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Using cumulative diet data and stable isotope analysis to determine trophic position of walleye *Sander vitreus* in a large, complex system

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Diet studies have traditionally been used to determine prey use and food web dynamics, while stable isotope analysis provides for a time-integrated approach to evaluate food web dynamics and characterize energy flow in aquatic systems. Direct comparison of the two techniques is rare and difficult to conduct in large, species rich systems. We compared changes in walleye *Sander vitreus* trophic position (TP) derived from paired diet content and stable isotope analysis. Individual diet-derived TP estimates were dissimilar to stable isotope-derived TP estimates. However, cumulative diet-derived TP estimates integrated from May 2001 to May 2002 corresponded to May 2002 isotope-derived estimates of TP. Average walleye TP estimates from the spring season appear representative of feeding throughout the entire previous year.

Keywords: δ^{13}C; δ^{15}N; cumulative diet assessment; Lake Oahe; *Sander vitreus*; trophic position

Introduction

Knowledge of food web dynamics and trophic relationships are important for understanding ecosystem functional dynamics. Historically, diet studies (i.e. gut content analysis) have been used to examine spatial and temporal patterns of prey use (Winemiller 1990; Vander Zanden & Rasmussen 1996). Diet studies provide a way to directly assess diet variability and breadth with high resolution. However, most diet studies only represent a 'snapshot in time' of overall diet composition and in species rich or large aquatic systems where labor and other costs are often too prohibitive to allow successful examination of large-scale spatial and temporal diet variation (Rybczynski et al. 2008).

Alternatively, stable isotope analysis (SIA) provides a time-integrated measure of carbon (δ^{13}C) and nitrogen (δ^{15}N), which reflects energy assimilated by consumers (Vander Zanden & Rasmussen 1999; Vander Zanden et al. 2000). SIA has been used extensively to assess energy flow and feeding relationships within aquatic food webs (Vander Zanden et al. 2000; Lake et al. 2001). Moreover, as analysis techniques are refined, the cost of SIA has decreased in many commercial laboratories (D. Clay, South Dakota State Precision Agriculture Laboratory, personal communication). However, comparisons between

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diet-derived trophic position (TP) and stable isotope-derived TP have rarely been conducted on the same individual (Overman & Parrish 2001; Rybczynski et al. 2008).

Here, both diet data and SIA are used to estimate TP in a predator (walleye *Sander vitreus*) from a large, complex system. We compared diet and SIA data to estimate their general and temporal comparability.

Methods

Lake Oahe, which extends from Bismarck, North Dakota to Pierre, South Dakota (372 km long, 3620 km shoreline, 1450 km^2 surface area), is the second largest of six impoundments of the Missouri River. Lake Oahe's fish assemblage is diverse and includes more than 15 potential sources of fish prey, numerous age-0 sport fish, and invertebrates.

Walleye were collected from six sampling sites equidistantly spaced through the reservoir using 45.7 m long experimental mesh gill nets (bar mesh from 15 to 51 mm) in May, July, and October 2001, and May 2002. We deployed gillnets randomly from three to 15 m in depth at sunrise and retrieved gillnets within 2 h. White muscle samples were taken from each walleye just below the first dorsal fin and frozen at −20 °C. Whole stomachs were removed from each walleye and preserved in ethanol.

Prey fish were collected with trap nets and bag seines in the daylight hours of July and October 2001, and May and January 2002 at each sampling site. Muscle samples from each prey fish were collected and processed in the same manner as walleye for SIA. Zooplankton were collected by towing a 0.5 m diameter mouth net with 63 μm mesh near the lake surface for five min. Because of Lake Oahe's depth (>50 m), a variety of macroinvertebrates were difficult to collect in sufficient numbers for a representative SIA sample but we did hand-collect adult mayflies (*Hexagenia* spp.) during night emergence. Whole invertebrates were used for SIA.

All tissue samples were dried at 60 °C until constant weight, then ground and homogenized prior to SIA. Zooplankton samples were first centrifuged then subsampled from the top and bottom layers. Muscle tissue samples and individual mayflies were first rinsed with deionized water. The samples were analyzed using a Europa 20−20 mass spectrometer (Europa Scientific, Ltd., UK) with Pee Dee belemnite limestone and atmospheric nitrogen as standards for δ^{13}C and δ^{15}N, respectively.

TP for each walleye was calculated from diet data using the equation,

$$\mathrm{TP}_{\mathrm{diet}} = S(W_i T_i) + 1,$$

where $\mathrm{TP}_{\mathrm{diet}}$ is the diet-derived TP of a walleye, W_i is the percent composition by weight of prey item i, and T_i is the TP of prey item i (Davis 2004). TP of diet items were estimated using the isotope baseline correction equation to eliminate errors in prey item estimates (Figure 1). TP was estimated for unidentified fish using the mean values of the most abundant prey fish items found in walleye diets.

To effectively compare diet data to isotope signatures, diet information must be time integrated to capture cumulative contribution to somatic growth. To derive a cumulative diet estimate for all seasons, W_i for each major diet item (constituting >1% by weight) was calculated for each season. Diet items were summed across seasons to derive total W_i of all prey taxa across seasons. This value was used to estimate a seasonal cumulative weighted mean for each diet. Cumulative diet contributions were calculated by summing

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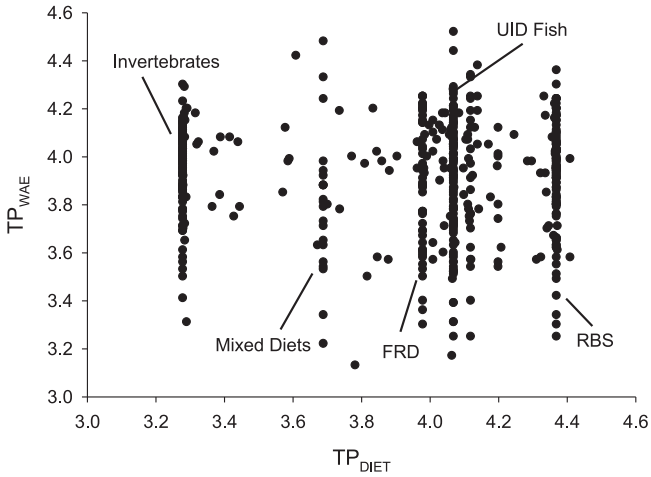

Figure 1. Comparison of isotope (TP_{WAE}) and diet (TP_{DIET}) derived walleye trophic position estimates for individual walleye. Vertical bands created by diet estimates represent walleye feeding on one prey type (except trophic position 3.7).
Note: Invertebrates = all macroinvertebrates in taxa list; mixed diets = different combinations of taxa in diets; FRD = freshwater drum; UID Fish = unidentified fish in diet; and RBS = rainbow smelt.

the weighted W_i of each diet item across dates. This cumulative mean W_i was used in the following equation:

$$\mathrm{WTP_{diet}} = \sum (W\mathrm{SUM}_i \times T_i) + 1$$

where $\mathrm{WTP_{diet}}$ is the weighted, integrated diet-derived estimate for the TP of each walleye, $W\mathrm{SUM}_i$ is the weighted, cumulative contribution across all seasons for each prey item, T_i is the TP of each prey item (see Table 1), and 1 is an increase of one trophic level for walleye TP (Davis 2004).

Isotope-derived TP (TP_{WAE}) was derived following procedures outlined by Vander Zanden et al. (1997) and Vander Zanden and Rasmussen (1999). Mayflies do not feed as adults, so isotope signatures during the adult stage would resemble signatures from their aquatic, larval life-stage. Thus, mayflies were used as a baseline standard. We then assumed a 3.4 enrichment factor (Vander Zanden et al. 1997) for a consumer.

Results

We collected 835 walleye with diet items present from May 2001 through July 2002. Walleye total length ranged from 122 to 688 mm, weighted from 14 to 2962 g, and aged from one to eight years. Over 2150 different diet items were identified from 24 different taxa in walleye stomachs including 9 invertebrate species and 15 fish species. From May 2001 to May 2002, mean W_i of diet items from all walleye sizes indicated that diets shifted from a large proportion of macroinvertebrates (63%) to a large proportion of fish (96%; Table 2).

TP estimates derived from walleye muscle isotopes were not strongly correlated with total length ($p < 0.001$, $df = 830$, $r^2 = 0.21$) or weight ($p < 0.001$, $df = 830$, $r^2 = 0.20$). Carbon isotope signatures were weakly correlated with TL ($p < 0.001$, $df = 830$, $r^2 = 0.30$) and weight ($p < 0.001$, $df = 830$, $r^2 = 0.30$). From May to October 2001,

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Table 1. Estimated trophic position for common prey taxa found in walleye diets. Trophic positions for taxa with subscripts were estimated using mayflies (*Ephemeridae* spp.) and *Daphnia* spp. as references. Trophic position for unidentified fish was estimated by calculating the mean trophic position from values of rainbow smelt, white bass, gizzard shad, freshwater drum, white crappie, yellow perch, and lake herring.

Taxa	TP	Taxa		TP
Zooplankton		Fish taxa		
Daphnia[a]	2.29	Johnny darter[a]	*Etheostoma nigrum*	3.41
		Rainbow smelt[a]	*Osermus mordax*	3.37
		White crappie[a]	*Pmoxis annularis*	3.20
Invertebrates:		Yellow perch[a]	*Perca flavescens*	3.14
Mayfly[a]	2.28	White bass[a]	*Morone chrysops*	3.12
Chironomid[b]	2.28	Emerald shiner[a]	*Notropis atherinoides*	3.01
		Freshwater drum[a]	*Aplodinotus grunniens*	2.98
		Lake herring[a]	*Coregonus artedi*	2.98
		Spottail shiner[a]	*Notropis hudsonius*	2.88
		Channel catfish[a]	*Ictalurus punctatus*	2.84
		Black bullhead	*Ameiurus melas*	2.84
		Gizzard shad[a]	*Dorosoma cepedianum*	2.69
		Unidentified fish[c]		3.07

[a]Estimate TP using baseline nitrogen correction.
[b]Estimated TP using mayflies as reference.
[c]Average of major prey fish contributors.

walleye TP declined while carbon signatures increased indicating a shift toward littoral prey resources. From October 2001 to May 2002, walleye TP increased while carbon signatures decreased indicating a shift toward a larger fish-based and pelagic diet.

Walleye TP_{diet} formed five discrete groups and each group represents a snapshot of walleye feeding habits (Figure 1). The lowest TP group ($TP_{diet} = 3.3$) was composed of invertebrates, followed by a mixed diet ($TP_{diet} = 3.7$), freshwater drum ($TP_{diet} = 4.0$), unidentified fish ($TP_{diet} = 4.1$), and rainbow smelt ($TP_{diet} = 4.4$). However, isotope estimates during the same sampling period indicated a population feeding at multiple trophic levels (from 3.18 to 4.57) within a single sampling period.

Mean walleye TP_{diet} generally increased from May 2001 to May 2002 (Figure 2). In May 2001, TP_{WAE} was larger than TP_{diet} (paired *t*-test; $t = 8.223$; $p < 0.001$). TP_{WAE} and TP_{diet} were similar in July 2001 ($t = 1.434$; $p = 0.153$) but TP_{WAE} was smaller than TP_{diet} in October 2001 ($t = -6.470$; $p < 0.001$) and May 2002 ($t = -6.940$; $p < 0.001$). There was no correlation between TP_{diet} and TP_{WAE} ($p = 0.11$, $r^2 = 0.005$). Walleye TP_{WAE} in October 2001 (3.80) were similar to cumulative WTP_{diet} integrated from May to October 2001 (3.82; Table 2). In addition, cumulative WTP_{diet} integrated from May 2001 to May 2002 (3.94) corresponded to May 2002 TP_{WAE} (3.98).

Discussion

Using cumulative diet-derived TP estimates from walleye, we exposed predicted seasonal patterns in TP of walleye (Kelso 1973; Hartman & Margraf 1992). These seasonal TP shifts imply changes in diets from benthivory to piscivory in a single year (Knight &

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Table 2. Cumulative TP values estimated from diet data from May to October 2001, October 2001 to May 2002, and May 2001 to May 2002. Time-integrated diet estimates were calculated from weighted means of diet composition and compared to mean isotope estimates (see text for details).

Taxa	Percent composition by weight (g)				
	May 2001	July 2001	October 2001	May 2002	TP
Zooplankton					
Daphnia spp.	3	0	0	0	2.29
Invertebrates					
Ephemerid mayflies	63	21	0	3	2.28
Unidentified invertebrates	2	2	0	0	–
Chironomid midges	0	5	0	0	2.28
Fish taxa					
Rainbow smelt	18	22	16	70	3.37
Unidentified fish	10	31	24	23	3.07
Emerald shiners	1	3	0	0	3.01
Yellow perch	0	5	2	1	3.14
White bass	0	5	18	1	3.12
Lake herring	0	1	3	0	2.98
Freshwater drum	0	3	19	1	2.98
Gizzard shad	0	0	11	0	2.69
White Crappie	0	0	4	0	3.20
Cumulative integrated diet trophic position					
May 2001–Oct 2001	3.82				
Oct 2001–May 2002	4.11				
May 2001–May 2002	3.94				
Mean isotopic trophic position					
May 2001–Oct 2001	3.80				
Oct 2001–May 2002	3.89				
May 2001–May 2002	3.89				

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Vondracek 1993). While muscle isotope-derived TP estimates can elucidate general shifts in fish diets (Vander Zanden et al. 2000), muscle isotope-derived TP estimates alone did not correspond to diet-derived walleye TP estimates when compared among individual fish. Thus, immediate diet shifts could be revealed through examining single sampling cumulative diet-derived TP estimates.

However, integrating diet cumulatively over time appeared to correspond to muscle isotope-derived TP. Thus, we revealed that the cumulative diet-derived TP corresponded closest to a May muscle isotope-derived TP estimate. From October 2001 to May 2002, isotope-derived walleye TP increased from 3.80 to 3.89, implying increased piscivory. Indeed, walleye consumption of spiny-rayed species and rainbow smelt increased from October 2001 to May 2002. October signatures should be more reflective of cumulative feeding through the growing season when metabolic rates and growth are fast (Sakano et al. 2005). When integrating diets from May 2001 to May 2002 to estimate cumulative diet-derived TP, the TP estimate (3.94) was only slightly larger than the isotope-derived walleye TP estimate (3.89). Cumulative, diet-derived estimates of walleye TP obtained

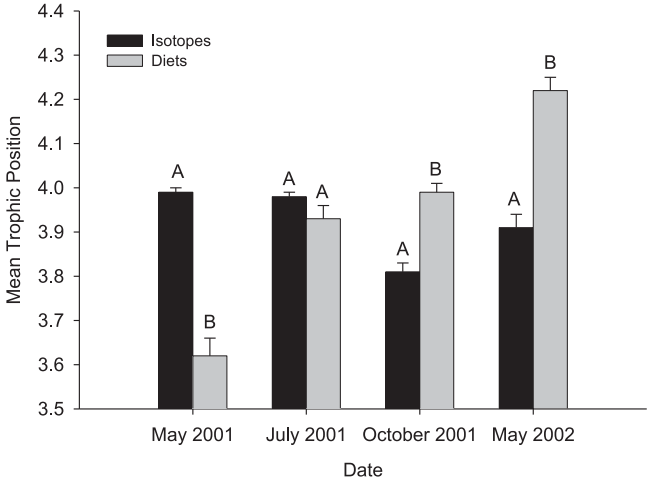

Figure 2. Comparison of lake-wide trophic position estimates for Lake Oahe walleye.
Note: Bars with the same letters are not significantly different between diet (TP_{DIET}) and isotope (TP_{WAE}) derived estimates of trophic position for each date. Error bars represent one standard error.

over the walleye growing season appear to reflect the annual isotope-derived walleye TP in May the following year.

Although Lake Oahe is a large, dynamic system and walleye in the reservoir can obtain energy from a large variety of prey resources, stable isotopes were able to track energy flow through the walleye food web. Using muscle tissue stable isotopes alone, changes in TP of the walleye population in Lake Oahe could be assessed as is traditionally done in smaller, less complex systems, but could only generalize the source of variation for such changes (e.g. diet changes of more or less fish versus invertebrates). However, by using a cumulative, diet-derived estimate of walleye TP that reasonably reflected TP derived from muscle isotopes, changes in walleye TP could be determined and one could deduce the source of variation (i.e. changes in specific diet items) in TP estimates. These results demonstrate that muscle isotope-derived predator TP estimates were reflective of the cumulative diet-derived TP estimates over a predator's growing season. The use of cumulative diet-derived TP estimates could also be beneficial for protected species when obtaining a muscle sample is not possible or desirable.

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