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Research Article

Carbon sources supporting fish growth in a north temperate lake

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Abstract. Lake consumers are supported by autochthonous organic matter produced by photosynthesis within the aquatic ecosystem and imported allochthonous material produced outside the ecosystem. To evaluate carbon sources that support fish growth, we enriched a 26 ha lake with inorganic ^{13}C. This labeled the autochthonous primary production and allowed us to determine the extent to which invertebrates in fish diets were supported by this autochthonous carbon. Fish autochthony was defined as the proportion ranging from 0 to 1 of fish growth derived from aquatic primary production. This proportion was calculated using the weighted average of each diet taxa's contribution to fish growth along with the autochthony of diet taxa estimated with dynamic models of δ^{13}C time series. Age 0 bluegill (*Lepomis macrochirus*) and yellow perch (*Perca flavescens*) had the highest autochthony (0.56, 0.57, respectively) because of greater use of zooplankton that were highly dependent on phytoplankton. Older fishes (age 1 and above) of all species had similar estimates of autochthony (mean = 0.47 standard deviation = 0.04) derived from feeding on either benthic invertebrates or other fishes. Proportional contribution of terrestrial prey (primarily terrestrial beetles) to fish growth was highest for bluegill (0.07–0.22) and substantially lower (<0.04) for largemouth bass (*Micropterus salmoides*) and yellow perch. Across species and ages ~ 45% of fish growth could not be attributed to terrestrial prey items or current autochthonous primary production. This residual detrital carbon source is a mixture of allochthonous material and autochthonous material derived from primary production prior to the ^{13}C addition. Fish growth and production in the study lake were not tightly coupled to the current season's primary production. Nearly half of the organic carbon supporting fish growth came from prior autochthonous primary production or allochthonous sources.

Key words. Stable isotopes; bioenergetics; allochthonous; autochthonous; detritus; benthic pathways.

Introduction

Food-web studies of lakes have quantified specific habitat and prey types that support fish populations but rarely determined the primary sources of organic carbon (Hecky and Hesslein, 1995; Vander Zanden and Vadeboncoeur, 2002). Organic matter that sup-

ports consumers can be produced within the ecosystem (autochthonous sources) or imported into the system (allochthonous sources). For lakes, food-web studies have traditionally focused on the autochthonous sources (phytoplankton, periphyton, macrophytes), assuming that the allochthonous sources (terrestrial inputs) are less important. There is growing evidence from streams (Nakano and Murakami, 2001; Kawaguchi et al., 2003), rivers (Finlay et al., 2002) and a few lakes (Carpenter et al., 2005; Mehner et al., 2005; Jansson et al., 2007) suggesting that allochthonous carbon sources are important subsidies to fish production. Much of the lake research has focused on allochthonous subsidies to zooplankton (Jones et al., 1999; Karlsson et al., 2003; Matthews and Mazumder, 2006; Jansson et al., 2007). Less is known about the relative roles of allochthonous and autochthonous carbon in supporting fish growth.

Quantifying the support of fish growth by organic carbon from different sources is difficult because terrestrial materials enter a lake through several pathways. Three forms of allochthonous carbon – dissolved, non-living particulates, and terrestrial organisms – can support lake food webs and contribute directly or indirectly to fish growth (Cole et al., 2006). Dissolved and particulate carbon represent the largest sources of terrestrial organic carbon to lakes, but uncertainty associated with the pathways and rates at which invertebrate consumers incorporate this carbon makes quantifying contributions to higher trophic levels difficult (Cole et al., 2006; Karlsson et al., 2007). Terrestrial organisms that support fish production span a wide taxonomic range and can function as consistent carbon sources throughout the growing season, or as infrequent but potentially large pulses associated with floods or insects that derive from terrestrial habitats (Mehner et al., 2005; Hodgson and Hansen 2005; Oliveira et al., 2006). In order to quantify carbon sources that support a fish community, an ecosystem approach is required to characterize multiple carbon pathways and account for contrasts in foraging behavior within and among fish species over a growing season.

Whole-lake additions of inorganic ^{13}C have proven successful in quantifying the source of carbon supporting consumers spanning multiple trophic levels (Cole et al., 2002; Pace et al., 2004). Benthic autochthonous primary production and allochthonous carbon have similar natural-abundances of δ^{13}C values, making it difficult to distinguish between these sources. ^{13}C enrichment labels the current autochthonous production in benthic and pelagic habitats and provides a means to separate in-lake and terrestrial sources. Using inorganic ^{13}C additions and a suite of time series models, Carpenter et al. (2005) estimated

that autochthonous carbon comprised 0.07–0.67 of fish growth in three different lakes, with the remaining growth attributed to allochthonous inputs. These experiments took place in small (< 3 ha) lakes with limited littoral habitats and simple fish communities. Thus, the importance of lake size, complexity of habitat, and/or food web structure is relatively unknown in determining carbon sources for fishes.
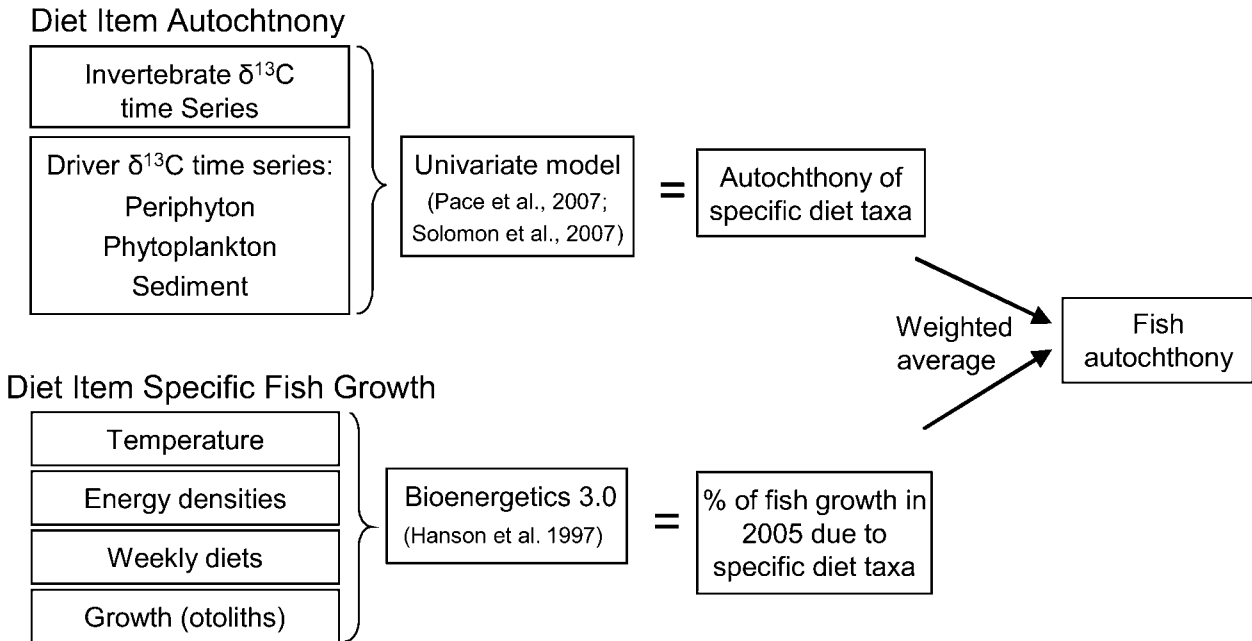
It is important to recognize that whole-lake ^{13}C additions estimate utilization of current autochthonous production because only the carbon fixed during the period of experimental addition is labeled. Autochthonous carbon fixed prior to the manipulation is not labeled, and the autochthony of organisms that assimilate this organic matter is therefore underestimated. The magnitude of the underestimate is small for pelagic consumers (Carpenter et al., 2005) but may be significant for benthic consumers (Solomon et al., 2008) and detrital pathways in general (Moore et al., 2004). For the purposes of this paper, we interpret our estimates as measures of current autochthony over the course of the experiment, or as lower bounds of autochthony over the complete lifespan of the consumer.

In 2005, we conducted a ^{13}C addition in a 26 ha, clear water lake to determine the importance of autochthonous carbon sources in supporting fish growth. We measured diets and growth rates for a number of age classes of three fish species and tracked the δ^{13}C of fish prey from May through October. We quantified the proportion of fish growth due to different diet taxa and used mass balance models to estimate the autochthonous carbon contributions to fish growth. Our objectives were to: 1) estimate the proportion of fish growth due to both autochthonous production during the ^{13}C addition and terrestrial prey directly consumed by fish; 2) use life history descriptions of major invertebrate taxa found in fish diets to assign fish growth to specific lake habitats; and 3) relate our findings to similar lake studies to explore potential factors that may influence the proportional importance of different carbon sources to fishes.

Methods

Site description and ^{13}C addition
Crampton Lake is located in a forested watershed of the University of Notre Dame Environmental Research Center (89° 32' W, 46° 13' N). This lake has a maximum depth of 18.5 m, a mean depth of 3.5 m and average nutrient levels in the mixed layer of 3.7 mg/L for dissolved organic carbon, 9.2 µg/L for total phosphorus, and 239 µg/L for total nitrogen during the open water season. This lake is more than 10 times

Diet Item Autochtnony

Invertebrate $\delta^{13}C$ time Series

Driver $\delta^{13}C$ time series:
Periphyton
Phytoplankton
Sediment

Univariate model
(Pace et al., 2007;
Solomon et al., 2007)

= Autochthony of specific diet taxa

Weighted average

Fish autochthony

Diet Item Specific Fish Growth

Temperature

Energy densities

Weekly diets

Growth (otoliths)

Bioenergetics 3.0
(Hanson et al. 1997)

= % of fish growth in 2005 due to specific diet taxa

Figure 1. Structure of data collection and analyses used to calculate fish autochthony estimates in Crampton Lake, 2005.

larger by area than sites of previous additions (Carpenter et al., 2005) and is larger than more than 80 % of the lakes in the Northern Highland Lake District of Wisconsin and the Upper Peninsula of Michigan (Hanson et al., 2007). The average 1 % light level during this study was 9 m and thermocline depth ranged from 2 to 6.5 m. The littoral zone contains macrophytes (predominantly *Sparganium* sp. and *Eriocaulon aquaticum*) and coarse woody material. Benthic substrates consist of mostly organic matter and fine sediments. Bluegill (*Lepomis macrochirus*), largemouth bass (*Micropterus salmoides*), and yellow perch (*Perca flavescens*), dominate the fish community (> 95 % biomass), with less abundant populations of pumpkinseed (*Lepomis gibbosus*), Johnny darter (*Etheostoma nigrum*), golden shiner (*Notemigonus crysoleucas*), and central mudminnow (*Umbra limi*) also present. The lake receives limited angling pressure and no harvest. Fish abundance, community structure, and overall biomass reflect the absence of fishing mortality.

To increase the ^{13}C of the lake's primary production, $NaH^{13}CO_3$ (> 99 % ^{13}C content) was added to the upper mixed layer each morning for 56 days from 13 June to 7 August 2005. The $NaH^{13}CO_3$ was dissolved in gas tight carboys filled with lake water, then pumped into the lake from a moving boat at a depth of 0.7 m while the boat traveled in a path that covered the entire lake area. This practice promoted dispersions throughout the mixed layer. ^{13}C additions elevated the $\delta^{13}C$ of lake water DIC from an initial value of approximately -12‰ to values in the range of 5‰ to

15‰. Dissolved ^{13}C values decreased within a week after the ^{13}C addition had ceased. Detailed information on the ^{13}C enrichment procedures are available in Carpenter et al. (2005) and Pace et al. (2007).

In this study we measured diet and growth for a number of age classes of three species of fishes and tracked the $\delta^{13}C$ of fish prey from May through October. For each species and age class of fishes that we considered, we determined the proportion of growth attributable to each prey taxon using bioenergetic modeling. Autochthony of those diet taxa was estimated by time series modeling of $\delta^{13}C$ measurements (as elaborated below). We combined these estimates in a weighted average to estimate fish autochthony (Fig. 1). Variability in both our estimates of prey taxa autochthony and bioenergetic estimates of prey contributions to fish growth were assessed through a Monte Carlo resampling approach. Our reported autochthony values are the mean and standard deviations from this approach.

Diet taxa autochthony
We fit dynamic models to $\delta^{13}C$ time-series of sampled invertebrates over the course of the addition and then used those results to estimate autochthony of fish diet taxa. Static mixing models, commonly used in natural abundance stable isotope studies, are not applicable because baseline $\delta^{13}C$ values change during the addition experiment. We used invertebrate autochthony estimates from previously published papers (Pace et al., 2007; Solomon et al., 2008) as well as estimates of autochthony using invertebrate $\delta^{13}C$

time-series sampled directly from fish diets. Weekly invertebrate $\delta^{13}C$ samples from diets (3–55 individuals) were collected from all fish species and size classes. Invertebrates were thoroughly rinsed with deionized water, dried at 60°C for 72 hours, and homogenized. Isotope analyses were conducted at the University of California, Davis Stable Isotope Laboratory.

We used the model of Solomon et al. (2008) to estimate the autochthonous proportion of diet taxa as given in equation 1:

$$X_t = w\,[\,(1-m)P_t + mP_{t-u}\,] + (1-w)\,S_t \qquad (1)$$

The value of (X_t) represents the $\delta^{13}C$ of an invertebrate prey taxon (X) on day t. Invertebrate $\delta^{13}C$ is modeled as a function of two drivers: $\delta^{13}C$ of periphyton (P_t) and $\delta^{13}C$ of a detrital resource representing organic matter in the sediments (S_t). Solomon et al. (2008) found no difference in autochthony estimates using the phytoplankton or periphyton time series. We used the periphyton time series for benthic invertebrate calculations as the indicator of autochthonous ^{13}C. Contribution of the current autochthonous carbon to a consumer is estimated by the parameter w $(0 \leq w \leq 1)$. Time lags between autochthonous production and its incorporation into the food web were estimated by contributions from the current autochthonous resource pool, then further divided into a fraction m $(0 \leq m \leq 1)$ from day t-u and a fraction (1-m) from day t. Previous studies demonstrated that this distinction substantially improved model fits (Pace et al., 2004). We used a profile likelihood analysis to find the value of u that minimized variance (Burnham and Anderson, 1998), and then estimated w and m by least squares using an optimization routine in the R statistical package. Uncertainty in our estimates of the model parameters m and w was estimated by bootstrapping the model residuals of the observed invertebrate $\delta^{13}C$. We added this randomly resampled residual error to the invertebrate $\delta^{13}C$ observations and refit the model (N = 1000) to create new estimates of m and w (Efron and Tibshirani, 1993). Uncertainty in our parameter estimates is represented as the standard deviation of these 1000 estimates. Previously published autochthony estimates and variability for Cladocera, Copepoda, and *Chaoborus sp.* were from Pace et al. (2007) and Diptera estimates were from Solomon et al. (2008). Additional details concerning primary producer and invertebrate $\delta^{13}C$ sample collection and processing are available in Pace et al. (2007) and Solomon et al. (2008).

Fish collection and analyses

The age classes analyzed for each fish species were chosen based on our ability to consistently sample diets from known age classes and to represent potential diet shifts within a species as associated with trophic ontogeny. The number of samples used to characterize the weekly diet of each fish group ranged from 4 -104 diets/week (average 13.5). During each week, sampling was conducted in both the littoral and pelagic zones to account for differences in lake habitats where fish were feeding. The majority of fish were collected in the littoral zone using a combination of angling and boat electrofishing. Weekly purse seining (June-August) in the deepest portion of the lake captured young of year yellow perch and bluegill during their pelagic phase but did not catch any older fishes. Gastric lavage was conducted on fish greater than 80 mm within 20 minutes of capture. Smaller fish were immediately euthanized with an overdose of MS-222 and stored on ice until their stomachs were dissected. Weekly collections during May-August were made during 3 time periods (0600–0800, 1300–1500, 1900–2100) in a given day to account for potential diel differences in diet. We assumed that the 0600–0800 samples would include prey consumed during the nocturnal periods. September and October diets were collected between 0900 and 1200. Additional diets collected during May and early June of 2006 supplemented early spring diet descriptions of age 1 bluegill (n = 55) and age 1 yellow perch (n = 64).

Fish diets were characterized for 33 different diet taxa. Benthic invertebrates and zooplankton were identified to order. Fish prey were identified to species and categorized based on whether they were young of year (YOY) or age 1+. Intact diet items were separated, counted, dried at 60°C for 72 hours and weighed to the nearest milligram. For partially digested or masticated items, counts were based on unique body parts (e.g. heads, tail spines). The dry weight of those items was based on counts and the average dry weight of that diet category.

Growth for a given age class and species was based on sectioned saggitae otoliths collected from fishes during May and June 2006. Otoliths were mounted in epoxy and a transverse section (~200 μm) was cut using a low speed saw. Interpreted annuli were measured along a radius centered at the origin and oriented perpendicular to annual growth marks. Change in length of an individual fish was estimated from the last annual growth increment (2005) using the direct-proportion back calculation method. Change in biomass of individual age classes was calculated from species-specific length-weight relationships developed from Crampton Lake over the

course of this study. Bioenergetics modeling used the average growth in 2005 for all individual fish in a given species and age class.

Bioenergetic modeling ascribed fish growth during 2005 to different diet taxa for bluegill ages: 0,1, 3, 4, and 6; yellow perch ages 0 and 1; and largemouth bass ages 1, 3, and 6. Model inputs were species and age specific average yearly growth (grams) and weekly diet proportions as well as daily mean water temperature measured at 1.5 m depths. Simulations were run from May-October 2005 except for age 0 fish simulations, which started when bluegill and yellow perch fry were first captured. We used the species and stage specific bioenergetic parameters found in Hansen et al. (1997) for each fish species. Predator and prey energy densities were based on literature values (Cummins and Wuycheck, 1971) and those summarized in Hansen et al. (1997).

Fish autochthony and carbon sources

Fish autochthony was calculated as a weighted average of fish growth due to specific diet taxa and autochthony estimates for those diet taxa (Fig. 1). We accounted for variability in our diet data and invertebrate autochthony estimates using a Monte Carlo resampling approach. For each week, individual fish diets were resampled with replacement and bioenergetic models were run to produce new estimates growth specific for each diet taxon. Diet item autochthony estimates were resampled based on their distributions and a new weighted average of fish autochthony was calculated. Herein, we report the average and variability of the autochthony estimates from 50 Monte Carlo simulations conducted for each species and age class. For rare diet items, we assumed autochthony followed a uniform distribution from 0 to 1 with a mean of 0.5. These rare diet items included: Amphibia, Amphipoda, Gastropoda, Hirudinea, Lepidoptera, and Bivalvia. For any species or age class of fishes, these prey items represented < 3 % of total fish consumption or growth by mass. We calculated the autochthony of juvenile bluegill, yellow perch, and largemouth bass first so these estimates could be used for calculating autochthony of piscivores.

We characterize the energy supporting fish growth into three categories: autochthonous, allochthonous, and detrital. Autochthonous carbon is represented by the average of our estimates. Allochthonous carbon is the fish growth attributable to terrestrial prey items directly consumed by fishes, and detritus represents the remaining portion. None of the species we considered consume detritus directly. We estimated how different lake habitats contribute to fish growth by categorizing fish diet taxa as terrestrial, pelagic, and benthic based on life history descriptions (Merritt

and Cummins, 1996; Smith and Pennak, 2001). Using this method provided the percentages of benthic, pelagic, and terrestrial taxa in prey fishes that contribute proportionally to piscivore growth.

Results

Autochthony of diet taxa

Pelagic and benthic invertebrates differed in their response to the ^{13}C addition (Fig. 2). Pelagic invertebrate carbon pools in Crampton Lake were more dependent on autochthonous carbon than those of benthic invertebrates (Pace et al., 2007; Fig. 2). Proportion autochthony was 0.69 for Cladocera and 0.98 for the dominant copepod, *Leptodiaptomus minutus* (Table 1). Trichoptera had the highest estimated autochthony of all benthic invertebrates (mean = 0.62, s.d. = 0.09), while Decapoda and Ephemeroptera had the lowest autochthony (mean = 0.23 and 0.10, respectively) (Table 1). The autochthonous carbon contribution of Diptera varied with depth (Fig. 2). High variability in $\delta^{13}C$ of diet-collected Diptera reflected variation in fish feeding over depth (Fig. 2). To account for this diet variability in fish autochthony estimates, we averaged the Diptera autochthony estimates from Solomon et al. (2008) and accounted for the increased uncertainty in the Monte Carlo simulations (s.d. = 0.15; Table 1). $\delta^{13}C$ of adult Odonata (range = −25.6 to −26.5) confirmed these diet items were correctly classified as terrestrial invertebrates (Fig. 2).

Carbon sources supporting fish growth

Back-calculated fish growth estimates from 2005 determined the change in biomass for each species and age class (Table 2). Although 33 potential diet categories were used to describe the diets, most of the growth for each species and age class was attributed to six or fewer diet categories (Fig. 3). For example, bluegill growth was primarily the result of feeding on Trichoptera, Odonata, Diptera, terrestrial invertebrates (predominantly Coleoptera) and Cladocera (Fig. 3). These same diet items made up the majority of age 0 yellow perch growth, whereas age 1 perch diets consisted mainly of Odonata (> 60 %). Zooplankton were only important to the growth of juvenile fishes, specifically age 0 and age 1 bluegill, and age 0 yellow perch (Fig. 3). Largemouth bass growth was principally attributed to fish prey, with age 0 and age 1 yellow perch and bluegill supporting the majority of bass growth (Fig. 3). Adult Odonata was the predominant terrestrial item contributing to largemouth bass growth, but diets also included Coleoptera, small mammals, and arachnids.
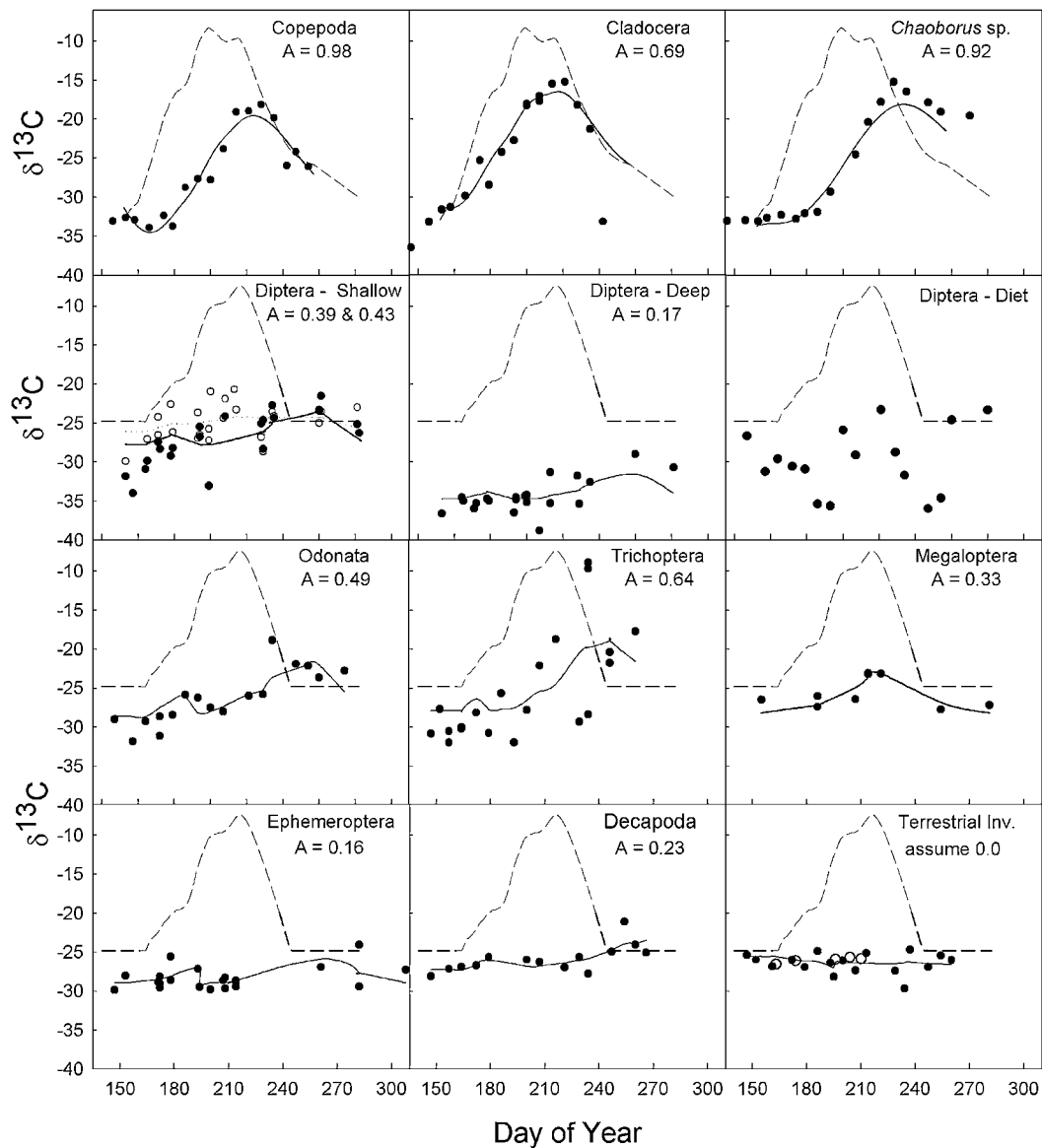
Figure 2. Measured (filled circles) and modeled (solid line) $\delta^{13}C$ for invertebrate taxa in Crampton Lake, 2005. The phytoplankton $\delta^{13}C$ time series (dashed line) was used for the top three pelagic invertebrate taxa. The periphyton $\delta^{13}C$ series was used for all benthic invertebrate and terrestrial taxa. Autochthony estimates from univariate models are noted in the upper right corner of each graph (”A = ”). The *Diptera – Shallow* panel shows Diptera $\delta^{13}C$ observations and model from depths of 1.5 m (open circles, dotted line) and 3.5 m (filled circles, solid lines). The *Terrestrial Inv.* panel includes samples from terrestrial Coleoptera, arachnids, and adult Odonata (open circles).

In general, autochthony was consistent among species but decreased slightly from age 0 to adult fish. Age 0 yellow perch and bluegill had the largest proportion of growth due to current autochthonous production, 0.65 (Fig. 4). Bluegill autochthony varied with ontogeny, decreasing to < 0.40 in ages 1–4 and then increasing slightly for age 6. Largemouth bass and yellow perch showed similar declines in autochthony with trophic ontogeny; however, the decreases were not as sharp as bluegill (Fig. 4). Average autochthony was 0.46 (s.d. = 0.05) for all fish species and age classes sampled.

The relative importance of terrestrial prey to fish growth differed between species and across ontogeny. Bluegill ages 1–6 had the largest proportion of growth directly attributable to terrestrial prey items (mean = 0.19, s.d. = 0.05; Fig. 5a). Conversely, no age classes of yellow perch or largemouth bass derived more than 0.04 of their growth from terrestrial prey items (Fig. 5a). Prey from benthic habitats contributed substantially more to bluegill and yellow perch growth than prey from pelagic habitats (means = 0.74 and 0.15, respectively; Fig. 5a). The proportion of fish growth not attributable to either autochthonous

Table 1. Autochthony estimates and standard deviations for fish diet taxa, Crampton Lake, 2005. For rare diet items we assumed autochthony followed a uniform distribution from 0 to 1 with a mean of 0.5. These include taxa within the Amphibia, Amphipoda, Gastropoda, Hirudinea, Lepidoptera, and Bivalvia. For any species or age class of fishes, these prey items combined represented < 3 % of total fish consumption or growth by mass.

Diet Item	Autochthony	s.d.	Source
Pelagic			
Cladocera	0.69	0.05	Pace et al. (2007)
Chaoborus sp.	0.92	0.03	Pace et al. (2007)
Copepoda	0.98	0.06	Pace et al. (2007)
Hydracarina	0.92	0.03	all zooplankton-Pace et al. (2007)
Unidentifiable Zooplankton	0.92	0.03	all zooplankton-Pace et al. (2007)
Leptodora kindti	0.92	0.03	all zooplankton-Pace et al. (2007)
Benthic			
Odonata	0.47	0.06	$\delta^{13}C$ time series from diet items
Decapoda	0.24	0.10	$\delta^{13}C$ time series from diet items
Trichoptera	0.62	0.09	$\delta^{13}C$ time series from diet items
Ephemeroptera	0.16	0.12	$\delta^{13}C$ time series from diet items
Megaloptera	0.19	0.14	$\delta^{13}C$ time series from diet items
Diptera	0.33	0.15	Mean all depths-Solomon et al. (2008)
Terrestrial			
Mammal	0.00	0.00	Assume zero
Terrestrial Invertebrate	0.00	0.00	Assume zero
Fish			
Yellow Perch YOY	0.57	0.07	Calculated this study
Yellow Perch Age1	0.47	0.03	Calculated this study
Bluegill YOY	0.56	0.06	Calculated this study
Bluegill Age1	0.38	0.04	Calculated this study
Largemouth Bass YOY	0.51	0.04	Calculated this study
Largemouth Bass Age1	0.56	0.04	Calculated this study
Johnny Darter	0.47	0.03	Assume Yellow Perch Age1
Central Mudminnow	0.47	0.03	Assume Yellow Perch Age1
Unidentifiable Fish	0.47	0.03	Assume Yellow Perch Age1

Table 2. Bioenergetic model parameters used in Bioenergetics 3.0 (Hanson et al., 1997) simulations for each fish species and age class from Crampton Lake, Wisconsin 2005. Differences in model time frame for age 0 fish reflect the first day age 0 fish of either species were captured.

Species	Age	Change in length (mm)	Growth (g)	Diets Examined	Model Time Frame	Spawning (% loss)	Bioenergetics Model Parameters Used
Bluegill	0	12–43	1.0	102	Jul 5–Oct 16	–	Kitchell et al. 1974, juvenile
Bluegill	1	43–73	4.1	507	May 19–Oct 16	–	Kitchell et al. 1974, juvenile
Bluegill	3	97–130	20.9	353	May 19–Oct 16	–	Kitchell et al. 1974, juvenile
Bluegill	4	139–163	29.4	407	May 19–Oct 16	12	Kitchell et al. 1974, adult
Bluegill	6	185–200	32.2	162	May 19–Oct 16	15	Kitchell et al. 1974, adult
Yellow Perch	0	13–57	1.5	73	Jun 1–Oct 16	–	Post 1990
Yellow Perch	1	63–90	4.0	128	May 19–Oct 16	–	Kitchell et al. 1977
Largemouth Bass	1	80–155	37.0	177	May 19–Oct 16	–	Rice et al. 1983
Largemouth Bass	3	250–293	115.8	225	May 19–Oct 16	–	Rice et al. 1983
Largemouth Bass	6	325–340	61.2	400	May 19–Oct 16	15	Rice et al. 1983

production or terrestrial prey was consistent (mean = 0.45, s.d. = 0.04) regardless of fish species or age (Fig. 5b).

Discussion

Contemporary autochthonous primary production supports approximately half of the fish production in this clear-water north temperate lake. These estimates represent a lower bound for fish autochthony because fish growth due to detrital sources is most likely composed of a mixture of autochthonous carbon fixed prior to the ^{13}C addition and allochthonous carbon. The ^{13}C addition is not able to distinguish sources within the detrital carbon pool, but diet data indicate this energy source is primarily passed to fish through benthic invertebrates. Previous whole-lake ^{13}C additions lacked detail on species-specific and habitat-specific benthic invertebrate $\delta^{13}C$ and autochthony estimates (Carpenter et al., 2005). Using samples from fish diets to track invertebrate $\delta^{13}C$ expedited
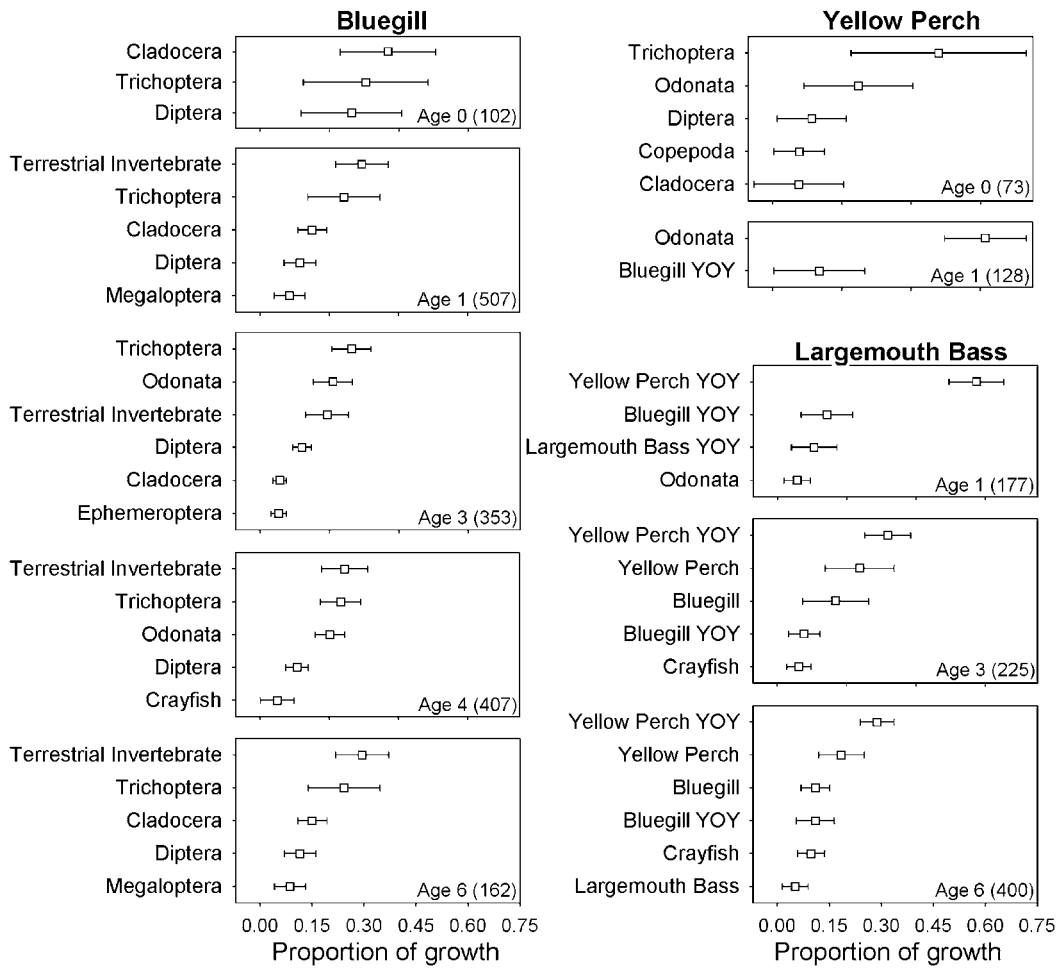
Figure 3. The contribution of specific diet taxa to bluegill (BLG), yellow perch (YWP), and largemouth bass (LMB) growth in Crampton Lake, 2005. Benthic invertebrate taxon names refer to larvae, pupae, and naiad stages. Open squares represent the mean of 50 bioenergetic simulations where individual fish diets from each week were resampled with replacement (Hanson et al., 1997). Error bars represent 2 standard deviations. Only diet taxa that comprised > 5 % of total growth are displayed.
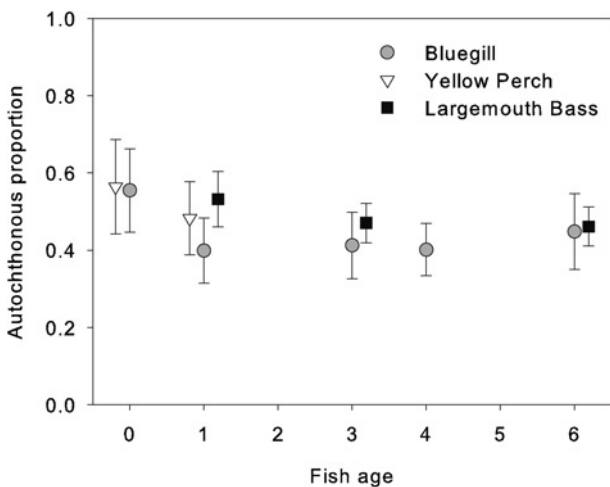

Figure 4. Mean autochthony for three fish species and multiple age classes in Crampton Lake, 2005. Error bars represent 2 s.d. of 50 Monte Carlo simulations.

sampling and ensured more accurate representation of taxa that contributed to fish production. These estimates represent the most well-constrained estimates of carbon sources for a lake fish community to date and indicate that fish production relies on, but is not tightly coupled to, current primary production.

In some clear-water lakes, primary production that occurs below the mixed layer can account for substantial portions of total lake primary production. This primary production can be consumed by zooplankton and thereby enter the food web (Matthews and Mazumder, 2006). Our ^{13}C addition methods do not label this production. Coloso et al. (2008) found, that 14–28 % of total lake primary production occurred below the mixed layer in Crampton Lake during 2005. To compute an upper bound for fish autochthony estimates, we reran our univariate time series models, assuming that only 72 % of autochthonous primary production (phytoplankton and periphyton) was la-
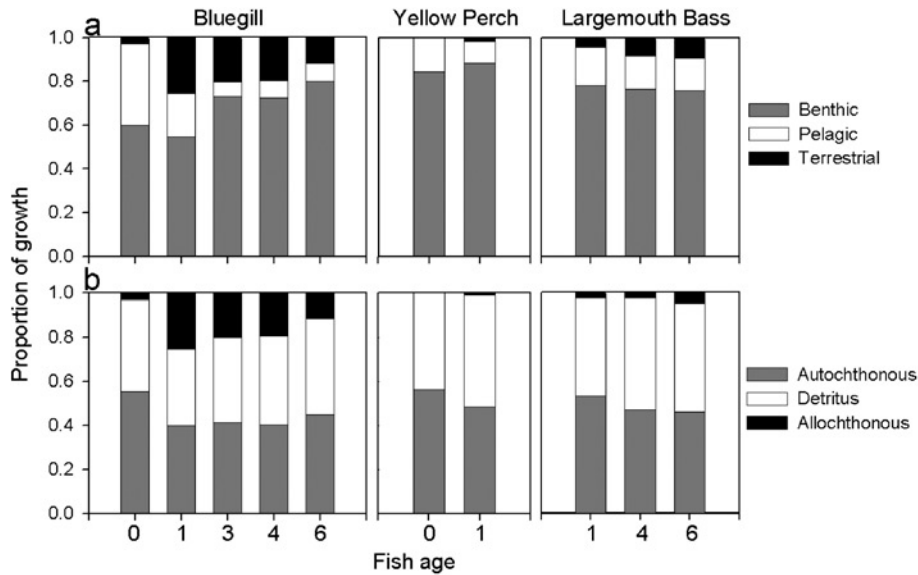
Figure 5. a. Proportion of fish growth attributed to specific lake habitats in Crampton Lake, 2005. Benthic, pelagic, and terrestrial proportions in prey fish contribute proportionally to piscivore growth. 5b. Proportion of fish growth attributed to different carbon sources. Allochthonous carbon (black fill) represents growth due to terrestrial prey items directly consumed by fish. The detritus category (white fill) represents fish growth not attributable to autochthonous primary production or terrestrial prey, rather then direct consumption of detritus by fishes. This detrital carbon pool is a mixture of autochthonous production prior to the ^{13}C labeling experiment and all forms of allochthonous carbon inputs.

beled. This increased our estimates of fish autochthony by an average of 16% (range = 13–20%) and the resulting range of fish autochthony was 54 to 76%. This upper bound is likely to be a substantial overestimate. Fish and zooplankton $\delta^{13}C$ data provide qualitative evidence that fish were not relying on autochthonous production below the mixed layer in Crampton Lake. Age 0 bluegills are obligate zooplanktivores during early life stages and primarily consume a variety of Cladocera. During the course of the ^{13}C addition, dorsal muscle $\delta^{13}C$ of these fish peaked at -11‰ at the same time the $\delta^{13}C$ of Cladocera from the mixed layer peaked at approximately -10‰, suggesting these fish were not consuming unlabeled Cladocera. Thus it is unlikely that primary production beneath the mixed layer provided a significant contribution to fish growth in our experiment.

The ^{13}C addition method can underestimate autochthony in fishes that consume detritivorous invertebrates because the detrital resource pool may include old unlabeled autochthonous production (Carpenter et al., 2005; Solomon et al., 2008). Detailed analyses of carbon flow in ^{13}C-labeled lakes showed that fish autochthony can be underestimated by 1% to 17% (Carpenter et al., 2005). Our analysis took a conservative approach because a large amount of fish growth cannot be attributed to either current autochthonous production or direct consumption of terrestrial prey items (Fig. 5b). This organic matter pool comprises a substantial and consistent propor-

tion of fish growth regardless of fish species or age and likely represents detrital support of fish production. Although detritus played a "central" role in early lake food webs descriptions (e.g. Lindeman, 1942), since then quantifying its importance to lake fish communities has been hampered by heterogeneity in the sources of detrital carbon and omnivory by benthic invertebrates that are the primary link of detrital energy to fish. The ubiquity and importance of detritus is supporting food webs is well recognized (Moore et al., 2004; Dodds and Cole, 2007) but understanding how detritus influences fish community composition and abundance is poorly understood. The ^{13}C addition provided an indirect method to estimate the importance of detrital resources to fish but additional research is needed to partition the relative importance of allochthonous and autochthonous carbon sources within the detrital pathway. Carbon isotope addition studies have the potential to determine the relative importance of autochthonous and allochthonous carbon but are limited by the logistics and expense as well as the complexities of cycling and time lags influencing detrital pools. Other isotopic approaches appear promising for delineating sources and evaluating relative support of food webs through detrital pools (e.g. Doucett et al., 2007).

Across fish species, autochthony estimates for age 1 and older fishes were remarkably similar. Bioenergetic estimates in figure 3 show that while the specific rank order of growth-contributing diet taxa

differed, the majority of bluegill and yellow perch growth was largely supported by the same few invertebrate taxa: Trichoptera, Odonata, Diptera, terrestrial invertebrates, and Cladocera. Likewise, piscivores diets were similar across trophic ontogeny and were predominately composed of age 0 and age 1 perch and bluegill. Because few taxa had a large influence on determining autochthonous production in fishes, the broad taxonomic resolution we used for classifying invertebrates in diets may have averaged over important differences in functional feeding groups within an order. Solomon et al. (2008) found substantial differences in Chironomidae (Diptera) autochthony with depth. As Diptera are a major diet item for all species and most age classes of fishes, a substantial proportion of our uncertainty in autochthony estimates may be related to autochthony differences in these important diet taxa. Autochthony of age 0 fish, both bluegill and yellow perch, was only slightly higher then older conspecifics and likely a result of greater reliance on pelagic zooplankton that were closely coupled to autochthonous production. During their pelagic life stages, age 0 fish autochthony would have likely been higher than we estimated, however much of the main period of production (growth) for these fish occurred after they shifted to littoral habitats where they feed primarily on benthic invertebrates.

We found the relative importance of terrestrial prey consumed by fish differs both within and between species. Mehner et al. (2005) also found strong interspecific variation in a lake where bleak, *Alburnus alburnus*, diet was >65% terrestrial invertebrates, yet perch, *Perca fluviatilis*, in the same lake consumed no terrestrials. In Crampton Lake, terrestrial particulate deposition, including terrestrial invertebrates, is highest near shore and declines exponentially with distance from shore (Preston et al., 2008). Consequently, fish habitat use relative to the littoral zone may explain differences in the importance of terrestrial prey items. Ontogenetic shifts in bluegill habitat use between pelagic and littoral areas have been well documented (Werner and Hall, 1988) and the importance of terrestrial prey to different ages of bluegill mirrors ontogenetic shifts in and out of near shore areas. Following a pelagic young of year stage, when gape likely limits terrestrial invertebrate consumption, predation risk relegates juvenile bluegill to near shore areas where particulate deposition is highest. Larger bluegills, less susceptible to predation, inhabit deeper waters relative to juveniles (Hall and Werner, 1977), where inputs of terrestrial invertebrates are reduced. Terrestrial invertebrates in bluegill diets were primarily coleopterans, in the family Scarabaeidae, which have also been identified as important prey supporting

stream brook trout populations (Utz et al., 2007). These beetles are associated with perennial shrubs and deciduous trees, suggesting that the vegetation composition of lake riparian areas could influence linkages between terrestrial invertebrates and fishes as in streams (Wipfli, 1997). A benefit of our detailed diet and bioenergetic approach as compared to sole reliance on techniques such as stable isotope analysis was the ability to clearly distinguish the relative importance of terrestrial prey from aquatic prey.

Our results contribute to a growing body of literature suggesting that in some systems, benthic rather than pelagic habitats are the primary energy pathway contributing to fish production (Hecky and Hesslein, 1995; Vadeboncoeur et al., 2002; Herwig et al., 2004). Across all species and ages we found that benthic invertebrates supported 74% of fish growth in 2005, as compared to 15% supported by pelagic invertebrates. The disproportionate importance of benthic areas is further highlighted by area-weighted estimates of secondary production where average pelagic invertebrate production ($40 \, g \, m^{-2} \, yr^{-1}$) is almost 10 times that of benthic invertebrate production ($4.4 \, g \, m^{-2} \, yr^{-1}$) (Babler et al., 2008). Vander Zanden et al. (2006) suggest that the larger body size and size range of benthic invertebrate prey relative to pelagic prey make feeding on benthos more energetically attractive to fish and subsequently increases the efficiency of this trophic link. Preferential and selective feeding on benthic prey would also increase the disparity between pelagic and benthic habitats as contributors to food web dynamics. The pelagic invertebrate community of Crampton Lake is dominated by small copepods (Pace et al., 2007) and lacks large *Daphnia* sp. that are commonly the important link between fish and the pelagic zone for small lakes in the Northern Highlands district (Carpenter et al., 2008). In the absence of a strong trophic link between pelagic invertebrates and fishes, autotrophic primary production in the Crampton Lake pelagic zone is likely an important energy source for fishes via the detrital carbon pool.

The number of studies determining the carbon sources that support fish production are limited (Carpenter et al., 2005) and the various features of ecosystems that influence support are poorly understood. Relative productivity, inputs of terrestrial organic matter, and ecosystem size and shape are likely to be significant features (Cole et al., 2006; Pace et al., 2007). For larger lakes, perimeter:area ratios decline and inputs of allochthonous carbon may become less significant relative to sources of autochthonous primary production. If this is true, then food webs and fish production in large lakes should be more autochthonous in comparison to smaller lakes, but

changes in the importance of autochthonous production may not be directly proportional to lake area. Instead, lake littoral zones may be substantially more efficient at transferring local terrestrial carbon inputs through food webs to fishes than adjacent pelagic habitats. In this case, lake size may have less influence on autochthonous support to fish production. We found the average fish community autochthony of Crampton Lake (0.46) within the range of values from multivariate autoregressive models (0.34 – 0.46) reported by Carpenter et al. (2005) for lakes that were 10–20 times smaller, by surface area. This similarity suggests that autochthonous support of fish does not increase simply with lake size. While larger than previous ^{13}C addition lakes we have studied, Crampton Lake is predominantly shallow, lacks a large hypolimnetic habitat, and contains no fish species that are obligate zooplanktivores throughout their life. Thus, deeper lakes with obligate planktivores may have greater autochthonous support and so lake size and morphometry may, through influencing fish species assemblage, ultimately influence the carbon source supporting fishes. Currently, comparative data on fish autochthony are too limited to provide strong tests of these possibilities.

Previous ^{13}C addition experiments suggest that the ratio of lake water color to chlorophyll *a* concentration is an indicator of the relative importance of allochthonous and autochthonous carbon to invertebrate carbon pools (Pace et al., 2007; Solomon et al., 2008). Color reflects the concentration of terrestrially-derived dissolved organic matter while chlorophyll *a* provides an index of autochthonous primary production. To assess this relationship, we plotted the average fish community autochthony from the present study of Crampton Lake with four previous ^{13}C addition experiments (see Carpenter et al., 2005) against color:chlorophyll *a* (Fig. 6). Fish community autochthony was inversely correlated with color : chlorophyll *a* ratio, suggesting this relationship may be a useful proxy for determining the relative importance of different carbon sources to fish production. Lakes with higher color relative to chlorophyll have lower autochthony. Stronger tests of this relationship require broader comparative data for many lake types and fish communities.

Multiple sources of information (accounting for fish carbon sources, whole-lake isotope enrichment, and bioenergetics modeling) illustrated the pathways and sources of carbon to fishes of different ages and species. Results converged on autochthony of around 45 %. This is consistent with trends in autochthony and color : chlorophyll *a* reported in previous studies. In general, only about half of the fish production in Crampton Lake and likely many others owes to a
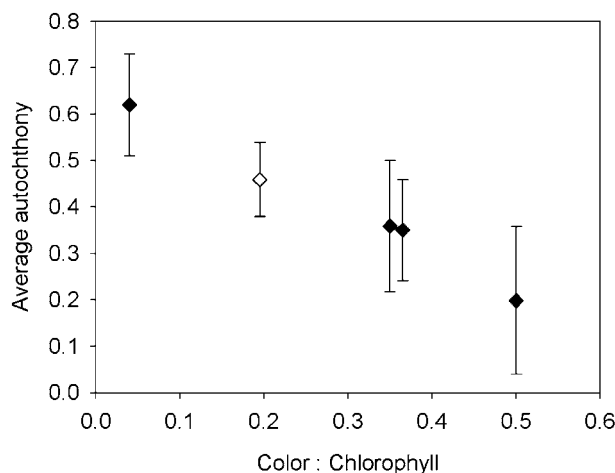
Figure 6. Relationship between average fish community autochthony and color : chlorophyll *a* ratio for five north temperate lakes where ^{13}C experiments were performed. Each filled diamond represents autochthony estimates from two different models in Carpenter et al., (2005). From left to right: Peter Lake- fertilized (N=6), Paul Lake (N=6), Peter Lake – unfertilized (N=6), and Tuesday Lake (N=6). The open diamond illustrates results from Crampton Lake, WI, 2005 (N=10). Error bars represent 1 s.d.

direct trophic transfer of the current season's primary production to fish production through consumption of intermediate prey. Nearly half of annual fish production owes to organic carbon that has passed through detrital food webs. This detrital carbon is comprised of mixed sources with variable turnover rates. Invertebrate taxa that dominate fish diets live primarily in littoral and benthic areas and these are key habitats through which detrital carbon supports fish production. Fish production is broadly correlated with measures of pelagic autochthonous production (Downing et al., 1990; Downing and Plante, 1993), but this relationship is based on both direct and indirect detrital trophic pathways. The patterns of allochthonous organic matter support of fish production among lake ecosystems remain poorly understood. Advances in our understanding will require better means for distinguishing sources and measuring rates for incorporation of detritus in lake food webs.

Acknowledgments

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