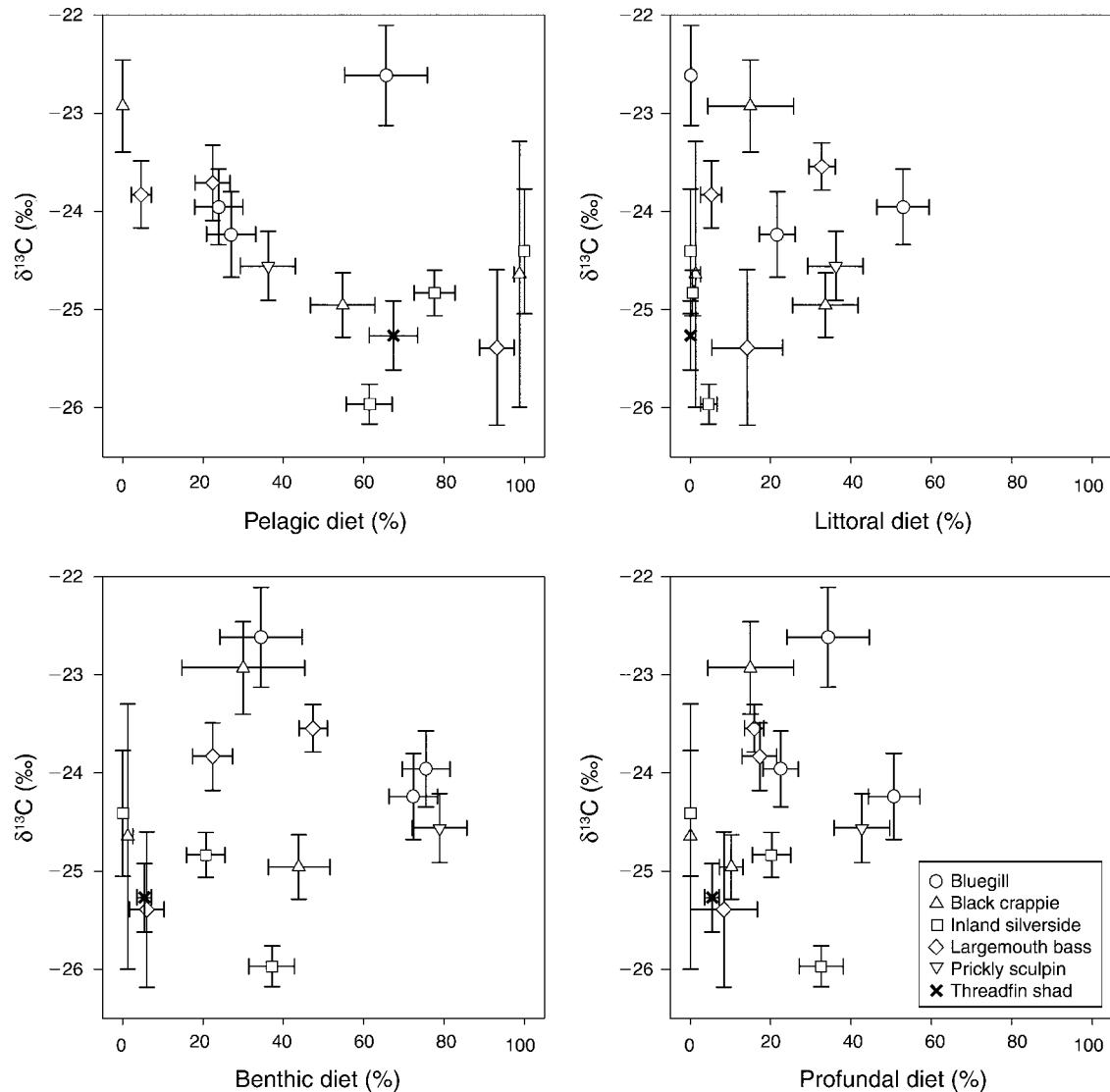


FIG. 5. Relationship between $\delta^{13}\text{C}$ values and habitat-specific diet resources (mean \pm SE) in six species of fish in Clear Lake. Benthic diet represents littoral and profundal items combined.

= 0.47, Fig. 5), indicating a greater reliance on benthic diet items associated with enriched carbon isotope values. However, the relationship between $\delta^{13}\text{C}$ and benthic diet was equivocal. Visually there appeared to be a trend toward increasing $\delta^{13}\text{C}$ values with increasing littoral and profundal diet; however, linear regressions showed no significant relationships ($P > 0.05$) between diet-based benthic foraging and stable carbon isotope ratios (littoral, $R^2 = 0.05$; profundal, $R^2 = 0.08$; total benthic, $R^2 = 0.04$; Fig. 5). The $\delta^{15}\text{N}$ and diet-based trophic position models had a strong linear correlation with one another ($R^2 = 0.93$). The slope of the relationship between the two (0.95) suggests that the assumed trophic enrichment value (3.4‰) adequately described the fractionation of $\delta^{15}\text{N}$ with trophic position. However, the regression intercept (-0.44)

indicates that the isotope-based index was nearly half a trophic level less than the diet-based estimates.

Mercury

Mercury concentrations varied dramatically across taxa, differing by three orders of magnitude from primary producers to adult largemouth bass (Fig. 6, Appendix C). Trophic position as indicated by $\delta^{15}\text{N}$ ratios was a strong predictor of Hg concentrations for all taxa combined ($R^2 = 0.89$, $P < 0.001$; Fig. 7); however, there was substantial variability within species. Mercury concentration also varied by foraging habitat, as indicated by both diet data and $\delta^{13}\text{C}$. Mercury concentrations increased with degree of littoral, profundal, and total benthic foraging and decreased with pelagic diet (Fig. 8). This pattern is

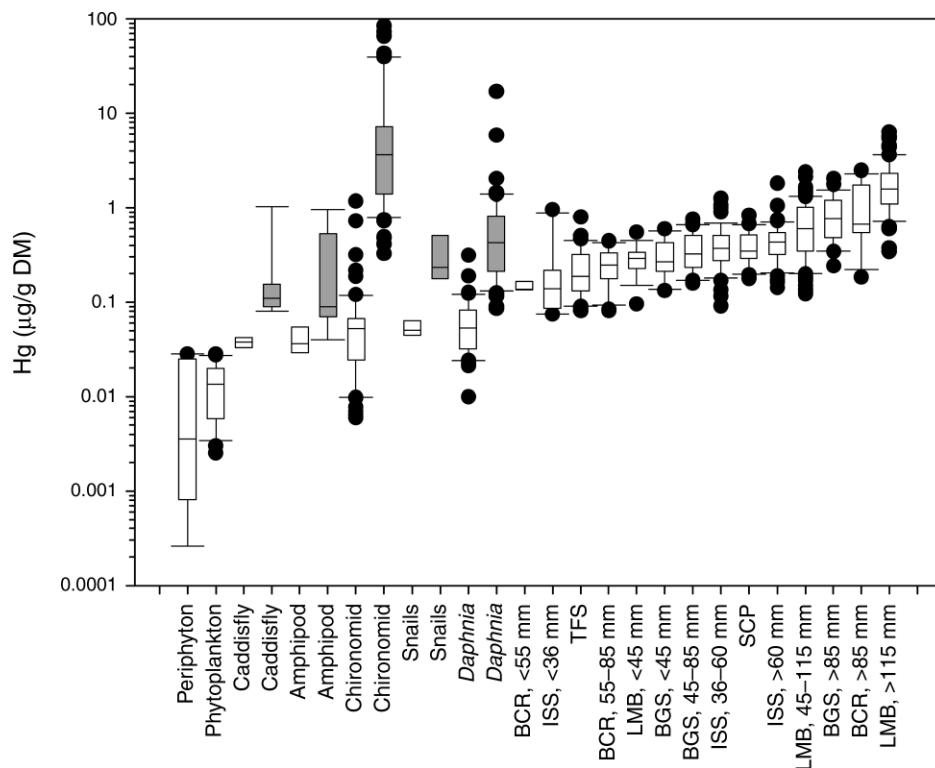


FIG. 6. Boxplots of mercury concentrations in the Clear Lake food web. Upper and lower box boundaries represent the 25th and 75th percentiles, and the center box line represents median values. Whiskers represent 10th and 90th percentiles. Open boxes for periphyton, phytoplankton, caddisfly, amphipod, chironomid, snails, and *Daphnia* are methylmercury (MeHg) concentrations, and gray boxes are total mercury (TotHg) concentrations. All fish values are TotHg concentrations (DM, dry mass). Species abbreviations are: BGS, bluegill; BCR, black crappie; ISS, inland silverside; LMB, largemouth bass; SCP, prickly sculpin; TFS, threadfin shad.

corroborated by $\delta^{13}\text{C}$, showing a significant positive correlation with Hg concentrations (Fig. 9).

Using an information theoretic approach (AIC), the most parsimonious model explaining Hg concentrations in Clear Lake fishes included species, trophic position, pelagic reliance, and length as main effects. This model clearly provided the best fit relative to the others in the candidate set as indicated by the next lowest ΔAIC value of 12.00 (Appendix D). However, the top model also included interaction terms between species and all three covariates, suggesting that each covariate differed among species with respect to its effect on fish Hg concentrations (Appendix D). Post hoc AIC analysis conducted for each species showed that the structure of the most parsimonious models varied among species (Appendix E), and length was the only factor that was consistently included in each model. Because ontogenetic changes in diet often were not linear and dynamics and retention time of Hg likely differ among different-aged fish, separate AIC analyses were conducted on young and adult fish for each species.

Black crappie.—For all black crappie the top model explaining Hg concentrations contained pelagic reliance and length as factors and, based on evidence ratios, was >2.8 times as likely as the next best model, which

included only length and had a ΔAIC value of 1.99 (Appendix E: Table E1). Variable weights were used to assess the importance of each factor, and the results indicate that across their entire size range, length (99%) was clearly the most important factor, followed by pelagic reliance (69%) and trophic position (28%). The top model for young-of-year fish (<85 mm) included both trophic position and length. The next best model, which included only length, had a ΔAIC value of 0.71. The addition of trophic position to length in the multiple regression model increased the R^2 from 0.21 to 0.30. In adult crappie (>85 mm) length alone accounted for 59% of the variability in Hg concentrations, and neither trophic position nor pelagic reliance substantially improved model fit. No other candidate models had ΔAIC values less than 2.00, and the next best model, which added pelagic reliance to length, had a ΔAIC of 2.50 and was 3.5 times less likely than the top model.

Bluegill.—For all ages of bluegill, the most parsimonious model included trophic position and length and had an R^2 value of 0.51 (Table 3). The only other competing model in the candidate set added pelagic reliance as a factor and had a ΔAIC value of 1.41 (Appendix E: Table E2). The difference in log-likelihood values of these two models was only 0.45, and there was

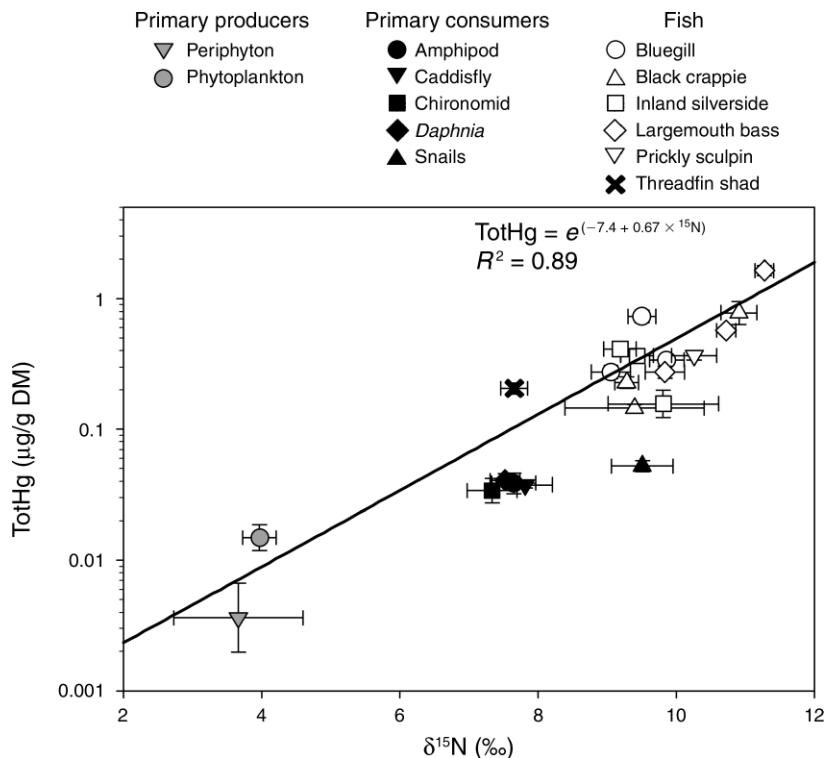


FIG. 7. Total mercury (TotHg) concentration (DM, dry mass) vs. $\delta^{15}\text{N}$ in the Clear Lake food web. Each symbol represents geometric (for TotHg) or arithmetic (for $\delta^{15}\text{N}$) means. Error bars represent $\pm\text{SE}$.

no difference in model R^2 values, indicating that the addition of pelagic reliance did not substantially help model fit. Both length and trophic position appear to be equally important as evidenced by their Akaike weights of 1.00 and 0.97, respectively.

When examined by age, Hg in YOY bluegill was also best predicted by a model that included trophic position and length and had an R^2 value of 0.29 (Table 3). Yet the best predictor of Hg concentrations in adult bluegill (>85 mm) was length alone (Table 3). However, this model provides a poor fit overall, only explaining 10% of the variability in Hg values. The addition of trophic position to the model only increased the R^2 to 0.12, and Akaike weights indicate that neither trophic position (0.22) nor pelagic reliance (0.24) are tremendously important to determining adult bluegill Hg concentrations in Clear Lake.

Inland silverside.—The top model for inland silversides across all sizes included trophic position, pelagic reliance, and length as factors and had an R^2 value of 0.13 (Table 3). Akaike weights of all three variables were nearly 1.00, indicating that each variable is equally important as the others. No other candidate models had ΔAIC values below 10, suggesting that the top model was substantially more likely than any others in the set (Appendix E: Table E3).

For young silversides (<60 mm), length alone was the best predictor of Hg concentrations, based on ΔAIC

values. The only other competing model contained both length and pelagic reliance and had a ΔAIC value of 0.92 (Appendix E: Table E3). Akaike weights indicate that the top model was 1.6 times more likely than its lone competitor in the candidate set, and the addition of pelagic reliance increased the R^2 value from 0.14 to <0.16. However, pelagic reliance was an important factor for large silversides (>60 mm), for which Hg concentrations were described best using pelagic reliance and length (Table 3). Length was still a more important variable than pelagic reliance, as suggested by the competing model, which contained only length and had a ΔAIC value of 0.19 (Appendix E: Table E3). Variable weights also indicate this order of relative importance, with length having the highest value (0.83), followed by pelagic reliance (0.55) and trophic position (0.31).

Largemouth bass.—The top model for the entire size range of largemouth bass explained 60% of the variability in Hg concentrations and contained trophic position, pelagic reliance, and length as independent variables (Table 3). No other candidate models had ΔAIC values <2.00, and variable weights (all ~ 0.98 –1.00) indicated that all three variables were equally important.

In YOY bass (<115 mm), Hg concentrations were best predicted by a combination of pelagic reliance and length ($R^2 = 0.59$; Table 3). The only competing model,

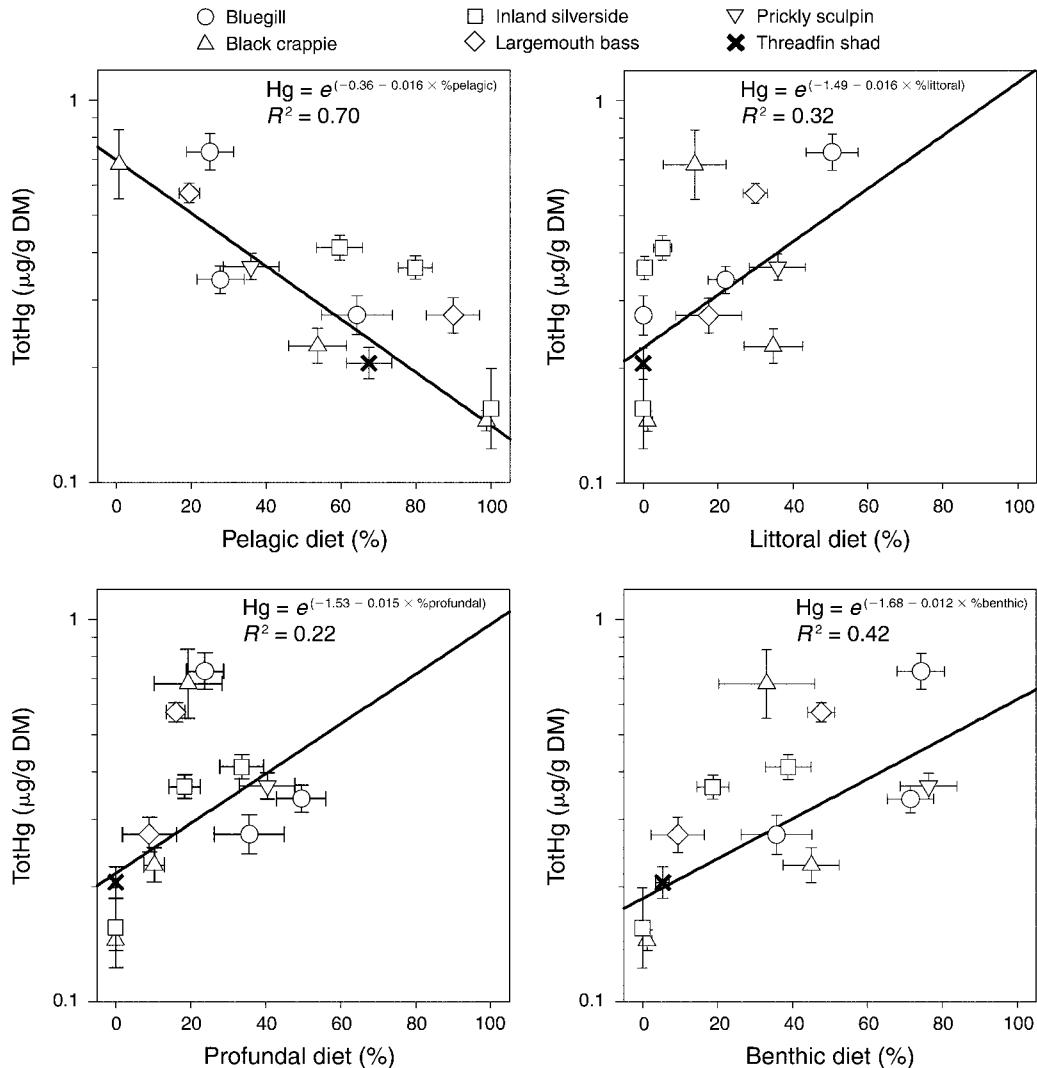


FIG. 8. Relationship between total mercury (TotHg; DM, dry mass) and habitat-specific foraging in six fish species, as determined by diet analysis. Each symbol represents geometric (for TotHg) or arithmetic (percentage of diet) means \pm SE.

which had a Δ AIC value of 0.76, also included trophic position. However, the addition of trophic position only improved the R^2 value to 0.60. Akaike weights indicate that the top model was 1.5 times more likely than its lone competitor. In adult bass (>115 mm) however, the top model included both length and trophic position (Table 3), which together explained 60% of the variability in Hg concentrations. The only other candidate model with a Δ AIC value of <2.00 contained only length but was nearly three times less likely than the top model.

Prickly sculpin.—Prickly sculpin Hg concentrations were also best described with a model composed of length and trophic position and had an R^2 value of 0.52 (Table 3). The model containing length alone was the only competitor in the candidate set, with a Δ AIC value of 1.17 (Appendix E: Table E5). Pelagic reliance did not appear to be of much importance in sculpin, with a variable weight of only 0.30, relative to trophic position

(0.59) or length (0.99), which clearly carried the most importance.

Threadfin shad.—Pelagic reliance and length together best predicted Hg concentrations in threadfin shad, explaining 46% of the variability in the data (Table 3). The model that also included trophic position had a Δ AIC value of 0.76 and only improved the R^2 value to 0.48. Log-likelihood values of the two models differed by less than 1.00, suggesting that the addition of trophic position did not add much value relative to the other variables (Appendix E: Table E6).

DISCUSSION

Diet was highly variable among all fish species and differed significantly among size classes for bluegill, black crappie, inland silverside, and largemouth bass, indicating clear ontogenetic diet shifts. Total mercury concentrations also varied significantly among species

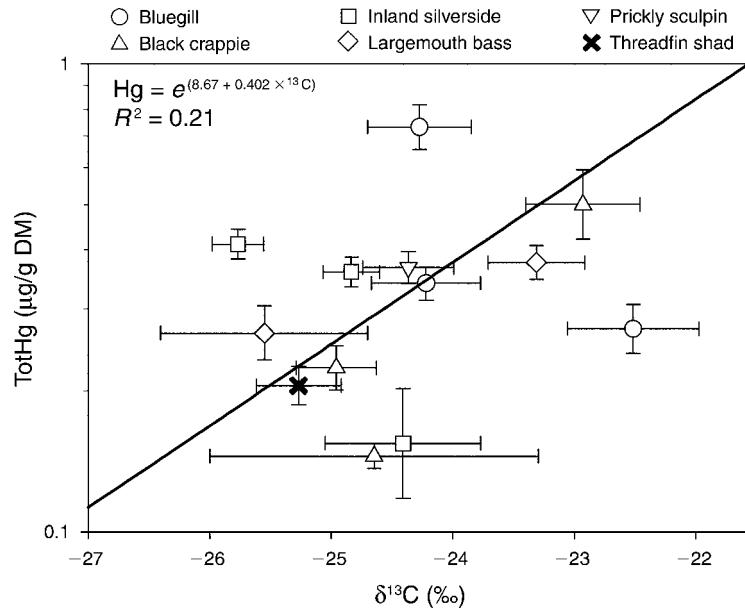


FIG. 9. Total mercury (TotHg; DM, dry mass) vs. $\delta^{13}\text{C}$ in six fish species. When corrected for length, species, and trophic position, $\delta^{13}\text{C}$ is correlated with Hg ($R^2 = 0.64$, $F_{1,485} = 47.52$, $P < 0.001$). On a species-specific basis, TotHg is correlated with $\delta^{13}\text{C}$ for bluegill ($R^2 = 0.47$, $P = 0.04$, $N = 73$), largemouth bass ($R^2 = 0.65$, $P < 0.001$, $N = 206$), and threadfin shad ($R^2 = 0.47$, $P < 0.001$, $N = 37$), but not black crappie ($P = 0.15$, $N = 42$), inland silverside ($P = 0.71$, $N = 111$), or prickly sculpin ($P = 0.48$, $N = 25$). Each symbol represents geometric (for TotHg) or arithmetic ($\delta^{13}\text{C}$) means \pm SE.

and size classes of fish. Across all taxa, stable isotopes and diet data indicated that Hg bioaccumulation in Clear Lake fish was influenced by both foraging habitat and trophic position, increasing with degree of benthic

foraging and trophic position. Baseline $\delta^{15}\text{N}$ ratios did not differ between benthic and pelagic prey. This suggests that the relationship between fish Hg and benthic diet was not a result of elevated trophic position,

TABLE 3. Top multiple regression models ($\Delta\text{AIC} = 0$) explaining mercury concentrations in Clear Lake fishes (see Appendix E for full list of candidate models).

Age†	Equation‡	R^2	Log-likelihood	AIC _c	Akaike weight§
Black crappie					
All	$\ln(\text{Hg}) = -1.69 - 0.61 \times \text{PR} + 0.01 \times \text{SL}$	0.72	-32.65	-56.23	0.5249
Juvenile	$\ln(\text{Hg}) = -1.28 - 0.50 \times \text{TP} + 0.014 \times \text{SL}$	0.30	-24.62	-39.41	0.3529
Adult	$\ln(\text{Hg}) = -1.57 + 0.008 \times \text{SL}$	0.59	-10.77	-13.35	0.6453
Bluegill					
All	$\ln(\text{Hg}) = -0.32 - 0.55 \times \text{TP} + 0.01 \times \text{SL}$	0.51	-58.47	-108.35	0.6471
Juvenile	$\ln(\text{Hg}) = -0.15 - 0.62 \times \text{TP} + 0.01 \times \text{SL}$	0.28	-43.99	-79.03	0.6920
Adult	$\ln(\text{Hg}) = -1.08 + 0.006 \times \text{SL}$	0.12	-17.17	-27.25	0.3126
Inland silverside					
All	$\ln(\text{Hg}) = -1.85 - 0.024 \times \text{TP} - 0.058 \times \text{PR} + 0.017 \times \text{SL}$	0.13	-83.36	-156.14	1.0000
Juvenile	$\ln(\text{Hg}) = -2.10 - 0.25 \times \text{PR} + 0.025 \times \text{SL}$	0.13	-33.89	-59.14	0.4476
Adult	$\ln(\text{Hg}) = -3.38 + 0.43 \times \text{PR} + 0.03 \times \text{SL}$	0.19	-36.64	-35.33	0.3000
Largemouth bass					
All	$\ln(\text{Hg}) = -1.56 - 0.305 \times \text{TP} - 0.59 \times \text{PR} + 0.006 \times \text{SL}$	0.60	-127.26	-244.01	0.9807
Juvenile	$\ln(\text{Hg}) = -1.69 - 0.69 \times \text{PR} + 0.02 \times \text{SL}$	0.59	-120.20	-232.12	0.5936
Adult	$\ln(\text{Hg}) = -1.75 + 0.39 \times \text{TP} + 0.004 \times \text{SL}$	0.60	-48.97	-89.13	0.4671
Prickly sculpin					
All	$\ln(\text{Hg}) = -0.95 - 0.24 \times \text{TP} + 0.016 \times \text{SL}$	0.52	-32.86	-55.36	0.4492
Threadfin shad					
All	$\ln(\text{Hg}) = -2.33 - 1.03 \times \text{PR} + 0.02 \times \text{SL}$	0.46	-32.12	-54.98	0.5933

† The length thresholds for juvenile fishes were 85 mm for black crappie and bluegill, 60 mm for silversides, and 125 mm for largemouth bass.

‡ Top multiple regression model for $\ln(\text{Hg})$ as determined by Akaike Information Criteria (AIC). Abbreviations are: PR, percentage of pelagic reliance (arcsine square-root transformed); TP, trophic position; SL, standard length (mm).

§ The likelihood of the model relative to others in the candidate set.

but due to greater Hg exposure associated with habitat-specific prey Hg concentrations. Further segregation of benthic prey into littoral and profundal taxa revealed that benthic subhabitat was an important distinction for interpreting fish Hg concentrations; the degree of profundal foraging was more strongly correlated with fish Hg concentrations than the degree of littoral foraging.

The AIC and multiple regression models indicate that trophic position, foraging habitat (quantified as percentage of pelagic reliance), and length were all very important in determining Hg concentrations in Clear Lake fish. However, the structure of the most parsimonious models and the relative importance of variables explaining Hg concentrations differed among fish species and between ages. Length was a component of all top multiple regression models and was at least as important as the other variables, particularly when examined across the entire size range of a species. All three variables were equally important for silverside and bass; however, the relative importance of foraging habitat was greater than trophic position for crappie and shad, whereas trophic position was more important than habitat in bluegill and sculpin. When separate AIC analyses were conducted for juvenile and adult fish of each species, foraging habitat had substantially higher variable weights than trophic position in 4 of 10 analyses (silverside <60 mm, silverside >60 mm, bass <115 mm, and shad), trophic position variable weights were higher in 4 of 10 analyses (crappie < 85 mm, bluegill <85 mm, bass >115 mm, and sculpin), and the variable weights were approximately equal in 2 of 10 analyses (crappie >85 mm and bluegill >85 mm). These results indicate that overall foraging habitat was at least as important as trophic position in determining fish Hg concentrations. The slopes of the foraging habitat component of multiple regression models indicate that Hg was negatively correlated with pelagic reliance and thus increased with increasing benthic diet. Interestingly, the parameter estimates for trophic position were negative for several analyses, indicating that Hg actually decreased with trophic position in some cases. This suggests that the increases in Hg with length and benthic foraging for many species outweighed the influence of trophic position.

The Hg mining along Clear Lake's shoreline has resulted in some of the most Hg-contaminated sediments ever reported (Suchanek et al. 2008b). Chironomid TotHg concentrations were also remarkably high and tracked the spatial trend of sediment concentrations, with samples near the mine much higher than in the rest of the lake (Suchanek et al. 2008a, c). However, MeHg concentrations in chironomids were one to two orders of magnitude lower than TotHg and showed no clear spatial trends, indicating that the inorganic fraction accounted for nearly all the Hg in chironomids in the Oaks Arm. In addition, chironomid abundance did not differ dramatically among arms of the lake (Suchanek et

al. 2008c), suggesting that their availability as prey also did not vary at this spatial scale. As a result, all things being equal, fish in the Oaks Arm near the mine were exposed to significantly more Hg from chironomids than from their other prey items.

Because of its toxicity and bioaccumulation potential, much of the recent literature has focused on MeHg as the species of importance for Hg bioaccumulation in aquatic systems, suggesting that the assimilation efficiency and bioaccumulation potential of inorganic Hg are too low to be of concern. In many circumstances this is likely the case, particularly in areas where inorganic Hg deposition is low and bioaccumulation is driven by MeHg production and availability. Allen et al. (2005) found that biomagnification was inversely correlated with chlorophyll *a* concentrations in a series of lakes, suggesting that biodilution regulated transfer of MeHg to higher trophic levels. Moreover, MeHg concentrations in biota were negatively correlated with pH, indicating that entry into the food web was controlled by water chemistry. In Lake Murray, Papua New Guinea, inorganic Hg concentrations actually decreased with trophic position, whereas MeHg accumulations were successively higher (Bowles et al. 2001). However, in systems in which Hg inputs are driven by a significant point source, the trophic dynamics of inorganic Hg may be equally important. For example, sites close to a point source in East Fork Poplar Creek, Tennessee, USA, had inorganic Hg as the dominant species in biota, whereas MeHg was dominant at downstream and reference areas (Hill et al. 1996, Southworth et al. 2000). These studies indicate that in systems dominated by inorganic point sources benthic infauna are likely to accumulate high inorganic Hg concentrations, some of which is accumulated in their prey. Although the assimilation efficiency of inorganic Hg is lower than that of MeHg (Wang and Wong 2003), the substantially elevated inorganic loads in Clear Lake chironomids may have corresponded to higher total Hg values in chironomid feeding fish.

In lakes, bioaccumulation of contaminants such as Hg generally follows energetic pathways (Vander Zanden and Rasmussen 1996). Not only can benthic productivity account for a large proportion of total primary productivity within lakes (Vadeboncoeur et al. 2003), but it is often intricately coupled to pelagic energy dynamics such that benthic energy supports a substantial proportion of upper trophic level production (Vadeboncoeur et al. 2002, Vander Zanden and Vadeboncoeur 2002). Thus, understanding the relative contributions of pelagic and benthic energy to successive trophic levels is critical to quantifying how contaminants move through food webs. In general, Hg bioaccumulation appears to be lower through benthic pathways than pelagic ones (Power et al. 2002, Allen et al. 2005); however, very few attempts have been made to understand the coupling of benthic and pelagic energy in higher trophic levels. Benthic secondary productivity has been shown to be correlated with pelagic energy

sources (Chandra et al. 2005) and may be strongly linked in eutrophic systems such as Clear Lake (Welch et al. 1988). Moreover, benthic Hg bioaccumulation pathways can be significant (Wong et al. 1997, Mason et al. 2000), suggesting that integration of both routes is required for proper assessment.

Clear Lake is relatively eutrophic, so energy fixation is dominated by pelagic pathways. Chlorophyll *a* concentrations and pelagic productivity rates can exceed 100 $\mu\text{g/L}$ (Tetra Tech, *unpublished manuscript*) and 2000 $\text{mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (Goldman and Wetzel 1963), respectively. Although there has been an increase in macrophyte development along the shoreline in recent years, water clarity in the littoral zone is still generally too low (summertime secchi measurements = 1.55 ± 0.14 m [mean \pm SE]; $n = 135$) to support substantial benthic carbon fixation. Moreover, in summer months the lake produces dense cyanobacteria blooms, effectively further shading benthic substrate along the shoreline. Yet Hg transfer to upper trophic levels appears to be strongly linked to benthic pathways, with Hg contamination and bioaccumulation directly related to degree of benthic foraging. However, the benthic conduit for Hg transfer was subsidized by pelagic energy resources. Profundal prey items, such as chironomid larvae, often derive much of their nutrients from detrital organic matter of pelagic origin (Goedkoop et al. 2000). Stable isotopes support this interpretation, with $\delta^{13}\text{C}$ ratios of profundal prey significantly depleted relative to those of littoral invertebrates.

These results highlight previous calls (Vander Zanden and Vadeboncoeur 2002) to integrate both gut content and stable-isotope data in studies to obtain robust estimates of foraging ecology and energy flow within and between systems. This is of particular importance in systems with strong coupling of benthic–pelagic carbon and in eutrophic systems in which the benthic $\delta^{13}\text{C}$ signature is obscured by the substantial pelagic carbon fixation. In this study, diet appeared to be a better indicator of foraging habitat of fishes than $\delta^{13}\text{C}$. Moreover, the variability in Hg concentrations was better explained with the diet data than carbon isotope ratios. Interestingly there were clear distinctions in $\delta^{13}\text{C}$ between littoral and pelagic invertebrates; however, the signatures of nearly all fish species were intermediate of these values, suggesting equal mixing of pelagic and littoral resources. Diet data indicated a strong reliance by fish on profundal invertebrates, which had $\delta^{13}\text{C}$ signatures matching those of many higher order consumers. Combining the two methods revealed the circuitous route that pelagic energy traveled from water column to benthos to fish.

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APPENDIX A

Habitat-specific designations for fish prey items (*Ecological Archives* A018-078-A1).

APPENDIX B

Mean percentage of diet of major prey items by fish species and size class (*Ecological Archives* A018-078-A2).

APPENDIX C

Mercury concentrations (geometric mean) in Clear Lake fishes (*Ecological Archives* A018-078-A3).

APPENDIX D

Akaike Information Criteria values and structure of candidate models describing mercury concentration in Clear Lake fishes (*Ecological Archives* A018-078-A4).

APPENDIX E

Akaike Information Criteria values and structure of candidate models describing mercury concentrations in black crappie, bluegill, inland silversides, largemouth bass, prickly sculpin, and threadfin shad (*Ecological Archives* A018-078-A5).