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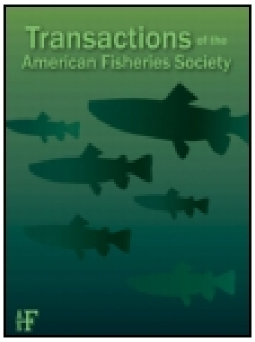

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[Article]

Ontogenetic Trophic Interactions and Benthopelagic Coupling in Lake Washington: Evidence from Stable Isotopes and Diet Analysis

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Abstract.—Stable isotopes of nitrogen and carbon and stomach content analysis were used to determine the trophic position and relative importance of benthic and pelagic pathways for different life stages and species of the major fishes and invertebrate prey in Lake Washington. Significant coupling of the benthic and pelagic pathways was evident in this complex food web across seasons and fish ontogenies. Among apex predators, cutthroat trout *Oncorhynchus clarkii* and northern pikeminnow *Ptychocheilus oregonensis* shifted ontogenetically from benthic omnivory to pelagic piscivory, whereas yellow perch *Perca flavescens* shifted from pelagic zooplanktivory to benthic piscivory. Apex predators continued to rely on benthic prey seasonally, particularly in winter and spring. Benthic pathways were less important to the current diets of apex predators than they were during the recovery from eutrophication in the 1970s. Surprisingly, the $\delta^{15}N$ values for copepods during winter and for zooplanktivorous longfin smelt *Spirinchus thaleichthys* and threespine sticklebacks *Gasterosteus aculeatus* were similar to those for top piscivores, whereas the significantly lower values for zooplanktivorous juvenile sockeye salmon *O. nerka* were more similar to expectations. Nitrogen and carbon isotope ratios of pelagic planktivores and invertebrates also varied seasonally. Mixing model results showed that stable isotopes and stomach contents were comparable for determining ontogenetic trends, but stable isotopes established these trends with many fewer samples and less variability and accurately portrayed ontogenetic trends when few stomach samples were available. However, stomach content analysis was critical in delineating seasonal trends in diets and for identifying specific prey species.

Much can be revealed about the structure and function of lake food webs by examining the relative importance of benthic and pelagic energy pathways to production of upper trophic-level species (Schindler and Scheuerell 2002; Vadeboncoeur et al. 2002; Vander Zanden and Vadeboncoeur 2002). Whole-lake benthic primary production is inversely related to phytoplankton production (Vadeboncoeur et al. 2001, 2003; Liboriussen and Jeppesen 2003), mainly because of light interception by phytoplankton. Despite the declining contribution of benthic primary production to whole-lake primary production with increasing lake trophic status, the contribution of benthic primary production to fish production does not necessarily follow the same trend.

Similar to whole-lake primary production, fish production is driven benthically in low-nutrient lakes because of limited pelagic resources (Carpenter et al. 1997; Jeppesen et al. 1997), and the importance of benthic pathways decreases as lake trophic status increases to mesotrophic levels (Persson et al. 1991; Carpenter et al. 1997; Jeppesen et al. 1997; Vander Zanden et al. 2003; Liboriussen et al. 2005). In nutrient-rich lakes, fish production becomes increasingly dependent on benthic pathways again; planktivorous fish are subsidized by benthos supported by high sedimentation of phytoplankton (Jeppesen et al. 1997), and increased turbidity reduces the ability of piscivores to forage visually for pelagic planktivores (Miner and Stein 1996; Beauchamp et al. 1999; De Robertis et al. 2003).

Food web processes operate at different temporal scales (diel, seasonal, annual) and also can differ ontogenetically within species. Ratios of the stable isotopes of nitrogen and carbon provide an integrated view of consumption over periods of months to years (Hesslein et al. 1993; MacAvoy et al. 2001), depending on how quickly the diet changes, individual growth rate, and the specific rate of new tissue production. Nitrogen isotopes generally reflect trophic position because the lighter isotope is preferentially excreted, leaving consumers approximately 3.4‰ higher (enriched) in the heavier isotope relative to their prey (Minagawa and Wada 1984; Vander Zanden and Rasmussen 2001). In contrast, consumers are typically less than 1‰ enriched in the heavy isotope of carbon relative to their food (Deniro and Epstein 1978; Vander Zanden and Rasmussen 2001). Carbon isotopes are often used to trace energy pathways within a system

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because pelagic carbon is depleted in the heavier isotope relative to carbon derived from bentholittoral sources (France 1995).

In contrast to the longer-term integrated dietary signal provided by stable isotope analysis (SIA), stomach content analysis (SCA) provides a "snapshot" of food habits over a day or less, depending on meal size and temperature (He and Wurtsbaugh 1993). While more labor intensive, SCA offers the advantage of identifying and measuring specific prey taxa rather than functional groups that might share similar isotopic signals, and can describe dietary changes at fine temporal scales (e.g., diel, monthly, or seasonal patterns) that contribute additional insight into trophic interactions.

Relatively few stable isotope studies of food webs have focused on western lakes, which typically contain simple food webs of low to moderate productivity. Lake Washington is relatively distinctive among large, deep western lakes because of its urbanized surroundings and very complex food web; the lake contains more than 29 resident or transient species of fish, including anadromous Pacific salmonids and the only land-locked population of longfin smelt *Spirinchus thaleichthys* in the United States (Wydoski 1972). Lake Washington is a well-known example of cultural eutrophication (during 1941–1968) and recovery thereafter (approximately 1968–1978) (Edmondson 1994). During recovery from eutrophication, fish production was dominated by benthic pathways (Eggers et al. 1978). Given its steep morphometry and current mesotrophic status, we would predict that current benthic contributions to upper-trophic level fishes would be low in Lake Washington and would be reduced from contributions during the recovery period. The primary research questions for this study included the following: To what extent do fish versus invertebrate prey and benthic versus pelagic prey contribute to the energy budgets of apex piscine predators in Lake Washington? Do trophic linkages between benthic and pelagic habitats shift ontogenetically among apex predators? Are top predators in Lake Washington more reliant on fish prey now than during the recovery from eutrophication? To answer these questions, we used a combination of SIA and SCA across sizes and seasons to corroborate current diet data for Lake Washington fishes. Because of the large number of samples collected for this effort, we were also able to explore the comparability of SIA and SCA in delineating ontogenetic trends in piscivory and benthivory among top predators in this system. We focused on temporal and ontogenetic trends because of the high mobility of most of the fishes studied; however, a spatial component was included for the relatively sedentary demersal fishes and invertebrates.

Study Area

Lake Washington is located in the Puget Sound basin between the cities of Seattle and Bellevue, Washington. The lake covers an area of 87.6 km^2 and has a length of 21 km, an average width of 2.4 km, an average depth of 33 m, and a maximum depth of 65 m (Arhonditsis et al. 2003). Stratification occurs in Lake Washington from May to early November; the thermocline is centered around 16 m, separating maximum epilimnetic temperatures of up to 22–24°C during August from hypolimnion temperatures that remain at 7–9°C year-round. Chlorophyll-*a* concentrations peak in May at approximately 12 μg/L in surface waters, while winter lows are approximately 2 μg/L. Secchi depths range from approximately 3.7 m during spring to 5.5 m during winter.

The abundant pelagic planktivore community of Lake Washington consists of juvenile sockeye salmon *Oncorhynchus nerka*, longfin smelt, threespine sticklebacks *Gasterosteus aculeatus*, and age-0 yellow perch *Perca flavescens*. Juvenile sockeye salmon reside for an average of 15 months in the lake before migrating to sea. Longfin smelt have a 2-year life span in Lake Washington, and even year-classes are 5–15 times more abundant than odd year-classes (Beauchamp 1994). Threespine sticklebacks live just 1 year in Lake Washington. The pelagic phase of age-0 yellow perch occurs during their first summer and fall. The benthic fish community is dominated by prickly sculpins *Cottus asper*, coastrange sculpins *C. aleuticus*, and peamouth *Mylocheilus caurinus*. Prickly sculpins were estimated to comprise 84% of the lake's fish biomass during the 1970s (Eggers et al. 1978). Currently, the dominant piscivores include cutthroat trout *O. clarkii* and northern pikeminnow *Ptychocheilus oregonensis* in pelagic and littoral regions and yellow perch and smallmouth bass *Micropterus dolomieu* in littoral regions. Smallmouth bass are much less abundant than the other three piscivores.

Methods

Field collections.—Fishes and invertebrates were collected from Lake Washington between October 2001 and November 2003 by means of gillnetting, midwater trawling, electrofishing, angling, snorkeling, scuba diving, minnow traps, conical nets, and submerged emergent traps. Large mobile fish were caught throughout the lake during the study. Pelagic forage fishes were collected by midwater trawl during October and March. Other pelagic biota, including bulk zooplankton, *Daphnia* spp., *Leptodora* spp., larval fish, and mysid shrimp *Neomysis mercedis*, were collected in 2002 from the top 20 m in the pelagic zone by use of either a 35-cm-diameter, 135-μm-mesh net (bulk zooplankton) or a 1-m-diameter, 1-mm-mesh net (all others). *Daphnia* and *Leptodora*, but not mysids, were available to both the small- and large-diameter nets and were not separated from bulk zooplankton when present. Sedentary benthic species, including prickly sculpins, signal crayfish *Pacifasticus leniusculus*, trichopteran larvae (limnephilids), and chironomid pupae were collected from the littoral zone (<1 m to 5 m depth) at up to three fixed locations, representing one relatively natural, undisturbed site (St. Edwards State Park [NE]) and two sites subject to significant human disturbance, such as shoreline development and storm drain outfalls (Magnuson Park [NW]; Mt. Baker Park [SW]). Large prickly sculpins (>75 mm total length [TL]) were also obtained from the profundal zone by midwater trawl during March 2002. Three freshwater mussels *Margeratifera margeratifera* were collected by scuba diving at 4.5–6.0 m depth at each of these three sites in August 2003. All specimens were immediately placed on ice until they could be processed.

Sample preparation.—Fishes and crayfish were measured to the nearest millimeter and weighed to the nearest 0.01 g. Fish stomachs were removed for SCA. Otoliths and scales were removed for age and growth analysis from cutthroat trout, yellow perch, and northern pikeminnow. Otoliths were the only aging structure used for sculpins. Approximately 0.5 g of muscle tissue was removed from the anterior dorsal area of individual fish and from the foot of unionid mussels for SIA. All other invertebrates and age-0 sculpins were analyzed as whole bodies and trichopteran larvae were removed from their cases. Muscle tissue and whole bodies were dried in a commercial convection oven at approximately 60°C. Dried tissue was ground to a fine powder in a porcelain mortar and weighed to 1.00 ± 0.02 mg in a tin capsule on a Cahn electrobalance.

Stable isotope analysis.—Stable isotopes were measured via continuous flow using a Carlo Erba 2100 elemental analyzer interfaced with a Thermo-Finnigan Deltaplus isotope ratio mass spectrometer at the Colorado Plateau Stable Isotope Laboratory at Northern Arizona University, Flagstaff. Stable isotope values (δ) were expressed as a ratio (R) of the heavy isotope to the light isotope ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) standardized with respect to internationally recognized reference materials as follows:

$$\delta(‰) = [(R_{\text{sample}}/R_{\text{reference}}) - 1] \times 1,000. \quad (1)$$

Every 10th sample was analyzed in duplicate; the average standard deviations between replicates were 0.11‰ for $\delta^{13}C$ and 0.07‰ for $\delta^{15}N$. The reference material was Vienna Pee Dee belemnite limestone for carbon and atmospheric N_2 for nitrogen.

The ^{13}C-depletion of lipids relative to that of other tissues (Deniro and Epstein 1977) can affect interpretation of stable isotopes in ecological contexts because it suggests a diet that is more depleted in ^{13}C than similar tissue containing less lipid. However, because lipid extraction can also alter stable nitrogen ratios (Pinnegar and Polunin 1999), lipid extraction was not performed on Lake Washington samples. Lipids were normalized using the method developed by McConnaughey and McRoy (1979) and validated by Kline (1997). This method uses C/N as a lipid surrogate (a ratio of 4.0 is considered normal) and adjusts $\delta^{13}C$ using a literature value of the average difference in $\delta^{13}C$ between lipid and protein. Normalized carbon isotope ratios ($\delta^{13}C$) increased by an average of 0.33 (SD = 0.90) across all samples. The $\delta^{15}N$ values of small prickly sculpins (TL < 75 mm) were adjusted for the use of whole bodies instead of muscle (i.e., $\delta^{15}N$ was increased by 0.78), based on the average difference between muscle and whole bodies for planktivores (two-sample t-test: df = 22, $P = 0.003$). Differences in $\delta^{13}C$ between muscle and whole bodies of planktivores were not significant ($P = 0.715$).

Algal contamination of bulk zooplankton.—Considerable amounts of algae were mixed with zooplankton in samples taken with the 153-μm-mesh plankton net, particularly in May. Because algae could artificially lower $\delta^{15}N$ values, we attempted to determine and correct for the proportion of algae in seasonal bulk zooplankton samples.

Using archived bulk zooplankton samples from the same sampling period in 2002 (D. E. Schindler Laboratory, School of Aquatic and Fishery Sciences, University of Washington), the percentage of algae in bulk zooplankton samples was calculated for samples from each season. Algae comprised 0.4% of the total biovolume of bulk zooplankton samples in winter, 37% in May, 3.4% in August, and 11.2% in December. These percentages revealed that only the spring bulk zooplankton sample contained appreciable amounts of algae. We normalized bulk zooplankton $\delta^{15}N$ by assuming an algal $\delta^{15}N$ of 7.1‰ (mean $\delta^{15}N_{Daphnia}$ – 3.4‰; i.e. approximately one trophic level below zooplankton). This adjustment resulted in a maximal increase in $\delta^{15}N$ of 1.84‰ for the May sample. Because the $\delta^{13}C$ of algae was not measured, it was not possible to normalize the $\delta^{13}C$ of bulk zooplankton samples for algal content.

Diet analysis.—Fish stomachs were stored in formalin and transferred to alcohol before analysis. Blotted wet weights of stomach contents and major prey groups were measured to the nearest 0.01 g for each nonempty stomach (Baldwin et al. 2000). The proportional gravimetric contribution of each prey category was computed for each stomach. Seasonal diets were obtained by averaging diet proportions for individuals within a size-class across months of each season; winter was January–March, spring was April–June, summer was July–September, and fall was October–December. For piscivores, three size-classes were used, based on previous diet data (Eggers et al. 1978; Beauchamp et al. 1992; Brocksmith 1999; Mazur 2004; Nowak et al. 2004), length-frequency modes, and scatter plots of the percentage of fish in the diet versus predator length (Mazur 2004).

Ideally, each size-by-season cell was represented by a minimum of 10 nonempty stomachs, though this was not always possible. With three size-classes delineated for each species, a minimum of 120 nonempty stomachs were desired for SCA (10 individuals × 4 seasons × 3 size-classes). We analyzed the stomach contents of 273 cutthroat trout, 825 northern pikeminnow, and 443 yellow perch. Of these samples, 21% of cutthroat trout, 41% of northern pikeminnow, and 52% of yellow perch stomachs were empty. Even with final nonempty stomach counts being much higher than the 120 minimum (215 for cutthroat trout, 488 for northern pikeminnow, and 211 for yellow perch), the minimum of 10 nonempty stomachs per season per size-class was achieved only for northern pikeminnow (Table 1). We used 23 cutthroat trout, 21 northern pikeminnow, and 43 yellow perch for SIA.

Historical comparison.—Annual proportions of benthic prey and fish prey in the current diets of northern pikeminnow and yellow perch in Lake Washington were compared with historical proportions from life history studies conducted during the recovery from eutrophication. For northern pikeminnow, seasonal proportions for large fish (>300 mm fork length [FL]) were averaged for the current and historical studies (Olney 1975). For yellow perch, seasonal proportions for spring, summer, and fall were averaged for adult fish (>139 mm), the largest size category in the historical study (Nelson 1976). Proportions for winter were not included in the annual yellow perch average for the current or historical study because relatively few winter samples were reported in the historical study. Cutthroat trout were not common in Lake Washington during the eutrophication recovery period, so no diet data were available (Eggers et al. 1978).

Mixing model.—We used a multi-source isotope mixing model, IsoSource (Phillips and Gregg 2003), to estimate the proportional contributions of fish versus invertebrate items and benthic versus pelagic items to the diets of the individual cutthroat trout, northern pikeminnow, and yellow perch sampled for SIA. Inputs to the model were the nitrogen and carbon isotope value for each individual and the nitrogen and carbon isotope values for the potential sources, incorporating a trophic fractionation of 3.4‰ for $\delta^{15}N$ and 0‰ for $\delta^{13}C$. Diet items were grouped into four sources: pelagic fishes, benthic fishes, pelagic invertebrates, and benthic invertebrates. Possible contributions from each source were examined in increments of 1%; the summed mass balance tolerance was 1%. Percent contribution of different prey types typically did not differ by more than 11% for cutthroat trout, 15% for northern pikeminnow, and 12% for yellow perch; therefore, we felt that results obtained using the average estimated contribution for each category did not misrepresent the data. This resulted in summed source contributions that ranged from 98% to 103% across individuals and averaged 100.4%. The stable isotope value for pelagic fishes in the model was the average value for longfin smelt, threespine sticklebacks, juvenile sockeye salmon, and age-0 yellow perch. Benthic fishes included both prickly and coastrange sculpins smaller than 100 mm, based on the sizes of sculpins observed in diets. The value for pelagic invertebrates was the average value for mysids and *Daphnia*. The value for benthic invertebrates was the average value for chironomids, trichopterans, and crayfish. For age-0 yellow perch (<100 mm), pelagic fishes were larval fish.

Statistical analyses.—All statistical procedures were performed using the Statistical Package for the Social Sciences, standard version 11.5 for Windows. Estimated proportional contributions of fish and benthic items derived from the isotope mixing model for individual cutthroat trout, northern pikeminnow, and yellow perch were compared with the proportions observed for each species in SCA. Proportions were averaged across individuals in 25-mm length increments. The average proportions from the mixing model exercise were compared with those from SCA for each species by use of simple linear regression. Significant regressions were compared with a 1:1 line of agreement such that the best agreement between the predicted and observed proportions included a slope of 1.0 and an intercept of 0.

Statistical tests were used to explore differences in metrics within species. Differences in planktivore weight between October and March samples (over their first winter) were tested with pairwise compari-

TABLE 1.—Percent contribution (by wet weight) of fish, benthos, and pelagic invertebrates to the diets of cutthroat trout, northern pikeminnow, and yellow perch by season and size-class. Rows do not add to 100% because benthic sculpins also contribute to fish percentage.

Species	Size-class (mm)	Season	*N*	% Fish	% Benthic sculpins	% Benthic invertebrates	% Mysids	% *Daphnia*
Cutthroat trout	113–199	Winter	2	0	0	50	50	0
		Spring	77	23	0	47	2	27
		Summer	1	0	0	0	0	100
		Fall	0	0	0	0	0	0
	203–299	Winter	4	67	0	33	0	0
		Spring	27	40	0	21	1	38
		Summer	11	41	9	0	0	59
		Fall	1	100	0	0	0	0
	300–530	Winter	18	68	6	28	4	0
		Spring	37	84	9	3	6	7
		Summer	27	92	<1	4	4	0
		Fall	10	88	0	12	0	0
Northern pikeminnow	118–199	Winter	30	46	<1	42	9	3
		Spring	50	43	<1	51	0	4
		Summer	40	15	1	47	1	35
		Fall	32	37	<1	48	1	13
	200–299	Winter	23	100	14	0	0	0
		Spring	64	85	<1	14	0	0
		Summer	97	60	2	23	0	17
		Fall	26	73	5	18	1	0
	300–530	Winter	19	96	21	4	0	0
		Spring	44	83	9	17	0	0
		Summer	44	87	<1	8	0	5
		Fall	19	86	<1	13	0	0
Yellow perch	63–99	Winter	9	10	1	14	72	1
		Spring	2	0	0	50	0	50
		Summer	0	0	0	0	0	0
		Fall	0	0	0	0	0	0
	100–224	Winter	28	8	0	32	60	0
		Spring	46	28	11	40	19	13
		Summer	66	3	3	21	4	72
		Fall	28	15	<1	6	67	11
	225–302	Winter	6	33	33	50	17	0
		Spring	14	93	65	7	0	0
		Summer	6	57	0	27	0	17
		Fall	6	67	0	33	0	0

sons (two-sample *t*-test) for each species. Seasonal differences in stable isotope ratios for longfin smelt were tested with one-way analysis of variance (ANOVA) and with pairwise comparisons (two-sample *t*-test) for threespine sticklebacks and sockeye salmon. Spatial differences in stable isotope composition among mussels, trichopteran larvae, and juvenile signal crayfish were tested for each species by one-way ANOVA. Relationships of stable isotope ratios with prickly sculpin length were tested by use of Pearson's correlation coefficient. If no relationship was found, differences in stable isotope ratios among sites were tested by ANOVA. For significant correlations with length, among-site differences in prickly sculpin stable isotope ratios were tested by an analysis of covariance (ANCOVA) in which length was used as a covariate. Tukey post hoc tests were used to identify differences between groups in ANOVA tests. A significance level of 0.05 was used throughout.

Results

Food Web Description

Among key species and life stages of consumers in the Lake Washington food web, trophic position ($\delta^{15}N$) was negatively correlated with benthic orientation ($\delta^{13}C$) ($r = -0.558$, $P < 0.001$) such that consumers with the highest $\delta^{15}N$ values (presumably indicating higher trophic levels) expressed the most pelagic carbon signals and lower trophic positions were generally more benthic (Figure 1). Mean $\delta^{15}N$ values ranged from 8.1‰ to 17.6‰, which encompassed roughly four trophic levels, assuming a fractionation of 3.4‰ between trophic levels (Minagawa and Wada 1984; Vander Zanden and Rasmussen 2001). Top piscivores in Lake Washington were identified as large cutthroat trout, northern pikeminnow, yellow perch, and smallmouth bass; their $\delta^{15}N$ signatures ranged from 15.8‰ to 17.6‰ (Table 2). Surprisingly, the pelagic planktivores (longfin smelt and threespine sticklebacks) exhibited high $\delta^{15}N$ values of 16.6–

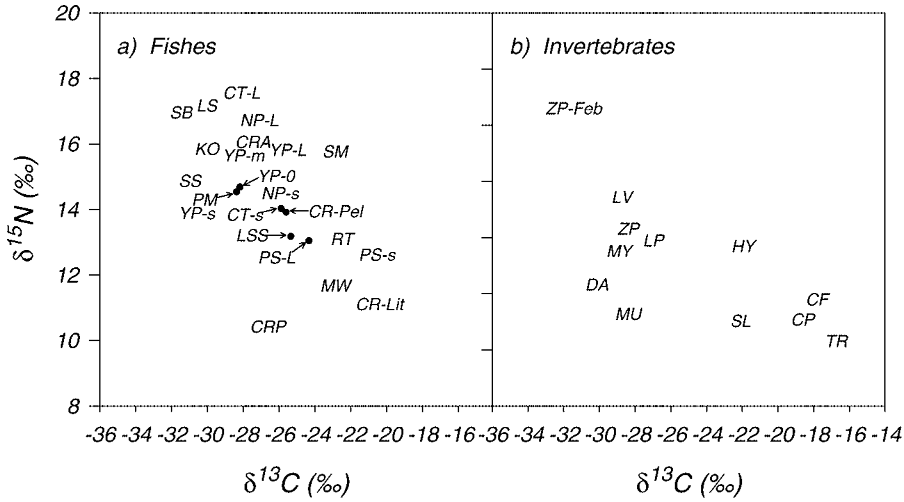

FIGURE 1.—Average stable isotope ratios of carbon and nitrogen for (**a**) major fishes and (**b**) invertebrates in Lake Washington by size and season when appropriate. The taxa and size-class codes in (a) are as follows: CR = coastrange sculpin (Pel = pelagic, Lit = littoral), CRA = crappies *Pomoxis* spp., CRP = common carp *Cyprinus carpio*, CT = cutthroat trout *Oncorhynchus kisutch*, KO = kokanee (lacustrine sockeye salmon), LS = longfin smelt, LSS = largescale sucker *Catostomus macrocheilus*, LV = larval fishes, MW = mountain whitefish *Prosopium williamsoni*, NP = northern pikeminnow, PM = peamouth, PS = prickly sculpin, SB = threespine stickleback, SM = smallmouth bass, SS = juvenile sockeye salmon, YP = yellow perch, L = large, M = medium, and S = small. The taxa codes in (b) are as follows: CF = age-0 crayfish, CP = chironomid pupae, DA = *Daphnia* spp., HY = Hydracarina, LP = *Leptodora* spp., MU = unionid mussels, MY = mysids, SL = stonefly (Plecoptera) larvae, TR = trichopteran larvae, and ZP = bulk zooplankton. Small invertebrates and prickly sculpins were analyzed as whole bodies. Nitrogen ratios for small prickly sculpins were corrected for the use of whole bodies as described in the text. The bulk zooplankton point with no season designation is the average value for spring, summer, and fall.

17.9‰, which were similar to those of the large piscivores. The $\delta^{15}N$ values of the other major forage fishes, juvenile sockeye salmon (14.9‰) and prickly sculpins (12.7‰), were 0.6–1.2 trophic levels lower than those of large cutthroat trout and northern pikeminnow. The $\delta^{15}N$ values of invertebrates generally ranged from 1.0 to 2.5 trophic levels below those of the large piscivores.

Distinct differences in $\delta^{13}C$ were evident between organisms associated with pelagic and littoral habitats (range = 19.3‰), allowing assessment of the relative contributions of benthic versus pelagic resources to upper trophic levels. The most pelagic members of the food web (i.e., with the most negative $\delta^{13}C$ values) included the pelagic planktivores (longfin smelt, threespine sticklebacks, juvenile sockeye salmon, and age-0 yellow perch) and pelagic invertebrates. The most littoral members of the food web were trichopteran larvae, age-0 crayfish, chironomid pupae, and littoral sculpins (Figure 1; Table 2).

Predatory Fishes: Ontogenetic Diet Shifts

Trends in $\delta^{15}N$ and $\delta^{13}C$ indicated that northern pikeminnow, cutthroat trout, and yellow perch underwent ontogenetic shifts in trophic position and energy pathways. Assuming an average shift in $\delta^{15}N$ of 3.4‰ between trophic levels (Minagawa and Wada 1984), $\delta^{15}N$ values increased by an average of 1.1 trophic levels through the ontogeny of northern pikeminnow ($\delta^{15}N$ = 13.0–16.9‰), 1.3 trophic levels for cutthroat trout ($\delta^{15}N$ = 13.4–17.6‰), and 0.5 trophic levels for yellow perch ($\delta^{15}N$ = 14.0–15.7‰; Table 2). All three piscivores increased trophic position with increasing length (Figure 2). For both cutthroat trout and northern pikeminnow, $\delta^{15}N$ values increased to a plateau of approximately 17.5‰ at approximately 300 mm FL. The $\delta^{15}N$ values for yellow perch larger than 175 mm also increased with increasing size and attained a plateau of approximately 16.0‰ at sizes greater than 260 mm.

These species exhibited different ontogenetic shifts between benthic–littoral versus pelagic energy pathways, based on size-related trends in $\delta^{13}C$ (Figure 3). As size increased, average $\delta^{13}C$ declined (became more pelagic) from −26.35‰ to −28.1‰ for cutthroat trout and from −24.7‰ to −27.3‰ for northern pikeminnow but increased (became more benthic) from −28.1‰ to −26.9‰ for yellow perch (Table 2). The smallest northern pikeminnow and cutthroat trout were relatively enriched in ^{13}C, and these species became

TABLE 2.—Stable isotope ratios of nitrogen and lipid-normalized carbon for Lake Washington biota by species, size- or age-class, (0+ refers to fish in their first year of life, 1+ to fish in their second year) and season when appropriate (min = minimum, max = maximum).

Species	Size-class, age-class, or season	N	δ^{15}N (‰)				δ^{13}C (‰)				FL			
			Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max
Cutthroat trout	Small	5	13.2	0.9	11.8	14.1	−26.4	2.0	−29.0	−24.1	177	18	148	195
	Medium	5	14.9	1.0	13.6	16.1	−25.4	1.3	−26.7	−23.5	247	21	211	262
	Large	13	17.6	0.6	16.8	18.3	−28.1	1.5	−29.6	−25.2	386	56	310	480
Northern pikeminnow	Small	4	13.0	2.5	9.7	15.2	−24.7	1.6	−25.8	−22.4	173	33	125	197
	Medium	6	15.4	1.1	14.1	17.1	−26.7	0.9	−27.8	−25.4	235	26	205	270
	Large	11	16.8	0.8	15.2	17.6	−27.3	1.0	−28.9	−25.0	416	55	337	530
Yellow perch	Small	12	14.6	0.7	13.4	15.6	−28.1	2.6	−31.0	−23.7	73	4	63	82
	Medium	13	14.0	0.5	12.4	14.5	−30.3	1.0	−31.5	−28.7	143	24	113	195
	Large	18	15.7	0.5	14.5	16.8	−26.9	1.6	−29.9	−23.9	259	31	222	320
Longfin smelt	Oct (0+)	5	16.6	0.4	16.1	17.2	−28.9	1.2	−30.2	−27.5	49	8	40	60
	Mar (1+)	17	17.9	0.6	16.8	18.8	−31.9	1.0	−34.0	−30.1	64	6	56	77
		19	16.7	0.5	15.7	17.9	−28.7	2.0	−31.4	−25.8	105	16	83	129
Threespine stickleback	Oct (0+)	5	16.6	0.3	16.3	17.1	−30.4	0.2	−30.8	−30.3	64	2	61	69
	Mar (1+)	9	17.2	0.4	16.5	17.8	−32.1	0.4	−32.5	−31.4	72	2	68	74
Kokanee		4	15.8	1.7	13.9	17.7	−30.2	2.9	−34.1	−27.2	222	47	178	275
		3	15.9	0.3	15.5	16.1	−29.8	0.1	−29.9	−29.7	320	13	307	332
Sockeye salmon	Oct (0+)	10	14.7	0.2	14.3	15.1	−30.9	0.5	−31.9	−30.2	104	9	90	114
	Mar (1+)	10	15.0	0.3	14.4	15.5	−31.1	0.6	−31.9	−29.8	114	7	103	125
Chinook salmon *Oncorhynchus tshawytscha*	Juvenile	5	13.6	0.2	13.5	14.0	−23.0	3.7	−29.3	−20.5	134	6	124	139
	Juvenile	5	14.3	0.4	14.0	14.9	−21.1	0.4	−21.6	−20.7	86	3	84	91
	Adult	5	15.5	1.2	14.6	17.6	−29.3	0.6	−30.0	−28.3	240	44	203	317
Rainbow trout *O. mykiss*		1	13.1		13.1	13.1	−22.5		−22.5	−22.5	277		277	277
Smallmouth bass		8	15.8	0.5	14.6	16.5	−22.9	1.8	−25.3	−20.4	293	62	236	395
Brown bullhead *Ameiurus nebulosus*		3	14.3	0.1	14.2	14.4	−25.4	0.7	−26.2	−24.8	259	69	181	308
Peamouth		5	14.5	0.3	14.2	15.0	−28.4	0.7	−29.2	−27.8	219	67	138	310
Largescale sucker		4	13.2	0.7	12.1	13.8	−25.3	2.3	−27.3	−22.4	311	104	168	404
Prickly sculpin	Small[a]	16	11.9	0.5	11.0	12.8	−20.5	1.8	−23.3	−17.4	45	14	25	75
	Medium	35	13.0	0.7	11.6	14.6	−24.2	2.7	−28.3	−19.2	110	10	87	128
	Large	6	13.1	0.5	12.5	13.6	−25.3	4.0	−29.5	−19.1	143	15	129	167
Coastrange sculpin	Pelagic[a]	5	13.9	0.5	13.3	14.6	−25.6	0.6	−26.6	−25.1	35	3	31	38
	Littoral[a]	5	11.1	0.6	10.7	12.0	−20.4	0.4	−20.7	−19.7	48	5	42	54
Pumpkinseed *Lepomis gibbosus*		4	14.3	0.9	13.2	15.5	−25.0	2.6	−28.2	−22.2	99	25	78	134
Crappies		3	16.0	0.9	15.0	16.6	−27.7	0.0	−27.7	−27.7	135	49	80	175
Mountain whitefish		3	11.7	1.8	10.6	13.7	−22.9	0.6	−23.3	−22.2	290	87	240	390
Common carp		1	10.4		10.4	10.4	−26.6		−26.6	−26.6	158		158	158
Larval fish		3	13.4	1.3	12.5	14.9	−28.8	2.9	−32.0	−26.8				
Leptodora spp.		3	11.9	0.9	10.8	12.5	−27.0	1.8	−28.0	−25.0				
Mysids	>10 mm	19	11.6	0.9	10.0	12.6	−29.4	1.6	−31.2	−26.4			10[b]	
	<10 mm	3	11.5	0.8	10.8	12.3	−30.8	1.0	−31.5	−29.7				10[b]
Daphnia spp.		6	10.3	0.3	9.9	10.6	−30.2	1.4	−31.5	−28.9				
Zooplankton[c]	Winter	3	16.6	0.1	16.4	16.7	−31.5	0.2	−31.8	−31.2				
	Spring	3	10.0	0.3	9.7	10.3	−25.2	0.4	−25.7	−24.8				
	Summer	3	12.8	0.2	12.5	13.0	−29.0	0.8	−29.9	−27.9				
	Fall	3	11.5	0.3	11.4	11.5	−30.9	0.2	−31.2	−30.7				
Hydracarina		3	11.7	0.1	11.6	11.7	−22.0	0.5	−22.3	−21.4				
Chironomids	Adult	1	7.9		7.9	7.9	−22.2		−22.2	−22.2				
	Pupa	3	9.1	0.4	5.8	9.6	−18.6	0.5	−26.6	−18.2				
Trichoptera	Larva	9	8.3	0.4	7.7	8.8	−16.8	2.1	−19.8	−14.9				
Stonefly	Larva	1	9.0		9.0	9.0	−22.1		−22.1	−22.1				
Snail[d]		1	8.1		8.1	8.1	−24.8		−24.8	−24.8				
Crayfish		10	9.8	0.7	8.7	10.6	−17.8	1.1	−18.9	−15.4	13[e]	0.34	13	14
Unionid mussel		9	9.3	0.3	8.7	9.6	−28.4	0.3	−29.1	−27.9	78	8	63	92

[a] Isotope values are for whole bodies.

[b] Carapace length.

[c] Bulk zooplankton samples; average algae-normalized seasonal values for δ^{15}N were 16.6, 11.9, 13.0, and 12.0‰.

[d] Chinese mystery snail *Cipangopaludina chinensis*.

[e] Total length.

increasingly ^{13}C-depleted with size, indicating a shift to more pelagic prey at larger sizes (Figure 3). In contrast to northern pikeminnow and cutthroat trout, yellow perch larger than 100 mm FL became increasingly ^{13}C-enriched with size (Figure 3), suggesting an increasingly benthic diet.

For juvenile yellow perch (66–85 mm), δ^{15}N values ranged from 13.4‰ to 15.6‰ and δ^{13}C ranged from

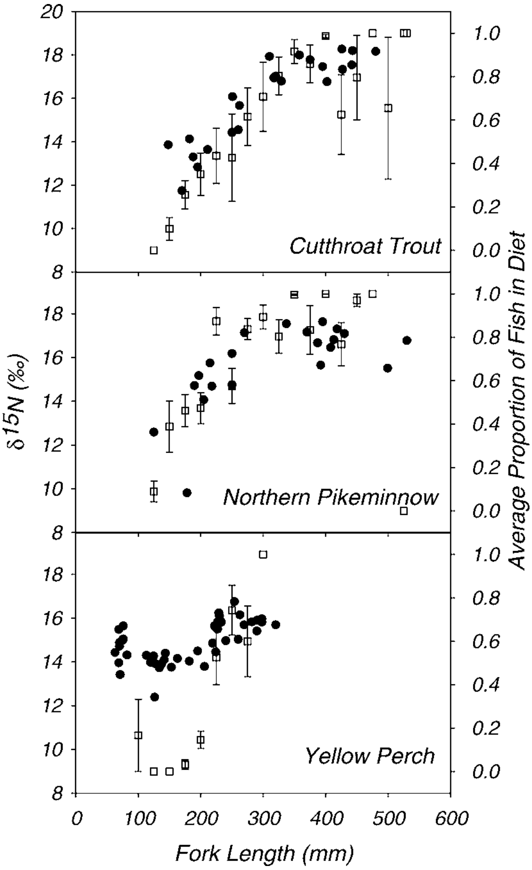

FIGURE 2.—Nitrogen stable isotope ratios as surrogates for trophic position (left axis; circles) and the proportion of fish in the diet (right axis; squares) for cutthroat trout, northern pikeminnow, and yellow perch in Lake Washington as a function of fish length. Stable isotopes are for individual fish; diet proportions are averages ± SEs for 25-mm increments.

−31.0‰ to −23.7‰. Juvenile yellow perch were caught by midwater trawl at the end of March and by beach seine in May; no difference was evident in either δ^{15}N (two-sample *t*-test: $P = 0.34$, df = 8) or δ^{13}C ($P = 0.61$) between the two sampling methods or periods. Within the juvenile life stage of yellow perch, δ^{15}N values were negatively correlated with δ^{13}C ($r^2 = 0.586$, $P = 0.010$), suggesting dietary specialization between individuals that ranged from feeding on benthic invertebrates to higher trophic-level pelagic prey (e.g., larval fish and carnivorous invertebrates).

Comparisons between Diets and Stable Isotopes

Trends in feeding habits inferred from SIA were corroborated by SCA. For cutthroat trout, northern pikeminnow, and yellow perch, the annual average proportion of fish prey in diets increased with increasing predator length and individual δ^{15}N values (Figure 2), demonstrating that increased piscivory was largely responsible for the increase in trophic position. The percentage of fish in the diet of yellow perch increased more rapidly than δ^{15}N as a function of length relative to the same relationship in cutthroat trout and northern pikeminnow; this was due to the higher reliance on small sculpins (lower δ^{15}N values than other forage fishes) by large yellow perch (16–30%) than by cutthroat trout and northern pikeminnow (<10%). The relatively higher δ^{15}N in small yellow perch than in small cutthroat trout and northern pikeminnow (Table 2) also contributed to the slower rise of δ^{15}N with length in yellow perch, owing to the higher δ^{15}N of pelagic larval fish and mysids

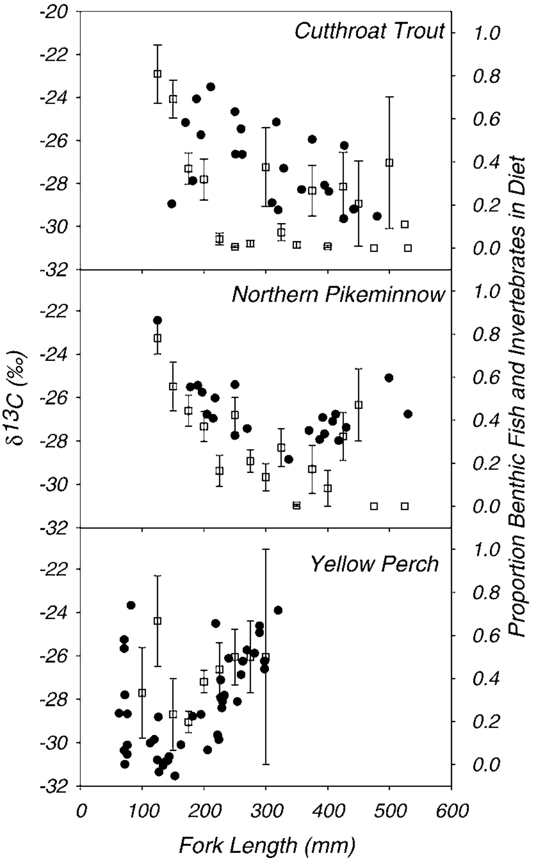

FIGURE 3.—Carbon stable isotope ratios (left axis; circles) inferring benthic orientation and the proportion of benthic fish and invertebrates in the diet (right axis; squares) for cutthroat trout, northern pikeminnow, and yellow perch in Lake Washington as a function of fish length. Stable isotope values are for individual fish; diet proportions are averages ± SEs for fish binned into 25-mm increments. The number of fish contributing to each mean is the same as in Figure 2.

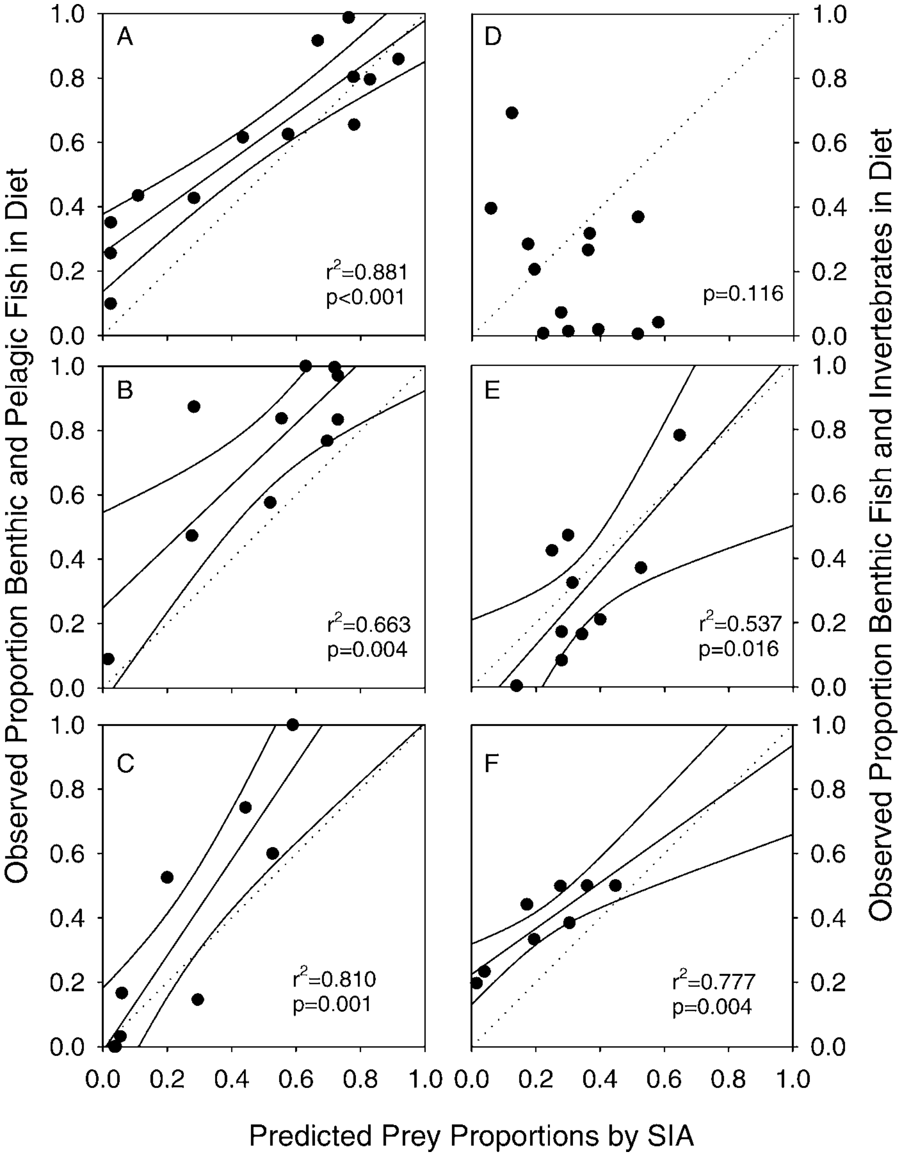

FIGURE 4.—Predicted versus observed prey proportions in the diets of cutthroat trout for individual fish grouped into 25-mm length increments. Panels **(A)**–**(C)** pertain to fish prey, panels **(D)**–**(F)** to benthic prey. The predicted proportions are summed diet proportions generated by the isotope mixing model as described in the text (SIA = stable isotope analysis). Each plot shows the 1:1 line of agreement. Regression lines and 95% confidence intervals are presented for significant regressions.

consumed by small yellow perch and the lower $\delta^{15}N$ of benthic invertebrates preferred by small cutthroat trout and northern pikeminnow (Table 1). The agreement of ontogenetic trends in stable nitrogen values with trends in the observed diet was supported by the stable isotope mixing model. Model predictions of the proportion of fish (benthic and pelagic) in the diet were significantly correlated with observed proportions of all fish in the diets of cutthroat trout, northern pikeminnow, and yellow perch (Figure 4a–c), and slopes were not significantly different from 1.0 at a confidence level of 95%. Intercepts for these regressions included 0 for cutthroat trout at a confidence level of 96% and for northern pikeminnow and yellow perch at a confidence level of 95%.

Trends in the annual average proportion of benthic items in the diet followed trends in individual $\delta^{13}C$ values (Figure 3), though the trends were less congruent than for trophic position (Figure 2), particularly for cutthroat trout. The estimated proportion of benthic prey in the annual diet of mid-size cutthroat trout was generally lower than was suggested by their $\delta^{13}C$ values. Among large cutthroat trout, benthic invertebrates were more prevalent in the diet during fall and winter (Table 1), periods for which diet was under-represented for mid-size cutthroat trout. These trends were also reflected in the results of the mixing model; the mixing model predictions of the proportion of benthic items in the diet were significantly correlated with observed diet proportions for northern pikeminnow and yellow perch but not for cutthroat trout (Figure 4d–f). The regression line had a slope of 1.0 for northern pikeminnow and yellow perch, but the intercept for northern pikeminnow was not significant ($P = 0.511$) and that for yellow perch was significantly greater than 0.

Predatory Fishes: Seasonal Diet Shifts

Among large cutthroat trout, benthic prey were most prevalent in the diet during winter months (Table 1) and largely consisted of chironomid pupae. Large northern pikeminnow and yellow perch relied heavily on benthic fish or invertebrate prey during winter and spring (Table 1). The single most common benthic prey consumed by yellow perch during both periods were small (32–98 mm) sculpins. Northern pikeminnow also focused on sculpins during winter, but consumed a diversity of benthic prey during spring, including sculpins, chironomids, crayfish, aquatic insects, gastropods, and trichopteran larvae.

Predatory Fishes: Historical Comparison

Benthic prey represented 18% of the diet of large northern pikeminnow during 2002–2003 and 68% during 1972. Benthic contribution to the diet of adult yellow perch (>139 mm) was 32% during 2002–2003 and 39% during 1974–1975. Fish represented 88% of the diet for large northern pikeminnow during 2002–2003 and 85% during 1972 and represented 26% of the diet for adult yellow perch (>139 mm) during 2002–2003 and 27% during 1974–1975. Consumption of sculpins by both northern pikeminnow and yellow perch in the 1970s was greater than that in 2002–2003, whereas consumption of pelagic fishes increased from 34% in the 1970s to 80% in 2002–2003 for northern pikeminnow and increased from 12% in the 1970s to 19% in 2002–2003 for yellow perch.

Planktivorous Pelagic Fishes

Seasonal differences in isotopic signatures were evident for longfin smelt, threespine sticklebacks, and juvenile sockeye salmon (Table 2). Changes in isotope ratios over the first winter were coincident with significant increases in weight for longfin smelt (*t*-test: $P < 0.001$) and threespine sticklebacks ($P < 0.001$) but not for juvenile sockeye salmon ($P = 0.527$). Age-1 longfin smelt grew substantially over the summer but showed almost no growth over the winter. From early fall to late winter (October–March), $\delta^{15}N$ values increased significantly for age-0 longfin smelt (ANOVA: $P < 0.001$; Tukey post hoc test: $P = 0.018$), threespine sticklebacks (*t*-test: $P = 0.019$), and sockeye salmon (*t*-test: $P = 0.048$). During the same period, $\delta^{13}C$ values decreased significantly for longfin smelt (ANOVA: $P < 0.001$; Tukey post hoc test: $P < 0.001$) and threespine sticklebacks (*t*-test: $P < 0.001$) but did not change for juvenile sockeye salmon (*t*-test: $P = 0.527$). For age-1 longfin smelt, $\delta^{15}N$ values declined and $\delta^{13}C$ values increased over time.

During late spring through fall, age-0 planktivores fed primarily on *Daphnia*, whereas copepods were the main component of the diet during winter through late spring (Figure 5). Age-0 longfin smelt also consumed mysids, benthos, and larval fish. Age-1 longfin smelt ate much more benthos and larval fish than did age-0 longfin smelt. Benthos became increasingly important to the diet of age-1 sockeye salmon during fall and winter.

Pelagic Invertebrates

Trophic position among most pelagic invertebrate samples was similar; $\delta^{15}N$ values ranged from 11.9‰ to 13.0‰. The exception was the winter sample of bulk zooplankton, which had a very elevated $\delta^{15}N$ value of 16.6‰ (Table 2) and was composed almost entirely of copepods (>99.9% by volume; *Eudiaptomu* : *Diacyclops* ≈ 2:1; J. Scheuerell, School of Aquatic and Fishery Sciences, University of Washington, personal communication), whereas *Daphnia* contributed 5–29% of the bulk zooplankton volume during the other seasons. The carbon source for pelagic invertebrates showed a shift across seasons; $\delta^{13}C$ increased through the winter and early spring and decreased thereafter, ranging from −31.7‰ to −25.2‰.

Benthic Species

Average stable isotope values for unionid mussels differed less than 0.5‰ among the three study sites for $\delta^{15}N$ (ANOVA: $P = 0.21$) or $\delta^{13}C$ ($P = 0.72$). For other benthic invertebrates, some spatial differences existed for both $\delta^{15}N$ and $\delta^{13}C$; however, trends were not consistent and only average values are reported (Table 2). For prickly sculpins that were pooled across all sites and seasons, $\delta^{15}N$ values were not correlated with size, but $\delta^{13}C$ exhibited a significant decline with increasing length (Figure 6). Trophic position of prickly sculpins

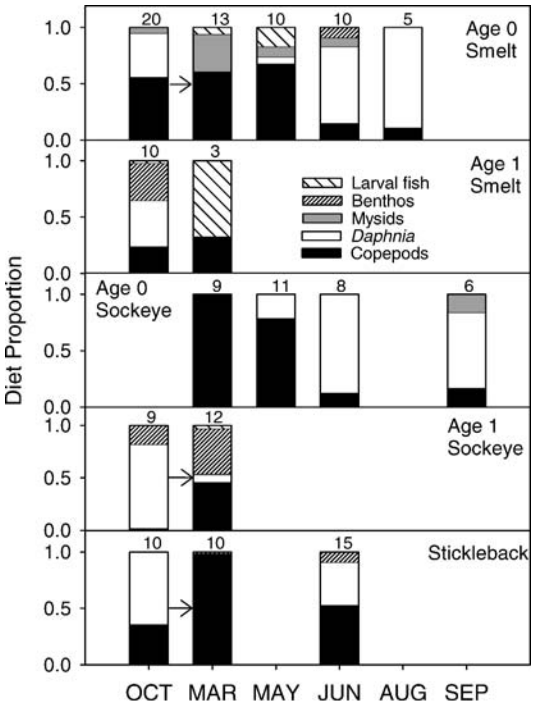

FIGURE 5.—Seasonal diet composition (proportion of stomach content wet weight) for longfin smelt, juvenile sockeye salmon, and threespine sticklebacks in Lake Washington. Sample sizes are shown for each average diet. Age-0 longfin smelt diets follow the strong year-class cohort through time starting in October 2002. Age-1 longfin smelt diets are for October 2003 (strong year-class) and March 2003 (weak year-class). Arrows indicate the period over which $\delta^{15}N$ increased significantly for age-0 fish.

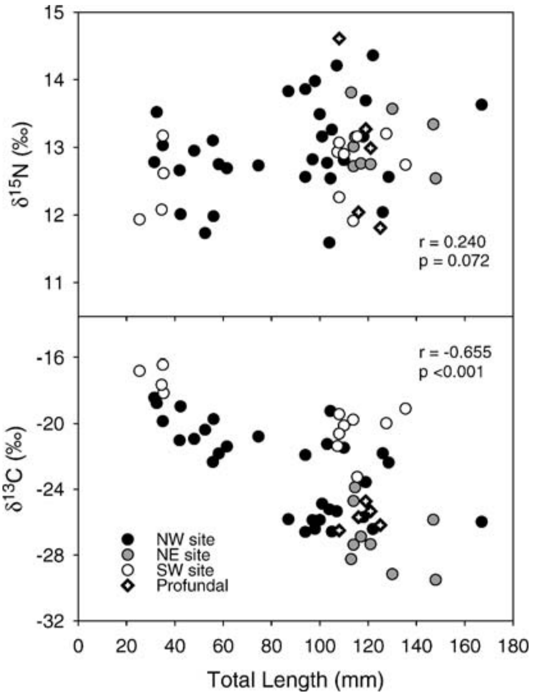

FIGURE 6.—Stable isotope ratios of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) in prickly sculpins from three littoral sites (northwest, northeast, and southwest) and one profundal site in Lake Washington. The $\delta^{15}N$ and $\delta^{13}C$ values for fish smaller than 75 mm are muscle corrected as described in the text. Test statistics are for all sites combined.

as indicated by $\delta^{15}N$ did not vary among the three littoral sites (ANOVA: $P = 0.497$), but significant differences in carbon source were present (ANCOVA with length as a covariate: $P < 0.001$). Among large prickly sculpins (>95 mm), $\delta^{13}C$ values were distinct at all three sites (ANOVA: $P < 0.001$); SW had the highest value, followed by NW and then NE (Tukey post hoc test: $P \leq 0.008$). The $\delta^{13}C$ values for large profundal sculpins were similar to those for large sculpins at the NE and NW sites but were significantly lower than the values at the SW site ($P < 0.001$).

Discussion

Stable isotope ratios and annual diet proportions both showed that cutthroat trout and northern pikeminnow in Lake Washington shifted ontogenetically from benthic omnivory to pelagic piscivory, whereas yellow perch smaller than 100 mm FL ate a highly variable diet of limnetic and benthic invertebrates then shifted first to pelagic zooplanktivory followed by benthic piscivory. The early variable feeding by juvenile yellow perch has also been reported for juvenile Eurasian perch *Perca fluviatilis* (Olsson et al. 2000; Burreau et al. 2004). Although the littoral area of Lake Washington occupies less than 20% of total surface area, littoral–benthic pathways contribute significantly to the energy budgets of different life stages or species of the major fishes in Lake Washington. Benthic–littoral production supported juvenile cutthroat trout and northern pikeminnow until they grew large enough to exploit the pelagic planktivore community. Conversely, yellow perch used relatively more pelagic resources as juveniles than as adults. Large yellow perch also consumed pelagic planktivores but to a lesser degree than did cutthroat trout and northern pikeminnow. Yellow perch did not grow as large as the other piscivores and showed less spatial–temporal overlap with the pelagic planktivores. Thus, yellow perch were relatively minor predators on the planktivore population. Instead, piscivory by yellow perch concentrated heavily on smaller-bodied benthic cottids. That all three of these species link benthic and pelagic prey across life history stages suggests that ontogenetic habitat coupling is common in Lake Washington fishes.

Values of δ^{15}N among Lake Washington benthic primary consumers ranged from 7.9‰ to 9.3‰. Indicative of a system impacted by anthropogenic inputs (Cabana and Rasmussen 1996), this finding was not surprising because Lake Washington is surrounded by human development and has a long history of human disturbance, including cultural eutrophication and recovery (Edmondson 1994). Currently, the lake receives outfall from combined sewer overflows (CSOs) that are being phased out but are still active during heavy storm events. In addition, the lake receives surface runoff from its urban tributaries and from the 65% of the shoreline composed of lawn, garden, or impervious surface (Toft 2001). Despite these and other human disturbances, there were no consistent spatial differences in stable isotope values at or near the base of the littoral food web among the three sites sampled for this study. Differences may have been observed had we sampled at extreme sites; for example, where specific inputs such as tributaries or active CSOs occur.

Reviews of the diets for common fish species in north-temperate lakes of North America found that secondary benthic production was vital in supporting production at higher trophic levels and that even "pelagic" fishes were at least partially supported by zoobenthos (Schindler and Scheuerell 2002; Vander Zanden and Vadeboncoeur 2002). This was certainly true of piscivores in Lake Washington; benthic prey contributed approximately 20% to the annual diets of the largest cutthroat trout and northern pikeminnow and represented 44% of the annual diet of yellow perch.

In other western lakes, stable isotope studies, alone or paired with diet studies, also showed ontogenetic shifts in diet among top predators (Johnson et al. 2002; Vander Zanden et al. 2003; Clarke et al. 2005), albeit for different dominant species (often lake trout *Salvelinus namaycush*, brown trout *Salmo trutta*, or bull trout *Salvelinus confluentus*). Similar to cutthroat trout and northern pikeminnow in Lake Washington, top predatory fishes in other western lakes became increasingly piscivorous as they grew, while contributions from benthic sources tended to decrease with size. In relatively oligotrophic lakes, the overall contribution of benthic prey to the diets of large piscivores was higher (Vander Zanden et al. 2003; Clarke et al. 2005) than for cutthroat trout and northern pikeminnow in Lake Washington and was comparable to that of Blue Mesa Reservoir, which possesses a similar trophic status as Lake Washington (Johnson et al. 2002). In the mesotrophic Lake Granby, δ^{13}C did not change with piscivore size (Johnson et al. 2002), but a lack of smaller lake trout confounded this finding. In general, benthic contributions to piscivore diets were inversely related to lake trophic status in these oligotrophic to mesotrophic western lakes, supporting the hypothesis that benthic contributions to fish production follow a bimodal distribution with lake trophic status.

Although cutthroat trout were not common enough during recovery from eutrophication to be included in historical diet studies (Eggers et al. 1978), historical data for northern pikeminnow and yellow perch indicate altered importance of benthic pathways to the diets of apex predators, consistent with our hypothesis. Benthic prey were much less important to northern pikeminnow in Lake Washington during the current study than during the recovery from eutrophication. The difference was due mostly to the lower importance of sculpins in the current diet of northern pikeminnow compared with that in 1972. Benthic prey were slightly less important to yellow perch in 2002–2003 than during the later stages of recovery from eutrophication. Sculpins were also less important in the diet of yellow perch in 2002–2003 than during 1974–1975. Reduced consumption of sculpins did not reduce the overall importance of fish to apex predators in Lake Washington; reduced consumption of sculpins was compensated by increased consumption of pelagic fishes for both species. Therefore, as the trophic status of Lake Washington shifted from eutrophic to the current mesotrophic state, the importance of benthic pathways to the production of top piscine predators was reduced in agreement with the theoretical importance of benthos for lakes at lower and higher, but not intermediate, trophic status.

Ontogenetic habitat coupling was also evident in prickly sculpins. Diet studies have reported an increased reliance on mysids as sculpins grow (Rickard 1980; Mazur 2004), substantiating the shift to more pelagic carbon signals with sculpin size. In addition, prickly sculpins moved out of the littoral zone as temperatures increased in Lake Washington (Rickard 1980), as has been observed for cottids in other lake systems (Ruzycki and Wurtsbaugh 1999), which would increase their accessibility to benthopelagic prey. Seasonal shifts between profundal and littoral habitats may help explain why the δ^{13}C values of profundal sculpins were indistinct from those of similar-sized sculpins caught in the littoral zone at the NW and NE sites. Large sculpins at the SW site had distinctly littoral values reflecting the difference in their location of capture ($<$1 m deep in an isolated boulder patch) compared with that of large sculpins at the NW and NE sites (5 m deep on featureless bottom substrate).

In addition to ontogenetic changes, cutthroat trout, northern pikeminnow, and yellow perch also exploited pelagic and benthic habitats across seasons. Because stable isotopes integrate dietary signal across seasons, SCA was very useful in demonstrating the seasonal importance of pelagic or benthic prey to the diets of large cutthroat trout, northern pikeminnow, and yellow perch. Pelagic planktivores were the most important prey in the annual diets of large cutthroat trout and northern pikeminnow (>75%) and represented more than 50% of the diet of large yellow perch during summer and fall. Benthic prey may therefore be an important dietary supplement for piscivores in Lake Washington. For example, the increased benthic contribution during winter and spring may be critical for maintaining fish condition when the availability of prey fish is limited. In other systems, piscivores switched from fish to benthic invertebrates when preferred prey became scarce (Hodgson and Kitchell 1987; Schindler et al. 1997; Baldwin et al. 2000). The ability of consumers to switch to alternative prey when preferred prey become scarce can impart greater stability to consumer populations (Post et al. 2000) by decoupling consumers from the dynamics of their preferred prey (Stein et al. 1995; Jeppesen et al. 1997; Schindler et al. 1997).

Nutrient translocation strengthens coupling of bentholittoral and pelagic habitats via lake mixing, when nutrients released in profundal waters from the detrital food chain are mixed throughout the water column. This process is potentially very influential because Lake Washington mixes throughout the winter, in contrast to many north-temperate lakes that only mix in spring and fall (Wetzel 1983). Bulk zooplankton samples (>135 μm) taken from Lake Washington at the end of winter exhibited higher δ^{15}N (16.6‰) than did samples from other seasons (11.9–13.0‰). In Lake Ontario, copepods and particulate organic matter (20–64 and 64–110 μm, respectively) showed elevated δ^{15}N during winter–spring but then dropped from approximately 18‰ to 10‰ at the onset of thermal stratification (Leggett et al. 2000). Leggett et al. (2000) postulated that to achieve such elevated δ^{15}N values, copepods may have fed on mixotrophic algae or members of the microbial loop using ^{15}N-enriched NH_4^+ made available by lake mixing. They suggested that the change to lower δ^{15}N values resulted from primary producers shifting to more ^{15}N-depleted NO_2^-/NO_3^- during stratification. A similar process could operate in Lake Washington. An alternative or further explanation could be that the winter sample of bulk zooplankton was composed almost entirely of copepods, whereas the remaining zooplankton samples were at least partially composed of *Daphnia*. Copepods are omnivorous (Thorp and Covich 2001), and carnivorous copepods have higher δ^{15}N values than herbivorous copepods (Kling et al. 1992) and cladocerans (Grey et al. 2001; Feuchtmayr et al. 2004). In addition, we might expect the cyclopoid copepods that dominated the zooplankton community during winter (Beauchamp et al. 2004) to be more carnivorous during the winter months when plant matter is much less abundant, thereby potentially further increasing the δ^{15}N of zooplankton during winter relative to that during other seasons. Further study of the trophic relationships of zooplankton and the δ^{15}N values of primary producers is needed to better understand these potential processes in Lake Washington.

The elevated δ^{15}N of zooplankton in Lake Washington during winter was probably responsible for the seasonal shifts in δ^{15}N observed in pelagic planktivores between October and March. Planktivores fed heavily on relatively ^{15}N-depleted *Daphnia* during their first summer and fall and then switched to ^{15}N-enriched copepods over the winter. Differences in the magnitude of the trophic shift for different planktivores could be related to differences in growth and diet composition over the winter period; threespine sticklebacks and age-0 longfin smelt grew over the winter, while juvenile sockeye salmon did not grow appreciably.

Vertical migration of macroinvertebrates can also transport nutrients from benthic–littoral to pelagic habitats. *Neomysis mercedis* in Lake Washington undertakes diel vertical migrations from daytime benthic refugia to the plankton-rich upper water column at night (Eggers et al. 1978; Murtaugh 1983). In Lake Washington, *N. mercedis* consumes both benthic and planktonic items (Murtaugh 1981), but the relative contribution of benthos to the diet has not been quantified. Whereas the stable carbon isotope ratio is helpful in identifying bentholittoral contributions to the diet, it cannot distinguish profundal carbon from limnetic carbon because they have the same carbon source (Vander Zanden and Rasmussen 1999). The δ^{15}N value of mysids (10.0–12.6‰) was similar to that of pelagic zooplankton ($\delta^{15}N = 11.9$–13.0‰, excluding February bulk zooplankton). With a trophic fractionation of approximately 3‰ (Gorokhova and Hansson 1999), mysids must have consumed a considerable proportion of very low trophic items like phytoplankton, benthic invertebrates, or detritus in Lake Washington. In general, mysids are considered omnivorous (Mauchline 1980). Based on evidence from SCA and SIA, the diet of *Mysis relicta* in Lake Ontario contained significant proportions of diatoms in spring and benthic amphipods in fall (Johannsson et al. 2001). Benthic prey were also important to pelagic *Mysis mixta* and *Mysis relicta* in the Baltic Sea, comprising 25–100% of their diet across sizes and seasons (Viherluoto et al. 2000). It is probable that benthic prey contribute significantly to the diet of *N. mercedis* in Lake Washington. As prey to both pelagic and benthic predators, *N. mercedis* is probably an important transporter of nutrients in Lake Washington because it migrates daily between benthic and pelagic habitats and consumes resources in both.

By means of fewer samples than required by the traditional SCA, SIA revealed ontogenetic shifts in trophic position and benthic orientation in cutthroat trout, northern pikeminnow, and yellow perch. In fact, the number of nonempty stomachs processed for SCA was at least five times the number of samples used in SIA. Although the ideal sample size needed for any given study will depend on the specific goals of that study and the temporal and ontogenetic scales of interest, sample ratios (SIA : SCA) of 1:9 cutthroat trout, 1:23 northern pikeminnow, and 1:5 yellow perch were effective in this study. Trends were also established with much less variability using SIA than SCA. Coefficients of variation (CV) for large apex predators indicated that for SCA to achieve the same CV as SIA, the number of samples would have had to increase by 190 times for cutthroat trout, 80 times for northern pikeminnow, and 340 times for yellow perch.

Owing to the relatively large number of samples processed for SCA, we were able to successfully demonstrate the comparability of SIA and SCA. Diet proportions derived by the mixing model from the stable isotope values were not expected to agree perfectly with the SCA estimates, because SIA and SCA were rarely conducted on the same individual and the results of SCA are inherently highly variable, especially when some size increments are represented by few individuals. Nonetheless, predicted proportions of fish and benthic prey from the mixing model generally agreed well with observed proportions in the diet. Some of the discrepancies between predicted and observed proportions warrant further explanation. For yellow perch, the predicted proportion of benthic prey in the diet was consistently lower than observed proportions. This discrepancy may have resulted from an assumption made when analyzing the diet data. Because it was not possible to distinguish between benthic and pelagic sculpin species in SCA and because most of the biomass in the lake is composed of benthic sculpins (Eggers et al. 1978), we assumed during SCA that sculpins in the diet of yellow perch were of benthic origin. If a significant proportion of these sculpins had in fact been of pelagic origin (i.e., the pelagic form of the coastrange sculpin), then the model predictions for benthic contributions to the diet of yellow perch would have better matched the observed proportions. Fish in the diet of northern pikeminnow was also under-predicted by the model relative to observed proportions. One explanation for this could be a trophic fractionation of less than 3.4‰ for δ^{15}N. Although few estimates of trophic level fractionation of ^{15}N have been reported for freshwater omnivores, fractionations of 2.3–3.8‰ were reviewed by Vander Zanden and Rasmussen (2001), who found that 70% of values were less than 3.4‰. In our model simulations, trophic fractionation values closer to 2.1‰ produced the best agreement between the predicted and observed proportions of fish in the diet of northern pikeminnow. Low sample sizes in certain seasons in SCA were probably responsible for the lack of agreement of predicted and observed proportions of benthic prey in the diet of cutthroat trout and probably decreased the agreement of predicted and observed values in general for the other species as well.

A further source of error in comparing the results of SIA and SCA was the effect of growth rate on the isotopic equilibrium between predators and prey. Because stable isotopes provided an integrated picture of consumption, periods of higher consumption and greater tissue production contributed more to the integrated isotope signal. By equally weighting monthly or seasonal diets, periods of higher consumption were underrepresented in the depiction of annual diets used in the mixing model. Diet proportions suggested by SIA should be more comparable to summed bioenergetically based consumption estimates (e.g., derived from Fish Bioenergetics 3.0: Hanson et al. 1997). The Wisconsin bioenergetics model calculates daily consumption of prey given diet proportions, predator growth, thermal regime, and prey energy densities.

Bioenergetics models could also be used to explore the enrichment in δ^{15}N observed in pelagic planktivores between October and March of their first year in the lake, by taking into account both patterns in prey δ^{15}N values and planktivore growth dynamics. Using seasonal δ^{15}N patterns in zooplankton similar to those observed in Lake Ontario, Harvey et al. (2002) used a bioenergetics model to simulate temporal patterns in δ^{15}N values in age-0, age-1, and adult alewives *Alosa pseudoharengus*. They were able to show that age-0 alewives could have higher δ^{15}N values than older alewives and that seasonal fluctuations in isotope ratios at the primary consumer level were still detectable at the secondary consumer level.

In conclusion, stable isotopes of nitrogen and carbon, in conjunction with SCA, showed that benthic and pelagic pathways contributed substantially to the production of different life stages and species of fish in Lake Washington. The predominant energy pathway for apex predators emanated from pelagic sources, whereas the most important benthopelagic coupling was formed by ontogenetic shifts in diet composition. Benthic pathways were critical to the early life stages of cutthroat trout and northern pikeminnow and to the older life stages of yellow perch. Furthermore, benthic production was an important supplement to seasonally available or insufficient supplies of preferred prey, such as the pelagic planktivores. We found that the importance of benthic pathways to apex predators was greater during recovery from eutrophication than currently; this finding is consistent with the hypothesized relationship between benthic contributions to fish production and lake trophic status. For the apex predators, SIA and SCA were comparable in delineating ontogenetic trends in piscivory and benthivory, although SIA established these trends with fewer samples and less variability. Used in combination, the two methods were complementary; stable isotopes provided integrated information on ontogenetic trends when stomach samples were seasonally limited, whereas stomach contents provided information on seasonal trends in diet that stable isotopes could not. Finally, bioenergetics models, in conjunction with stable isotope ratios, may be useful in further defining trophic interactions in Lake Washington, as well as exploring the seasonal influence of changing diets on stable isotope dynamics at lower trophic levels.

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