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Habitat use by fishes of Lake Superior. II. Consequences of diel habitat use for habitat linkages and habitat coupling in nearshore and offshore waters

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Diel migration patterns of fishes in nearshore (15–80 m depth) and offshore (>80 m) waters of Lake Superior were examined to assess the potential for diel migration to link benthic and pelagic, and nearshore and offshore habitats. In our companion article, we described three types of diel migration: diel vertical migration (DVM), diel bank migration (DBM), and no diel migration. DVM was expressed by fishes migrating from benthopelagic to pelagic positions and DBM was expressed by fishes migrating horizontally from deep to shallow waters at night. Fishes not exhibiting diel migration typically showed increased activity by moving from benthic to benthopelagic positions within demersal habitat. The distribution and biomass of fishes in Lake Superior was characterized by examining 704 bottom trawl samples collected between 2001 and 2008 from four depth zones: ≤40, 41–80, 81–160, and >160 m. Diel migration behaviors of fishes described in our companion article were applied to estimates of areal biomass (kg ha^{-1}) for each species by depth zone. The relative strength of diel migrations were assessed by applying lake area to areal biomass estimates for each species by depth zone to yield estimates of lake-wide biomass (metric tonnes). Overall, species expressing DVM accounted for 83%, DBM 6%, and non-migration 11% of the total lake-wide community biomass. In nearshore waters, species expressing DVM represented 74% of the biomass, DBM 25%, and non-migration 1%. In offshore waters, species expressing DVM represented 85%, DBM 1%, and non-migration 14% of the biomass. Of species expressing DVM, 83% of total biomass occurred in offshore waters. Similarly, 97% of biomass of non-migrators occurred in offshore waters while 83% of biomass of species expressing DBM occurred in nearshore waters. A high correlation ($R^2 = 0.996$) between lake area and community biomass by depth zone resulted in 81% of the lake-wide biomass occurring in offshore waters. Accentuating this nearshore-offshore trend was one of increasing estimated total areal biomass of the fish community with depth zone, which ranged from 13.71 kg ha^{-1} at depths ≤40 m to 18.81 kg ha^{-1} at depths >160 m, emphasizing the importance of the offshore fish community to the lake ecosystem. The prevalence of diel migration expressed by Lake Superior fishes increases the potential of fish to link benthic and pelagic and shallow and deepwater habitats. These linkages enhance the potential for habitat coupling, a condition where habitats become interconnected and interdependent through transfers of energy and nutrients. Habitat coupling facilitates energy and nutrient flow through a lake ecosystem, thereby increasing productivity, especially in large lakes where benthic and pelagic, and nearshore and offshore habitats are often well separated. We propose that the application of biomass estimates to patterns of diel migration in fishes can serve as a useful metric for assessing the potential for habitat linkages and habitat coupling

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in lake ecosystems, and provide an important indicator of ecosystem health and function. The decline of native Lake Trout and ciscoes and recent declines in exotic Alewife and Rainbow Smelt populations in other Great Lakes has likely reduced the capacity for benthic-pelagic coupling in these systems compared to Lake Superior. We recommend comparing the levels and temporal changes in diel migration in other Great Lakes as a means to assess changes in the relative health and function of these ecosystems.

Keywords: Great Lakes, fish communities, diel migration

Introduction

Large lake ecosystems have been traditionally understood by studying pelagic communities in offshore waters, the predominant habitat in these ecosystems. As a result, the contribution of nearshore and benthic habitats to foodwebs and whole-lake energy budgets has not been adequately addressed (Schindler and Scheuerell, 2002; Vadeboncoeur et al., 2002; Vander Zanden and Vadeboncoeur, 2002). Fish have been identified as a primary linkage or coupler of energy flow between nearshore and offshore habitats of lakes (Schindler and Scheuerell, 2002; Vadeboncoeur et al., 2002; Vander Zanden and Vadeboncoeur, 2002). Movement of energy between nearshore and offshore habitats can be traced through foodwebs because carbon fixed in benthic and pelagic habitats have different isotope signatures (France, 1995; Hecky and Hesslein, 1995; Keough et al., 1996; Harvey and Kitchell, 2000; Sierszen et al., 2006).

Diet and stable isotope studies of Lake Superior fishes (Dryer et al., 1965; Anderson and Smith, 1971; Conner et al., 1993; Harvey and Kitchell, 2000; Harvey et al., 2003; Ray et al., 2007; Isaac et al., 2012; Gamble et al., 2011a, b) have led to the development of Lake Superior foodweb models (Kitchell et al., 2000; Gorman et al., 2010a; Stockwell et al., 2010a, Gamble et al., 2011a, b). An important feature of these proposed foodwebs is the recognition of benthic and pelagic pathways of energy production and consumption. For example, the δC^{13} signature of siscowet Lake Trout (*Salvelinus namaycush siscowet*), a deepwater form of Lake Trout, indicates a diet based on both pelagic and benthic sources, whereas the signature for lean Lake Trout (*Salvelinus namaycush namaycush*), the shallow water form of Lake Trout, indicates a diet dominated by benthic sources (Harvey et al., 2003). The use of both benthic and pelagic sources of energy by siscowet Lake Trout is supported by diet studies showing they consume primarily benthic Deepwater Sculpin (*Myoxocephalus thompsonii*) and burbot (*Lota lota*), and pelagic Kiyi (*Coregonus kiyi*) and other coregonines (Fisher and Swanson, 1996; Sitar et al., 2008; Gamble et al., 2011a). Observed patterns of diel vertical migration (hereafter DVM) in *Mysis duluviana* (hereafter *Mysis*), Kiyi, and siscowet Lake Trout (Jensen et al., 2006; Hrabik et al., 2006; Stockwell et al., 2010c; Ahrenstorff et al., 2011) suggest that siscowet feed largely on Deepwater Sculpin and burbot by day and pelagic Kiyi by night. Kiyi, in turn, feed on *Mysis*, which feed on detritus and benthos by day and on plankton in the pelagic zone by night (Beeton and Bowers, 1982; Johannsson et al., 2001, 2003). Deepwater Sculpin feed primarily on *Mysis* and the benthic macroinvertebrate *Diporeia hoyi* (hereafter *Diporeia*) (Gamble et al., 2011a, b). DVM is expressed by *Mysis*, Kiyi, and siscowet Lake Trout; Kiyi track movement of *Mysis* from deep demersal layers at day to near the metalimnion at night and siscowet track and prey upon kiyi (Hrabik et al., 2006; Jensen et al., 2006; Stockwell et al., 2010c; Ahrenstorff et al., 2011). Bollens et al. (2011) would describe this pattern of linked diel migrations as a "cascade of migrations" driven by successive trophic levels of predation. Thus, in deep, offshore waters of Lake Superior, DVM of fishes appears to be driven by DVM of invertebrate prey, thereby promoting the coupling of benthic and pelagic habitats.

Adult Cisco (*Coregonus artedi*) occupy offshore pelagic habitat where they feed on zooplankton and express shallow DVM (Ahrenstorff et al., 2011; Gorman et al., 2012b). Because adult Cisco express limited DVM, and because most are likely too large to serve as prey for most siscowet Lake Trout (Stockwell et al., 2010c; Gorman et al., 2012b), they are a minor contributor to benthic-pelagic coupling in offshore waters (Ahrenstorff et al., 2011). Instead, Cisco undergo seasonal migration to spawn in nearshore waters where they deposit gametes in demersal habitat with energy derived from the offshore pelagic habitat (Stockwell et al., 2009; Stockwell et al., 2010a). In nearshore waters, juvenile Cisco live in demersal habitat and, upon maturity, assume a pelagic existence in offshore waters, thus completing the coupling of nearshore and offshore

habitats (Stockwell et al., 2006, 2009, 2010b; Gorman et al., 2012b). In nearshore waters of Lake Superior, additional benthic-pelagic linkages are effected by DVM of Bloater (*Coregonus hoyi*) and Rainbow Smelt (*Osmerus mordax*) (Harvey and Kitchell, 2000; Yule et al., 2007; Gamble, 2011a, b; Gorman et al., 2010; 2012b). Linkages between deep and shallow demersal habitats result from diel bank migration (hereafter DBM) of Lake Whitefish (*Coregonus clupeaformis*) from deeper demersal waters in the day to shallower demersal waters at night (Yule et al., 2007, 2008; Gorman et al., 2012b).

Previously, we described the diel patterns of habitat migration in the fish communities of nearshore and offshore waters in the Apostle Islands region of Lake Superior (Gorman et al., 2012b) to gain a more comprehensive understanding of the capacity of the Lake Superior fish community to provide linkages across benthic and pelagic and nearshore and offshore habitats. We found a diversity of species-specific habitat associations and diel migration behaviors that varied with ontogenetic stage. All sizes of some species showed strong DVM (Cisco, Bloater, Kiyi, and Rainbow Smelt) over depths ranging from <31 m to >90 m, but for siscowet Lake Trout, only adults present at depths >90 m exhibited strong DVM. All life stages of Lake Whitefish and lean Lake Trout exhibited DBM, but for siscowet Lake Trout, only juveniles exhibited DBM. Finally, the sculpin species did not show evidence of diel migration, but exhibited increased nocturnal activity. In this study we applied the species- and ontogenetic-specific diel migration patterns we described for fishes in the Apostle Islands region (Gorman et al., 2012b) to biomass estimates for the lake-wide fish community of Lake Superior. Our goal was to assess the relative magnitude of diel migration that contributes to linkage of benthic and pelagic and nearshore and offshore habitats in Lake Superior. Finally, we discussed the potential for fish-mediated linkages to promote ecosystem health and function through habitat coupling in the Great Lakes.

Methods

The magnitude of diel migration in the Lake Superior fish community was assessed by applying species-specific diel migration patterns (DVM, DBM, or no migration; Table 1) that we described for fishes in the Apostle Islands region (Gorman et al., 2012b) to lake-wide biomass estimates for each species by depth zone. Lake-wide biomass

Table 1. Fishes of nearshore and offshore waters of Lake Superior showing principal diel migration behavior. DVM: diel vertical migration; DBM: diel bank migration (from Gorman et al., 2012b).

			Diel Migration	
Species	Scientific name	Species code	Juveniles	Adults
lean Lake Trout	*Salvelinus namaycush namaycush*	LLT	DBM	DBM
hatchery Lake Trout	*Salvelinus namaycush namaycush*	HLT	DBM	DBM
siscowet Lake Trout	*Salvelinus namaycush siscowet*	SLT	DBM	DVM
Cisco	*Coregonus artedi*	CIS	DVM	DVM
Bloater	*Coregonus hoyi*	BTR	DVM	DVM
Kiyi	*Coregonus kiyi*	KIY	DVM	DVM
shortjaw cisco	*Coregonus zenithicus*	SJC	DVM	DVM
Lake Whitefish	*Coregonus clupeaformis*	LWF	DBM	DBM
Pygmy Whitefish	*Prosopium coulteri*	PWF	DBM	DBM
Rainbow Smelt	*Osmerus mordax*	RBS	DVM	DVM
Longnose Sucker	*Catostomus catostomus*	LNS	DBM	DBM
Burbot	*Lota lota*	BUR	none	none
Trout-Perch	*Percopsis omiscomaycus*	TRP	DVM	DVM, DBM
Ninespine Stickleback	*Pungitius pungitius*	NSS	DVM, none	DVM, none
Slimy Sculpin	*Cottus cognatus*	SLS	none	none
Spoonhead Sculpin	*Cottus ricei*	SPS	none	none
Deepwater Sculpin	*Myoxocephalus thompsoni*	DWS	none	none

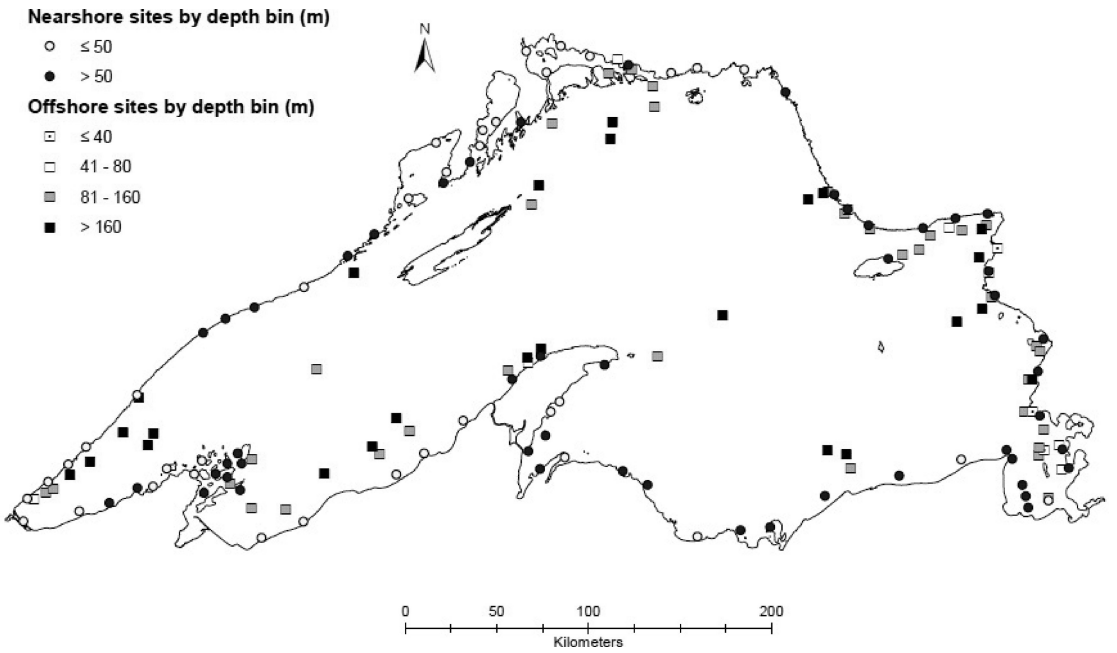

Figure 1. Sampling locations and depth bins for characterizing habitat use by fishes of Lake Superior, 2001–2008. Shown are 86 nearshore bottom trawl sampling sites (circles) and 71 offshore bottom trawl sampling sites (squares).

estimates of fishes were derived from day bottom trawl samples taken in nearshore (15–80 m depth; 86 sites, 550 samples) and offshore (>80 m depth; 71 sites, 154 samples) waters of Lake Superior during May–July of 2001–2008 (Figure 1). These data were obtained using the same trawling methodology described in our companion article on diel migration patterns in the Apostle Islands region (Gorman et al., 2012b) and are the same methodology used in assessments of regional and lake-wide trends in fish community biomass (Stockwell et al., 2006, 2007; 2010a, b; Gorman and Hoff, 2009; Gorman et al., 2010; 2011, 2012a; Yule et al., 2010). The trawl samples were widely distributed across the lake and taken at depths ranging from 15 to >300 m. Catch data were sorted by depth range into the following depth bins: 0–40, 41–80, 81–160, and >160 m. Though data from these surveys were divided into slightly different depth bins than those reported in our companion article (Gorman et al., 2012b), we judged them to be similar enough to apply our findings for diel migration. For each species and depth bin we estimated mean areal biomass (kg ha^{-1}) and expanded these estimates to the lake area contained in the depth bins. We estimated lake area for each depth bin from area polygons created with ArcGIS 9© software applied to unpublished bathymetry data of Lake Superior.

Because adult Cisco are largely pelagic and their abundance is underrepresented in day bottom trawl samples (Stockwell et al., 2006, 2007; Yule et al., 2007; Gorman et al., 2012b), we used biomass estimates from lake-wide acoustic surveys (Stockwell et al., 2006, 2007). For Kiyi, we applied areal biomass estimates based on day bottom trawl samples taken from depths of 121–160 m to depths >160 m. This was done because Kiyi occupy demersal strata during the day, where they are vulnerable to bottom trawls, but appear to be bathymetrically limited to depths <200 m. At greater depths, Kiyi are suspended off the lake bottom (Stockwell et al. 2010a–c). Two additional species in the lake-wide data set not represented in our Apostle Islands study were hatchery Lake Trout, which is derived from lean Lake Trout stocks and is functionally similar, and Longnose Sucker (*Catostomus catostomus*), a demersal species of inshore and nearshore waters (Table 1). Based on sampling of inshore waters (<15 m depth) of the Apostle Islands and Isle Royale, longnose sucker appear to express nocturnal DBM (Gorman and Moore, 2009).

Bubble plots were generated to visualize changes in the diel vertical distribution of the fish community by depth zone. Based on information on the vertical distribution of Lake Superior fishes from our companion article (Gorman et al., 2012b)

and other sources (Hrabik et al. 2006; Yule et al. 2007, 2008; Stockwell et al., 2010a–c), we assigned fishes to a classification of vertical strata as follows: 0 – benthic (on the lake bottom); 1 – benthopelagic (just above the lake bottom); three pelagic strata within the hypolimnion, 2 – deep hypopelagic, 3 – mid-hypopelagic, and 4 – upper hypopelagic; 5 – metapelagic (pelagic stratum contained within the metalimnion); and 6 – epipelagic (pelagic stratum contained within the epilimnion). These vertical strata are pictured in a diagram in our companion article (Gorman et al, 2012b, Figure 9a). The demersal zone represents a combination of benthic and benthopelagic strata and is the habitat sampled by bottom trawls. Plots were generated by integrating information on diel migration and vertical distribution of fishes with estimates of areal biomass (kg ha^{-1}) and total biomass by depth zone. Total biomass was estimated by weighting areal biomass by the area of a depth zone.

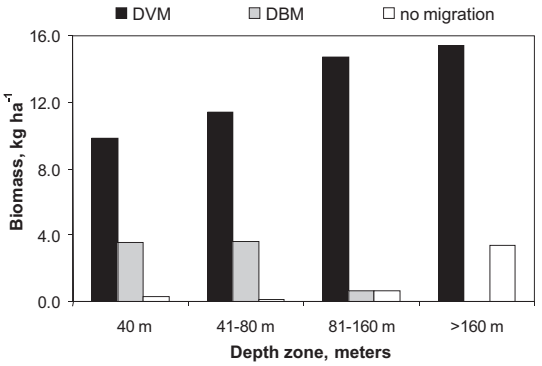

Figure 2. Summary of diel migration of Lake Superior fishes expressed as areal biomass (kg ha^{-1}) by depth zone. Principal contributors to DVM (diel vertical migration) included Cisco, Bloater, Kiyi, Rainbow Smelt, and siscowet Lake Trout. The principal contributors to DBM (diel bank migration) included Lake Whitefish, Pygmy Whitefish, and lean Lake Trout. Deepwater Sculpin was the principal species that did not express diel migration but showed increased activity at night. Data presented here are from Table 2.

Results

Fish community areal biomass increased with depth, ranging from 13.71 kg ha^{-1} at depths ≤40 m to 18.81 kg ha^{-1} at depths >160 m (Table 2; Figure 2). Species expressing DVM (principally Cisco, siscowet Lake Trout, Kiyi, Bloater, and Smelt) accounted for 81% of the areal biomass across all depths (Tables 2 and 3; Figure 2). Those species expressing DBM (principally Lake Whitefish, Pygmy Whitefish, and lean Lake Trout) accounted for 12% of the areal biomass across all depths, and those showing no migration accounted for 7% (Tables 2 and 3; Figure 2). The fraction of areal biomass represented by species expressing DVM increased with depth, from 72% at depths ≤40 m to a peak of 92% at depths of 81–160 m and declining to 82% at depths >160 m (Table 2; Figure 2). Conversely, the fraction of areal biomass represented by species expressing DBM decreased from 26% at depths ≤40 m to zero at depths >160 m (Table 2; Figure 2). The proportion of areal biomass represented by non-migrators was low (1–2%) at depths ≤80 m and was dominated by burbot, but increased sharply from 4% at depths of 81–160 m to 18% at depths >160 m due largely to increased areal biomass of Deepwater Sculpin (Tables 2 and 3; Figure 2).

Diel shifts in the vertical distribution of the fish community across depth zones were visualized with bubble plots that integrated estimates of areal biomass and diel vertical distribution of fishes (Figure 3). During the day, 62% of the overall community areal biomass occurred in the pelagic strata, ranging from 56% at depths ≤40 m to 64% in the 81–160 m depth interval (Figure 3). A small decline to 61% in the deepest >160 m depth zone was due to the sharp increase in areal biomass of Deepwater Sculpin (Table 3). Daytime pelagic areal biomass was dominated by Cisco, which represented 98% of the biomass across all depth zones. During the night, 82% of the overall community areal biomass occurred in the pelagic strata, ranging from 73% at depths ≤40 m to 92% at depths 81–160 m. Increased areal biomass of Deepwater Sculpin at depths >160 m resulted in a decrease in the proportion of pelagic areal biomass in this depth zone at night (82%) compared to the 81–160 m depth zone. DVM expressed by species migrating from demersal strata during the day to pelagic strata at night decreased the proportion of Cisco in the areal biomass of pelagic species at night, down to 68–82% across depth zones. At depths ≤80 m, 36% of the daytime demersal areal biomass shifted to the pelagic strata at night compared to 81% and 58% in 81–160 m and >160 m depth zones, respectively. At depths ≤80 m, the high areal biomass of demersal Lake Whitefish resulted in a lower proportion of demersal community biomass shifting to the pelagic strata at night. Compared to the 81–160 m depth zone, the high areal biomass of Deepwater Sculpin at depths >160 m resulted in a smaller proportion the

Table 2. Summary of lake area by depth zone and estimated lake-wide community biomass (metric tonnes) and areal biomass (kg ha^{-1}) of Lake Superior fishes by diel migration behavior and depth zone. DVM – diel vertical migration; DBM – diel bank migration. ≤80 m and >80 m represent nearshore and offshore depth zones, respectively. *Proportion-1* represents fractions of biomass by diel migration behavior within a depth zone. *Proportion-2* represents fractions of biomass by diel migration behavior across depth zones (lake-wide).

	Estimated lake area		Areal biomass, kg ha^{-1}/ *proportion-1*				Lake-wide biomass, metric tonnes */proportion-1/proportion-2*			
Depth Zone	hectares	*proportion*	DVM	DBM	no migration	Total	DVM	DBM	no migration	Total
≤40 m	903067	*0.11*	9.84/*0.72*	3.57/*0.26*	0.30/*0.02*	13.71	8887/*0.72*/*0.07*	3220/*0.26*/*0.40*	272/*0.02*/*0.02*	12380/*1.00*/*0.09*
41–80 m	985164	*0.12*	11.38/*0.75*	3.62/*0.24*	0.14/*0.01*	15.14	11214/*0.75*/*0.10*	3568/*0.24*/*0.43*	134/*0.01*/*0.01*	14916/*1.00*/*0.11*
81–160 m	2216619	*0.27*	14.73/*0.92*	0.64/*0.04*	0.65/*0.04*	16.02	32654/*0.92*/*0.28*	1415/*0.04*/*0.17*	1448/*0.04*/*0.09*	35508/*1.00*/*0.25*
>160 m	4104850	*0.50*	15.44/*0.82*	0.00/*0.00*	3.36/*0.18*	18.81	63391/*0.82*/*0.55*	20/*0.00*/*0.00*	13790/*0.18*/*0.88*	77201/*1.00*/*0.55*
All depths	8209700	*1.00*	12.85/*0.81*	1.96/*0.12*	1.11/*0.07*	15.92	116138/*0.83*/*1.00*	8223/*0.06*/*1.00*	15643/*0.11*/*1.00*	140005/*1.00*/*1.00*
≤80 m	1888231	*0.23*	10.60/*0.76*	3.25/*0.23*	0.17/*0.01*	14.02	20102/*0.74*/*0.17*	6788/*0.25*/*0.83*	406/*0.01*/*0.03*	27296/*1.00*/*0.19*
>80 m	6321469	*0.77*	15.09/*0.85*	0.32/*0.02*	2.40/*0.13*	17.80	96036/*0.85*/*0.83*	1435/*0.01*/*0.17*	15237/*0.14*/*0.97*	112709/*1.00*/*0.81*
All depths	8209700	*1.00*	12.85/*0.81*	1.96/*0.12*	1.11/*0.07*	15.92	116138/*0.83*/*1.00*	8223/*0.06*/*1.00*	15643/*0.11*/*1.00*	140005/*1.00*/*1.00*

Table 3. Summary of biomass of Lake Superior fishes by diel migration and depth zone. A – estimated areal biomass (kg ha^{-1}), B – estimated lake-wide biomass. DVM – diel vertical migration, DBM – diel bank migration. Estimates of Cisco areal biomass are based areal biomass estimates from Stockwell et al. (2006). Species codes are listed in Table 1.

A.	Species, diel migration, and areal biomass (kg ha^{-1})																
Depth	DVM								DBM					Non- migration			
Zone	CIS	SLT*	KIY	BTR	RBS	SJC	NSS†	TRP††	LWF	LNS	LLT	PWF	HLT	DWS	BUR	SLS	SPS
≤ 40 m	7.84	0.03	0.00	0.31	1.56	0.00	0.04	0.08	2.38	0.80	0.29	0.00	0.06	0.00	0.26	0.03	0.01
41–80 m	9.45	0.36	0.02	1.38	0.42	0.03	0.04	0.05	2.19	0.18	0.38	0.47	0.04	0.01	0.08	0.04	0.01
81–160 m	10.05	2.68	1.31	0.54	0.02	0.13	0.00	0.00	0.45	0.01	0.06	0.12	0.00	0.58	0.06	0.01	0.00
>160 m	11.22	2.52	1.69	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.30	0.05	0.00	0.00
Total	9.64	1.40	0.76	0.56	0.50	0.04	0.02	0.03	1.26	0.25	0.18	0.15	0.02	0.98	0.11	0.02	0.01
B.	Species, diel migration, and lake-wide biomass (metric tonnes)																
Depth	DVM								DBM					Non- migration			
Zone	CIS	SLT*	KIY	BTR	RBS	SJC	NSS†	TRP††	LWF	LNS	LLT	PWF	HLT	DWS	BUR	SLS	SPS
≤40 m	7083	26	2	282	1409	1	35	76	2150	725	265	3	51	0	238	26	8
41–80 m	9309	358	18	1357	410	29	41	51	2160	176	371	464	38	12	76	37	9
81–160 m	22274	5947	2894	1201	43	280	7	1	992	32	126	259	5	1295	125	23	5
>160 m	46046	10329	6950	54	3	10	0	0	0	20	0	0	0	13554	224	9	3
Total	84712	16660	9864	2894	1865	320	83	128	5302	953	762	726	94	14861	663	95	25

*At depths ≤80 m, most SLT were juveniles and subadults and exhibited DBM, and at depths >80 m, most were large adults and exhibited DVM.

†Most NSS exhibited a mixture of DVM and non-migration.

††Small TRP exhibited DVM and adults exhibited mostly DVM and some DBM.

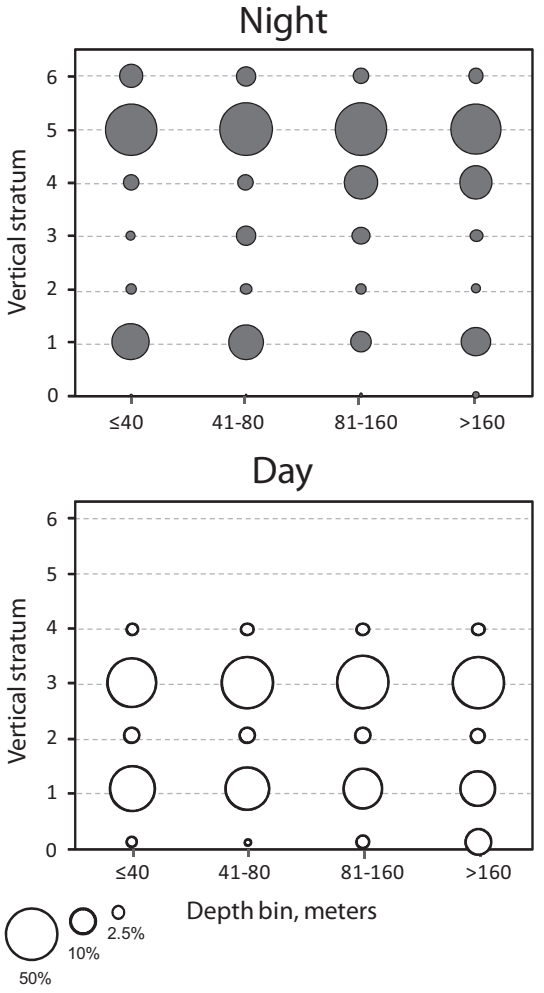

Figure 3. Diel changes in the vertical distribution of the Lake Superior fish community expressed as the proportion of areal biomass (kg ha^{-1}) by depth zone and vertical stratum. Relative strengths of diel vertical migration within a depth zone are indicated by the size of the bubbles and shifts in vertical distribution. The proportion of areal biomass in each stratum is represented by the size of the bubble and sum to 100% within each depth bin (column) for each diel period (day or night panel). Vertical strata are as follows: 0 – benthic; 1 – benthopelagic; 2 – deep hypopelagic; 3 – mid-hypopelagic; 4 – upper hypopelagic; 5 – metapelagic; 6 – epipelagic. The demersal zone is defined as the combination of benthic and benthopelagic strata. These vertical strata are pictured in a diagram in our companion article (Gorman et al. 2012b, Figure 9a). Data presented here are from Tables 2 and 3 and information on vertical distribution of Lake Superior fishes are derived from our companion article (Gorman et al., 2012b) and from Hrabik et al. (2006) and Stockwell et al. (2010a, b, c).

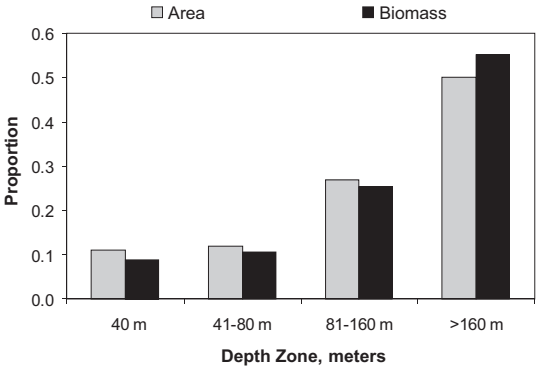

Figure 4. Proportion of depth zone by lake area and proportion of lake-wide fish community biomass by depth zone in Lake Superior. Data presented here are summarized from Table 2.

demersal community biomass shifting to the pelagic strata at night. Over all depth zones, 58% of the demersal community areal biomass shifted to pelagic strata at night.

Weighting areal biomass by lake area for each depth bin yielded somewhat different results because deeper depth bins represented larger fractions of the total lake area (Table 2). Thus, total community biomass and lake area by depth bin were highly correlated ($R^2 = 0.996$) such that 81% of the lake-wide community biomass occurred in offshore waters and 55% at depths >160 m (Table 2).

The bulk of the lake-wide fish community biomass expressed DVM; 83% overall, ranging from 72% at depths ≤40 m to 92% at depths of 80–160 m (Table 2; Figure 4). Overall, 83% of the lake-wide biomass of fish expressing DVM occurred in offshore waters. Species contributing most to DVM lake-wide (in decreasing order of biomass) were Cisco, siscowet Lake Trout, Kiyi, Bloater, and Rainbow Smelt (Table 3). Moving from shallow to deeper depth bins, Cisco and Rainbow Smelt were the principal species contributing to DVM at depths ≤40 m; Cisco and Bloater were the principal species in the 41–80 m depth bin; Cisco, adult siscowet Lake Trout, Bloater, and Kiyi all contributed in the 81–160 m depth bin; and Cisco, adult siscowet Lake Trout, and Kiyi contributed most in the deepest >160 m depth bin (Table 3).

Fish expressing DBM represented 6% of the lake-wide fish community biomass, ranging from 26% in the ≤40 m depth bin to 0% at depths >160 m (Table 2; Figure 5). Overall, 83% of the lake-wide biomass of fish expressing DBM occurred in nearshore waters. Species contributing most to

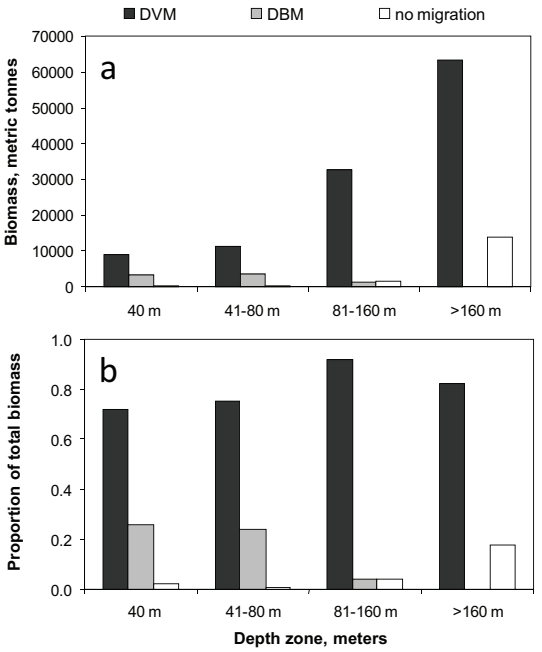

Figure 5. Summary of diel migration of Lake Superior fishes expressed as lake-wide community biomass by depth zone. (a) Lake-wide biomass by diel migration and depth zone. (b) Proportion of lake-wide biomass by diel migration and depth zone. Principal contributors to DVM (diel vertical migration) included Cisco, Bloater, Kiyi, Rainbow Smelt, and adult siscowet Lake Trout. The principal contributors to DBM (diel bank migration) included Lake Whitefish, Pygmy Whitefish, lean Lake Trout and juvenile siscowet Lake Trout. Deepwater Sculpin was the principal species that did not express diel migration but showed increased activity at night. Data presented here are from Table 2.

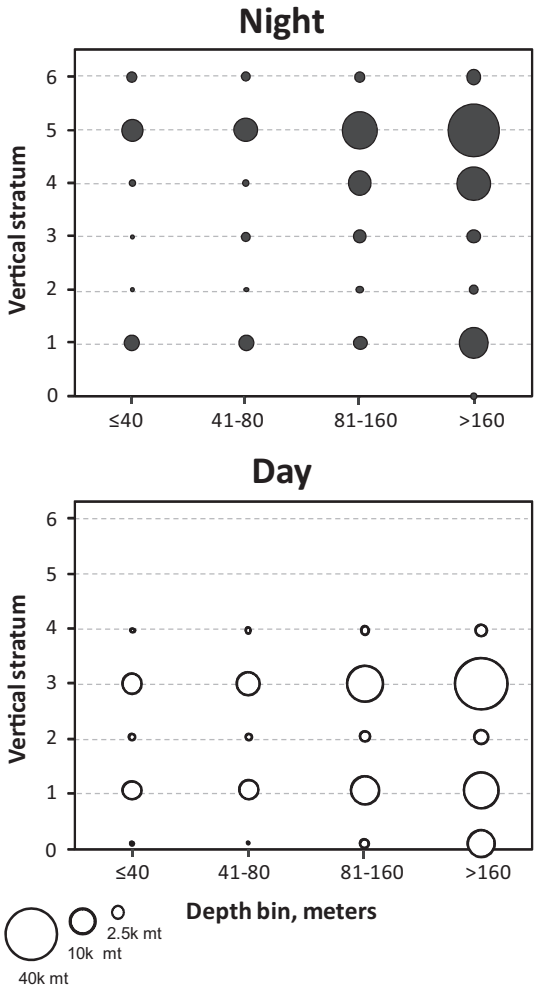

Figure 6. Diel changes in the vertical distribution of the Lake Superior fish community expressed as the proportion of total biomass (metric tonnes, mt) by depth zone and vertical stratum. Relative strengths of diel vertical migration within a depth zone are indicated by the size of the bubbles and shifts in vertical distribution. The amount of areal biomass in each stratum is represented by the size of the bubble and sum to the total biomass within each depth bin (column) for each diel period (day or night panel). Values for total biomass are found in Table 2. Vertical strata are defined as: 0 – benthic; 1 – benthopelagic; 2 – deep hypopelagic; 3 – mid-hypopelagic; 4 – upper hypopelagic; 5 – metapelagic; 6 – epipelagic. The demersal zone is defined as the combination of benthic and benthopelagic strata. These vertical strata are pictured in a diagram in our companion article (Gorman et al. 2012b, Figure 9a). Data presented here are from Tables 2 and 3 and information on vertical distribution of Lake Superior fishes are derived from our companion article (Gorman et al., 2012b) and from Hrabik et al. (2006) and Stockwell et al. (2010a, b, c).

DBM lake-wide were, in decreasing order of importance, Lake Whitefish, Longnose Sucker, lean Lake Trout (all ages), Pygmy Whitefish, and juvenile siscowet Lake Trout (Table 3). At depths >80 m, principal contributors to DBM were, in decreasing order of importance, Lake Whitefish, Pygmy Whitefish, and lean Lake Trout (Table 3).

Fish expressing no migration represented 11% of lake-wide biomass, ranging from 2% at depths ≤80 m to 18% at depths >160 m (Table 2; Figure 5). Overall, 97% of the lake-wide biomass of fish expressing no migration occurred in offshore waters where Deepwater Sculpin accounted for 95% of the biomass of non-migrating species. At depths ≤80 m, burbot and Slimy Sculpin were the principal non-migrating species (Table 3).

Bubble plots expressing areal biomass weighted by the area of the depth zone (Figure 6) provide a contrast to bubble plots using unweighted data

(Figure 3) and permit visualization of diel shifts in the vertical distribution of lake-wide fish community biomass by depth zone. The increasing proportion of lake-wide community biomass with depth, as indicated by the increasing sizes of bubbles with depth, underscores the importance of the offshore fish community. The fraction of lake-wide fish community biomass increased from 9% (12380 mt) at depths ≤40 m to 55% (77201 mt) at depths >160 m (Table 2; Figure 6). The fraction of total biomass represented by species expressing DVM increased with depth, ranging from 7% at depths ≤40 m to 55% at depths >160 m (Table 3). For species expressing DBM within the demersal strata, the fraction of total biomass decreased with depth, from 40% at depths ≤40 m to 0% at depths >160 m (Table 3). The fraction of total biomass represented by non-migrating species within demersal strata increased with depth, ranging from 2% at depths ≤40 m to 88% at depths >160 m (Table 3). As with comparisons based on areal biomass, Lake Whitefish was the primary factor in the sharp reduction in fractional biomass of species expressing DBM at depths > 80 m, and Deepwater Sculpin was the primary factor in the sharp increase in the fractional biomass of non-migratory species at depths >160 m (Tables 2 and 3).

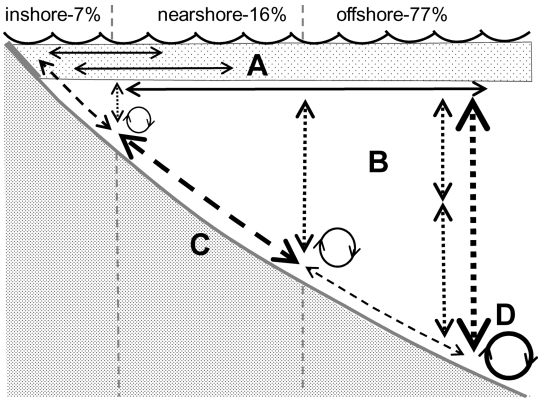

Figure 7. Conceptual diagram of habitat linkages and potential coupling of habitats of Lake Superior by migration and movement of fishes. Coupling habitats by fish-mediated linkages facilitate the transfer of energy across lake habitats (Schindler and Scheuerell, 2002; Stockwell et al., 2010a). Inshore habitat (0–15 m depth), nearshore (15–80 m depth), and offshore (>80 m depth) represent 7%, 16%, and 77% of the surface area of Lake Superior, respectively (Gorman et al., 2010a). Maximum depth of the epilimnion and metalimnion is represented by the shaded upper stratum. Horizontal linkages (A, C) connect inshore, nearshore, and offshore habitats by ontogenetic shifts in habitat use and diel and seasonal migration. Ontogenetic shifts and seasonal migration in the pelagic zone (A) is exemplified by Rainbow Smelt and Cisco. Vertical linkages (B) connect benthic and demersal habitats to pelagic habitats on a diel basis (diel vertical migration, DVM). DVM is exemplified by Rainbow Smelt, juvenile Cisco, Bloater, Kiyi, and adult siscowet Lake Trout. In offshore waters, adult Cisco express shallow DVM (short upper arrow), and Bloater express attenuated DVM (short lower arrow). Kiyi and adult siscowet Lake Trout exhibit strong DVM in offshore waters (bold long arrow). Diel bank migration (DBM) of fishes within the demersal strata (C) is exemplified by Lake Whitefish and lean Lake Trout. Circular forms (D) indicate species that show increased nocturnal activity by moving from benthic to benthopelagic strata at night but do not express DVM or DBM. Species represented by D include Sculpins and Burbot. In nearshore waters, Burbot is the primary contributor to increased nocturnal activity and, Deepwater Sculpin is the primary contributor in offshore waters.

Discussion

Stockwell et al. (2010a) recently synthesized information on migratory behavior and diet in fishes from offshore waters of Lake Superior and proposed a model of habitat coupling in which fish migration linked energy and nutrient pathways between benthic and pelagic habitats, and between nearshore and offshore waters. They hypothesized that benthic-pelagic coupling in offshore waters was driven primarily by DVM of the invertebrate *Mysis*, Kiyi, and siscowet Lake Trout, and nearshore-offshore coupling was driven primarily by seasonal migrations of adult cisco. Stockwell et al. (2010c) noted that the large size of adult Cisco rendered them less vulnerable to predation and their shallow DVM (migration from mid-hypopelagic to metapelagic stratum) reduced their contribution to linking benthic and pelagic habitats in deep offshore waters. Building on Stockwell et al. (2010a, c), we summarize our findings on diel migration and habitat linkages in Lake Superior from Gorman et al. (2012b) and this study in Figure 7. Our findings indicate that the strength of vertical linkages, as expressed by DVM (Figure 7, B), increase with bathymetric depth. In nearshore waters, major contributors to DVM include Cisco, Bloater, and Rainbow Smelt. In offshore waters DVM is driven primarily by high biomass of siscowet Lake Trout and kiyi. The strength of horizontal linkages expressed by DBM (Figure 7, C) decreases with depth and was driven primarily by the high biomass of Lake Whitefish and secondarily by the biomass of Longnose Sucker and lean Lake Trout in nearshore waters. Increased nocturnal activity (no migration), in which fishes move from the benthic to the benthopelagic

stratum (Figure 7, D), increased with depth, and in offshore waters is attributed to the increased biomass of Deepwater Sculpin. Also, the high biomass of Deepwater Sculpin in the benthopelagic stratum of offshore habitat likely facilitates linking benthic-pelagic habitats because they are heavily consumed by siscowet Lake Trout in offshore waters (Ray et al., 2007; Gamble et al., 2011a). Ontogenetic shifts in horizontal distribution of fishes (pelagic and demersal) serve to segregate juvenile and adult life stages and potentially contribute to energy transfer from nearshore to offshore waters over intervals of one or more years (Figure 7, A and C), depending on the appearance of new cohorts of fish, which for Cisco, Bloater, and Kiyi can vary by one to eight or more years (Bronte et. al., 2003; Gorman and Hoff, 2009). When production in lake habitats becomes dependent on these transfers, migration of fish and invertebrates across habitats drive coupling of habitats. The magnitude of diel migration in fishes expressed by applying biomass estimates to linkages in Figure 7, serves as a useful metric for assessing the potential for habitat linkages and habitat coupling in lake ecosystems, and thus provides an indicator of ecosystem health and function.

The high correlation between lake area by depth zone and community biomass resulted in most (81%) of the lake-wide biomass occurring in offshore waters >80 m depth. The increasing level of community areal biomass with increasing depth emphasizes the importance of the offshore fish community to the Lake Superior ecosystem and the importance of fish-mediated linkages to effect the flux of energy and nutrients between nearshore and offshore habitats. Species that exhibit DBM may facilitate linking deeper and shallower habitats and included Lake Whitefish, Longnose Sucker, lean Lake Trout, and Pygmy Whitefish (this study). Cisco was the predominant species in the Lake Superior fish community, representing 51% of the total community biomass. Although Cisco was preeminent in the pelagic strata as a result of its use of pelagic habitat, its shallow DVM likely reduces its contribution to benthic-pelagic coupling. However, adult Cisco likely link nearshore and offshore habitats by seasonal migration (Stockwell et al., 2010a, c).

Comparison of the magnitude of diel migration exhibited by the lake-wide fish community in this study with that from the Apostle Island region (Gorman et al., 2012b) showed similar migration patterns. However, because the maximum depth sampled in the Apostle Islands region was limited to depths <120 m, no comparison was possible with the >160 m lake-wide depth zone. In both studies, the proportion of the total areal community biomass expressing DVM and no migration increased with increasing depth. Also, both studies showed decreasing proportions of DBM with increasing depth. Notable differences included a smaller proportion of DVM and a larger proportion of DBM in the shallower depth zones of the Apostle Island region (≤90 m). This difference was caused by the high relative biomass of Lake Whitefish in the Apostle Islands region compared to lake-wide estimates. The higher proportion of species exhibiting no migration in waters >160 m deep observed in this study can be attributed to the higher biomass of Deepwater Sculpins at depths >160 m compared to the deepest depth bin in the Apostle Islands study (91–120 m). Overall, diel migration was expressed by >93% of the fish community areal biomass in both the Apostle Island region and the whole lake and >98% of the migrating areal biomass can be attributed to native species; mostly Cisco, Bloater, Kiyi, Lake Whitefish, and siscowet Lake Trout.

In their review of Deepwater Ciscoes of the Great Lakes, Eshenroder and Burnham-Curtis (1999) hypothesized that this group evolved to exploit abundant *Mysis* that undergo DVM. In particular, Eshenroder and Burnham-Curtis (1999) suggested that larger body size is related to a higher proportion of body lipids, resulting in less reliance on the air bladder for buoyancy and increased ability for DVM, which would result in an increased efficiency of predation on *Mysis*. This same principal applies to siscowet Lake Trout, except that DVM capability in siscowets should improve their ability to prey on both Kiyi and Deepwater Sculpin. Consistent with the predictions of Eshenroder and Burnham-Curtis (1999), Gorman et al. (2012b) found that larger bloater were distributed in deeper waters and expressed DVM. For Kiyi, Gorman et al. (2012b) did not detect differences in depth distribution and DVM by size, however, life history information on Kiyi remain scant. The expression of DVM and distribution of large siscowet in deep offshore waters (Hrabik et al., 2006; Ahrenstorff et al., 2011; Gorman et al., 2012b) are consistent with the predictions of Eshenroder and Burnham-Curtis (1999).

In the lower Great Lakes the decline of native ciscoes and Lake Trout likely reduces the capacity for these systems to benefit from diel migration (Eshenroder and Burnham-Curtis, 1999). The reduced expression of diel migration in these

systems likely results in reduced energy transfers between habitats and potentially reduced trophic efficiency. The recent expansion of dreissinids (Zebra Mussels *Dreissena polymorpha* and Quagga Mussels (*D. rostriformis bugensis*) in the Lower Great Lakes may exacerbate the loss of trophic transfers by sequestering nutrients and reducing primary and secondary production in the offshore benthic and pelagic strata (Nalepa et al., 2006, 2009a, b; 2010; Vanderploeg et al., 2010; Fahnenstiel et al., 2010; Pothoven et al., 2010a, b; Mida et al., 2010). The sharp declines in fish densities observed in lakes Michigan and Huron have been correlated with the expansion of dreissinids (Riley et al., 2008, 2010; Madenjian et al., 2010, 2012). These communities have undergone sharp reductions in fishes capable of DVM (particularly native Bloater and exotic Alewife [Alosa pseudoharengus] and Rainbow Smelt) between demersal and pelagic habitats since 1995. The remarkable changes in fish communities of lakes Michigan and Huron observed over the past 30+ years underscore the sensitivity of Great Lakes ecosystems to impairment stemming from loss of native species and invasion and expansion of exotic species. Temporal changes in the relative proportions of DVM, DBM, and no migration in Great Lake ecosystems can serve to track changes in ecosystem function and health. When the relative magnitudes of diel migration are assessed by species and depth zone and compared across the Great Lakes over time, a greater understanding of the changes that have occurred in these ecosystems will be attained, which will lead to an increased ability to predict future changes, recognize limitations, and suggest possible remediation strategies.

Conclusions

The results of our study underscore the contention expressed by Vander Zanden and Vadeboncoeur (2002) and Vadeboncoeur et al. (2002) that the contribution of the benthic energy pathway in lake ecosystems is too often underestimated relative to the pelagic pathway, and there is a need to better describe how fish movement may facilitate coupling these two principal pathways. Expanding on the hypotheses of Eshenroder and Burnham-Curtis (1999), the high degree of diel migration, especially DVM, exhibited by the Lake Superior fish community suggests that the native species that dominate the community have evolved diel migration behavior to more efficiently utilize benthic and pelagic resources in a large oligotrophic lake. We expect the high degree of DVM by fishes we observed in offshore waters of Lake Superior to facilitate coupling of benthic and pelagic habitats. Similarly, we expect DBM we observed between shallow nearshore (<40 m depth) and deep nearshore (40–80 m) waters by lake whitefish (an invertivore) and lean Lake Trout (a piscivore) to facilitate coupling of the demersal habitats (benthic and benthopelagic strata) in shallow and deep nearshore waters. The coupling of demersal habitats across depth zones may provide additional energy pathways that feed into the benthic-pelagic pathway in offshore waters. The coupling of habitats and their primary production by fish movement may help to explain the higher trophic transfer efficiencies observed in aquatic ecosystems (Hairston and Hairston, 1993).

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