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# Habitat coupling in a large lake system: delivery of an energy subsidy by an offshore planktivore to the nearshore zone of Lake Superior

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## SUMMARY

1. We hypothesised that the autumn spawning migration of Lake Superior cisco (*Coregonus artedii*) provides a resource subsidy, in the form of energy-rich cisco eggs, from the offshore pelagic to the nearshore benthic community over winter, when alternate prey production is likely to be low.
2. We tested this hypothesis using fish and macroinvertebrate surveys, fish population demographics, diet and stable isotope analyses, and bioenergetics modelling.
3. The benthic, congeneric lake whitefish (*C. clupeaformis*) was a clear beneficiary of cisco spawning. Cisco eggs represented 16% of lake whitefish annual consumption in terms of biomass, but 34% of energy (because of their high energy density: >10 kJ g wet mass<sup>-1</sup>). Stable isotope analyses were consistent with these results and suggest that other nearshore fish species may also rely on cisco eggs.
4. The lipid content of lake whitefish liver almost doubled from 26 to 49% between November and March, while that of muscle increased from 14 to 26% over the same period, suggesting lake whitefish were building, rather than depleting, lipid reserves during winter.
5. In the other Laurentian Great Lakes, where cisco populations remain very low and rehabilitation efforts are underway, the offshore-to-nearshore ecological link apparent in Lake Superior has been replaced by non-native planktivorous species. These non-native species spawn in spring have smaller eggs and shorter incubation periods. The rehabilitation of cisco in these systems should reinstate the onshore subsidy as it has in Lake Superior.

*Keywords:* cisco, eggs, foraging, whitefish, winter ecology

## Introduction

The transfer of energy across habitats can have important consequences for ecological community dynamics and ecosystem processes (e.g. Polis, Anderson & Holt, 1997). For example, predators can alter ecosystem properties across habitats directly through consumption and the translocation of nutrients, and indirectly through predator-induced prey habitat and foraging shifts effects

(Schmitz *et al.*, 2008; Schmitz, 2010). Connections between different habitats also may facilitate the export of primary production to food-limited habitats, resulting in greater overall production than would be the case with disconnected habitats (e.g. Cloern, 2007).

Highly mobile organisms such as fish can couple seemingly disconnected habitats. Semelparous Pacific salmon (*Onchorynchus spp.*) move marine-derived nutrients to coastal ecosystems where they have a significant

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impact on freshwater and terrestrial production (e.g. Kline *et al.*, 1993). Similarly, migratory iteroparous fish, such as alewife (*Alosa pseudoharengus*; Durbin, Nixon & Oviatt, 1979), blueback herring (*A. aestivalis*; MacAvoy *et al.*, 2000) and rainbow smelt (*Osmerus mordax*; Saunders, Hachey & Fay, 2006), move nutrients and may be taken by predators as they move within and among habitats seasonally. In addition to nutrients, egg deposition may represent significant pulses of food resource in coastal marine (e.g. Willson & Womble, 2006) and river (Heintz, Wipfli & Hudson, 2010) systems. In lakes, energy fluxes between benthic and pelagic habitats facilitated by fish movement are considered important processes in whole-lake food webs (e.g. Schindler & Scheuerell, 2002).

Loss of native fishes resulting from overfishing or invasive species may disrupt ecological processes (Zimmerman & Krueger, 2009). For example, cisco (*Coregonus artedii*) was a major component of fish assemblages in all the Laurentian Great Lakes (Smith, 1995) but collapsed by the middle of the 20th Century in most of the lakes (Lawrie & Rahrer, 1973). Among the Laurentian Great Lakes, Superior is unique because its food web is currently dominated by native species, including rehabilitated cisco populations (Stockwell *et al.*, 2009). Cisco are an important prey for native piscivores because their relatively large size provides a high net energy return (Mason, Johnson & Kitchell, 1998; Kaufman *et al.*, 2006). Additionally, a diet of cisco, compared to one of non-native species, such as alewife, does not induce thiaminase-related recruitment failure in piscivores (e.g. Brown *et al.*, 2005), a condition similar to M74 syndrome in Baltic salmon (*Salmo salar*; e.g. Lundström *et al.*, 1999). Thus, the presence of cisco in Lake Superior provides an opportunity to test hypotheses about the role of native fish in habitat coupling and ecosystem processes in a large lake environment.

In this study, we examined the role of cisco in the movement of energy from offshore to nearshore habitats. Adult cisco are primarily planktivorous (e.g. Gamble *et al.*, 2011a), occupy offshore pelagic waters in Lake Superior (Stockwell *et al.*, 2006; Stockwell *et al.*, 2010) and move nearshore to spawn in late autumn (Yule *et al.*, 2009). Their eggs incubate over winter and hatch in April and May and thus may provide an energy-rich resource for benthic predators from late autumn to spring. Previous studies in Lake Superior and the other Great Lakes indicate the macroinvertebrates *Mysis* and *Diporeia* are important prey for fish from spring to autumn (e.g. Owens & Dittman, 2003; Gamble *et al.*, 2011a,b; Isaac *et al.*, 2012). Therefore, we hypothesised

that cisco eggs act as a resource subsidy and support the nearshore benthic community in winter, when macroinvertebrate production is likely to be low (Stockwell *et al.*, 2010). If true, cisco eggs should be an important diet for benthic fish throughout winter. Additionally, if cisco eggs have stable isotopic values distinct from invertebrate prey, this should be reflected in isotopic values of benthic fish between autumn and spring. In particular, cisco eggs should have a higher  $\delta^{15}\text{N}$  than invertebrate prey, reflecting their higher trophic status, and a lower  $\delta^{13}\text{C}$  because of the pelagic origin of their carbon (France, 1995) and high lipid content. Alternatively, the nearshore production of benthic invertebrate prey may be sufficiently high that the comparative contribution of cisco eggs is negligible. We would then expect to see the winter diet of benthic fish dominated by invertebrates and their stable isotopic values reflecting that diet. We test these hypotheses using results from fish and macroinvertebrate surveys, fish population demographics, diet and stable isotope analyses, and bioenergetics modelling and discuss the consequences of our findings with regard to the importance of native fish in ecosystem processes.

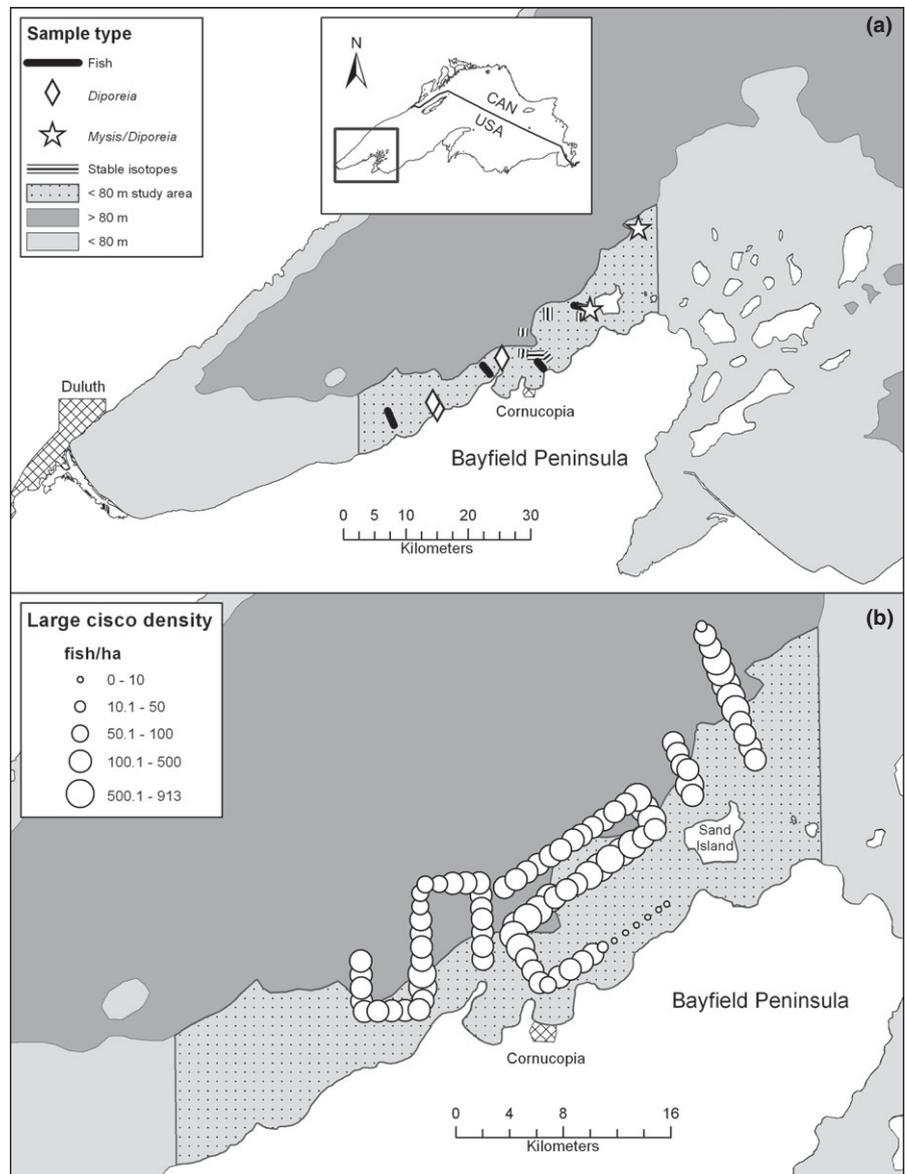
## Methods

### Study system

Lake Superior is the largest freshwater lake by area in the world (82 000 km<sup>2</sup>), averages 150 m in depth, and is highly oligotrophic (Munawar, 1978). This study was conducted within the Wisconsin south shore region in the western arm of the lake, which is characterised by a mix of nearshore (<80 m) and offshore (>80 m) habitats (Fig. 1). Cisco currently represent 63% of the total fish biomass in offshore areas in the western arm (T.R. Hrabik, unpubl. data), the amphipod *Diporeia* spp. represent 50% of benthic invertebrate biomass in the 0–80 m stratum of the western arm (J.V. Scharold, unpubl. data), and overall biomass of the diel vertical migrator *Mysis diluviana* is five to six times that of *Diporeia* (Kelly *et al.*, 2011).

### Macroinvertebrate sampling

Details of our sampling of *Mysis* and *Diporeia* can be found in Isaac *et al.* (2012). Briefly, *Mysis* was sampled at night with a vertically towed 1-m<sup>2</sup> net (1000- $\mu\text{m}$  mesh tapered to 250- $\mu\text{m}$  mesh with a 63- $\mu\text{m}$ -mesh bucket) from 2 m off bottom to the surface, and *Diporeia* was sampled during the day with a 0.046-m<sup>2</sup> Ponar grab. For



**Fig. 1** Study area along the Wisconsin south shore in the western arm of Lake Superior. (a) Sampling sites for *Mysis* and *Diporeia* biomass estimates, lake whitefish density estimates, and fish and invertebrates stable isotope samples. (b) Acoustic transects and density estimates of spawning-sized cisco (from Yule *et al.*, 2009). Note different spatial scales between the two panels.

each *Mysis* and *Diporeia* sample, all individuals were counted and measured. We used mass-length regressions (USGS Great Lakes Science Center and Duluth-EPA, unpubl. data) to convert individual lengths of *Mysis* and *Diporeia* to dry mass and to estimate the biomass ( $\text{kg ha}^{-1}$ ) of each. *Mysis* and *Diporeia* were collected at two and five sites, respectively (Fig. 1). One *Mysis* site was sampled in spring, summer and autumn of 2005, and the other site was sampled only in autumn that year. One *Diporeia* site was sampled in each of the three seasons, one site was sampled only in the autumn, and the remaining *Diporeia* sites were sampled only in the summer of 2005. Four (*Mysis*) and three (*Diporeia*) replicate samples were collected during each sampling event at each site. Replicates were used to estimate the

mean biomass for each macroinvertebrate for each site/season, and each of these site/season estimates was then used to estimate the annual mean ( $\pm\text{SE}$ ) biomass for *Mysis* ( $N = 4$ ) and *Diporeia* ( $N = 7$ ). Annual mean biomass per unit area was then multiplied by the area of the Wisconsin south shore  $<80$  m (45 760 ha) to estimate the overall annual biomass (kg).

#### *Cisco spawning movements*

Cisco abundance in the nearshore habitat increases drastically between early and late autumn in Wisconsin waters of Lake Superior (Yule *et al.*, 2009). The spawning cisco population of the western arm was estimated during November 2006 using acoustic methods and

midwater trawl samples (see Yule *et al.*, 2009). Adult cisco ( $\geq 250$  mm) densities were estimated at 93 and 133 fish  $\text{ha}^{-1}$  for nearshore ( $< 80$  m) and offshore ( $> 80$  m) zones, respectively. For the present study, we used observations from Yule *et al.* (2009) to estimate mean ( $\pm$ SE) adult cisco density in the study area (Fig. 1b). We assumed all adults spawned and all spawning occurred in the nearshore zone (Stockwell *et al.*, 2009; Yule *et al.*, 2012). Cisco caught in midwater trawl samples during the 2006 survey were processed to determine sex ratio, size structure and mass-length relationships, following Yule *et al.* (2008). Ovaries were collected to develop a mass versus fecundity relationship, following Yule *et al.* (2006), and to estimate egg energy density with bomb calorimetry (Parr 6200 Oxygen Bomb Calorimeter; Parr Instrument Company, Moline, IL, U.S.A.). Data were used to estimate the biomass of eggs deposited and their energetic equivalence assuming all eggs were spawned. Yule *et al.* (2006) found a majority of the variance associated with estimates of cisco egg deposition in the Apostle Islands region of Lake Superior resulted from variance in estimates of spawner density. Therefore, we estimated the variance in egg deposition based on the variance in spawner density alone and assumed that the variance in the other factors (sex ratio, size structure, the mass-length relationship and the mass-fecundity relationship) contributed negligibly to uncertainty in egg deposition.

#### Lake whitefish sampling

Numerical densities of lake whitefish (*C. clupeaformis*; hereafter 'whitefish') were estimated from an annual spring bottom trawl survey of the nearshore zone, conducted during daylight by the U.S. Geological Survey Great Lakes Science Center (see Stockwell *et al.*, 2007 for details) that included four sites along the Wisconsin south shore (Fig. 1). We averaged density estimates from 3 years (2005–07) to smooth among-site and interannual variability in the years surrounding the 2006 cisco spawner survey. Abundance was calculated by multiplying mean density by the area of the study region (45 760 ha). These estimates were then used to scale up individual whitefish consumption estimates (see below).

Samples of whitefish diet in winter were taken from fish caught commercially near Sand Island (Fig. 1) between December 2009 and April 2010, with an additional collection there in December 2011. Whitefish were harvested with overnight bottom-set gill nets, except in one instance when fish were harvested by trap net (April 2010). Fish were returned to the laboratory for

immediate processing. Stomach contents were emptied into a Petri dish, and prey items were sorted, blotted and weighed to the nearest 0.01 g. Diet proportions were summarised by month from December to April, pooling across years when available.

#### Consumption estimates

Isaac (2010) recently estimated lake-wide, annual prey consumption by Lake Superior fish using a bioenergetics modelling approach. Here, we refine that work to estimate consumption by whitefish resident along the Wisconsin south shore. Estimates of whitefish consumption were developed with the Wisconsin bioenergetic model (Kitchell, Stewart & Weininger, 1977) using the parameters for a generalised coregonid (Rudstam, Binkowski & Miller, 1994), except that we applied the respiration parameter for whitefish from Madenjian *et al.* (2006).

The bioenergetics models were run at a daily time step for one year beginning on 1 January. Estimates of length-at-age and mass-length relationships for whitefish (Isaac, 2010) were used to assign start and end masses for each year class (Table 1). Daily model temperature was based on linear interpolation between mean observed bottom water temperatures of 3.9 °C in May, 7.2 °C in August and 6.6 °C in October (Isaac, 2010), and a compiled estimate of 2.5 °C in January (Assel, Croley & Schneider, 1994). Model inputs for age-at-maturity and spawning date were taken from Isaac (2010), and percentage mass loss to spawning was taken from Madenjian *et al.* (2006) (Table 1). Spring (May–June), summer (July–August) and autumn (September–November) diet proportions were taken from Gamble *et al.* (2011b), and winter (December–April) diet proportions were obtained during the present study (Table 2).

**Table 1** Model inputs for lake whitefish start and end weights, age-at-maturity, spawning date and percentage mass loss to spawning for each age class used in the bioenergetics modelling. Per cent mass loss due to spawning was taken from Madenjian *et al.* (2006). All other inputs were taken from Isaac (2010)

Age class	Start mass (g)	End mass (g)	Spawning date	% Mass loss to spawning
2	90.9	158.7	n/a	0.0
3	158.7	248.5	n/a	0.0
4	248.5	360.2	n/a	0.0
5	360.2	493.1	November 1	5.2
6	493.1	646.0	November 1	5.2
7	646.0	817.0	November 1	5.2
8	817.0	1 004.0	November 1	5.2
9	1 004.0	1 111.5	November 1	5.2

**Table 2** Diet proportions by wet mass for whitefish used to estimate annual consumption. Data were taken from Gamble *et al.* (2011b), except for diet composition of whitefish in the months of December–April which were derived from the present study. Data for February were linearly interpolated between December and March. Energy density is in  $\text{kJ g}^{-1}$  wet. Other category for whitefish includes clams and leeches

Month	<i>Mysis</i>	<i>Diporeia</i>	Cisco eggs	Chironomids	Other
May–June	0.87	0.13	0.00	0.00	0.00
July–August	0.47	0.43	0.00	0.00	0.11
September–November	0.69	0.30	0.00	0.01	0.00
December	0.00	0.00	0.99	0.00	0.01
January	0.00	0.00	1.00	0.00	0.00
March	0.00	0.29	0.25	0.32	0.14
April	0.00	0.00	0.09	0.38	0.53
Energy density	3.537*	4.386*	10.312 <sup>‡</sup>	2.427 <sup>†</sup>	3.064

\*Gardner *et al.* (1985).

†Cummins & Wuycheck (1971).

‡Present study.

Daily consumption estimates of each prey type were derived for an individual fish in each whitefish year class (ages two to nine). The numerical density of each year class was estimated by apportioning whitefish total densities ( $\text{fish ha}^{-1}$ ) to year classes based on an age-length key and length-frequency distributions (Isaac, 2010). Total densities for whitefish were taken from the annual spring bottom trawl survey as described above. The annual consumption estimate for each individual for each year class was multiplied by year class density and then summed across year classes to estimate annual consumption on a per hectare basis. These estimates were then multiplied by 45 760 ha to estimate overall whitefish annual and winter consumption for the study region. We compared annual and winter consumption estimates with the sum of estimates of standing stock and annual production for both *Mysis* and *Diporeia*, the standing stock of cisco eggs and their energetic equivalents. Production was estimated by multiplying standing stock by annual production to biomass ratios (P/B) for *Mysis* (3.21; Isaac, 2010) and *Diporeia* (0.80; Auer, Cannon & Auer, 2009).

Because we found cisco eggs to be an important part of whitefish diet, we ran an additional bioenergetics simulation to evaluate the extent to which an individual whitefish would have to compensate for the absence of the eggs (e.g. if the cisco stock collapsed) by feeding on other prey to achieve the same growth. To do this, we simulated whitefish growth using starting and ending masses for an age-six individual (Table 1) and altered

their dietary composition. We extended the per cent diet composition for September–November until March (Table 1) and then evenly allocated the per cent of the diet composition that was cisco eggs in March and April to the remaining (consumed) diet items in each month. We ran a simulation for one year, with all other inputs and parameters the same as described above, and estimated the per cent increase in biomass consumption.

#### Stable isotope analyses

We sampled the fish community between Cornucopia and Sand Island during November 2009 and April–May 2010 using bottom trawl and midwater trawl gear (Fig. 1) to collect tissue samples for stable isotope analyses. This area was chosen because (i) it was known to support a high density of spawning cisco (Yule *et al.*, 2009), (ii) the stomach samples for whitefish were available through the winter from a commercial fishing operation and (iii) past sampling showed the fish assemblage in the area was species rich (USGS, unpubl. data). We attempted to collect 10 individuals of smaller-bodied fish species and 10 juvenile and 10 adults of larger-bodied species. Small-bodied species included the following: rainbow smelt, ninespine stickleback (*Pungitius pungitius*), slimy sculpin (*Cottus cognatus*) and spoonhead sculpin (*Cottus renei*). Larger-bodied species included the following: shortjaw cisco (*Coregonus zenithicus*), cisco, bloater (*Coregonus hoyi*) and whitefish. Individuals were frozen in the field and kept frozen until laboratory processing. In the laboratory, individuals were thawed and muscle and liver samples were collected from whitefish. Perga & Gerdeaux (2005) demonstrated that, in European whitefish (*C. lavaretus*), tissues with more rapid turnover, such as liver, reflect the recent diet more closely than does muscle during periods of slow growth. Muscle samples from other members of the fish assemblage were also collected, as were cisco ovaries from autumn 2009 spawners in the study region and cisco eggs from whitefish stomachs, when collected in sufficient numbers throughout winter. *Mysis* and *Diporeia* samples for stable isotope analyses were collected in the autumn and spring at a 73-m deep station between Cornucopia and Sand Island (Fig. 1). Additionally, *Diporeia* samples were collected at 25- and 108-m-deep stations in the same vicinity during spring. Macroinvertebrate samples were frozen until laboratory processing.

For stable isotope analyses, samples (1–3 g wet) were dried at 65 °C for 48 hr in aluminium boats and homogenised with a mortar and pestle. For each dried sample, an aliquot of 0.9–1.1 mg, measured to the nearest

0.001 mg, was placed in a tin capsule. Samples were analysed for  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ , % N and % C using a Costech ECS4010 elemental analyser (Costech Analytical Technologies, Inc, Valencia, CA, U.S.A.) coupled with a DELTA<sub>plus</sub> XP isotope ratio mass spectrometer (Thermo Scientific, Bremen, Germany) at the University of New Hampshire Stable Isotope Laboratory. Carbon and nitrogen isotope data are reported in  $\delta$  units (‰) according to  $([R_{\text{sample}}/R_{\text{standard}}]-1) \times 1000$ , where R is the ratio  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$  (Peterson & Fry, 1987), and the standard was Vienna Pee Dee belemnite (VPDB) for carbon and atmospheric  $\text{N}_2$  for nitrogen. The  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values were normalised on the VPDB and AIR scales with IAEA CH6 ( $-10.4\text{‰}$ ), CH7 ( $-31.8\text{‰}$ ), N1 ( $0.4\text{‰}$ ) and N2 ( $20.3\text{‰}$ ).

Commercially available reference materials were used to confirm the accuracy and precision of stable isotope analyses. Means ( $\pm$ SD) were  $9.2 \pm 0.1\text{‰}$  for  $\delta^{15}\text{N}$  and  $-25.4 \pm 0.2\text{‰}$  for  $\delta^{13}\text{C}$  for bolete ( $n = 59$ ; true values =  $9.2$  and  $-25.4\text{‰}$  for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , respectively), and  $0.6 \pm 0.1\text{‰}$  for  $\delta^{15}\text{N}$  and  $-27.0 \pm 0.1\text{‰}$  for  $\delta^{13}\text{C}$  for NIST15 ( $n = 69$ ; true values =  $0.7$  and  $-27.0\text{‰}$  for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , respectively).

We estimated per cent lipid (L) of whitefish samples using the equation  $L = 93/(1 + (0.246 \cdot C : N - 0.775)^{-1})$ , where C : N is the molar C : N ratio (McConnaughey & McRoy, 1979). Molar C : N was derived by converting mass-based C : N measurements from stable isotope analyses to molar. Fagan *et al.* (2010) concluded that arithmetic estimation of lipids from C : N data was not reliable. In contrast, other studies have found highly significant statistical relationships between C : N and measured lipid content (e.g. Kiljunen *et al.*, 2006; Logan *et al.*, 2008; Abrantes *et al.*, 2012). To illustrate seasonal changes in whitefish tissue composition, we present both per cent lipid, calculated according to McConnaughey & McRoy (1979), and C : N ratios. To examine some isotopic shifts more closely, we calculated lipid-corrected  $\delta^{13}\text{C}$  values for muscle, according to Kiljunen *et al.* (2006), and liver, according to Logan *et al.* (2008).

Circular statistics (Batschelet, 1981) were used to test whether the stable isotope values of the fish assemblage shifted in a manner consistent with a diet of cisco eggs over the winter. Following Schmidt *et al.* (2007), we used average  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values to represent the food-web coordinates ( $x$ ,  $y$ ) for each fish species and life-stage (adult or juvenile, when available) in autumn and spring. We estimated the magnitude ( $r$ ) and direction (or angle) of change ( $\theta$ ) in food-web space between the two time periods for each species and then tested for

directional change among species using Rayleigh's test for circular uniformity (Schmidt *et al.*, 2007).

## Results

### Cisco eggs and macroinvertebrate availability

The relationship between ovary mass (range = 12.8–124.4 g) and female mass (range = 124–764 g) was statistically significant ( $F = 308$ ,  $P < 0.0001$ ,  $r^2 = 0.89$ ,  $n = 41$ ) and described by  $Y = 0.148 \cdot X - 6.901$ , where Y is ovary mass (g) and X is female mass (g). Based on this fecundity–mass relationship, the 2006 mean ( $\pm$ SE) adult cisco density ( $366 \pm 24 \text{ ha}^{-1}$ ) in the study area, sex ratio (66% female) and size structure of the spawning cisco population in the western arm of Lake Superior (Yule *et al.*, 2009), we estimate that cisco deposited  $11.5 \pm 0.8 \text{ kg ha}^{-1}$  of eggs, giving a total of  $526 \pm 34$  metric tons (mt) in the whole study area during 2006 (Fig. 2). Energy density of cisco ovaries averaged ( $\pm$ SE)  $10.3 \pm 0.2 \text{ kJ g}^{-1}$  wet mass ( $n = 10$  fish). Given the biomass of cisco eggs and their mean energy density, the total energy value of cisco eggs deposited along the Wisconsin south shore of Lake Superior was  $5421 \pm 355$  gigajoules (GJ; Fig. 2).

Other prey available to benthic fish over winter, as measured by the estimated standing stock of the macroinvertebrates *Mysis* and *Diporeia*, was  $359 \pm 161$  mt and  $1684 \pm 472$  mt, respectively (Fig. 2). Cisco eggs therefore represented 20% of available prey by biomass. On an energetic basis, however, cisco eggs represented 39% of available prey (Fig. 2) because of their higher energy density (Table 2).

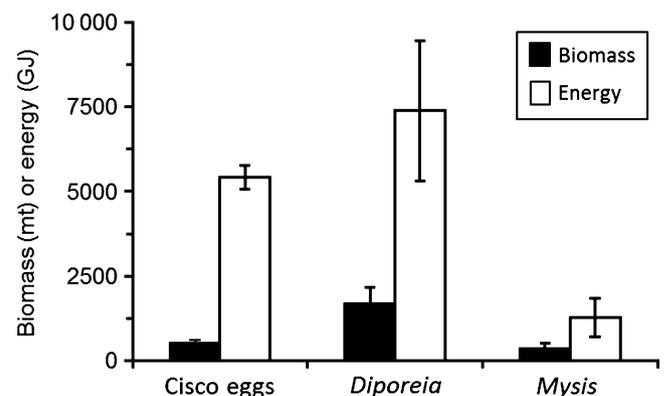


Fig. 2 Average ( $\pm$ SE) biomass (solid bars) and energy (open bars) of major benthic prey resources in the Wisconsin south shore region of Lake Superior over the winter (cisco eggs) and throughout the year (*Diporeia* and *Mysis*).

**Table 3** Average ( $\pm$ SE) total prey biomass and cisco egg biomass found in whitefish stomachs collected between December 2009 and April 2010 and in December 2011. Total lengths are reported as average values ( $\pm$ SE), and empty stomachs are per cent of number of stomachs examined

Date	No. stomachs	Total length (mm)	% Empty Stomachs	Total prey biomass (g)	Cisco egg biomass (g)
December 2009	5	451 $\pm$ 12.2	0	22.1 $\pm$ 3.65	22.1 $\pm$ 3.65
January 2010	6	450 $\pm$ 6.6	0	13.3 $\pm$ 3.26	13.3 $\pm$ 3.26
March 2010	20	460 $\pm$ 3.0	75	0.4 $\pm$ 0.19	0.1 $\pm$ 0.11
April 2010	15	459 $\pm$ 4.2	53	0.1 $\pm$ 0.07	<0.1 $\pm$ 0.02
December 2011	20	436 $\pm$ 4.2	0	24.7 $\pm$ 1.78	23.9 $\pm$ 1.82

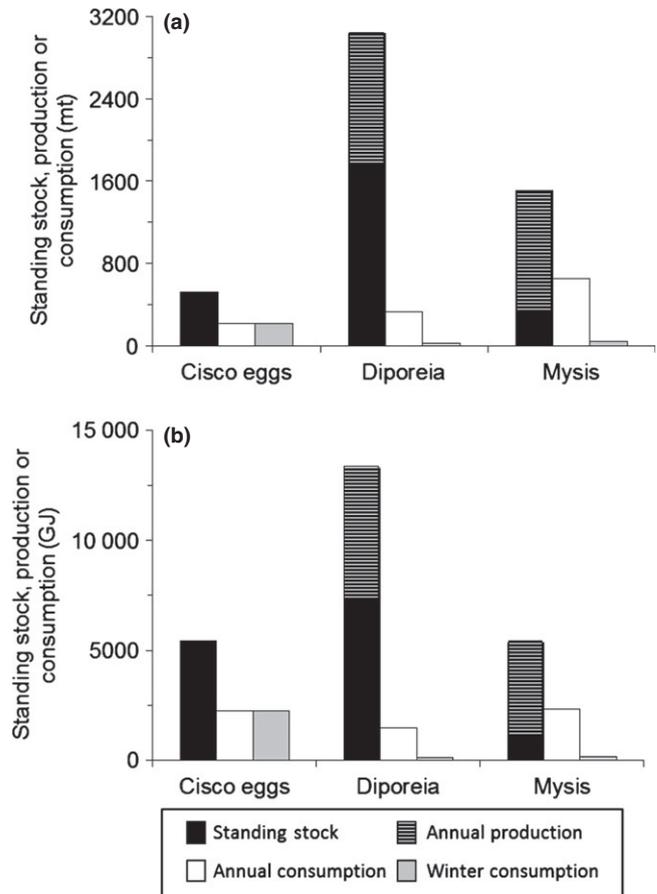
### Lake whitefish consumption

To characterise the winter diet, a total of 66 whitefish were collected on five separate dates from December 2009 to April 2010 and December 2011 (Table 3). A mean ( $\pm$ SE) of 22.1  $\pm$  3.65 and 13.3  $\pm$  3.26 g of cisco eggs were found in whitefish stomachs in December 2009 and January 2010, respectively, which contributed 100% of the observed gut contents on these dates (Tables 2 & 3). Eggs from whitefish stomachs were genetically identified as cisco (W. Stott, USGS, unpubl. data). Stomach samples from whitefish collected during December 2011 ( $N = 20$ ) contained an average of 23.9  $\pm$  1.82 g of cisco eggs (Table 3). The amount of cisco eggs found in whitefish stomachs in March and April 2010 dropped to 0.1  $\pm$  0.11 and <0.1  $\pm$  0.02 g, respectively, but overall prey content in stomachs also dropped and the per cent of empty stomachs increased compared to December and January (Table 3).

Total annual consumption by whitefish along the Wisconsin south shore region of the western arm of Lake Superior was estimated at 1351 mt of prey. Annual consumption was dominated by *Mysis* (657 mt, or 49% of total estimated biomass consumed), *Diporeia* (333 mt, 25%) and cisco eggs (216 mt, 16%; Fig. 3a). Estimated annual consumption of *Diporeia*, *Mysis* and cisco eggs was lower than estimated available supplies for each (11, 43 and 41%, respectively; Fig. 3a).

Consumption by whitefish during the winter (December–April) was estimated at 396 mt of prey. Winter whitefish consumption was dominated by cisco eggs (216 mt, or 54% of total biomass consumed in winter), whereas demand for *Mysis* (39 mt, 10%) and *Diporeia* (29 mt, 7%) was much lower than in the rest of the year (Fig. 3a).

Considered on an energetic basis, cisco eggs represented 34% of the whitefish diet annually, because of their much greater energy density (10.312 kJ g<sup>-1</sup> wet) compared to *Mysis* (3.537 kJ g<sup>-1</sup> wet) and *Diporeia* (4.386 kJ g<sup>-1</sup> wet). Whitefish consumed an estimated 2224 GJ of cisco eggs, 2323 GJ of *Mysis* and 1460 GJ of *Diporeia* over the course of a year (Fig. 3b). In the winter,



**Fig. 3** (a) Standing stock of *Mysis*, *Diporeia*, and cisco eggs (black bars), annual production of *Mysis* and *Diporeia* (horizontal striped bars), and annual (open bars) and winter (grey bars) consumption demand by lake whitefish for the three primary prey types on the Wisconsin south shore region of Lake Superior. (b) Same as (a) except on an energy basis. Standing stock estimate of cisco eggs is taken from 2006. Standing stock and annual production estimates of macroinvertebrates are taken from spring, summer and autumn collections in 2005.

cisco eggs represented 79% of the energy consumed by whitefish (Fig. 3b).

To evaluate the importance of cisco eggs for whitefish annual energy intake, cisco eggs were modelled as 'dropped from the diet'. The estimated annual consumption of prey biomass by an age-six whitefish would need

to increase 32% to compensate for the absence of eggs to grow at the observed rate.

#### Stable isotope analyses and lipid estimates

Stable isotope values of cisco eggs collected during November were significantly different from values for *Mysis* and *Diporeia*. Mean November values ( $\pm$ SE) were  $-28.8 \pm 0.1\text{‰}$  for  $\delta^{13}\text{C}$  and  $6.5 \pm 0.1\text{‰}$  for  $\delta^{15}\text{N}$  for cisco eggs compared to  $-27.4$  and  $4.0\text{‰}$  for *Mysis* and  $-26.9$  and  $4.4\text{‰}$  for *Diporeia* (Table 4). Because whitefish  $\delta^{15}\text{N}$  values for muscle and liver tissue in November ( $6.8 \pm 0.1$  and  $5.9 \pm 0.2\text{‰}$ , respectively) were similar to cisco eggs and appeared greater than *Mysis* and *Diporeia*, we expected a shift in whitefish stable isotope values to higher  $\delta^{15}\text{N}$  values through the winter if cisco eggs were a major component of their diet.

Whitefish muscle  $\delta^{15}\text{N}$  values increased significantly from autumn to spring ( $F_{0.05(2), 5, 47} = 6.8$ ,  $P < 0.0001$ ,  $r^2 = 0.42$ ) with a maximum mean difference of  $0.9\text{‰}$  between the months of November and March (Fig. 4a). Liver  $\delta^{15}\text{N}$  values also increased significantly from autumn to spring ( $F_{0.05(2), 5, 48} = 43.0$ ,  $P < 0.0001$ ,  $r^2 = 0.82$ ), with a maximum mean difference of  $2.2\text{‰}$  between the months of November and March (Fig. 4b). The  $\delta^{13}\text{C}$  values for muscle and liver both decreased over winter ( $F_{0.05(2), 5, 47} = 3.3$ ,  $P = 0.0118$ ,  $r^2 = 0.26$  for muscle;  $F_{0.05(2), 5, 48} = 4.3$ ,  $P < 0.0028$ ,  $r^2 = 0.31$  for liver) with both tissues showing significant differences between November and March (Fig. 4).

Per cent lipid estimates of whitefish liver changed significantly over the winter months ( $F_{0.05(2), 5, 48} = 15.2$ ,  $P < 0.0001$ ,  $r^2 = 0.61$ ). Estimates ( $\pm$ SE) almost doubled between November ( $26 \pm 0.7\%$ ) and January ( $48 \pm 2.3\%$ ), with a peak in March ( $49 \pm 2.5\%$ ; Fig. 5). These trends were mirrored by average liver C : N ratios ( $\pm$ SD), which increased from  $4.8 \pm 0.2$  in November to  $8.0 \pm 1.5$  in March. Whitefish muscle lipid content also changed significantly over the winter months ( $F_{0.05(2), 5, 48} = 4.1$ ,  $P = 0.0034$ ,  $r^2 = 0.30$ ), with a steady increase between November and March (Fig. 5). Mean muscle C : N also increased from  $3.9 \pm 0.3$  in November to  $4.8 \pm$  in March.

Lipid-corrected  $\delta^{13}\text{C}$  values for whitefish liver and muscle tissues indicated that seasonal decreases in liver and muscle  $\delta^{13}\text{C}$  were driven by those increases in lipid content. Mean uncorrected liver  $\delta^{13}\text{C}$  declined (November to March) by  $2.1\text{‰}$  (from  $-24.5$  to  $-26.6\text{‰}$ ; Fig. 4b), whereas lipid-corrected values decreased by only  $0.4\text{‰}$  (from  $-22.8$  to  $-23.2\text{‰}$ ;  $t = 1.4$ ,  $P = 0.20$ , d.f. = 16). Mean uncorrected muscle  $\delta^{13}\text{C}$  declined (November to March) by  $1.3\text{‰}$  (from  $-24.4$  to  $-25.7\text{‰}$  Fig. 4a), whereas average lipid-corrected values decreased by only  $0.3\text{‰}$  (from  $-22.8$  to  $-23.1\text{‰}$ ;  $t = 1.2$ ,  $P = 0.24$ , d.f. = 16).

The  $\delta^{13}\text{C} - \delta^{15}\text{N}$  biplot of muscle tissue samples from fish assemblage members between autumn 2009 and spring 2010 is consistent with a diet of cisco eggs over the winter (Fig. 6a). All fish species showed a similar trajectory through food-web space (average  $\theta \pm$  circular

**Table 4**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (‰) for cisco eggs, *Mysis*, and *Diporeia* between autumn 2009 and spring 2010. When more than one sample was available, the average ( $\pm$ SE) is reported. Sample sizes are shown in parentheses. Cisco eggs were taken from spawning cisco (November) or from lake whitefish stomachs (remaining time periods). Station depths from which macroinvertebrate samples were collected are indicated (parenthetically) in left column

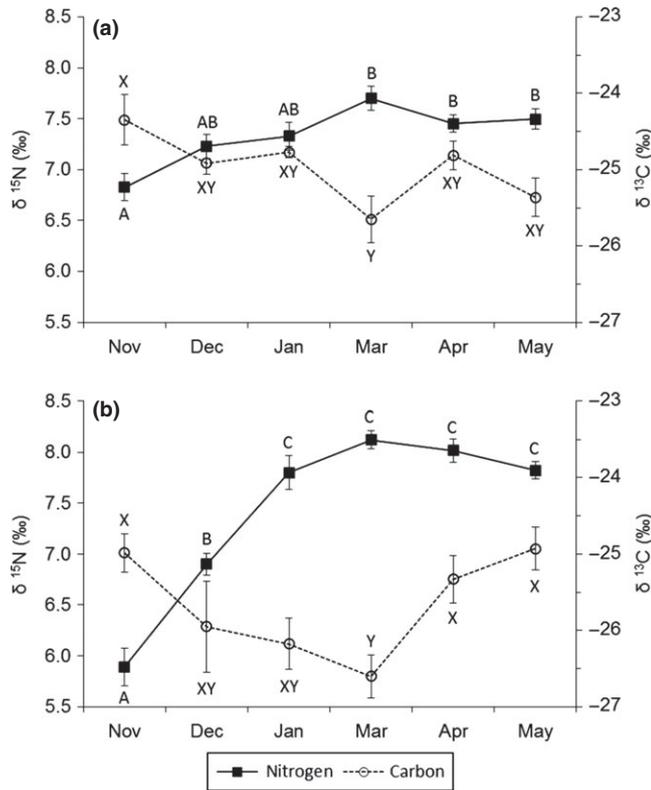
Prey Item	November	December	January	March	April	May
Cisco eggs						
$\delta^{13}\text{C}$	$-28.8 \pm 0.1$ (9)	$-28.4$ (1)	$-29.0 \pm 0.06$ (2)	$-28.5$ (1)		$-28.0$ (1)
$\delta^{15}\text{N}$	$6.5 \pm 0.1$ (9)	$6.5$ (1)	$6.9 \pm 0.01$ (2)	$7.0$ (1)		$6.4$ (1)
<i>Mysis</i>						
(73 m) $\delta^{13}\text{C}$	$-27.4^A$ (1)				$-28.3$ (1)	
(73 m) $\delta^{15}\text{N}$	$4.0^B$ (1)				$7.1$ (1)	
<i>Diporeia</i>						
(25 m) $\delta^{13}\text{C}$					$-28.6$ (1)	
(25 m) $\delta^{15}\text{N}$					$4.3$ (1)	
(73 m) $\delta^{13}\text{C}$	$-26.9^C$ (1)				$-27.1$ (1)	
(73 m) $\delta^{15}\text{N}$	$4.4^D$ (1)				$6.0$ (1)	
(108 m) $\delta^{13}\text{C}$					$-27.3$ (1)	
(108 m) $\delta^{15}\text{N}$					$7.3$ (1)	

<sup>A</sup>Significantly different from cisco eggs in November (one-sample  $t$ -test,  $t = 9.9$ , d.f. = 8,  $P < 0.0001$ ).

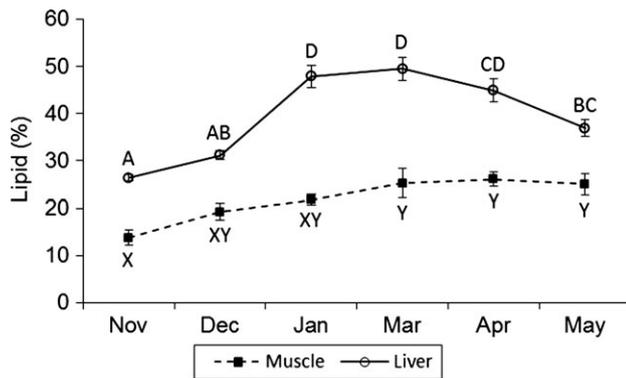
<sup>B</sup>Significantly different from cisco eggs in November (one-sample  $t$ -test,  $t = 20.7$ , d.f. = 8,  $P < 0.0001$ ).

<sup>C</sup>Significantly different from cisco eggs in November (one-sample  $t$ -test,  $t = 13.4$ , d.f. = 8,  $P < 0.0001$ ).

<sup>D</sup>Significantly different from cisco eggs in November (one-sample  $t$ -test,  $t = 17.1$ , d.f. = 8,  $P < 0.0001$ ).



**Fig. 4** Mean ( $\pm$ SE)  $\delta^{13}\text{C}$  (open circles; uncorrected for lipids) and  $\delta^{15}\text{N}$  (closed squares) trajectories for (a) muscle and (b) liver samples of lake whitefish from November 2009 to May 2010. Estimates labelled with the same letter indicate no significant difference among months for each tissue type and isotope (Tukey's honestly significant difference test;  $\alpha = 0.05$ ). ABC lettering refers to  $\delta^{15}\text{N}$  tests and XY lettering refers to  $\delta^{13}\text{C}$ .



**Fig. 5** Mean ( $\pm$ SE) per cent lipid estimates for liver (open circles) and muscle (closed squares) samples of lake whitefish from November 2009 to May 2010. Estimates labelled with the same letter indicate no significant difference among months for each tissue type (Tukey's honestly significant difference test;  $\alpha = 0.05$ ). ABCD lettering refers to liver tests and XY lettering refers to muscle tests.

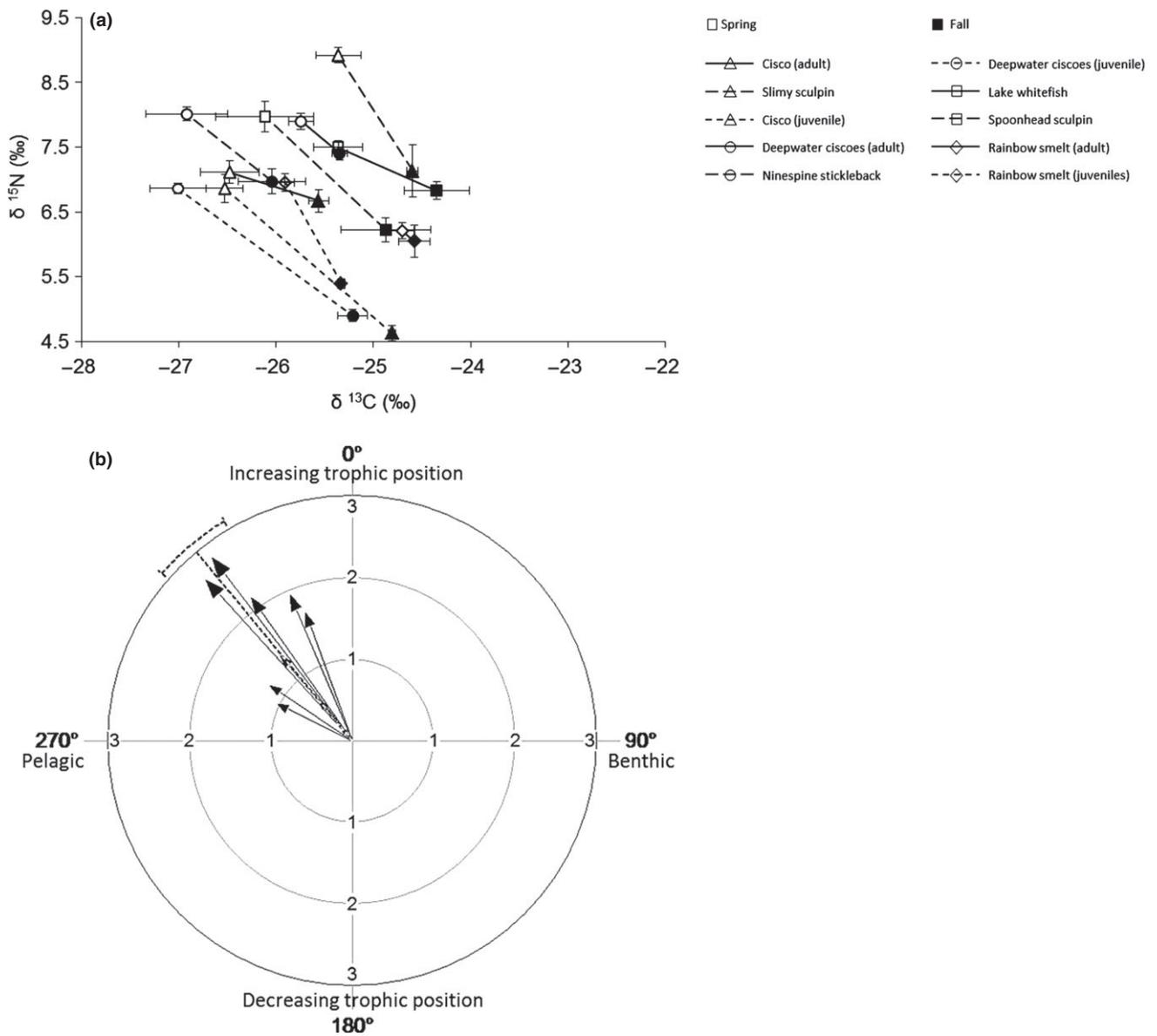
$SD = 320 \pm 13^\circ$ , range of  $\theta = 296\text{--}340^\circ$ , Rayleigh's  $Z = 9.5$ ,  $P < 0.0001$ ; Fig. 6b). However, the changes cannot unequivocally be attributed to a diet dominated by

cisco eggs because the isotopic values of *Mysis* and *Diporeia* also shifted closer to the value of cisco eggs sometime between autumn and spring (Table 4). The  $\delta^{15}\text{N}$  values for *Mysis* and *Diporeia* samples, collected at the same 73-m-depth station as the previous autumn, increased by 3.1 and 2.0‰, respectively. Additionally,  $\delta^{15}\text{N}$  values for *Diporeia* in April showed a positive trend with depth, increasing from 4.3‰ at 25-m depth to 7.3‰ at 108-m depth (Table 4), consistent with the findings of Sierszen, Peterson & Scharold (2006). The  $\delta^{13}\text{C}$  values were within the range of variation expected for these depths (Sierszen *et al.*, 2006).

## Discussion

Awareness of the importance of habitat coupling has grown over the last two decades (Polis *et al.*, 1997; Schindler & Scheuerell, 2002; Loreau, Mouquet & Holt, 2003). Our findings indicate that cisco provide a substantial spatial resource subsidy from offshore pelagic to nearshore benthic habitats in the Wisconsin south shore region of Lake Superior. On a biomass basis, cisco eggs represented 16% of annual and 54% of winter (December to April) consumption by whitefish. On an energetic basis, cisco eggs represented 34% of annual and 79% of winter consumption. On an annual time scale, only *Mysis* represented a greater source of energy for whitefish in our study region, at 36%. The availability of cisco eggs, and their high energy density compared to other available prey, may explain their extensive use by whitefish during the winter. Furthermore, the reduced cost of foraging on eggs versus mobile prey probably provides additional energetic gain through reduced foraging costs. Diet and bioenergetics simulations were corroborated by significant isotopic shifts in whitefish livers during the winter period. Lipid-corrected liver and muscle  $\delta^{13}\text{C}$  showed small seasonal changes, indicating that lipid accumulation drove the patterns in whitefish isotope data. Although *Mysis* and *Diporeia* developed isotope values similar to those of cisco eggs over winter, the small energetic demand predicted for those macroinvertebrates relative to that predicted for eggs, based on winter diet analyses and bioenergetics modelling, points to egg consumption as the cause for the seasonal isotopic shifts in whitefish tissues. Taken together, our results indicate a strong linkage between offshore secondary production and the dominant nearshore benthivore, whitefish, via the dominant offshore planktivore, cisco.

Cisco eggs are clearly of major importance for whitefish in our study region. To our knowledge, there is no previous documentation of this or other similar findings



**Fig. 6** (a) Biplot of average ( $\pm$ SE)  $\delta^{13}\text{C}$  (uncorrected for lipids) and  $\delta^{15}\text{N}$  values of muscle samples taken from fish species captured in the Wisconsin south shore region of Lake Superior in autumn 2009 (solid symbols) and spring 2010 (open symbols): adult (circles with solid lines,  $N = 13$  for autumn,  $N = 18$  for spring) and juvenile (circles with short-dashed lines,  $N = 6$  for autumn,  $N = 20$  for spring) ‘deepwater ciscoes’ (i.e. bloater and shortjaw cisco combined); adult (triangles with solid lines,  $N = 10$  for autumn,  $N = 13$  for spring) and juvenile (triangles with short-dashed lines,  $N = 9$  for autumn,  $N = 10$  for spring) cisco; adult (diamonds with solid line,  $N = 10$  for autumn,  $N = 10$  for spring) and juvenile (diamonds with short-dashed lines,  $N = 10$  for autumn,  $N = 12$  for spring) rainbow smelt; adult lake whitefish (squares with solid lines,  $N = 8$  for autumn,  $N = 10$  for spring); ninespine stickleback (circles with long-dashed lines,  $N = 7$  for autumn,  $N = 10$  for spring); spoonhead sculpin (squares with long-dashed lines,  $N = 10$  for autumn,  $N = 4$  for spring); and slimy sculpin (triangles with long-dashed lines,  $N = 3$  for autumn,  $N = 11$  for spring). (b) Arrow diagram for directionality (angle of change  $\theta$ ) for each fish species and life-stage in Panel (a). Each arrow represents the direction and magnitude of change for a single species or life-stage between autumn (origin) and spring (tip of arrow). The length of the arrow represents the magnitude of change for that species. The mean angle of change ( $\mu$ ) among all species and life-stages is represented by the straight dashed line, and its 95% confidence interval is represented by the curved dashed line on the rim.

in the Laurentian Great Lakes. Only two other published studies in the last 50 years have found fish eggs to constitute more than 3% of the stomach contents of whitefish. Lumb *et al.* (2007) found unidentified fish eggs to represent 20% of stomach contents (by biomass) for

whitefish captured in the autumn and 13% in the spring in Lake Erie. Herbst, Marsden & Lantry (2013) found fish eggs to compose 42% of the diet (by biomass) for whitefish <800 g in spring in Lake Champlain. It appears that a paucity of winter diet information is at

**Table 5** List of lake whitefish diet studies from North America over the last 50 years and the reported seasons from which diet samples were collected. List excludes studies on larval diets

Study	Lake(s)	Diet sampling?			
		Spring	Summer	Fall	Winter
Anderson & Smith (1971)	Superior	Y	Y	Y	Y
Ihssen <i>et al.</i> , 1981;	Ontario, Huron, Simcoe, Opeongo	N	Y	N	N
Tohtz (1993)	Flathead	Y	Y	Y	Y
Hoyle <i>et al.</i> (1999)	Ontario	U	U	U	U
Pothoven <i>et al.</i> (2001)	Michigan	Y	Y	Y	N
Owens & Dittman (2003)	Ontario	Y	Y	Y	N
Stafford, Hansen & Stanford (2004)	Flathead	Y	N	Y	N
Pothoven (2005)	Michigan	Y	Y	Y	N
Hoyle (2005)	Ontario	N	Y	N	N
Madenjian <i>et al.</i> (2006)	Michigan	Y	Y	Y	N
Pothoven & Nalepa (2006)	Huron	Y	Y	N	N
Lumb <i>et al.</i> (2007)	Erie, Ontario	Y	Y	Y	N
Nalepa, Pothoven & Fanslow (2009)	Huron	Y	Y	N	N
Rennie, Sprules & Johnson (2009)	Huron	Y	Y	Y	N
Claramunt <i>et al.</i> (2010)	Michigan, Superior	Y	Y	N	N
Macpherson <i>et al.</i> (2010)	Huron	Y	N	Y	N
Gamble <i>et al.</i> (2011a,b)	Superior	Y	Y	Y	N
Herbst <i>et al.</i> (2013)	Champlain	Y	Y	Y	Y

Y, yes; N, no; U, unreported.

least partly responsible for these patterns (Table 5). However, the relatively intact native fish community of Lake Superior, with large populations of both cisco and whitefish, enabled us to detect this trophic linkage that may currently be weak or absent in the other Great Lakes.

Isotopic shifts in other benthic nearshore fish suggest that cisco eggs also may be an important part of their diet during the winter. However, the lack of samples over the course of the winter, together with concurrent isotopic shifts in other major prey sources (*Mysis* and *Diporeia*) between autumn and spring, makes it difficult to determine the degree to which isotopic shifts in the fish assemblage are due to a diet of cisco eggs. On the one hand, the shifts in the macroinvertebrate values are consistent with seasonal lipid accumulation that has been described for boreal invertebrates (Syväranta & Rautio, 2010), and in Lake Superior might be linked to winter consumption of cisco eggs. Seale & Binkowski (1988) did not find evidence for *Mysis* consumption of bloater eggs from Lake Michigan in laboratory experiments, but *Mysis* did consume embryonic bloaters. On the other hand, seasonal oscillations of isotopic signals in aquatic biota are well known, with  $^{13}\text{C}$ -depletion and  $^{15}\text{N}$ -enrichment during winter resulting from temporal changes in nutrient pools and subsequent uptake by primary producers and consumers (e.g. Woodland *et al.*,

2012). Higher in the food web,  $^{15}\text{N}$ -enrichment during winter and other seasons has been associated with starvation over a wide range of animals including fish (e.g. Chérel *et al.*, 2005; Colborne & Robinson, 2013). Therefore, patterns in the fish assemblage observed, based solely on isotopic shifts between autumn and spring samples, may result from a combination of mechanisms. However, our sampling of whitefish through the winter and our multi-pronged approach (diets, bioenergetics analysis, isotopes and lipids) suggest cisco eggs are an important part of the whitefish diet in winter and, moreover, for the entire year. By sampling during winter, we uncovered an important whitefish–cisco interaction that would otherwise have been obscured. Future winter collections of fish and invertebrates will be important for assessing the potential impacts of cisco eggs and other seasonal processes on the broader nearshore community. Application of multiple natural tracers (e.g. stable isotopes and essential fatty acids) would also provide better insight.

While we are confident in the interpretation of our results, there are several caveats that may have bearing on our findings. Our winter consumption estimates are based on relatively few stomach samples ( $N = 66$ ). Consumption of cisco eggs by whitefish, however, has been known among commercial fishermen for decades, is more prevalent when cisco spawning stocks are high

and, unlike our findings, can be high in March and April (C. Bronte, US Fish and Wildlife Service, pers. comm.). Additionally, despite our modest sample size, whitefish diet composition was consistent across consecutive months (December 2009 and January 2010) and across years (December 2009 and 2011), when eggs were presumably most available to whitefish. Both of these anecdotal and scientific observations suggest cisco egg predation by whitefish is a real and consistent phenomenon in this part of Lake Superior. A second caveat is that our winter diet data were taken from commercially captured fish >400 mm. We assumed the diet of these fish to be representative of all sizes modelled (age-2+). Whitefish are known to undergo ontogenetic dietary shifts related to prey size (e.g. Pothoven & Nalepa, 2006). However, cisco eggs range in diameter from 1.8 to 2.1 mm and therefore do not impose gape limitations on any whitefish age-classes. Our ability to use mixing models (Phillips & Gregg, 2001) to quantify the nutritional contribution of cisco eggs to whitefish using isotope data was limited by the similarity in the isotopic values of macroinvertebrate and eggs in the spring. However, lipid-corrected isotope data, lipid estimates based upon C : N ratios obtained through isotope analyses, and bioenergetic modelling provided further evidence of the seasonal importance of cisco egg consumption. A final caveat is that our *Mysis* and *Diporeia* isotopic values were based on very few samples. Sierszen *et al.* (2011) reported isotopic values for *Mysis* (2.4–4.2‰ for  $\delta^{15}\text{N}$  and –26.1‰ for  $\delta^{13}\text{C}$ ) and *Diporeia* (1.0–3.5‰ for  $\delta^{15}\text{N}$  and –27.3 to –26.8‰ for  $\delta^{13}\text{C}$ ) captured in the same depth zone (30–80 m) throughout Lake Superior in late summer and early autumn. Their values are similar to ours from November, suggesting consistent separation of *Mysis* and *Diporeia* isotopic values from cisco eggs at the start of winter.

Future studies may be improved by comparing benthic fish growth from areas or lakes with and without spawning cisco (e.g. Botton & Loveland, 2011). Our whitefish diet and community isotope samples were collected from a region of Lake Superior characterised by large spawning aggregations of cisco (Selgeby, 1982; Yule *et al.*, 2009). At this time, the relevance of our findings to the rest of Lake Superior is unknown, but more detailed spatial analyses incorporating a wider range of cisco and whitefish densities, growth and foraging would help evaluate the broader applicability of our results.

If our energy transport hypothesis is true, we would expect lower spring lipid values in the absence of cisco egg deposition, akin to the observed declines in growth and condition of whitefish in Lakes Huron, Michigan

and Ontario associated with declines in *Diporeia* (e.g. Mohr & Nalepa, 2005). In our simulation of the absence of cisco eggs in the diet of an age-six whitefish from December to April, the whitefish had to consume 32% more prey biomass to realise the same growth. This suggests that feeding on cisco eggs over the winter is likely to represent a significant component of their annual diet, without which they would need to increase their foraging activity to compensate (for example, see Fig. 5 in Pothoven & Madenjian, 2008). After spawning, fish are energy-depleted and having an adequate supply of prey is very likely to be important for their recovery and future reproductive output (e.g. Burton & Idler, 1987). Our results suggest that the energy reserves of whitefish after spawning in the Wisconsin south shore region of Lake Superior recover over winter as a result of cisco egg availability. Further, the energy they obtain over winter may have longer-term implications for their subsequent growth and reproduction (Beauchamp, Collins & Henderson, 2004). Our results provide an example of important processes that may be affecting whitefish during the winter, a poorly studied season (Table 5). Further studies of winter feeding and food-web interactions may shed light on these processes in Lake Superior and the other Great Lakes.

Historical fluctuations in cisco abundance probably resulted in variable deposition of eggs in nearshore areas. Coupling between offshore and nearshore habitats may have been stronger when cisco populations were much more abundant in Lake Superior (Cox & Kitchell, 2004) and the other Great Lakes (Stockwell *et al.*, 2009). Where cisco populations have been greatly reduced or lost, this offshore–nearshore coupling is absent; cisco have been replaced by non-native planktivorous species that spawn in spring and have short incubation periods (e.g. rainbow smelt and alewife). This altered assemblage of prey fish does not support such strong movements of energy across habitats. The extent to which extant native fish in these lakes would benefit from a rehabilitated fish assemblage that includes cisco remains unknown. These processes have not yet been clearly elucidated, partly because cisco have been examined primarily as planktivores (e.g. Link, Selgeby & Keen, 2004; Young & Yan, 2008) and as prey (e.g. Hrabik *et al.*, 2006; Negus *et al.*, 2008), but also because changes in the fish assemblage in the other Great Lakes may have suppressed or eliminated those processes. Our work demonstrates that by coupling offshore pelagic and nearshore benthic production, cisco may carry out an additional, and possibly more important, ecosystem process than simply serving as a prey fish for apex predators.

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