

Partial diel vertical migration in an omnivorous macroinvertebrate, *Mysis diluviana*

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Abstract Partial migration, whereby only a portion of a population migrates, has just recently received attention in aquatic systems. Partial diel vertical migration (DVM) has received even less attention but could significantly influence our understanding of trophic interactions and nutrient movement in open water systems. Recent work in the Baltic Sea shows differences in isotope composition between benthic and pelagic *Mysis salemaai* sampled at night, suggesting that partial DVM may be fixed at the individual level. Historic observations of North American *M. diluviana* suggest partial DVM in this species, but this behavior has largely been ignored in the literature. We used length, occurrence of gravid females, and body $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{34}\text{S}$, and C:N ratio as

markers to test for differences among adult *M. diluviana* collected from benthic and pelagic habitats at night in Lake Champlain, USA. We found differences in body length and occurrence of gravid females between pelagic- and benthic-caught *M. diluviana* and differences in C:N between pelagic- and benthic-caught non-gravid individuals, consistent with life stage and body condition hypotheses for partial migration. Partial DVM of *M. diluviana* could have significant impacts on population assessments which could bias food web models used in basic research and management.

Keywords *Mysis diluviana* · DVM · Partial migration · Isotope · Body condition

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Introduction

Partial migration occurs when some individuals in a population migrate while others remain resident (Chapman et al., 2011). Although extensively studied in birds (Lundberg, 1988), partial migration has received less attention in aquatic systems (Chapman et al., 2012). Fish and macroinvertebrates exhibit partial horizontal (Brodersen et al., 2011) and diel vertical migrations (Brodersen et al., 2008; Mehner & Kasprzak, 2011; Ogonowski et al., 2013), although examples are limited.

Diel vertical migration (DVM) in aquatic organisms has been hypothesized to be the largest

synchronized movement of animal biomass in the world (Hays, 2003), transporting energy and nutrients vertically in the water column (Longhurst & Harrison, 1988; Schnetzer & Steinberg, 2002). Predator avoidance is a common explanation for DVM, enabling organisms to take advantage of food-rich surface waters at night, while limiting their vulnerability to visual predators during the day (Clark & Levy, 1988; Lampert, 1989; Loose & Dawidowicz, 1994). However, many other environmental factors such as light and temperature affect DVM behavior (Lampert, 1989; Pearre, 2003; Mehner, 2012), all of which could differentially impact individuals based on life stage or reproductive status and thus lead to variation in migration behavior among individuals within populations.

Mysis diluviana (Audzijonytė & Väinölä, 2005) (hereafter *Mysis* when referring to this species) is a common macroinvertebrate in North America that exhibits pronounced DVM throughout its range (e.g., Beeton & Bowers, 1982; Ahrenstorff et al., 2011). *Mysis* prefers cold (<8°C) and deep (>50 m) lakes, typically exhibiting maximum densities in areas with bathymetric depths >100 m (Carpenter et al., 1974; Kelly et al., 2011). *Mysis* is omnivorous and feeds on both benthic and pelagic food sources (Johannsson et al., 2001; Sierszen et al., 2011). Thus, *Mysis* is able to forage in benthic and pelagic environments with DVM providing an important benthic–pelagic link, transporting benthic-derived nutrients to pelagic environments and vice versa (Sierszen et al., 2011, 2014; Oliver et al., 2014).

Despite extensive documentation of and research on *Mysis* DVM (op. cit.) and its proximate cues such as light, temperature and predator density (Boscarino et al., 2009a, b, 2010), and historical observations of epibenthic mysids during nighttime (Morgan, 1980; Bowers, 1988), partial DVM in *Mysis* has received little attention. Morgan (1980) hypothesized that the sudden absence of gravid *Mysis* in pelagic tows in Lake Tahoe during November and December was the result of gravid *Mysis* occupying benthic habitat at night to reduce predation risk, consistent with the asset protection principle (Clark, 1994). Partial DVM may also reflect differences in fasting ability or body condition (body condition hypothesis) or hunger and satiation (hunger/satiation hypothesis) among individuals (Pearre, 2003; Chapman et al., 2011) where individuals only perform DVM when hungry. Finally,

Mysis could represent phenotypically different ecotypes, simplified as one migratory and one benthic-resident population (c.f. Lundberg, 1987; Ogonowski et al., 2013).

Partial DVM in *Mysis* spp. in the Baltic Sea was described several decades ago (Rudstam et al., 1989) and more recently (Ogonowski et al., 2013). Using stable isotopes as markers of differences in foraging arenas, Ogonowski et al. (2013) found that *M. salemaai* (Audzijonytė & Väinölä, 2005) exhibited isotope differences within the population. They concluded that a portion of the population was migratory, occupying the pelagic environment at night (presumably feeding on zooplankton), while remaining individuals were epibenthic day and night, feeding on detritus and benthic invertebrates. Consequently, observations of epibenthic mysids at night in North America (Morgan, 1980; Bowers, 1988) may also reflect fixed resident and migrant populations in *Mysis*.

In this study, we first determined whether *Mysis* exhibit partial DVM in Lake Champlain, USA, by sampling benthic and pelagic habitats at night. We then explored support for three hypotheses to explain partial DVM. Decision to migrate is associated with (1) the asset protection principle whereby reproductive status determines migration similar to observations in Lake Tahoe (Morgan, 1980); (2) body condition as measured by carbon to nitrogen ratio (C:N) as an estimate of lipid content, similar to what has been found in other partially migrating animals (Brodersen et al., 2008; Chapman et al., 2012); and (3) distinct population polymorphisms/ecotypes similar to *M. salemaai* in the Baltic Sea (Ogonowski et al., 2013). The hypotheses were explored using data on demographics, foraging habitat history (stable isotopes) and body condition (C:N ratios) of benthic and pelagic *Mysis* caught at night.

Methods

Study area

Mysis were sampled at three sites in Lake Champlain, USA (Fig. 1): Split Rock (SR; 44°16'972"N, -073°19'448"W), Main Site (MS; 44°28'526"N, -073°18'241"W), and Cumberland Head (CH; 44°38'462"N, -073°22'926"W). The primary physical difference among sites was depth; SR was the

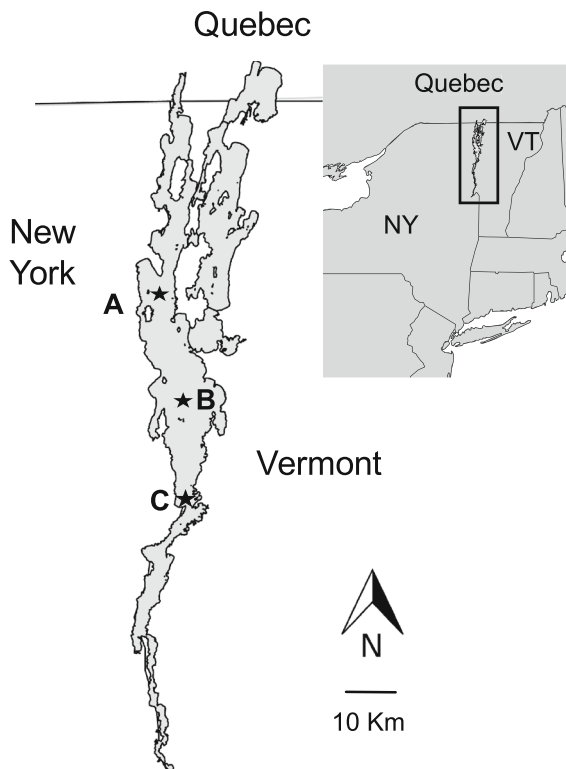


Fig. 1 Cumberland Head (A), main site (B), and Split Rock (C) sampling sites for *Mysis* collections in Lake Champlain, November 2013

deepest (≈ 120 m) followed by MS (≈ 100 m) and CH (≈ 70 m).

Sampling

Mysis were sampled on several occasions during November 2013 to acquire average isotope composition and distribution for the month. Samples were pooled across dates during analyses. Samples were collected starting 1 h after nautical twilight and continued through the night ($\approx 18:00$ – $02:30$) in early (4-Nov, only site MS and benthic *Mysis* from SR), middle (13- and 14-Nov, all sites), and late November (19- and 20-Nov, all sites). The order in which sites were sampled was rotated across dates to account for any bias of sampling time. Prior to sampling, a conductivity–temperature–depth probe was deployed to measure thermal profiles at each site. Water temperature was between 8 and 10°C with little or no stratification at all three sites on all sampling dates. Moon phase ranged from just after new moon on 4-Nov (moon rise = 09:44) to almost full on 20-Nov

(moon rise = 20:10), with partly cloudy skies on all nights.

Pelagic *Mysis* were collected using a combination of oblique and discrete tows with a Tucker trawl (opening = 3.6 m²; mesh = 1000 μ m; cod end = 250 μ m) at water column depths 0–50 m. Benthic-caught *Mysis* were collected using an epibenthic sled (opening = 0.1 m²; mesh = 1000 μ m; cod end = 250 μ m) and represent only individuals within ≈ 0.5 m from the bottom.

Epibenthic transects were approximately 0.5 km, while Tucker trawl transects were approximately 1.5 km to ensure sufficient numbers of pelagic-caught *Mysis*. No catch per unit effort was measured. Benthic- and pelagic-caught samples from each site were placed in separate coolers filled with chilled lake water for transport to the laboratory. Within 10 h of collection, a target of 100 individual *Mysis* were haphazardly chosen from each date–site–habitat event, measured to the nearest mm from the tip of the rostrum to the base of telson, assessed for embryos or eggs, and individually frozen at -20°C in 2-ml centrifuge tubes.

Partial migration is defined as any population with migratory dimorphism (Chapman et al., 2011). Previous studies of *Mysis* have suggested that all or the vast majority of individual *Mysis* migrate each night (Shea & Makarewicz, 1989). Therefore, if *Mysis* were captured in night benthic sled tows, the sample site population was classified as partially migratory. Additionally, we set a target number of 100 *Mysis* per date–site–habitat sample, thereby reducing the likelihood that *Mysis* captured in the water column by chance during deployment and retrieval of the benthic sled would impact the sample.

The size of *Mysis* (max length 20–25 mm tip of rostrum to base of telson), abundance, and habitat (deep, open water) makes mark-recapture studies an impractical method to evaluate individual migration characteristics. We therefore used stable isotopes as markers to test for DVM differences among individuals. $\delta^{13}\text{C}$ of consumers differs between benthic and pelagic habitats because of variable reliance on particulate organic matter which is generally low in ^{13}C (France, 1995; Peterson, 1999). $\delta^{15}\text{N}$ of consumers differs with prey trophic level (Post, 2002), and benthic diets presumably contain a different proportion of low and high trophic level foods than pelagic diets. Finally, C:N ratio varies with diet composition, and can be used as a metric of body

condition (high ratio associated with high fat content; Post et al., 2007). Stable isotopes change slowly over time (McMahon et al., 2013) and, therefore differences between benthic- and pelagic-caught mysids would suggest a sustained difference in habitat use. Ogonowski et al. (2013) found these markers to differ between benthic- and pelagic-caught *M. salemaai*. We used $\delta^{34}\text{S}$ as an additional marker because the water column can be enriched in ^{34}S compared to lake sediments (Croisetièrè et al., 2009).

Length–frequency histograms were used to assess population size structure. Ten non-gravid *Mysis* from the most common size range across all samples (13–16 mm) were randomly chosen from each date–site–habitat group for C:N ratio and carbon and nitrogen stable isotope analyses. Whole dried individuals were milled into a fine powder using a mortar and pestle, and 0.75–0.85 mg of the sample was transferred to 3.5- × 5-mm tin capsules (Costech Analytical Technologies Inc). Using whole individuals provided sufficient material to run duplicate samples per individual of carbon and nitrogen to assess precision.

The non-gravid mysids (10 per site, date and habitat) were analyzed for both carbon and nitrogen isotopes at the University of Wyoming Stable Isotope Facility using continuous-flow settings on a Costech 4010 Elemental Analyzer coupled to a Thermo Delta Plus XP IRMS. Results are expressed in parts per thousand (‰) and denoted as δ according to the equation:

$$\delta X = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] * 1000$$

where X is ^{15}N or ^{13}C , R is the corresponding ratio $^{15}\text{N}:^{14}\text{N}$ or $^{13}\text{C}:^{12}\text{C}$, and the standard was Vienna Pee Dee belemnite (VPDB) for carbon and atmospheric N_2 for nitrogen. For quality control, 36-UWSIF- Glutamic 1, 39-UWSIF-Glutamic 2, and UWSIF01 Liver were used for measurement of standard quality assurance ($n = 2$ per 24 samples). The standard deviations for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of 36-UWSIF- Glutamic 1 and 39-UWSIF-Glutamic 2 were ± 0.2 and ± 0.05 ‰, ± 0.1 and ± 0.04 ‰, respectively, and the standard deviations of UWSIF01 Liver were ± 0.1 ‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Standard deviations of duplicate samples were 0.04 for $\delta^{15}\text{N}$ and 0.34 ‰ for $\delta^{13}\text{C}$. Any samples that failed or had unusually high or low levels of C or N as noted by the stable isotope facility were removed from analysis.

Sulfur stable isotope analyses were conducted on other individual mysids than those used for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (five 13–16 mm non-gravid individuals per site, habitat, and date, except from Nov. 4 due to incomplete sampling of sites on that date). Analyses were done on an Elementar vario ISOTOPE cube interfaced to a SerCon 20-22 IRMS (Sercon Ltd., Cheshire, UK) continuous-flow isotope-ratio mass spectrometer at the University of California Davis stable isotope facility. To account for variation in analysis, IAEA S-1, S-2, and S-3 were used as standard reference materials throughout sample measurement. The overall standard deviation for $\delta^{34}\text{S}$ was 0.18 ‰ for S-1, 0.22 ‰ for S-2 and 0.14 ‰ for S-3.

Statistical analysis

Differences in the numbers of gravid females between habitats and sites were evaluated using Chi Square test of Association. Samples from each site and habitat were pooled across date, and analysis was conducted on the total values for each site–habitat replicate.

To test for differences in length among sites and habitats, two-way analysis of variance (ANOVA) was used with habitat, site, and their interaction as principal factors. To assess possible differences in mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, we conducted a two-way analysis of covariance (ANCOVA) with habitat, site, and their interaction as principal factors and C:N mass ratio and length as covariates. C:N was used as a covariate because $\delta^{13}\text{C}$ can be influenced by lipid content, and C:N correlates with lipids (Post et al., 2007), while size was used to account for any size-related changes in diet. To assess differences in C:N and $\delta^{34}\text{S}$ at each site, two-way ANCOVAs were used with the same principal factors, but only length was used as a covariate. All analyses were conducted using R version 3.1.1 (R Core Team 2015) using the FSA (Ogle, 2014) and car (Fox & Weisburn, 2011) packages with $\alpha = 0.05$ and adjusted with a Bonferroni correction for multiple comparisons.

Results

Evidence for partial migration

Mysis were collected on bottom at night at all sites, consistent with the definition of partial migration

(Chapman et al., 2011). Our target sample of 100 individuals was generally achieved within the first two to three benthic sled tows suggesting that densities were fairly high, though exact catch per unit effort and density were not quantified.

Mysis length and gravid females

A total of 1496 *Mysis* were measured and assessed for gravidity. However, because only benthic individuals were sampled from SR on 4-Nov due to equipment issues, these samples were removed from further consideration leaving 1396 individuals in the analysis. *Mysis* length ranged from 6 to 23 mm with a mean (\pm SD) of 13.9 ± 3.0 mm (S1). Benthic- and pelagic-caught *Mysis* had almost identical length ranges (6–22 and 6–23 mm, respectively). Benthic-caught *Mysis*, however, had a higher mean body length than pelagic-caught *Mysis* (ANOVA $F_{1,1390} = 42.6$, $P < 0.001$, mean difference = 1.1 mm; Fig. 2). *Mysis* lengths also differed among sites (ANOVA $F_{2,1390} = 41.5$, $P < 0.001$; Fig. 2) and were driven in part by differences between benthic- and pelagic-caught *Mysis* increasing with site depth (Fig. 3). Our shallowest site, CH, had similar mean lengths between benthic- and pelagic-caught individuals (difference = -0.59 mm), while the difference at our deepest site, SR, was 3.1 mm. The variation among sites led to a significant habitat:site interaction (ANOVA $F_{2,1390} = 42.8$, $P < 0.001$).

The proportion of the sampled *Mysis* found to be gravid was higher in benthic samples than pelagic-caught samples (Fig. 4; Table 1; χ^2 $P < 0.001$). Additionally, the proportion of gravid *Mysis* within our samples varied by site (χ^2 $P < 0.001$). Only 32 out of 200 of *Mysis* (8%) sampled at CH were gravid, while 113 out of 623 (18%) of those sampled at MS and 98 out of 373 (26%) of those sampled at SR were gravid (Fig. 4). In addition, the difference between benthic-caught and pelagic-caught gravid females increased with site depth (Fig. 3).

Stable isotope analysis

Mysis $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ varied by site but not by habitat (Fig. 2; Table 2). Further, C:N had a positive relationship with $\delta^{13}\text{C}$ and was therefore a significant covariate for $\delta^{13}\text{C}$, (Table 2; Post et al., 2007), but length did not have an impact on either *Mysis* $\delta^{13}\text{C}$ or

$\delta^{15}\text{N}$ composition. $\delta^{34}\text{S}$ was not significantly different between habitats or sites (Fig. 2).

Overall, *Mysis* C:N was higher in benthic-caught individuals but did not vary among sites (Fig. 2; Table 2). Additionally, length was a significant covariate for C:N. The difference in C:N between habitats was largest at SR, our deepest site, and smallest at CH, our shallowest site (Fig. 3).

Discussion

Our results provide evidence that Lake Champlain *Mysis* exhibit partial DVM, adding to the list of systems where *Mysis* spp. have been observed on the bottom at night (Moen & Langeland, 1989; Rudstam et al., 1989; Ogonowski et al., 2013). Despite no quantitative assessment, the proportion of *Mysis* remaining on the bottom at night in November appears substantial. In all cases, our target number of 100 *Mysis* was surpassed within three benthic sled tows, while a much larger sampling effort was required to collect sufficient numbers of pelagic specimens. The observed catch rates appear to indicate that benthic densities were at least comparable to pelagic densities in contrast to Lake Ontario where catches from nighttime benthic sled tows were negligible (Shea & Makarewicz, 1989). Additionally, recent benthic-pelagic collections at night in Lake Champlain across seasons confirm our observations (Stockwell, unpublished data).

The larger average size of benthic-caught *Mysis* compared to pelagic-caught *Mysis* at the two deeper sites may indicate that large individuals are less migratory than smaller ones. The difference in size could be due to size-selective predation in the water column that decreases the abundance of larger *Mysis* (e.g., Holliland et al., 2012). Alternatively, larger *Mysis* with sufficient energy reserves to forego energy-rich zooplankton may remain on the bottom as a strategy to avoid predation risk. However, the observed size differences were driven in part by the lack of migration of larger gravid females, which were 4.4 mm longer on average than non-gravid *Mysis*. Gravid females constituted a higher proportion of the sampled populations in benthic versus pelagic habitats at the two deeper sites, which partially supports the asset protection hypothesis (Hypothesis 1; Clark, 1994). The relatively small effect size of the overall

Fig. 2 Mean ($\pm 95\%$ CI) $\delta^{34}\text{S}$, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ composition, and C:N mass ratio of non-gravid *Mysis* 13–16 mm in length, and mean ($\pm 95\%$ CI) length of all *Mysis* measured ($n = 1396$) from benthic (B) and pelagic (P) habitats from the three sites in November 2013

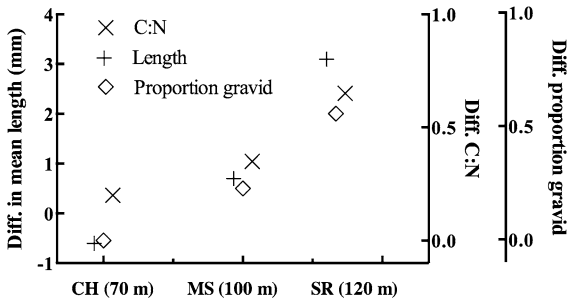
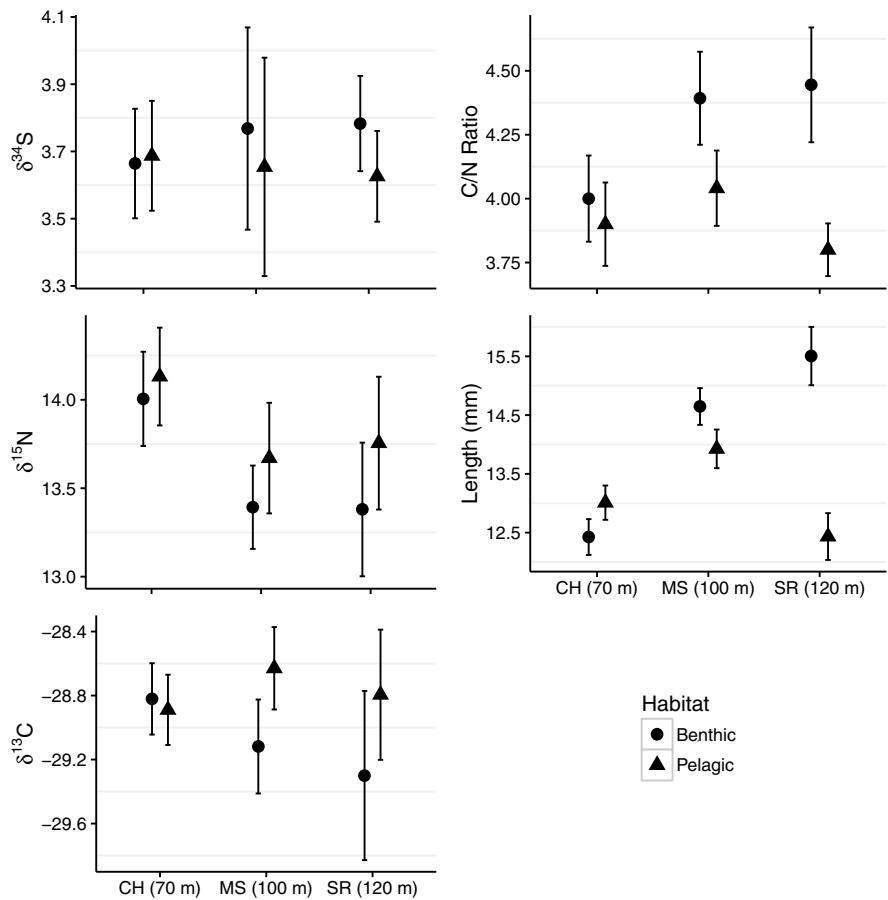


Fig. 3 Differences between *Mysis* mean length (mm), C:N, and proportion of gravid females by site depth (CH \approx 70 m, MS \approx 100 m, SR \approx 120 m) in Lake Champlain, November 2013

average length difference between benthic- and pelagic-caught individuals (1 mm), the size overlap between *Mysis* that migrate and those that remain on bottom, and observations of gravid females in pelagic samples, however, suggest that size and life stage differences cannot fully explain partial migration behavior.

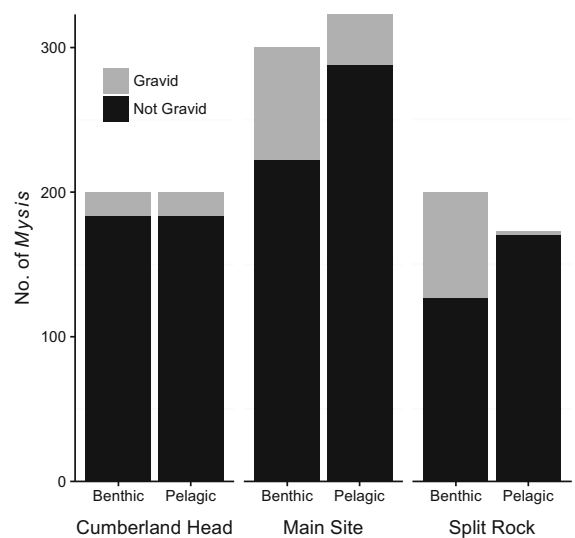


Fig. 4 Number of *Mysis* identified as gravid (gray) or non-gravid (black) in benthic and pelagic habitats at each site in Lake Champlain, November 2013

Table 1 Mean (\pm SD) *Mysis* length (L), number gravid *Mysis* observed for *n* individuals, and mean (\pm SD) C:N of ten non-gravid 13–16 mm individuals over all dates, sites, and habitats in Lake Champlain in November 2013

Site	Habitat	n	Mean L (mm)	No. gravid <i>Mysis</i>	Mean C:N
SR	Benthic	200	15.5 \pm 3.55	73	4.45 \pm 0.48
	Pelagic	173	12.4 \pm 2.66	2	3.80 \pm 0.22
MS	Benthic	300	14.6 \pm 2.75	78	4.39 \pm 0.46
	Pelagic	323	13.9 \pm 3.00	35	4.04 \pm 0.37
CH	Benthic	200	12.4 \pm 2.19	16	4.00 \pm 0.35
	Pelagic	200	13.0 \pm 2.09	16	3.90 \pm 0.34

Table 2 Results of two-way ANCOVAs testing for differences in Lake Champlain *Mysis* isotopic composition and C:N ratios among non-gravid individuals caught in November 2013 from three different sites in benthic and pelagic habitats

Factors	$\delta^{13}\text{C}$			$\delta^{15}\text{N}$		C:N		$\delta^{34}\text{S}$	
	df	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Habitat	1	3.83	0.053	4.61	0.033	29.92	<0.001*	1.10	0.298
Site	2	6.89	0.001*	7.13	0.001*	3.42	0.036	0.01	0.989
Habitat:site	2	1.86	0.160	0.45	0.637	4.50	0.013	0.40	0.671
C:N	1	145.85	<0.001*	0.45	0.503	NA	NA	NA	NA
Length	1	0.36	0.550	0.02	0.899	7.11	0.009*	0.30	0.587

NA indicates variables that were not part of the analysis. *F* values that were significant following a Bonferroni correction for multiple comparisons are denoted with asterisks

* Significant following Bonferroni correction

Notably, non-gravid benthic-caught individuals had an average C:N ratio 9% higher than non-gravid pelagic-caught individuals at MS and 17% higher at SR, representing a potential difference in tissue lipid content of 2.5% at MS and 4.6% at SR based on dry mass (Post et al., 2007). *Mysis* with higher lipid content were captured on the bottom where predation risk is likely lower (Harrington et al., 2015), while *Mysis* with lower lipid content (lower nutritional status) may migrate to pelagic waters to access higher density and presumably more energy-rich prey, but at a presumably increased risk of predation. However, the difference in lipid content between benthic-caught and pelagic-caught *Mysis* at CH was less than 1%, again suggesting other factors likely contribute to partial DVM. Nonetheless, the differences in C:N at two out of three sites support that condition may be one factor in migration choice (Hypothesis 2).

Contrary to results from Ogonowski et al. (2013), we found no differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ between benthic- and pelagic-caught *Mysis*. Diet differences,

such as those expected between epibenthic *Mysis* with no DVM and vertically migrating pelagic individuals, may not necessarily result in different isotopic signatures (c.f. Phillips & Gregg, 2003; Sweeting et al., 2005; Brett, 2014). Consequently, the absence of significant differences in isotope composition in the present study precludes us from rejecting distinct ecotypes of *Mysis* (Hypothesis 3). However, because length and C:N differed between habitats, partial migrations are likely true partial migrations and not simply the result of continuous re-distributions of the *Mysis* population in the water column throughout the night. Nonetheless, to conclusively test Hypothesis 3 that *Mysis* partial migration is related to fixed population polymorphism, we recommend that future studies use additional markers such as fatty acids (Brett, 2014) and *Mysis* stomach content analyses (O'Malley & Bunnell, 2014).

Mysis exhibited partial migration at all sites. The effect size of demographics and C:N between benthic- and pelagic-caught *Mysis*, however, differed among

sites and increased with depth. In Lake Superior, isotope composition of *Mysis* changed with depth and was attributed to decomposition of detritus as it sinks to the bottom (Sierszen et al., 2011). The depths of our study sites (70–120 m), however, were shallower than assessed by Sierszen et al. (2011; 120–300 m), and we saw no large differences in *Mysis* isotope composition with depth. Thus, the differences in *Mysis* demographics and C:N by depth found in the present study were more likely associated with *Mysis* feeding or migration behavior among sites than depth-mediated isotope changes in detritus.

Interpretation of our results is limited to the month of November when stratification in Lake Champlain is negligible. At this time, the distributions of predators and prey are presumably more vertically homogenous than during stratified periods, likely limiting the energetic advantage near the surface and decreasing the presumed predator refuge near the bottom. Pelagic productivity, thermal stratification, and presence of predators are proximate factors known to impact the depth to which *Mysis* migrate at night during May through September (Boscarino et al., 2007, 2009b). However, *Mysis* continue to migrate even when stratification breaks down and may even migrate closer to the surface in autumn than in the spring (Beeton, 1960; Ahrenstorff et al., 2011). Therefore, evaluating *Mysis* distribution and condition during other months when stratification and predator densities are more distinct may help further elucidate the drivers of partial DVM. However, the presence of two alternative migration strategies in November implies that bimodal behaviors do exist in *Mysis* at certain times of the year. Surveys of Lake Champlain suggest partial that DVM occurs year round (Stockwell, unpublished data).

Research identifying individual differences in the migration traits of invertebrates, and specifically in vertically migrating invertebrates, is underrepresented in aquatic ecology research. To the best of our knowledge, our work and that of Ogonowski et al. (2013) are the only studies that have directly identified and assessed the benthic component of partial migration behavior of *Mysis* spp. While other studies have discussed partial DVM (Morgan, 1980; Bowers, 1988; Rudstam et al., 1989), the predominant focus of *Mysis* DVM research continues to be on individuals that have migrated into the water column. Our results partially support both the body condition and the asset

protection hypotheses as explanations of partial DVM. However, neither hypothesis was supported at all sites. Despite inconsistencies among sites, our findings suggest that partial migration may be a non-random process. Non-random partial DVM of *Mysis* adds complexity to our understanding of DVM and necessitates more detailed description of benthic and pelagic distributions of *Mysis* to determine when and why individuals migrate. We propose that future studies of vertically migrating organisms account for potential partial migration by expanding sampling techniques to better represent non-migratory individuals (e.g., Shea & Makarewicz, 1989; Stockwell et al., 2010). Selective sampling techniques that do not account for the full distribution of the target species could bias abundance estimates (e.g., Stockwell et al., 2006). The key role *Mysis* play in food webs (e.g., Ellis et al., 2011; Gamble et al., 2011; Isaac et al., 2012) makes understanding impacts of *Mysis* on both benthic and pelagic communities essential for estimates of energy flow and connectivity in food web and ecosystem models (Kitchell et al., 2000; Stewart et al., 2010; Bunnell et al., 2011).

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