Habitat use by fishes of Lake Superior. I. Diel patterns of habitat use in nearshore and offshore waters of the Apostle Islands region

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*Diel patterns of distribution of fishes in nearshore (15–80 m depth) and offshore (>80 m) waters of the Apostle Islands region of Lake Superior were described using bottom trawls, mid-water trawls, and acoustic gear during day and night sampling. These data revealed three types of diel migration: diel vertical migration (DVM), diel bank migration (DBM), and no migration. DVM was expressed by fishes migrating from benthopelagic to pelagic strata and DBM was expressed by fishes migrating horizontally from deeper waters in the day to shallower waters at night while remaining within the benthopelagic stratum. Most fishes that did not exhibit diel migration showed increased nighttime densities as a result of increased activity and movement from benthic to benthopelagic strata. Rainbow Smelt (*Osmerus mordax*), Cisco (*Coregonus artedi*), Bloater (*C. hoyi*), Kiyi (*C. kiyi*), juvenile Trout-Perch (*Percopsis omiscomaycus*), and adult siscowet (*Salvelinus namaycush siscowet*) exhibited DVM. Lake Whitefish (*C. clupeaformis*), lean Lake Trout (*Salvelinus namaycush namaycush*), and juvenile siscowet exhibited DBM. Adult Trout-Perch and adult Pygmy Whitefish (*Prosopium coulteri*) exhibited a mixture of DBM and DVM. Burbot (*Lota lota*), Slimy Sculpin (*Cottus cognatus*), Spoonhead Sculpin (*C. ricei*), and Deepwater Sculpin (*Myoxocephalus thompsonii*) did not exhibit diel migration, but showed evidence of increased nocturnal activity. Ninespine Stickleback (*Pungitius pungitius*) exhibited a mixture of DVM and non-migration. Juvenile Pygmy Whitefish did not show a diel change in density or depth distribution. Species showing ontogenetic shifts in depth distribution with larger, adult life stages occupying deeper waters included, Rainbow Smelt, lean and siscowet Lake Trout, Lake Whitefish, Pygmy Whitefish, Ninespine Stickleback and Trout-Perch. Of these species, siscowet also showed an ontogenetic shift from primarily DBM as juveniles to primarily DVM as adults. Across all depths, fishes expressing DVM accounted for 73% of the total estimated community areal biomass (kg ha⁻¹) while those expressing DBM accounted for 25% and non-migratory species represented 2% of the biomass. The proportion of total community biomass exhibiting DVM increased with depth, from 59% to 95% across ≤30 m to >90 m depth zones. Along the same depth gradient, the proportion of total community biomass exhibiting DBM declined from 40% to 1%, while non-migrators increased from 1% to 4%. These results indicate that DVM and DBM behaviors are pervasive in the Lake Superior fish community and potentially provide strong linkages that effect coupling of benthic and pelagic and nearshore and offshore habitats.*

Keywords: Great Lakes, fish communities, diel migration, habitat linkages, habitat coupling

Introduction

Diel vertical migration (DVM) of zooplankton and fish is a conspicuous feature of biological communities of oceans and lakes, and is responsible for a large vertical flux of energy and nutrients in the world's oceans, commonly referred to as the "biological pump" (Longhurst and Harrison, 1988; Longhurst and Williams, 1992; Legendre and Rivkin, 2002; Putzeys and Hernández-León, 2005). Predation likely drives most of this behavior (Zaret and Suffern, 1976; Wright et al., 1980; Gliwicz, 1986; Bailey, 1989; Bollens and Frost, 1989, 1991; Lampert, 1989; Ohman et al., 1983; Scheuerell and Schindler, 2003) and the effect of predation of one trophic level on another can cause "cascading migrations of organisms" (Bollens et al., 2011). In lake ecosystems, these migrations of organisms provide linkages to transfer energy and nutrients across habitats, effectively coupling them so that they become interdependent (Schindler and Scheuerell, 2002; Vadeboncoeur et al., 2002; Vander Zanden and Vadeboncoeur, 2002).

Cascading migrations driven by predation is evident in Great Lakes biological communities. The Opossum Shrimp *Mysis duluviana* (hereafter *Mysis*) undergoes DVM to increase the likelihood of encountering food (zooplankton) which also expresses DVM (Johannsson et al., 2001, 2003; Beeton and Bowers, 1982) and minimizing the likelihood of being preyed on by fish (Gal et al., 2006; Boscarino et al., 2007, 2009). In offshore waters of Lake Superior, fish and their invertebrate prey *Mysis* undergo DVM. Kiyi (*Coregonus kiyi*), the predominant deep-water cisco in Lake Superior, track movement of *Mysis* from deep demersal layers during the day to near the metalimnion at night, and the piscivore siscowet (*Salvelinus namaycush siscowet*), a deep-water form of Lake Trout, track and prey upon Kiyi (Hrabik et al., 2006; Jensen et al., 2006; Stockwell et al., 2010c; Ahrenstorff et al., 2011). Thus, in offshore waters of Lake Superior, DVM of invertebrate prey results in DVM behavior in fishes, thereby providing linkages that promote the flux of energy and nutrients between benthic and pelagic habitats. 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, 2011b). Linkages between deep and shallow demersal habitats result from diel bank migration (hereafter DBM) of Lake

Whitefish (*Coregonus clupeaformis*) from deeper waters in the day to shallower waters at night (Yule et al., 2007, 2008).

Previously, we conducted a study using multiple gears in day and night sampling periods to determine the best approach for achieving closer to absolute estimates of areal biomass (kg ha^{-1}) of Lake Superior fishes (Yule et al., 2007, 2008). Our sampling of fishes across three depths (30, 60, and 120 m) with bottom trawls during the day and, bottom trawls, mid-water trawls, and acoustics at night, revealed evidence of diel migration of fish. During the day, most species except for cisco (*Coregonus artedi*) were concentrated near or on the lake bottom (demersal), while at night many species were absent from bottom trawl samples. Mid-water trawl samples and acoustic data indicated that these fishes had migrated vertically off the bottom (Bloater, Kiyi, Rainbow Smelt, and Ninespine Stickleback (*Pungitius pungitius*)). Sampling at three depths provided evidence that for most species, larger individuals were found in deeper water, and Lake Whitefish underwent DBM at night. Unlike other fishes, adult cisco were present almost entirely in pelagic habitat. These results, and those described in recent papers on DVM of Lake Superior fishes (Hrabik et al., 2006; Jensen et al., 2006; Stockwell et al., 2010b; Ahrenstorff et al., 2011), suggest that diel migration of fish between habitats provides potential for coupling nearshore and offshore and benthic and pelagic habitats by fish. To test the validity of models of trophic linkages (Stockwell et al., 2010a) and proposed foodwebs (Kitchell et al., 2000; Gorman et al., 2010a; Stockwell et al., 2010a; Gamble et al., 2011a, 2011b), greater information is needed to describe the distribution and movement of fishes and their life stages across Lake Superior habitats.

The goal of our research was to describe the diel periodicity of migration of the Lake Superior fish community between benthic and pelagic and nearshore and offshore habitats, thereby identifying potential habitat linkages that contribute to habitat coupling. To accomplish this goal, we characterized the distribution of fishes and their life stages by diel period across nearshore and offshore waters in the Apostle Islands region of Lake Superior.

Methods

Sampling of fish communities was conducted in the Apostle Islands region of Lake Superior between
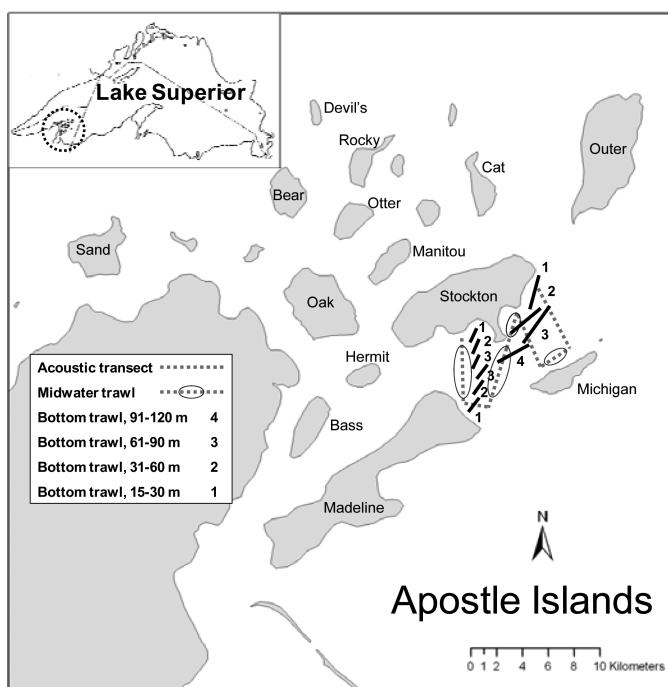
Figure 1. Location of fish community sampling transects in the Apostle Islands region of Lake Superior.

Stockton Island to the northwest, and Madeline and Michigan Islands to the southeast (Figure 1). This area was chosen for study because it is representative of the Lake Superior fish community and habitats; previous work in this area has demonstrated that it contains most of the fish species found in Lake Superior and includes a range of habitats from 15 to >100 m depth (Yule et al., 2007, 2008). We define nearshore (15–80 m) and offshore (>80 m) waters in Lake Superior according to Horns et al. (2003) and elaborated upon by Gorman et al. (2010b).

Bottom trawl transects, 1 to 3 km long, with overlapping depths ranges, were located at depths between 15 m and 120 m in the following depth bins: 15–30 m, 31–60 m, 61–90 m, and 91–120 m (Table 1; Figure 1). Fishes in demersal strata (benthic and benthopelagic; Figure 9a) were sampled along transects during both day and night with 12-m bottom trawls and catch data were expressed as areal density (number of fish ha^{-1}) and areal biomass (kg ha^{-1}) as described in Yule et al. (2007). Sampling was conducted during twelve periods between mid-May to mid-October, 2004–2005 and 2007–2008 (Table 1). Effort (number of transects sampled) was distributed across seasons as follows: spring – 14, summer – 22, fall – 16 (Table 1). After completing daytime sampling of bot-

tom trawl transects, the same transects were re-sampled with bottom trawls during the following night (36 h later). The next night we used a combination of a 15-m mid-water trawl and acoustic gear to sample the pelagic waters of the study area as described in Yule et al. (2007). Fishes captured in bottom and mid-water trawls were identified to species, counted, individually measured total length (hereafter TL) to the nearest mm, and weighed to the nearest gram. For each species, individuals were assigned to size classes that represented life stages from juvenile to adult (Table 2), thus allowing us to characterize ontogenetic changes in habitat use.

Vertical distributions of predominant pelagic species in the water column were described from acoustic and mid-water trawl samples taken at night in a similar fashion to Yule et al. (2007). Sampling each night commenced 30 minutes after the start of nautical twilight and ended 1–2 h before nautical twilight ended. The path of the acoustic and mid-water trawl transects traversed ∼30 km and was positioned over or near the bottom trawl transects (Figure 1). We did not use acoustic and midwater trawl data collected in 2004–2005 as that sampling was more limited in coverage (Yule et al., 2007). Acoustic and mid-water trawl transects were

Table 1. Description of bottom trawl transects and sampling effort. (A) depth statistics of bottom trawl sampling transects. (B) sampling dates, season, and effort for bottom trawl tows, expressed as the number of day/night pairs.

(A) Trawl transect depth statistics

	Depth Bin			
	1	2	3	4
Target depth range, m	15–30	31–60	61–90	91–120
Mean starting depth, m	20.1	28.8	56.8	115
Mean ending depth, m	31.6	60	89	116
Average depth, m	27.4	47.4	69.2	115.6
Median depth, m	26.7	44.2	69.4	115.5
Median interquartile range, m	24–31	42–47	65–73	115–116

(B) Sampling schedule

Year	Date	Season	Depth Bin				Total pairs
			1	2	3	4	
2004	15–16 Jul	Summer	1		1	1	3
	29–30 Jul	Summer	1		1	1	3
	31 Aug–1 Sep	Summer	1	1		1	3
	14–16 Sep	Fall	1		1	1	3
2005	5–6 Jul	Summer	1	1		1	3
	20–21 Jul	Summer	1		1	1	3
	13–15 Sep	Fall	1		1	1	3
	8–9 Oct	Fall	1	1		1	3
2007	30 May–1 Jun	Spring	2	2	2	1	7
2008	19–21 May	Spring	2	2	2	1	7
	29–31 Jul	Summer	2	2	2	1	7
	14–17 Oct	Fall	2	2	2	1	7
	Total pairs		16	11	13	12	52

sampled four times: 1–2 June 2007, and 21–22 May, 31 July–1 August, and 15–16 October 2008.

Acoustic data were collected with a BioSonics DT-X echosounder equipped with 6.7° (half-power beam width) circular split-beam transducer with an operating frequency of 120 kHz. The transducer was deployed with a 1.2-m-long tow body to a depth of 0.8 m. The transducer emitted 3 pings s^{-1} with a pulse duration of 0.4 ms. A mark threshold of -75 decibels (dB) was used during data collection. Vessel position during travel was measured with a differentially corrected global positioning system accurate to ≤1 m. Acoustic fish densities were processed with Echoview$^{©}$ post-processing software (version 4.50.47.12136, SonarData Pty LTD, Australia) using methods described in Yule et al. (2007). A bottom tracking algorithm in Echoview was used to establish a line 0.5 m above the bottom, and this software-generated line was double-checked to ensure bottom echoes were properly excluded. A second line was added 3 m below the transducer to exclude echoes in the transducer near field. Embedded vessel position data was used to define 1,000-m intervals on echograms and each interval was further divided into 10-m high cells from the surface line to the bottom exclusion line. Using the single target detection – split beam (method 1), we created an echogram of single targets using single echo detection criteria recommended by Rudstam et al. (2009). Thresholds for the mean volume backscattering strength (S_v) and single target echograms were set at -66 and -60 dB, respectively. Fish density (number ha^{-1}) in each cell was calculated using the echo integration method.

Four mid-water trawl samples were collected during each sampling event to interpret the

Table 2. Fishes and their size classes found in the nearshore and offshore waters of the Apostle Islands region of Lake Superior.

Species	Scientific name	Species code	Small (juveniles)	Medium (sub-adults, adults)	Large (adults)
				Size class, mm total length (TL)	
lean Lake Trout	*Salvelinus namaycush namaycush*	LLT	≤225	226–400	>400
siscowet	*Salvelinus namaycush siscowet*	SLT	≤225	226–400	>400
Cisco	*Coregonus artedi*	CIS	≤185	186–250	>250
Bloater	*Coregonus hoyi*	BTR	≤165	166–225	>225
Kiyi	*Coregonus kiyi*	KIY	≤130	131–200	>200
Shortjaw Cisco	*Coregonus zenithicus*	SJC	na	186–250	>250
Lake Whitefish	*Coregonus clupeaformis*	LWF	≤225	226–415	>415
Pygmy Whitefish	*Prosopium coulteri*	PWF	≤100	>100	
Rainbow Smelt	*Osmerus mordax*	RBS	≤100	>100	
Burbot	*Lota lota*	BUR	≤226	226–400	>400
Trout-Perch	*Percopsis omiscomaycus*	TRP	≤74	>74	
Ninespine Stickleback	*Pungitius pungitius*	NSS	≤53	>53	
Slimy Sculpin	*Cottus cognatus*	SLS	≤43	44–70	>70
Spoonhead Sculpin	*Cottus ricei*	SPS	≤45	46–72	>72
Deepwater Sculpin	*Myoxocephalus thompsoni*	DWS	≤47	48–88	>88

acoustic echograms. The mid-water trawl was towed in a stepped-oblique fashion (Kirn and LaBar, 1991; Fabrizio et al., 1997) from roughly 5 m below the surface to roughly 5 m above the bottom, down to a maximum depth of 80 m at the deepest site sampled (116 m).

Based on prior knowledge of the distribution of Lake Superior pelagic species (Myers et al., 2009), we stratified the study area into shallow (≤40 m depth) and deep bathymetric depth zones (>40 m). The 40-m depth demarcation was useful because stepped-oblique mid-water trawl samples collected no adult deepwater ciscoes (Bloater, Kiyi, and Shortjaw Cisco *C. zenithicus*) in the shallow zone. Acoustic target strength distributions from each depth zone were consistent with the size distributions of fishes captured in the mid-water trawl samples during each event. In the shallow zone, we separated adult Cisco from small-bodied (<150–mm TL) pelagic species using a −44.59 dB cutting-edge (Myers et al., 2009). All targets in the shallow zone ≥−44.59 dB were classified as adult Cisco, while targets <−44.59 dB, were apportioned to Rainbow Smelt and Ninespine Stickleback based on their relative proportions in mid-water trawl catches samples during each sampling event.

We observed a distinct group of fish in the deep depth zone during each sampling event having target strengths ranging between −52 and −33 dB (modal TS of −39 dB to −41 dB). These targets were consistent with adult deepwater ciscoes (Fleischer et al., 1997). When apportioning acoustic densities to species in the deep zone, we assumed that all targets at depths >40 m from the surface were deepwater ciscoes and used their relative proportions in each sampling event to estimate their respective densities. Apportionment in the upper 40 m of the water column in the deep zone was done using the same methods described earlier for the shallow zone. To simplify presentation, we report only average vertical distribution patterns for each species calculated by averaging densities in each 10-m strata over the four 2007–2008 sampling events.

Bottom trawls were only effective in sampling fishes in the demersal zone and acoustics and midwater trawls were only effective in sampling pelagic zone (Yule et al., 2007, 2008). To facilitate analysis of vertical distribution of fishes, we assigned fishes to a classification of vertical strata as follows: 0 – benthic (on the lake bottom); 1 – benthopelagic (within ∼1.0 m of the lake bottom); three pelagic strata above the benthopelagic stratum and

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) (Figure 9a). We note that the demersal zone represents a combination of benthic and benthopelagic strata and represents the habitat sampled by bottom trawls. Sculpins were assigned to the benthic stratum because of their well-established benthic habitat association and lack of an air bladder (Hubbs and Lagler, 1958; Scott and Crossman, 1973; Berra, 2007). Other species and size classes were assigned to other vertical strata depending on capture in bottom or midwater trawls, and the size distribution of acoustic targets in the water column as detected by acoustic gear.

The diel migration pattern exhibited by a species' size class was determined by comparing densities estimated from bottom trawl samples partitioned by depth bin and diel period (day vs. night bottom trawls). We recognized four diel patterns (Figure 2). Species that did not show distinct differences in density or depth distribution between diel periods (Figure 2a), and those species that showed increased densities at night over the same depth distribution (Figure 2b), were classified as non-migrators. Increased densities of non-migrators at night represent evidence of increased nocturnal activity or daytime trawl avoidance. Species that did not show distinct differences in densities between day and night but showed significant shifts in density from deeper to shallower depth bins were classified as expressing DBM (Figure 2c). Species that showed significant reductions in daytime densities over all depth bins at night and were caught in the pelagic strata at night in midwater trawls were classified as expressing DVM (Figure 2d). Nighttime vertical distributions of species exhibiting DVM were described from acoustic and mid-water trawl catch data.

ANOVA was used to determine the significance of diel changes in densities of fishes measured with bottom trawl sampling gear across depth bins. Prior to statistical analysis, density estimates were log-transformed ($\log_{10}(x+1)$) to resolve presence of zero catch data. Two-way ANOVA was used to detect significant changes in densities across depths and between diel periods. Significant interaction between depth and diel period was interpreted as a diel change in distribution across depth bins. Significant differences were recognized for probabilities ≤0.05, and near-significant differences were noted for prob-
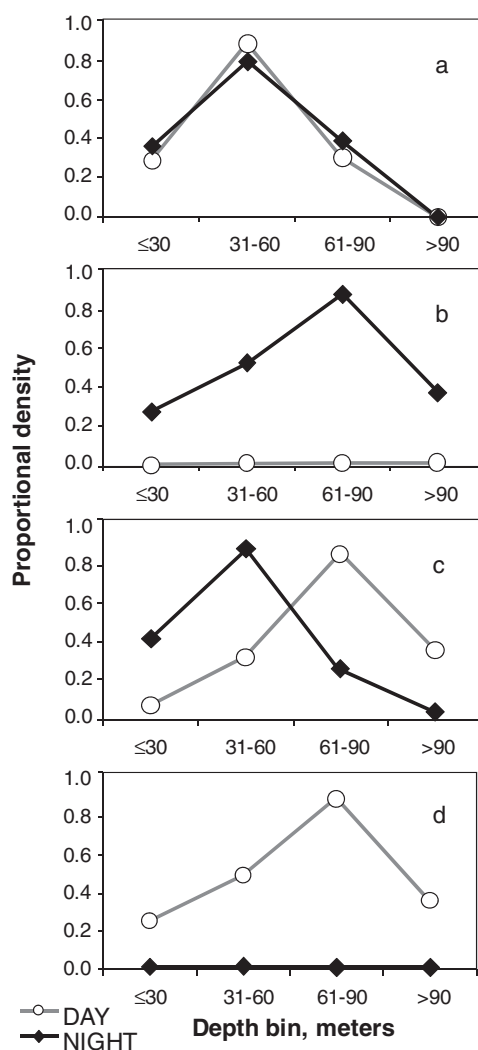
Figure 2. Hypothetical examples of diel changes in density and depth distribution of fishes. (a) No change; (b) increased nocturnal activity or daytime net avoidance; (c) diel bank migration (DBM); and (d) diel vertical migration (DVM).

abilities between >0.05 and 0.10. Statistical analyses were conducted with PAST (PAleontological STatistics) software (Hammer et al., 2009).

The relative strengths of diel migration patterns (DVM, DBM, no migration) expressed by fishes in our study area were evaluated by comparing areal biomass (kg ha^{-1}) of each species and size class estimated from bottom trawl catch data averaged over all sample periods by diel pattern and depth bin (≤30, 31–60, 61–90, >90 m). For each species and size class, estimated areal biomass from the diel period that yielded the largest value was used, as these were judged closer to absolute. Estimates

of areal biomass for cisco were based on acoustic data as these were judged closer to absolute; Stockwell et al. (2006) and Yule et al. (2007) showed that adult Cisco are pelagic and poorly represented in bottom trawl catches. Similarly, we used biomass estimates based on acoustic data for Bloater, Shortjaw Cisco, and Kiyi when these were greater than estimates based on bottom trawl catches. We visualized changes in the diel vertical distribution of the fish community by depth zone with bubble plots that integrated information on diel migration and vertical distribution together with estimates of areal biomass by depth zone.

Results

A total of 52 day-night bottom trawl pairs were collected across all years (Table 1). Overall, we collected 15 fish species represented by 38,927 individuals in bottom trawls, 24,081 in the day and 14,846 in the night (Table 3A). Density and composition of the fish community changed by diel period and depth as estimated by bottom trawl samples; overall, fish density declined more than 50% during night (Table 3B). Composition across all depth bins shifted from one consisting largely of Rainbow Smelt (49%), Lake Whitefish, (15%), Deepwater Sculpin (12%), and Bloater (10%) during the day, to Deepwater Sculpin (38%) and Lake Whitefish (32%) at night (Table 3; Figure 3). The most abundant species in the shallowest depth bin (15–30 m) during the day was Rainbow Smelt (94%). At night, overall fish density in the shallow depth bin declined more than four-fold largely as a result of the near-absence of Rainbow Smelt, but was partially offset by 14-fold increase in Lake Whitefish density, which represented 82% of the night catch (Table 3; Figure 3). In the 31–60 m depth bin, Lake Whitefish and Rainbow Smelt dominated daytime catches (57% and 23%, respectively), while Lake Whitefish dominated nighttime catches (60%). In the 61–90 m depth bin, daytime catches were dominated by Bloater (35%) and Lake Whitefish (29%), while at night overall fish density declined nearly three-fold and the composition shifted to a relatively even distribution of Ninespine Stickleback (27.8%), the Deepwater Sculpin (26.0%), Bloater (15.1%), and Lake Whitefish (12.9%). In the deepest depth bin (91–120 m), Deepwater Sculpin dominated both daytime and nighttime catches (62.8% and 75.3%, respectively).
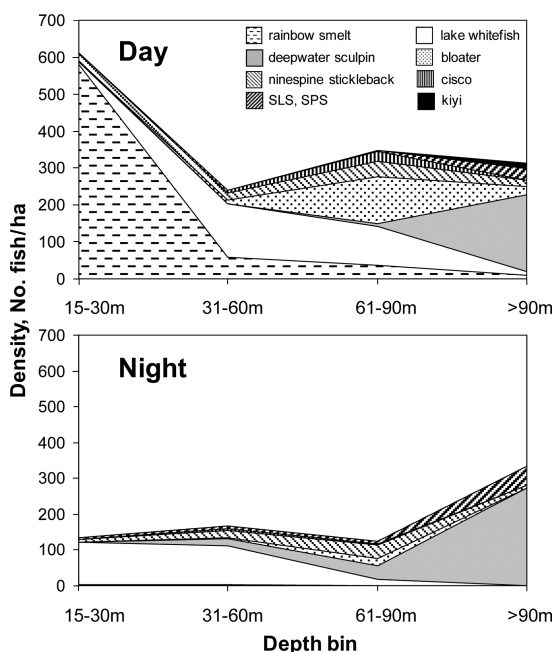
Figure 3. Summary of diel changes in density and depth distribution of principal fishes of the Apostle Island region of Lake Superior as revealed from day and night bottom trawl sampling. SLS: Slimy Sculpin; SPS: Spoonhead Sculpin (Table 2).

A total of 157 and 864 fish were caught in mid-water trawls towed over shallow (≤40 m) and deep (>40 m) zones, respectively. Three pelagic species were caught in the shallow zone; adult Cisco (>250 mm TL) was predominant (46% by number), followed by Rainbow Smelt (42%), and Ninespine Stickleback (12%). Bloaters were predominant (48%) in the deep zone, followed by Ninespine Stickleback (20%), Rainbow Smelt (15%), and adult Cisco (10%). Other species captured in low numbers in the deep zone included Spoonhead Sculpin, Shortjaw Cisco, Kiyi, Slimy Sculpin, Deepwater Sculpin, and Pygmy Whitefish.

Most species and their size classes showed significant differences in densities across depths and between diel periods based on bottom trawl samples (Table 4; Figures 4–8). Significant interaction terms indicated density was affected by a combination of depth and diel period; for example, some species and their size classes (e.g. Cisco, Bloater, Lake Whitefish, lean Lake Trout, siscowet, and Trout-Perch) showed a shift in depth distribution between day and night (Table 4; Figures 4, 6 and 7). Although data in Figure 6 suggest that lean Lake Trout shifted their depth distribution to shallower water at night, the ANOVA interaction term was not significant

Table 3. Number of fish captured (A) and mean densities from bottom trawl samples (B) in the Apostle Islands region of Lake Superior by depth bin and diel period. Density is expressed as number of fish per hectare.

(A) Number of fish captured

| | | | Depth Bin | | | | | | | |
| | All Depths | | 1 (15–30 m) | | 2 (31–60 m) | | 3 (61–90 m) | | 4 (91–120 m) | |
Species	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
lean Lake Trout	69	50	9	16	20	21	39	12	1	1
siscowet	75	53	0	11	2	8	14	20	59	14
Cisco	530	76	6	15	81	37	424	19	19	5
Bloater	1978	234	0	3	92	37	1465	187	421	7
Kiyi	322	4	0	0	0	0	4	2	318	2
Shortjaw Cisco	41	17	0	0	17	1	23	16	1	0
Lake Whitefish	3420	2691	144	1410	1538	1054	1540	213	198	14
Pygmy Whitefish	92	73	9	13	12	20	71	40	0	0
Rainbow Smelt	10776	55	9626	25	509	27	412	2	229	1
Burbot	16	77	2	34	1	20	2	8	11	15
Trout-Perch	335	57	76	25	203	27	56	5	0	0
Ninespine Stickleback	1073	686	280	52	183	189	454	368	156	77
Slimy Sculpin	954	3511	140	1163	69	551	150	806	595	991
Spoonhead Sculpin	614	1668	9	95	2	190	11	295	592	1088
Deepwater Sculpin	3786	5594	2	18	6	274	87	452	3691	4850
Totals	24081	14846	10303	2880	2735	2456	4752	2445	6291	7065

(B) Mean densities

| | | | Depth Bin | | | | | | | |
| | All Depths | | 1 (15–30 m) | | 2 (31–60 m) | | 3 (61–90 m) | | 4 (91–120 m) | |
Species	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
lean Lake Trout	1.2	1.0	0.5	1.0	1.6	2.3	2.8	0.9	0.1	0.0
siscowet	1.0	0.9	0.0	0.7	0.2	0.7	1.0	1.2	3.0	0.8
Cisco	8.4	1.5	0.3	1.1	6.3	3.5	27.3	1.3	0.8	0.4
Bloater	39.2	6.2	0.0	0.2	8.8	3.3	127.9	21.2	23.2	0.5
Kiyi	3.8	0.1	0.0	0.0	0.0	0.0	0.3	0.1	16.3	0.1
Shortjaw Cisco	2.3	1.1	0.0	0.0	3.3	0.2	4.4	3.5	0.4	0.0
Lake Whitefish	61.6	64.1	8.4	117.9	144.2	109.2	104.9	18.1	9.8	0.8
Pygmy Whitefish	1.7	1.4	0.6	1.0	1.0	1.6	5.3	3.0	0.0	0.0
Rainbow Smelt	202.8	1.5	580.2	2.9	59.3	2.7	37.5	0.2	10.2	0.0
Burbot	0.3	1.6	0.4	2.4	0.1	1.9	0.2	0.7	0.7	1.2
Trout-Perch	2.5	0.4	0.0	0.8	7.5	0.7	3.9	0.1	0.0	0.0
Ninespine Stickleback	25.3	17.6	22.7	5.9	20.3	19.9	42.0	38.9	15.3	8.0
Slimy Sculpin	3.4	10.4	0.5	4.0	0.9	8.3	1.1	5.8	12.0	23.7
Spoonhead Sculpin	4.4	7.9	0.0	0.8	0.0	0.6	0.1	2.9	19.1	29.7
Deepwater Sculpin	49.4	76.3	0.1	1.1	0.5	19.6	5.7	36.4	207.5	271.5
Totals	407.4	191.9	613.7	140.0	253.8	174.5	364.3	134.2	318.3	336.8

Table 4. Probabilities of equal mean densities from two-way ANOVA of the effect of diel period, depth and interaction (interact) between diel period and depth on density of fishes of the Apostle Islands region of Lake Superior based on day and night bottom trawl samples. Bold values represent probabilities ≤ 0.05. Values in italics represent probabilities >0.05 and <0.1.

| Species	All			Small (juveniles)			Medium or large (sub-adults, adults)			Large (adults)		
	Depth	Diel period	Interact	Depth	Diel period	Interact	Depth	Diel period	Interact	Depth	Diel period	Interact
lean Lake Trout	**0.001**	0.587	0.267	**0.037**	0.390	0.346	**0.009**	0.292	0.435	0.364	**0.019**	0.411
siscowet	**0.004**	0.698	**0.007**	0.153	0.396	0.150	0.157	**0.027**	0.288	**0.001**	0.849	**0.002**
Cisco	**<0.000**	0.140	**0.014**	**0.024**	**0.021**	**0.048**	**<0.001**	*0.066*	0.137	0.290	0.956	**0.018**
Bloater	**<0.001**	**<0.001**	**<0.001**	*0.074*	**<0.001**	**0.035**	**<0.000**	**0.017**	*0.066*	**<0.000**	**0.005**	**0.002**
Kiyi	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.012**	**0.002**	**<0.001**	**0.003**	**<0.001**	**<0.001**	**0.007**	**<0.001**
Shortjaw Cisco							**0.008**	*0.080*	0.179			
Lake Whitefish	**<0.001**	0.601	**0.002**	**<0.001**	0.336	**<0.001**	**<0.001**	0.115	**<0.001**	0.720	**<0.001**	**0.019**
Pygmy Whitefish	**<0.001**	0.968	0.4464	**0.007**	0.291	0.560	**<0.001**	0.581	0.1569			
Rainbow Smelt	*0.100*	**<0.001**	0.918	**0.001**	**<0.001**	0.164	0.296	**<0.001**	**<0.001**			
Burbot	0.429	**0.005**	0.643	*0.088*	*0.073*	0.633	0.877	**0.005**	0.759			
Trout-Perch	**0.014**	*0.065*	0.611	**0.025**	0.209	0.830	**0.018**	*0.077*	**0.011**			
Ninespine Stickleback	0.382	0.287	0.706	0.838	0.846	0.938	0.149	*0.075*	0.557			
Slimy Sculpin	**0.009**	**<0.001**	0.178	*0.100*	**0.001**	0.208	**0.003**	**<0.001**	0.162	**<0.001**	**<0.001**	0.496
Spoonhead Sculpin	**<0.001**	**<0.001**	**0.004**	0.126	**<0.001**	*0.059*	**<0.001**	**<0.001**	**0.021**	**<0.001**	**0.015**	0.768
Deepwater Sculpin	**<0.001**	**<0.001**	*0.053*	**<0.001**	**0.003**	0.962	**<0.001**	**0.001**	0.945	**<0.001**	**0.046**	**0.008**
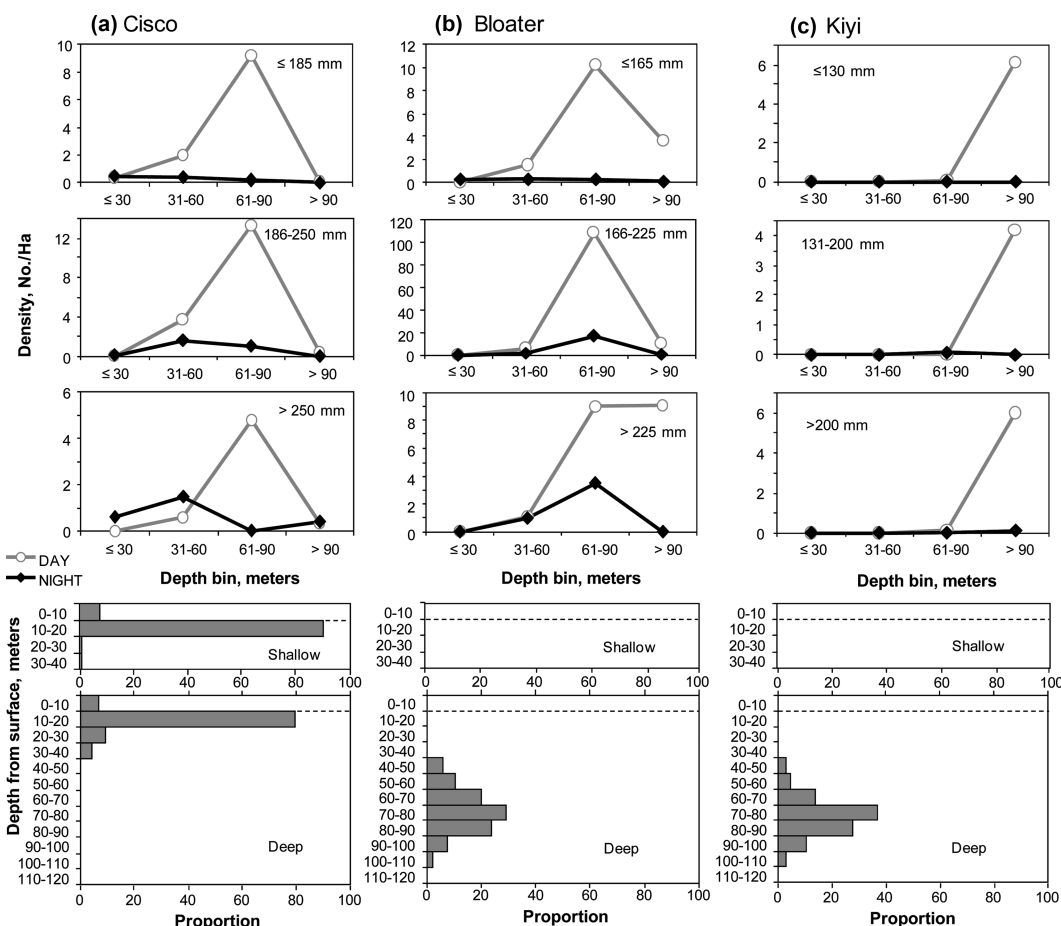
Figure 4. Diel changes in density and depth distribution for Cisco, Bloater, and Kiyi in the Apostle Island region of Lake Superior. Upper panels show depth distributions of various size classes of fish from day and night bottom trawl samples taken over four depth ranges. Lower two panels show night water column distribution of all sizes of fish estimated from results of acoustic and midwater trawl sampling. Panel labeled "shallow" shows water column distribution estimated from transects covering ≤40 m depths. Panel labeled "deep" shows water column distribution estimated from transects covering 41–120 m depths. Dashed line indicates approximate epilimnion-metalimnion boundary. Approximate depth ranges for the epilimnion, metalimnion and hypolimnion are 1–10, 10–20, and 20–120 m, respectively.

(P = 0.267). This was likely the result of strongly unequal variances arising from abundant zero-catches during the day at the shallowest depths sampled.

The clearest examples of DVM were expressed by Cisco, Bloater, Kiyi, and Rainbow Smelt (Figures 4 and 5), while the clearest example of DBM was shown by Lake Whitefish, with diel distribution of lean Lake Trout also consistent with DBM (Figure 6). Some species expressed a combination of DVM and DBM, such as siscowet and adult Trout-Perch (Figures 6 and 7). Examples of species not exhibiting a shift in depth distribution included small Pygmy Whitefish, large Spoonhead Sculpin, and medium and large Deepwater Sculpin (Figures 7

and 8). Examples of increased densities within depth bins at night included small Ninespine Stickleback, all sizes of Slimy Sculpin, small Spoonhead Sculpin, and small Deepwater Sculpin (Figures 5 and 8). Burbot showed increased catches at night, but the pattern varied with size class; small burbot showed increased density at night with the same depth distribution; however, larger burbot showed increased densities in shallower depth bins at night (Figure 7).

Small (juvenile) and large (adult) size classes of many species showed distinct depth distributions. A common pattern in daytime bottom trawl catches was for smaller (juvenile) size classes to be more
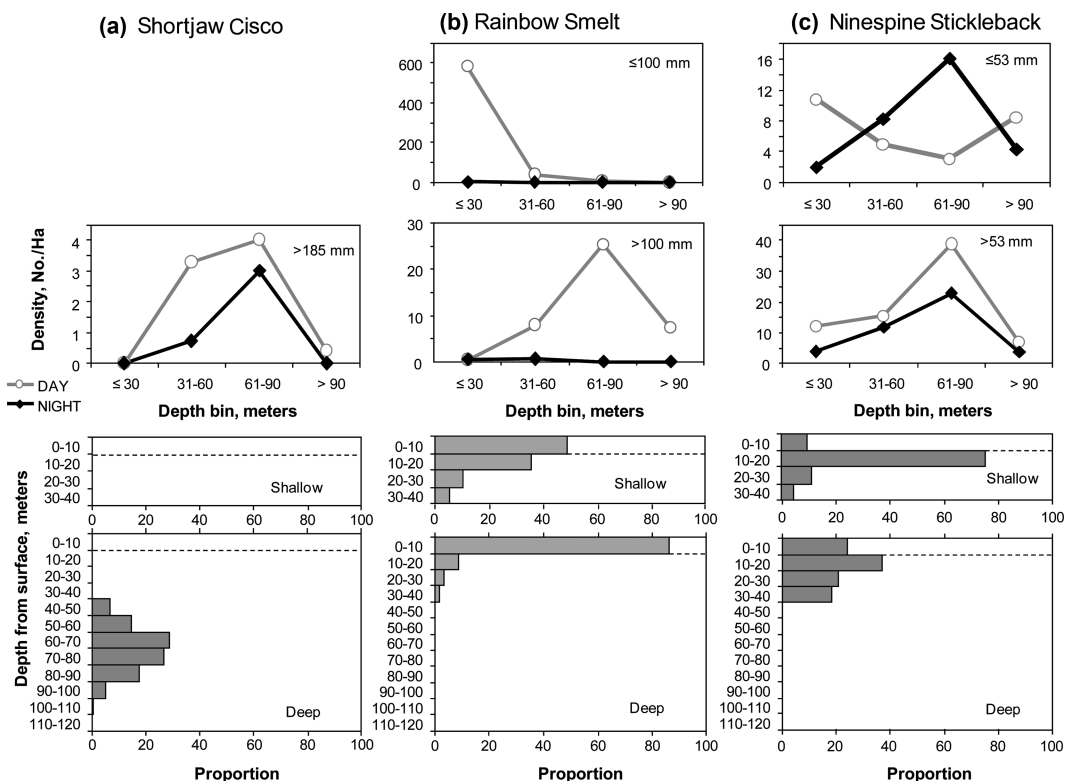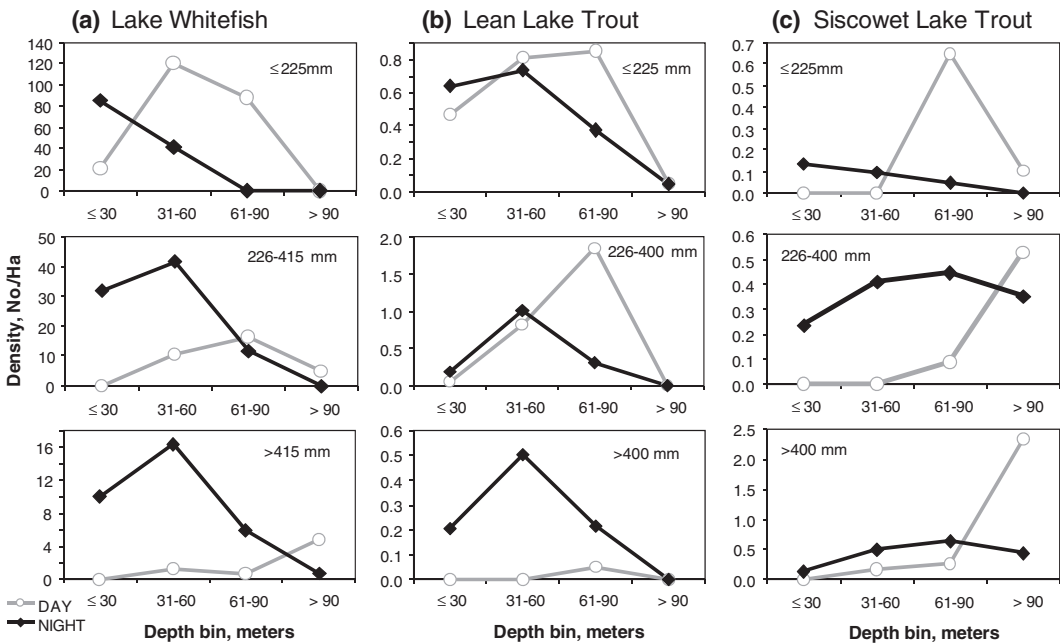
Figure 5. Diel changes in density and depth distribution for Shortjaw Cisco, Rainbow Smelt, and Ninespine Stickleback in the Apostle Island region of Lake Superior. Upper panels show depth distributions of various size classes of fish from day and night bottom trawl samples taken over four depth ranges. Lower two panels show night water column distribution of all sizes of fish estimated from results of acoustic and midwater trawl sampling. Panel labeled "shallow" shows water column distribution estimated from transects covering ≤40 m depths. Panel labeled "deep" shows water column distribution estimated from transects covering 41–120 m depths. Dashed line indicates approximate epilimnion-metalimnion boundary. Approximate depth ranges for the epilimnion, metalimnion and hypolimnion are 1–10, 10–20, and 20–120 m, respectively.

abundant in shallower depth bins compared to larger adults. This was most clearly exhibited by Rainbow Smelt, Bloater, lean and siscowet Lake Trout, Lake Whitefish, Pygmy Whitefish, Trout-Perch, and slimy and Deepwater Sculpins (Table 5; Figures 4–8). Moreover, juveniles and adults of some species showed concordant shifts in depth distribution with diel period. This was most apparent for Lake Whitefish, siscowet, and Trout-Perch (Figures 4–7). However, adults of some species (Cisco, Bloater, and Lake Whitefish) were observed to occupy a wider range of depths at night (Table 5; Figures 4 and 6). Compared to adults, higher proportions of juveniles of some species (lean and siscowet Lake Trout and Lake Whitefish) were present in the shallowest depth bin at night (Table 5; Figure 6).

Diel shifts in species distributions can link habitats across depth zones and vertical strata (Table 5). For the 15 species collected in our study, as many as

15 horizontal and 15 vertical linkages were possible. Horizontal linkages were composed of eight species distributed across depth zones 1–4; three species distributed across depth zones 1–3; and three species distributed across depth zones 2–4. One species was restricted to depth zone 4. Vertical linkages were composed of four species using benthic and benthopelagic strata; five species using benthopelagic and hypopelagic strata; two species using benthopelagic through metapelagic strata; two species using benthopelagic through epipelagic strata. Two species were restricted to the benthopelagic stratum. Different size classes within species may show different vertical and horizontal distributions. For example, small (juvenile) and large (adult) siscowet occupied different ranges of depth zones and only adults showed evidence of DVM (Table 5; Figure 6).

To better visualize community-level diel patterns of depth and vertical distribution, we integrated the
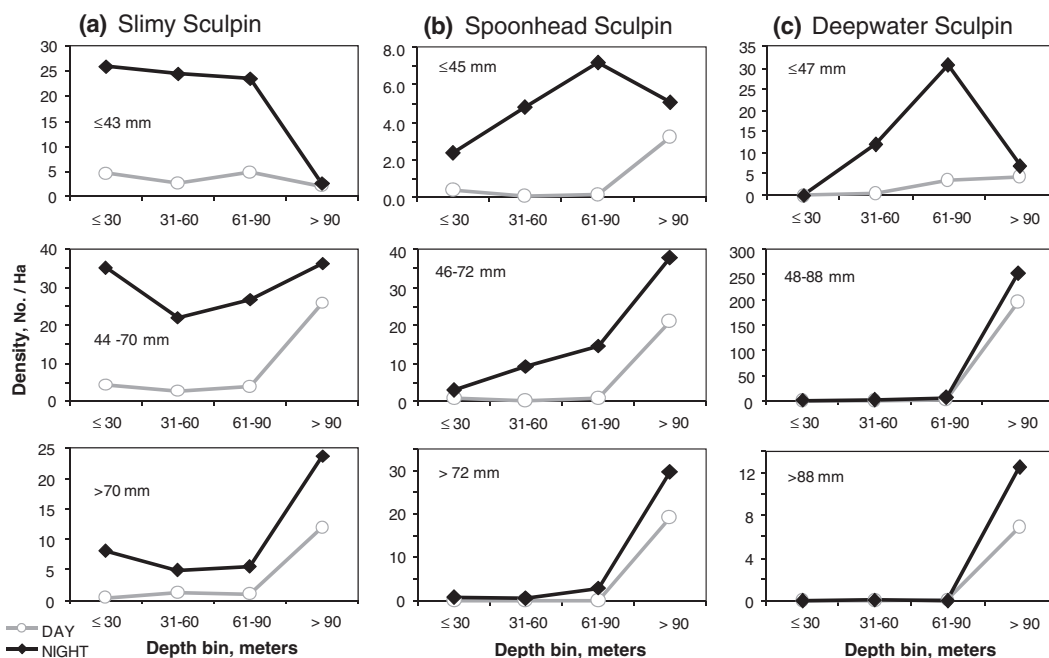
Figure 6. Diel changes in density and depth distribution for Lake Whitefish, lean Lake Trout, and siscowet in the Apostle Island region of Lake Superior. Panels show depth distributions of three size classes of fish from day and night bottom trawl samples taken over four depth ranges.

results of principal demersal and pelagic species into a summary schematic (Figure 9). Cisco, Bloater, Kiyi, Rainbow Smelt and adult siscowet expressed strong DVM between demersal and pelagic habitats. Adult Cisco migrated from the benthopelagic and mid-hypopelagic strata to the metapelagic stratum at night (Figures 4 and 9). Bloater and Kiyi migrated from the benthopelagic stratum to the deep

and mid-hypopelagic strata at night (Figures 4 and 9). Rainbow Smelt migrated from the benthopelagic stratum to the metapelagic and epipelagic strata at night (Figures 5 and 9). Adult siscowet migrated from the benthopelagic stratum during the day to as far as the epipelagic stratum at night (Figures 6 and 9). Lake Whitefish and lean Lake Trout expressed DBM between shallow and deep nearshore
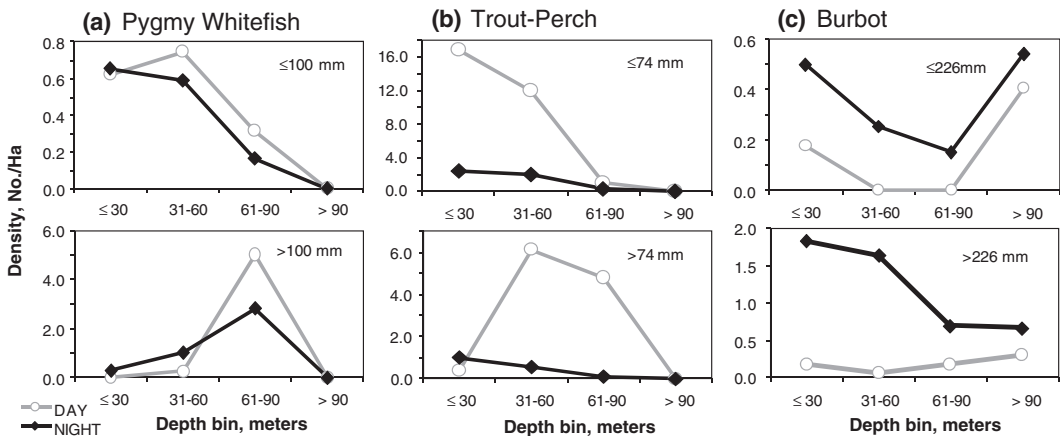
Figure 7. Diel changes in density and depth distribution for Pygmy Whitefish, Trout-Perch, and burbot in the Apostle Island region of Lake Superior. Panels show depth distributions of two size classes of fish from day and night bottom trawl samples taken over four depth ranges.

Figure 8. Diel changes in density and depth distribution for Slimy, Spoonhead, and Deepwater Sculpin in the Apostle Island region of Lake Superior. Panels show depth distributions of three size classes of sculpins from day and night bottom trawl samples taken over four depth ranges.

and offshore habitats within the benthopelagic stratum (Figures 6 and 9). Juvenile siscowet exhibited a pattern of DBM similar to lean Lake Trout (Figure 6). Shortjaw Cisco, Ninespine Stickleback, Pygmy Whitefish, Trout-Perch and burbot did not contribute significantly to overall community areal biomass and were omitted from Figure 9. Sculpins did not express DBM or DVM; however, our results suggest that sculpins moved from benthic to benthopelagic habitat between day and night.

Relative strengths of diel migration behaviors of fishes in our study area were evaluated by comparing areal biomass (kg ha^{-1}) of each species by diel pattern and depth zone (Table 6). Estimated total areal biomass of the fish community was similar in the ≤30, 61–90, and >90 m depth zones but was higher in the 31–60 m depth zone, largely as a result of increased areal biomass of Cisco and Lake Whitefish (Table 6; Figure 10a). Overall, DVM was the most common diel migration behavior averaged across all depth bins (73% of total community areal biomass), followed by DBM (25%) and no migration (2%). Expression of DVM increased with depth, from 59% of total community areal biomass in the ≤30 m depth zone to 95% in the >90 m depth zone (Figure 10b). Conversely, expression of DBM decreased

from 40% of total areal biomass in the ≤30 m depth zone to 1% at depths >90 m. Non-migratory species represented a small proportion of community areal biomass but increased with depth, ranging from 1% at depths ≤90 m to 4% at depths >90 m (Figure 10). Principal contributors to DVM expressed as areal biomass (≥1 kg ha^{-1} in a depth zone) included, in decreasing order of importance: Cisco, Bloater, Rainbow Smelt, Shortjaw Cisco, Kiyi, and adult siscowet (Table 6). The principal contributor to DBM was Lake Whitefish. Principal non-migratory species with areal biomass ≥0.2 kg ha^{-1} in a depth zone included Burbot, Slimy Sculpin, Spoonhead Sculpin, and Deepwater Sculpin.

Diel shifts in the vertical distribution of the community across depth zones were visualized with bubble plots that integrated estimates of areal biomass and diel vertical distribution of fishes from Figures 4–8 and Tables 5 and 6 (Figure 11). During the day, community areal biomass was roughly evenly divided between demersal and pelagic strata in all depth zones (Figure 11); 51–55% of the areal biomass occurred in the pelagic strata of which 96% consisted of Cisco. The preeminence of Cisco in the pelagic strata during the day was the result of its use of pelagic habitat and dominance in the fish

Table 5. Diel habitat distributions and linkages of fishes of the Apostle Islands region of Lake Superior. Shown are habitat distributions (vertical strata and depth zone) of juveniles and adults of each species along with the type of habitat shifts (DVM, DBM, or none). Habitat linkages are inferred by diel shifts in distributions across strata or depth zones. Ontogeny identifies the principal habitat shift associated with juvenile and adult life history stages; "depth" indicates a change in depth distribution. Vertical strata are defined as: 0 – benthic; 1 – benthopelagic; 2 – deep hypopelagic; 3 – mid-hypopelagic; 4 – upper hypopelagic; 5 – metapelagic; 6 – epipelagic (Figure 9a). Depth zones are defined as: 1 – ≤ 30 m; 2 – 31–60 m; 3 – 61–90 m; 4 – >90 m depth.

| | | Juveniles | | | | | Adults | | | | |
| | | | Vertical strata | | Depth zone | | | Vertical strata | | Depth zone | |
Species	Ontogeny	Habitat Shift	Day	Night	Day	Night	Habitat Shift	Day	Night	Day	Night
lean Lake Trout	depth	DBM	1	1	1–3	1–3	DBM	1	1	2–3	1–3
siscowet	depth; DBM to DVM	DBM	1	1–2	3–4	1–4	DVM	1	2–5*	3–4	1–4
Cisco	depth	DVM	1	3–5*	2–3	2–3	DVM	2–3	3–5*	2–4	1–4
Bloater	depth	DVM	1	3	2–3	2–3	DVM	1	2–3	2–4	2–4
Kiyi	none	DVM	1	3	4	4	DVM	1	3	4	4
Shortjaw Cisco	depth	–	–	–	–	–	DVM	1	2–3	2–4	2–4
Lake Whitefish	depth	DBM	1	1	2–3	1–2	DBM	1	1	2–4	1–3
Pygmy Whitefish	depth; none to DBM, DVM	none	1	1	1–3	1–3	DBM, DVM	1	1–2	2–3	2–3
Rainbow Smelt	depth	DVM	1	5–6	1	1–2	DVM	1	4–6	2–4	1–4
Burbot	none	none	0–1	1	1–4	1–4	none	0–1	1	1–4	1–4
Trout-Perch	depth; DVM to DVM, DBM	DVM	1	1–2	1–2	1–2	DVM, DBM	1	1–2	2–3	1–2
Ninespine Stickleback	depth	DVM, none	1	1–3	1–4	1–4	DVM, none	1	1–6	1–4	1–4
Slimy Sculpin	depth	none	0	1	1–3	1–3	none	0	1	1–4	1–4
Spoonhead Sculpin	depth	none	0	1	1–4	1–4	none	0	1	3–4	3–4
Deepwater Sculpin	depth	none	0–1	1	3–4	2–4	none	0–1	1	4	4

*Some fish may enter the epipelagic stratum at night.

community; Cisco represented 51% of the community areal biomass across all depth zones (Table 6). During the night, most of the areal community biomass was found in the pelagic strata, and the proportion increased with depth, from 61% at depths ≤30 m to 95% at depths >90 m (Figure 11). At depths ≤60 m, the high biomass of demersal Lake Whitefish resulted in a lower proportion of daytime demersal community biomass shifting up into the pelagic strata at night (Cisco being absent from this group); in the ≤30 m depth zone only 19% of the daytime demersal biomass shifted to the pelagic strata at night compared to 27% in 31–60 m depth zone. At depths of 61–90 m, 64% of the daytime demersal biomass shifted to the pelagic strata, and at depths >90 m, this figure increased to 94%. Overall, 49% of the daytime demersal biomass shifted to pelagic strata at night.

Discussion

Our study demonstrates that diel migration is a prominent feature of the fish community of the Apostle Islands region of Lake Superior and confirms earlier work in nearshore (Yule et al.,

Table 6. Diel migration and estimated areal biomass (kg ha^{-1}) of fishes by depth zone for the Apostle Islands region of Lake Superior based on bottom trawl catch data except as noted. DVM – diel vertical migration. DBM – diel bank migration.

| | Species, principal diel migration, and areal biomass estimates (kg ha^{-1}) | | | | | | | | | | | | | | | |
| | DVM | | | | | | | | DBM | | | No migration | | | | TOTAL |
Depth Zone	CIS*	BTR	RBS	SJC	KIY	SLT**	NSS†	TRP††	LWF	LLT	PWF‡	BUR	DWS	SLS	SPS	
≤30 m	22.85	2.06	0.70	0.00	0.00	0.00	0.07	0.04	17.29	0.16	0.00	0.39	0.00	0.14	0.01	43.72
31–60 m	26.99	2.56	2.96	0.74	0.00	0.10	0.08	0.06	21.87	0.50	0.01	0.33	0.02	0.09	0.04	56.35
61–90 m	22.91	8.63	3.54	1.49	0.01	0.22	0.11	0.03	6.03	0.54	0.06	0.15	0.04	0.11	0.06	43.93
>90 m	22.31	10.63	0.36	2.36	3.79	1.46	0.12	0.00	0.45	0.00	0.00	0.16	1.01	0.21	0.24	43.10
Total	23.76	5.97	1.89	1.15	0.95	0.45	0.10	0.03	11.41	0.30	0.02	0.26	0.27	0.14	0.09	46.77

*Iincludes estimates based on acoustic and mid-water trawl catch data (CIS, BTR, SJC, KIY).

**At depths ≤90 m, most SLT were juveniles and sub-adults and exhibited DBM, and at depths >90 m, most were large adults and exhibited DVM.

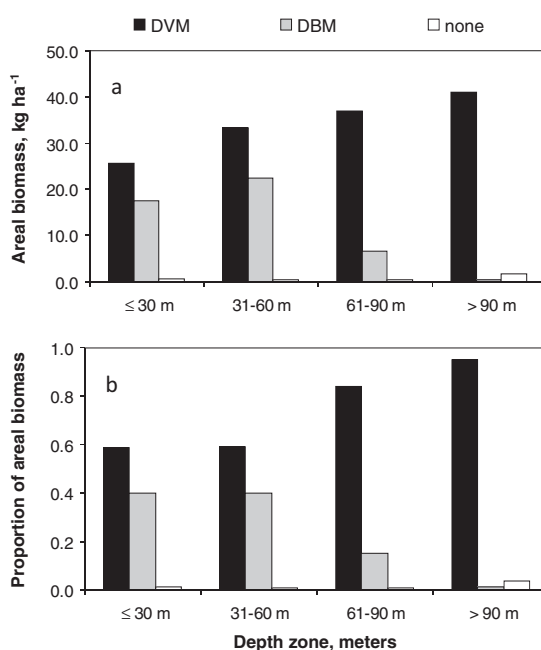† Most NSS exhibited a mixture of DVM and non-migration.

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

‡Juvenile PWF exhibited non-migration while adults exhibited a mixture of DBM and DVM.
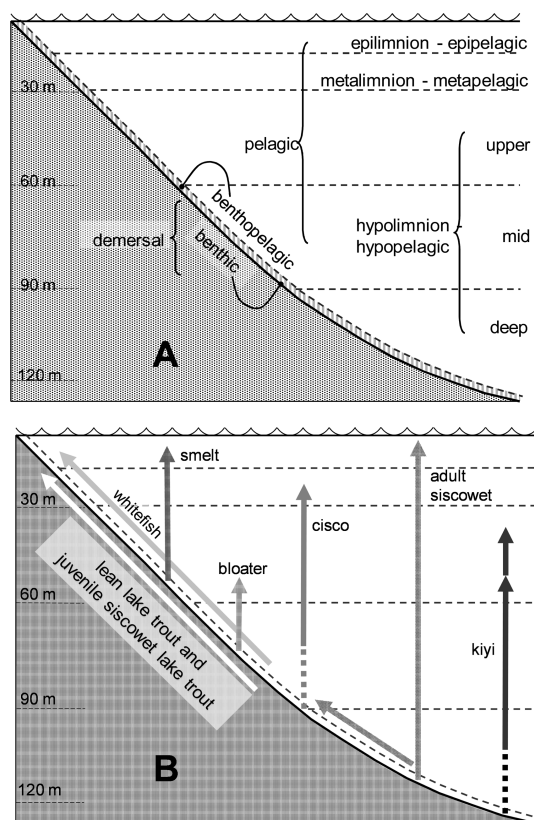
Figure 9. Schematic of nocturnal migration by principal fishes of the Apostle Islands region of Lake Superior. (a) Vertical strata relative to lake classification scheme. (b) night migration of principle fishes of Lake Superior. Rainbow Smelt, Cisco, Bloater, Kiyi, and adult siscowet Lake Trout show upward migration (DVM), whereas Lake Whitefish and lean Lake Trout show up-the-bank migration (DBM). Arrows indicate maximum relative vertical or horizontal nocturnal migration. Fishes return to their original distributions by dawn, completing the diel cycle of migration (Hrabik et al., 2006; Stockwell et al., 2010a; Ahrenstorff et al., 2011). All species except for Cisco occupy the demersal stratum during the day, whereas most adult cisco occupy the mid-hypopelagic stratum, indicated by a vertical dashed line. During the day, Kiyi are demersal at depths up to 225 m, but in deeper areas of Lake Superior, Kiyi occupy the deep-hypopelagic stratum (>225 m) during the day, indicated by dashed lines (Hrabik et al., 2006; Stockwell et al., 2010c; Ahrenstorff et al., 2011). At night kiyi ascend higher in the upper midpelagic stratum in offshore waters (upper arrow, Hrabik et al., 2006; Ahrenstorff et al., 2011) than we observed in the Apostle Islands.

Figure 10. Summary of diel migration by fishes of the Apostle Islands region of Lake Superior by depth zone. (a) Estimated total areal biomass (kg ha^{-1}) by diel migration and depth zone. (b) Proportion of estimated total areal biomass by diel migration and depth zone. Principal contributors to DVM (diel vertical migration) included Cisco, Bloater, Shortjaw Cisco, Rainbow Smelt, and siscowet Lake Trout. The principal contributors to DBM (diel bank migration) included Lake Whitefish and lean Lake Trout. Principal species that did not express diel migration but showed increased activity at night included burbot, Deepwater Sculpin, Slimy Sculpin and Spoonhead Sculpin. Data presented are summarized from Table 6.

2007, 2008) and offshore (Hrabik et al., 2006; Stockwell et al., 2006, 2010a; Ahrenstorff et al., 2011) regions of the lake. Moreover, our results demonstrate the potential for DVM and DBM by fish to provide linkages for transferring energy and nutrients between nearshore and offshore waters and benthic and pelagic strata (Figures 9–11). Our finding of estimated areal biomass >43 kg ha^{-1} across all depth zones (Table 10; Figure 10a), suggests that the relative strengths of diel migration are potentially similar in nearshore and offshore waters. Further, we found that the contributions of DVM and DBM to the relative strengths of diel migration changed in opposite directions with increasing depth, with DVM increasing and DBM decreasing. Although both DBM and DVM likely contribute to habitat linkages in nearshore waters of Lake Superior, DVM is the dominant contributor in offshore waters. Stockwell et al. (2010c) noted that adult Cisco in offshore waters of Lake Superior may have a diminished role in linking benthic-pelagic habitats because they exhibit shallow DVM, i.e. from mid-pelagic to metapelagic strata (Stockwell et al., 2010c; depths >90 m, this study). We found
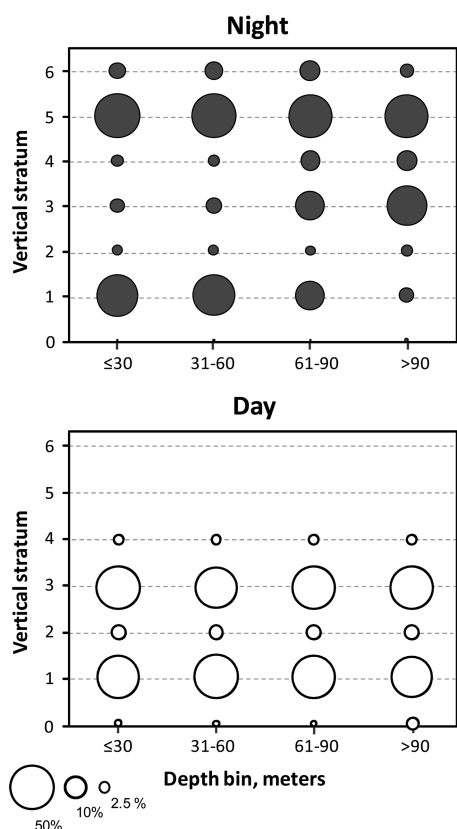
Figure 11. Diel changes in the vertical distribution of the fish community of the Apostle Island region of Lake Superior expressed as the proportion of areal biomass (kg ha^{-1}) by depth bin and vertical stratum. Relative strengths of diel vertical migration within a depth zone are indicated by the 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, defined in Figure 9a, 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.

that Cisco represented 51% of the community areal biomass in the Apostle Islands region, resulting in a reliance on other species that expressed deep DVM from demersal to pelagic strata to provide linkages between benthic and pelagic habitats. In nearshore habitat ≤60 m deep, species exhibiting DVM from demersal to pelagic strata represented only 6–11% of the community areal biomass. In deeper habitat >60 m depth, this figure increased to 32–43%. Thus, the potential for fish-mediated benthic-pelagic coupling in offshore waters is considerable, but weaker in nearshore waters. We observed that in

habitat ≤90 m deep, juvenile Cisco were common in demersal strata during daytime (Figure 4) and exhibited DVM at night and thus may contribute to benthic-pelagic linkages in nearshore habitats. Also, during periods when strong year classes of Cisco appear, juveniles are abundant in nearshore waters and exhibit DVM from demersal to pelagic strata (Yule et al., 2007). Thus, we conclude that the potential for benthic-pelagic coupling is considerable in both nearshore and offshore waters of Lake Superior. The principal species contributing to vertical habitat linkages via DVM include cisco, Bloater, Rainbow Smelt, Shortjaw Cisco, Kiyi, and adult siscowet. The potential for lateral coupling of shallow and deep habitats within the nearshore zone is also considerable. The principal species contributing to horizontal linkages via DBM are Lake Whitefish, lean Lake Trout, and juvenile siscowet.

We did not address seasonal variation in diel migration in this study, as our previous work found little seasonal variation in diel migration patterns between summer and fall (Yule et al., 2007, 2008). Ahrenstorff et al. (2011) also found little seasonal variation in patterns of DVM of *Mysis*, Kiyi, and siscowet in deep offshore waters, though Cisco showed reduced DVM during fall. For this reason we focused on providing greater resolution of the depth distribution and movement of fishes and ontogenetic changes in diel migration and distribution and across habitats. Although our research was limited to the Apostle Islands region, we argue that the patterns of diel migration in fishes we observed are generally applicable to other portions of the lake and note that our results are largely concordant with those from studies that include large portions or the entire lake (Hrabik et al., 2006; Stockwell et al., 2010c; Ahrenstorff et al., 2011). Future research should integrate information on diel and seasonal migration, biomass, diet, consumption, and excretion by each species to estimate the relative contribution of fishes to coupling of Lake Superior habitats.

Many fishes in our study showed ontogenetic shifts in habitat use, i.e. younger life stages occupied shallower depths and, together with complementary patterns of DVM and/or DBM, were partially segregated from adult life stages in deeper waters. Species showing the clearest patterns of ontogenetic shifts in habitat use along with complementary patterns of diel migration included Rainbow Smelt, Lake Whitefish, Pygmy Whitefish, Trout-Perch, and lean Lake Trout. Unlike these species, siscowet showed

an ontogenetic shift in diel migration along with habitat use; juveniles expressed primarily DBM in nearshore waters while large adults expressed primarily DVM in offshore waters. This result is consistent with Stockwell et al.'s (2010c) observation that only large siscowet were captured in midwater trawls at night while a mix of small and large siscowet were caught in day bottom trawls. DBM expressed by juvenile siscowet is also consistent with the results of Harvey et al.'s (2003) stable isotope analysis and Ray et al.'s (2007) diet study of Lake Superior Lake Trout. Harvey et al.'s (2003) results showed that juvenile siscowet utilized nearshore production. Ray et al. (2007) showed that siscowet diets included a substantial fraction of nearshore prey fishes, particularly Rainbow Smelt. However, in deep, far offshore waters of Lake Superior, shallow banks are absent and juvenile siscowet are not able to undergo DBM. To account for their absence in night samples (Stockwell et al., 2010c), we hypothesize that juvenile siscowet in deep offshore waters move up into the deep hypopelagic stratum at night where they are not vulnerable to bottom or midwater trawls.

Ciscoes (Cisco, Bloater, and Kiyi) did not express striking ontogenetic shifts in use of demersal habitat occupied during daylight hours. Kiyi, in particular, showed no shift in depth distribution during daytime across size classes. Likewise, Cisco showed no differences in daytime depth distributions occupied by small and large fish. However, large Cisco are less demersal during the day than juvenile stages (Stockwell et al., 2006; Yule et al., 2007; present study), and reflects an ontogenetic shift from use of demersal habitat in daytime by juveniles to pelagic habitat by adults. Only Bloater showed differences in depth distribution by size; the daytime depth distribution of larger adults expanded into deeper waters (>90 m) compared to smaller fish. This result may explain the high abundance of large Bloater in offshore waters of Lake Superior in the 1960–1970s (Dryer, 1966; Peck, 1977). Gorman (2012) showed that most Bloaters during this period were old, large adults, a population condition that appeared to be the result of chronic recruitment failure in the 1950–1970s.

Though DVM was found to be the dominant form of diel migration expressed by fishes in the Apostle Island region of Lake Superior fishes and likely has the greatest potential to link benthic and pelagic habitats, the proportion of total community biomass that vertically migrates varied with species

and depth. Our results showed that adult and juvenile cisco were present in the benthopelagic and mid-hypopelagic strata during the day and migrated to the metapelagic stratum at night. During the day, juveniles represented >80% of the relative density of cisco in the benthopelagic stratum in depths up to 90 m. At greater depths (>90 m), cisco were nearly absent in demersal bottom trawl samples. Evidence from lake-wide surveys indicate that adult cisco are present in the mid-hypopelagic strata (60–90 m from surface) during the day in deep offshore waters of Lake Superior (Stockwell et al., 2009, 2010c). Because adult cisco are largely pelagic and are only intermittently present in the demersal zone, they are not likely to contribute appreciably to linkage of benthic and pelagic habitats, however, seasonal migration of cisco may contribute significantly to linkage of offshore and nearshore waters of Lake Superior (Stockwell et al., 2009, 2010a, 2010c). While adult cisco may not contribute significantly to benthic-pelagic coupling, juvenile cisco, which express deep DVM from demersal to pelagic strata (Yule et al. 2007; this study), are likely to be significant contributors of during years that follow strong recruitment events, particularly in nearshore waters.

In our study, Kiyi migrated from the benthopelagic stratum to the deep and mid- hypopelagic strata at night, but others have shown Kiyi in open waters of Lake Superior to migrate higher at night, to the upper hypopelagic stratum (Hrabik et al., 2006; Stockwell et al., 2010c; Ahrenstorff et al., 2011). In deep offshore waters >225 m depth, Kiyi occupy the deep hypopelagic stratum during day and migrate to the upper hypopelagic stratum at night (Stockwell et al., 2010c). Thus, kiyi may serve as an important link between benthic and pelagic habitats in depths where they are abundant in the benthopelagic stratum during the day (>90 m to 225 m depth), a depth range representing about 50% of the lake area. Bloater are strongly benthopelagic during the day and relatively abundant in depths ranging from 60 to 120 m (Selgeby and Hoff, 1996). Unlike Kiyi, Bloater are absent or rare or in deepwater habitat >120 m, so their contribution to linking benthic-pelagic habitats in Lake Superior is limited to the 27% of the lake area with depths ≤120 m. Adult siscowet are potentially the strongest fish link between benthic and pelagic habitats in Lake Superior; they are abundant at all depths >90 m, which encompasses about 75% of the lake area, and migrate between the benthopelagic and pelagic strata daily (Hrabik et al., 2006).

We found that sculpins exhibited no discernible pattern of diel migration; however, the increased densities we observed during night bottom trawling at depths ≤90 m suggests increased activity at night, expressed as movement from the benthic to the benthopelagic stratum where fish are more vulnerable to capture in bottom trawls. Many studies have demonstrated that sculpins hide by day and are active at night (Hubbs and Lagler, 1958; Scott and Crossman, 1973; Hoekstra and Janssen, 1985; Greenberg and Holtzman, 1987) and show increased nocturnal feeding (Hoekstra and Janssen, 1985; Brandt, 1986; Greenberg and Holtzman, 1987; Selgeby, 1988), which would explain increased nocturnal capture rates in bottom trawls (Brandt 1986, Potter and Fleischer 1992, this study). In Lake Ontario, Brandt (1986) attributed decreased daytime captures of sculpins at depths <60 m to visual avoidance of the trawl. We argue that because sculpins are small and lack an air bladder (Berra, 2007) they are not able to effectively swim out of the path of bottom trawls like pelagic fish, but remain tight to the lake bottom and hide under debris and in crevices, thus rendering them less vulnerable to capture in bottom trawls. Brandt (1986) and Kraft and Kitchell (1986) found capture and feeding rates of sculpins was similar during day and night at depths >60–80 m, suggesting that at profundal depths, the loss of a diel light cycle results in continuous feeding and activity. Our results are congruent with these studies and showed less difference between day vs. night densities of sculpins in bottom trawls at depths >90 m (Figure 8). Our results also showed that smaller sculpins were more abundant at depths ≤90 m and showed strong diel differences in densities, while larger sculpins were more abundant at depths >90 m and showed less diel differences in density. However, in all cases nocturnal densities were higher for all sculpin species at depths >90 m. Though sculpins do not appear to contribute measurably to linking benthic and pelagic habitats, their continuous activity at depths >90 m makes them more vulnerable to Lake Trout predation. The Deepwater Sculpin, which is relatively abundant in offshore waters, is a common food item in the diet of siscowet (Fisher and Swanson, 1996; Ray et al., 2007; Sitar et al., 2008; Gamble et al., 2011a). Thus, Deepwater Sculpin indirectly contribute to linking benthic and pelagic habitats in deep offshore waters of Lake Superior by serving as benthic prey to adult siscowet expressing DVM. Furthermore, the generally deeper daytime depth distribution of siscowet compared to lean Lake Trout is consistent with siscowet consuming more Deepwater Sculpin and lean Lake Trout consuming more Rainbow Smelt (Gamble et al., 2011b).

Significantly lower day-time densities of adult lean Lake (>400 mm TL) and adult Lake Whitefish (>415 mm TL) suggest these larger fish may be evading the bottom trawl during day sampling (Table 4; Figure 6). Lean Lake Trout were infrequently captured at depths >90 m, and the 61–90 m depth bin was the modal daytime depth bin for all size classes. The shift to the 31–60 m modal depth at night with increased density of large Lake Trout is suggestive of daytime trawl avoidance in the 61–90 m depth bin (Figure 6). There were no significant differences in densities of smaller trout between day and night (Table 4), so day bottom trawl catches may provide reasonable estimates of density for juvenile and sub-adult lean Lake Trout. Likewise, there were no significant differences in daytime and nighttime densities of juvenile and sub-adult Lake Whitefish. Though daytime densities of adult Lake Whitefish were significantly lower than at night (Table 4), light levels in the >90 m modal daytime depth should be exceedingly low, casting some doubt in the ability of adult Lake Whitefish to avoid the bottom trawl; our results show that they are easily caught in bottom trawls at night (Figure 6). We suggest that at depths >90 m, adult Lake Whitefish may be suspended several meters off the bottom, just above the path of our bottom trawl. Overall, our results suggest that night bottom trawling yields the best estimates for densities of adult lean Lake Trout and Lake Whitefish.

Conclusions

The high degree of diel migration exhibited by the fish community of the Apostle Islands region of Lake Superior underscores the thesis of Vander Zanden and Vadeboncoeur (2002) and Vadeboncoeur et al. (2002) that fish serve as important links that couple lake habitats by interdependent transfers of energy and nutrients thus facilitating production in lake ecosystems. The prevalence of DVM expressed by the fish community in our study demonstrates that the potential for linkage of benthic and pelagic habitats in Lake Superior is considerable and facilitates coupling of these habitats. This observation is supported by studies of Lake Superior foodwebs where stable isotope signatures indicate that primary

production from benthic and pelagic pathways is integrated into the fish community (Harvey et al., 2003; Sierszen et al., 2006; Gamble et al., 2011a, 2011b). Our results highlight the importance that native species (Cisco, Bloater, Kiyi, and siscowet) play in providing benthic-pelagic linkages in Lake Superior through DVM. Also, our results suggest that DBM exhibited by native Lake Whitefish, which accounts for 97% of all DBM expressed as areal biomass, likely serves as the primary linkage of demersal habitats in shallow inshore and deeper nearshore waters ≤90 m deep. In our follow-up article (Gorman et al., 2012), we applied species-specific diel migratory behaviors described for the fishes of the Apostle Islands region to the lake-wide fish community of Lake Superior. Our whole-lake assessment addresses the potential for diel migration in the Lake Superior fish community to foster benthic-pelagic and inshore-nearshore demersal linkages, and allows us to characterize diel migration as an attribute of the lake ecosystem. Lake Superior is in a relatively natural state compared to other Great Lakes and has retained its native fish assemblage (Barbiero et al., 2001; Bronte et al., 2003; Gorman and Hoff, 2009; Ryan et al., 2012), and thus serves as a baseline for understanding the contribution of diel migration to habitat coupling in a relatively undisturbed Great Lakes ecosystem. Because diel migration provides linkages that effect habitat coupling and facilitate production through energy and nutrient flux, we believe the level of diel migration exhibited in a fish community provides an important indicator of ecosystem health and function.

Acknowledgements

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