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Size-mediated control of perch–midge coupling in Lake Erie transient dead zones

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Abstract Transient ecosystem-level disturbances such as oxygen depletion (hypoxia) in aquatic systems modulate species distributions and interactions. In highly eutrophic systems, hypoxic areas (“dead zones”) have expanded around the world, temporarily preventing many demersal predators from accessing their food resources. Here, we investigate how yellow perch (*Perca flavescens*), an exploited, cool-water mesopredator, interact with their dominant invertebrate prey in benthic habitat–non-biting midge (chironomid) larvae–as bottom-water hypoxia develops in central Lake Erie (United States–Canada) during summer. We apply linear mixed-effects models to individual-level data from basin-wide field surveys on size-based interactions between perch and midge larvae under varying habitat conditions and resource attributes. We test if 1) midge populations (larval body size and density) differ among habitat states (unstratified normoxia, stratified normoxia, and stratified hypoxia); and 2) size-based perch–midge interactions (predator–prey mass ratio

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or PPMR) differ among habitat states with varying temperature and midge density. Midge populations remained highly abundant after bottom-water oxygen depletion. Despite their high densities, midge larvae also maintained their body size in hypoxic water. In contrast, perch on average consumed relatively smaller (by up to ~64%) midges (higher PPMR) in warmer and hypoxic water, while prey size ingested by perch shrunk less in areas with higher midge density. Our analysis shows that hypoxia-tolerant midges largely allow perch to maintain their consumer–resource relationships in contracted habitats through modified size-mediated interactions in dead zones during summer, revealing plasticity of their trophic coupling in the chronically perturbed ecosystem.

Keywords Food web · Trait-mediated · Foraging · Body size · Great Lakes · Hierarchical modeling

Introduction

Ecosystem state modulates energy fluxes that fuel primary and secondary production through trophic interactions in aquatic systems (Carpenter et al. 1985; Benndorf et al. 2002). However, ecosystem-level perturbations by human activities such as nutrient enrichment, pollution, and habitat destruction have disrupted species performance, populations, species assemblages, and food webs in many systems (Lotze et al. 2011; Lotze and Milewski 2004). In particular, areas with low dissolved oxygen (DO) concentration (hypoxia–defined hereafter as ≤2 mg O_2 l^{-1}) or "dead zones" induced by excessive nutrient loading have expanded (Diaz and Rosenberg 2008) and become of ecological importance worldwide, modifying species distributions and interactions (e.g., Mesa et al. 2005; Taylor et al. 2007). Although eutrophication may promote some warm-water herbivore (e.g., invasive carps) production (Djemali et al. 2017), further expansion of dead zones may have implications for ecosystem services such as fisheries production and distribution of cool- and cold-water species in these perturbed systems (Breitburg 2002; Breitburg et al. 2009).

Spatial and temporal variation in ecosystem properties such as temperature can drive individual-level processes of trophic interactions among ectotherms through prey accessibility and predator behavior (bottom-up control, Persson 1986; Diehl 1992; Abrahams et al. 2007). Moreover, natural and human-induced disturbances such as surface water warming and droughts may further constrain aquatic predator–prey interactions (Abrahams et al. 2007; Domenici et al. 2007). In eutrophic systems, when thermally stratified, hypoxia often develops as DO concentration declines to stressful levels for organisms below the pycnocline or thermocline. Hypoxia effects on predator–prey interactions thus likely depend on the tolerances (and resulting spatial redistributions) of the predator and the prey to hypoxia (Kolar and Rahel 1993; Abrahams et al. 2007). In some cases, spatial overlap between predators and prey may increase as their habitat sizes shrink as DO concentration declines (Costantini et al. 2008; Brandt et al. 2011). In bottom waters, resilient predators may experience higher prey availability as sediment-dwelling organisms are forced by hypoxia (or anoxia) to surface and become vulnerable to predation (Pihl et al. 1992; Roberts et al. 2012). By contrast, sensitive predators may miss foraging opportunities in benthic habitat and switch to alternative prey resources (e.g., from zoobenthos to zooplankton, Pothoven et al. 2009) as they escape into shallow oxygenated nearshore areas or into oxygenated surface waters (Magnuson et al. 1985; Zhang et al. 2009).

Stability and strength of predator–prey interactions also depend on species traits (Emmerson and Raffaelli 2004). Body size is such a trait that may filter environmental variability through physiological responses (e.g., temperature-dependent metabolism) and in turn govern ecological processes (e.g., size-dependent prey capture) in trophic interactions and energy transfer (Barnes et al. 2010; Brose et al. 2006; Woodward and Warren 2007; Goto and Wallace 2011). In hypoxic bottom-waters of thermally stratified systems, because of limited time for searching and handling prey, some predators may consume prey differently (Brante and Hughes 2001; Shin et al. 2005). Further, because of hypoxia-induced shifts in prey spatial distribution, these predators may also experience modified accessibility to size-structured resources (Pihl et al. 1992). Variability in predator–prey body mass ratio may thus reflect integrated processes in organisms and the environment modified by transient ecosystem disturbances (Woodward and Warren 2007; Nakazawa et al. 2011).

Here, we investigate consequences of summer bottom-water oxygen depletion for trophic coupling by yellow perch (*Perca flavescens*) in benthic habitats of a large, eutrophic system, Lake Erie (United States–Canada; Fig. 1). Its largest (central) basin (~11,000 km^2) of Lake Erie has been experiencing increasingly

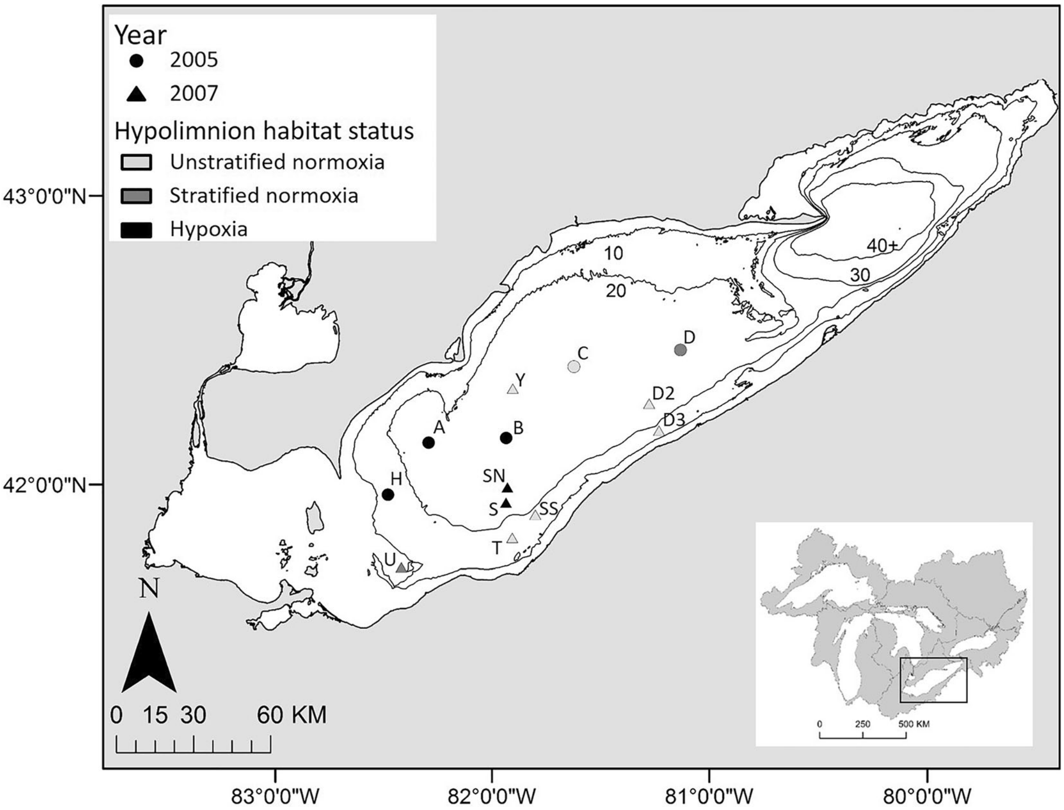

Fig. 1 Locations (A, B, D, and H in 2005, and B, S, T, U, Y, D2, D3, SN, and SS in 2007) of field survey stations in central Lake Erie. Contour lines (10 m) indicate bathymetry; gray areas indicate land; and white areas indicate water

widespread seasonal (late summer/early fall) hypoxia during recent decades because of human-driven environmental changes (Rucinski et al. 2010; Scavia et al. 2014). Recent ecosystem state shifts likely have induced a series of extreme events such as massive harmful algal blooms (Michalak et al. 2013), which may modify food web balance and threaten cool- and cold- water fisheries production (Scavia et al. 2014). Lake Erie yellow perch are a productive, cool-water mesopredator that supports one of largest capture fisheries in North American freshwaters (Roseman et al. 2008), with annual lake-wide total (commercial and recreational) harvest ranging from over 2700 to 5000 metric tons (~95% from Ontario and Ohio waters) during 2000–2015 (Belore et al. 2016). A benthic stage of perch bridges the gap between the planktivorous larval stage and the piscivorous adult stage, allowing them to grow out of size-dependent predation risk. Unlike many other predators, some perch continue to ingest zoobenthos such as chironomid (non-biting midge) larvae and pupae in hypoxic bottom waters (Roberts et al. 2009, 2012). We use individual-level data sets from large-scale field observations to examine variability in a size-mediated interaction between perch and midge larvae–a dominant benthic invertebrate–under varying habitat conditions and resource attributes to test the following questions: 1) do the quality and quantity of resources–midge populations (larval body size and density)–differ among bottom-water habitat states (stratification and oxygen depletion)?; and 2) do size-mediated consumer–resource links (perch–midge body size ratio) differ among habitat states with varying temperature and food density gradients?

Materials and methods

Central Lake Erie field surveys

We collected yellow perch (juveniles and adults) and non-biting midge larvae as part of large-scale scientific surveys, International Field Years of Lake Erie (IFYLE; www.glerl.noaa.gov/res/projects/ifyle/), conducted at

13 stations in the central basin of Lake Erie across two years (2005 and 2007). We sampled at three to five stations on June 17–21, August 15–18, September 17–19, and October 13–14 of 2005, and August 27–30 and September 17–20 of 2007 (Table 1 and Fig. 1). Detailed sample collection and processing methods were documented previously in Pothoven et al. (2009) and Roberts et al. (2009). Briefly, we conducted bottom (13 mm mesh lining) and mid-water (6.4 mm mesh lining) trawling every four hours over a 24-h sampling period along a five km transect at each station on each sampling date. Once collected, we identified, counted, and immediately stored fish samples at −20 °C until processing for diets in the laboratory. In the same cruises, we also collected zoobenthos once during each 24-h period in triplicate at the middle and endpoints of each site transect using a Ponar grab sampler (250 μm mesh; sampling area = 0.046 m^{-2}; $n = 9$ per station and date). Depth-specific water temperature and dissolved oxygen data were recorded using a CTD (Conductivity, Temperature, and Depth), fluorometer and dissolved oxygen sensor (Sea-Bird Electronics, Bellevue, WA, USA) every 24 h at each east–west five-km station transect ($n = 3$ per station). We identified seven thermally unstratified normoxia (>2 mg O_2 l^{-1}), eight stratified normoxia, and six stratified hypoxia (≤ 2 mg O_2 l^{-1}) events during 2005 and 2007 surveys (Table 1).

In the laboratory, we measured the total mass (g wet) of each perch; in total, we processed 1126 fish from the 2005 and 2007 surveys [see Roberts et al. (2012, 2009) for detailed diet analysis]. We identified, counted, and measured (nearest 0.0001 mm) the body length ($n = 5375$ individuals, at least 20 individuals per fish sample when available) of midges in 433 perch stomachs (Table 2). Similarly, we identified, counted, and measured the body length ($n = 3935$ individuals, at least 20 individuals per sample when available) of midges in Ponar grab samples (Table 2). When parts of the body were missing (and fewer than 20 individuals were available), we measured the head capsule width (mm) and estimated the total body length (mm) using the following regression derived from the survey samples: ln(total body length) = 1.48 × ln(head width) + 3.37 ($R^2 = 0.99$). We then converted body length to mass

Table 1 Environmental characteristics of bottom-water (hypolimnion) habitats at survey stations in central Lake Erie during 2005 and 2007

Year	Month	Station	Temperature (°C)	Dissolved oxygen (mg O^2 l^{-1})	Hypolimnion thickness (m)	Hypolimnion habitat status
2005	June	A	9.6	9.0	8.8	normoxia
2005	June	B	8.7	10.5	9.8	normoxia
2005	June	C	9.0	9.0	NA	unstratified
2005	June	D	10.2	11.2	7.5	normoxia
2005	August	B	10.3	4.6	9.3	normoxia
2005	August	D	13.0	4.8	3.1	normoxia
2005	August	H	11.7	2.7	4.1	normoxia
2005	September	A	11.6	1.1	5.8	hypoxia
2005	September	B	11.3	1.5	6.1	hypoxia
2005	September	H	15.6	0.9	2.0	hypoxia
2005	October	B	18.8	7.5	NA	unstratified
2007	August	B	11.8	2.1	7.0	normoxia
2007	August	S	12.8	1.4	2.5	hypoxia
2007	August	T	23.9	6.6	NA	unstratified
2007	August	U	20.5	4.1	2.5	normoxia
2007	August	Y	23.8	6.9	NA	unstratified
2007	September	B	12.1	1.0	4.5	hypoxia
2007	September	D2	20.8	6.7	NA	unstratified
2007	September	D3	20.9	6.8	NA	unstratified
2007	September	SN	12.7	1.4	2.5	hypoxia
2007	September	SS	18.6	4.5	NA	unstratified

Table 2 Mean body mass and biomass density of non-biting midge (chironomid) larvae in the sediment, mean body mass and consumed biomass of midges in yellow perch (*Perca flavescens*) stomachs, and mean body mass and biomass of perch from central Lake Erie field surveys during 2005 and 2007

			Midge larvae									Yellow perch		
			Sediment					Perch stomach						
Year	Month	Station	Mass (SE, mg)	*n*	Density (SE, g • m^{-2})	Proportion(SE)	*n*	Mass (SE, mg)	*n*	Biomass (SE, mg)	Proportion(SE)	Mass (SE, g)	*n*	Biomass (kg hr.$^{-1}$)
2005	June	A	22.27(0.14)	134	1.45(0.05)	0.43(0.02)	8	10.35(0.01)	843	51.15(1.44)	0.98(0.001)	16.12(0.03)	42	4.4
2005	June	B	11.64(0.08)	149	0.67(0.08)	0.14(0.01)	8	8.39(0.02)	406	109.50(5.84)	0.99(0.001)	17.42(0.01)	24	1.0
2005	June	C	14.12(0.09)	149	1.66(0.10)	0.32(0.03)	8	10.10(0.01)	575	N/A	N/A	15.57(0.01)	27	1.8
2005	June	D	4.85(0.02)	141	0.19(0.01)	0.01(0.00)	8	11.03(0.02)	500	29.71(0.68)	0.93(0.005)	17.05(0.01)	29	5.8
2005	August	B	3.99(0.02)	270	0.36(0.02)	0.21(0.02)	8	6.61(0.02)	305	75.50(4.85)	0.94(0.014)	17.47(0.01)	18	5.1
2005	August	D	2.00(0.01)	319	1.64(0.07)	0.14(0.01)	8	2.37(0.00)	517	14.92(0.89)	0.83(0.020)	16.47(0.01)	32	15.7
2005	August	H	11.66(0.05)	269	3.04(0.10)	0.16(0.02)	8	7.00(0.08)	66	65.40(20.39)	0.99(0.005)	16.09(0.09)	6	5.2
2005	September	A	14.17(0.07)	209	3.96(0.12)	0.75(0.01)	8	6.16(0.01)	345	101.05(4.18)	0.99(0.005)	18.44(0.01)	15	1.7
2005	September	B	8.01(0.04)	209	0.95(0.04)	0.21(0.02)	8	N/A	N/A	N/A	N/A	N/A	N/A	1.7
2005	September	H	12.21(0.09)	139	0.79(0.07)	0.35(0.04)	8	10.69(0.02)	514	14.61(0.71)	1.00(0.001)	18.34(0.01)	29	24.7
2005	October	B	6.81(0.04)	193	0.86(0.16)	0.34(0.04)	8	5.30(0.01)	329	66.27(6.83)	1.00(0.001)	17.76(0.01)	22	11.3
2007	August	B	3.30(0.04)	139	0.41(0.03)	0.57(0.02)	8	14.17(0.67)	20	9.09(1.70)	1.00(0.001)	13.89(0.03)	14	1217.9
2007	August	S	13.30(0.06)	271	1.61(0.02)	0.96(0.00)	8	2.01(0.04)	44	29.52(13.45)	1.00(0.001)	22.71(0.03)	3	696.5
2007	August	T	1.56(0.04)	44	0.02(0.00)	0.67(0.07)	8	N/A	N/A	N/A	N/A	N/A	N/A	1871.1
2007	August	U	5.68(0.05)	149	0.01(0.00)	0.23(0.04)	8	N/A	N/A	N/A	N/A	N/A	N/A	1284.0
2007	August	Y	11.20(0.06)	271	2.65(0.06)	0.97(0.00)	8	N/A	N/A	N/A	N/A	N/A	N/A	510.6
2007	September	B	4.73(0.03)	232	0.44(0.02)	0.59(0.01)	8	N/A	N/A	N/A	N/A	N/A	N/A	0.0
2007	September	D2	10.78(0.04)	279	2.50(0.07)	0.71(0.01)	8	4.13(0.02)	820	53.98(1.70)	0.92(0.003)	15.34(0.01)	41	34,793.6
2007	September	D3	28.47(0.17)	126	1.41(0.10)	0.63(0.01)	8	N/A	N/A	2.64(0.19)	0.71(0.046)	16.13(0.02)	9	10,200.0
2007	September	SN	9.68(0.08)	179	0.65(0.05)	0.78(0.02)	8	4.11(0.02)	32	114.0(26.90)	0.97(0.009)	23.90(0.01)	3	672.0
2007	September	SS	29.35(0.35)	43	0.33(0.02)	0.77(0.02)	8	N/A	N/A	4.78(1.88)	0.12(0.048)	20.45(0.01)	13	21,895.0

Midge larval body masses were determined from individuals in the sediment and perch stomachs (*n* = the number of midge larva samples). Proportion in the sediment indicates the proportion of midge larvae in total zoobenthos biomass in the sediment (*n* = the number of Ponar grab sample replicates); proportion in perch stomachs indicates the proportion of midge larvae in total perch diet biomass (*n* = the number of fish samples). Perch biomass is estimated from CPUE from bottom trawl surveys. N/A = not available using the following power function derived from Lake Erie midges from the 2005 survey: Body mass = 0.0013 × (total body length)$^{2.69}$ × 10^{-3} (T. Nalepa, NOAA-GLERL, personal communication).

Statistical modeling

We tested for effects of 1) bottom-water habitat conditions on attributes of prey populations (midge larva body mass and biomass density), and 2) habitat conditions and prey attributes on predator–prey (yellow perch–midge larvae) mass ratio. For predator–prey mass ratio (PPMR), we used 'individual-link PPMRs'–mass of an individual perch divided by mass of an individual midge in a perch stomach–to minimize potential bias associated with averaging of prey mass (Woodward and Warren 2007; Nakazawa et al. 2011). Further, we used a linear mixed-effects model to account for 1) the unbalanced, hierarchical nature (non-independence) of our field surveys (multiple prey items ingested by individual fish collected on different survey dates at the same station) (Zuur et al. 2009; Barnes et al. 2010), and 2) interannual and spatial variability in the onset of thermal stratification and bottom-water oxygen depletion (Table 1).

Midge larvae in the sediment

We tested for significance of fixed effects, bottom-water habitat state (nominal: unstratified normoxia, stratified normoxia, or stratified hypoxia) and mean temperature in the hypolimnion (°C; for unstratified stations, mean temperatures of the entire water column were calculated), on midge body mass (mg) and biomass density (g m^{-2}) as a response variable with survey station (n = 13) as a random intercept. Midge biomass density was also added as a fixed effect for the models with body mass as a response variable to test for density dependence.

Perch–midge interactions

We tested if habitat conditions and prey attributes contribute to variation in individual-level perch–midge mass ratio; we tested for significance of four survey-level fixed effects; 1) bottom-water habitat state, 2) temperature, 3) midge density, and 4) perch biomass. We evaluated the following full model for perch k at station j (with survey station and perch as random intercepts):

$$\begin{aligned}\log_{10}\left(PPMR_{jk}\right) = {} & \beta_1 \times state_j + \beta_2 \times \log_{10}\left(temp_j\right) + \beta_3 \times \log_{10}\left(dens_j\right) + \beta_4 \times \log_{10}\left(biom_j\right) \\ & + \beta_5 \times state_j \times \log_{10}\left(temp_j\right) + \beta_6 \times state_j \times \log_{10}\left(dens_j\right) + \beta_7 \times \log_{10}\left(temp_j\right) \times \\ & \log_{10}\left(dens_j\right) \\ & + \left(b_j{}^S + b_k{}^P\right) + \varepsilon_{jk} \\ & \qquad b_j{}^S \sim N\left(0, \sigma^2\right), b_k{}^P \sim N\left(0, \sigma^2\right), \varepsilon_{jk} \sim N\left(0, \sigma^2\right)\end{aligned}$$

where βs are fixed effect coefficients; $PPMR_{jk}$ is perch: midge mass ratio for perch k at station j, $state_j$, $temp_j$, $dens_j$, and $biom_j$ are bottom-water state, temperature, midge density in the sediment, and perch CPUE from the bottom trawl surveys (kg hr.$^{-1}$) at site j, $b_j{}^S$ and $b_k{}^P$ are normally distributed random effect intercepts (jth *station* and kth *fish ID*, respectively) with mean of zero and variance of σ^2, and ε_{jk} is a normally distributed error term with mean of zero and variance of σ^2. PPMRs may vary with the time of the day (e.g., diel activities) or predator size (e.g., size-dependent foraging efficiency). However, our preliminary exploratory analysis showed that adding the terms of sampling time of the day or perch mass was not supported by our data and did not improve the model fit (based on a difference in Deviance Information Criterion or ΔDIC ≥7, Spiegelhalter et al. (2002); ΔDIC = 2.7 and 5.3, respectively); we thus did not test further for these terms in model evaluation.

We followed the two-step protocol of Zuur et al. (2009) to develop the linear mixed-effects models; we first evaluated the model structure of random effects (intercepts); *station* (n = 13) and individual *fish ID* (n = 433) as random intercepts separately and in combination (non-hierarchically and hierarchically structured) with ΔDIC ≥7 as a threshold (Spiegelhalter et al. 2002). The model with the selected random effects was subsequently evaluated for fixed effects. We evaluated the model convergence for random effects and fixed effects using restricted maximum likelihood and maximum likelihood, respectively (Zuur et al. 2009). The variance structures were evaluated visually for homogeneity and normality with plots of residuals and covariates. All the models were fit using a function, lmer, of an R package, lme4 (ver. 1.1–12). As reference, we also estimated pseudo-R^2 for a model with varying intercepts using a function, r.squaredGLMM, from an R package, MuMIn (Nakagawa and Schielzeth 2013; Johnson 2014). All the response variables were $\log_{10}$-transformed; temperature and prey covariates were $\log_{10}$-transformed and centered.

Results

Biomass density and body mass of midge larvae in the sediment

Biomass density of midge larvae in the sediment varied from 0.01 to 3.96 g m^{-2} and differed among bottom-water habitat states. Under normoxia, mean density was 2.5-fold greater when stratified than when unstratified (0.25 vs. 0.10 g m^{-2}, respectively; Fig. 2a, Table 3). Further, mean density was 1.9-fold greater under hypoxia than stratified normoxia (0.47 vs. 0.25 g m^{-2}, respectively; Fig. 2a, Table 3). Mean bottom-water temperature in central Lake Erie varied from 8.7 to 20.5 °C when stratified and from 9.0 to 23.9 °C when unstratified during summers of 2005 and 2007 (Table 1). However, including the temperature term did not improve the model fit (Table 3).

Individual body mass of midge larvae in the sediment varied from 1.6 to 29.4 mg and differed among bottom-water habitat states. Under normoxia, mean body mass was 1.2-fold greater when unstratified than when stratified (10.5 vs. 8.8 mg, respectively; Fig. 2b, Table 3). Further, when stratified, mean body mass was 1.4-fold greater under hypoxia than normoxia (12.1 vs. 8.8 mg, respectively; Fig. 2b, Table 3). Mean body mass was negatively correlated with bottom-water temperature (ΔDIC = 13.3; Table 4). Moreover, including the interaction term, habitat state × temperature, improved the model fit (ΔDIC = 20.7; Table 3), revealing that the linear correlation between mean body mass and temperature was stronger when stratified. Including the midge density term did not improve the model fit (ΔDIC = 3.8; Table 3).

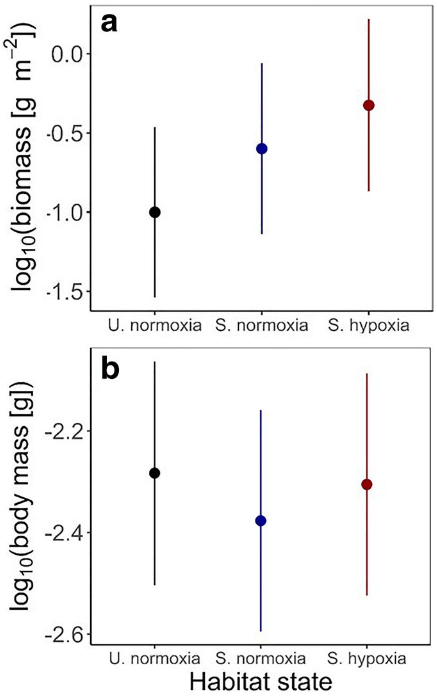

Fig. 2 Biomass density (**a**) and body mass (**b**) of non-biting midge (chironomid) larvae in the sediment under varying bottom-water habitat states (unstratified normoxia, stratified normoxia, and stratified hypoxia) in central Lake Erie. Circles and error bars indicate mean ± 95% confidence intervals estimated by the selected linear mixed-effects models with habitat state as a fixed effect and *station* as a random intercept for biomass density as a response variable or with habitat state and temperature as fixed effects and *station* as a random intercept for body mass as a response variable (Table 3). In (**b**), the temperature effect is controlled by fixing at mean values across all surveys

Perch–midge body mass ratios

Individual body mass of midge larvae in yellow perch stomachs varied from 2.0 to 14.2 mg with 29.9% of total variation found within individual fish and 28.6% among fish. Midge body mass in stomachs increased with perch body mass (ΔDIC = 23.1) and differed among bottom-water habitat states (ΔDIC = 11.4; Fig. 3a–c, Table 4). Under normoxia, realized perch–midge mass ratios were on average 1.3-fold greater (perch consuming smaller midges) when unstratified than when stratified (3836:1 vs. 2894:1, respectively; Fig. 4a, Table 4). Further, when stratified, realized perch–midge mass ratios were 1.6-fold greater under hypoxia than normoxia (4754:1 vs. 2894:1, respectively; Fig. 4a, Table 4). Perch–midge mass ratios were positively correlated with bottom-water temperature (ΔDIC = 44.7, Fig. 4b, Table 4);

Table 3 Model selection results for linear mixed-effects models with non-biting midge (chironomid) larva body mass and biomass density in the sediment as response variables

Model	DIC	ΔDIC	R^2_m	R^2_c
Midge larva biomass density				
(random effect only: *station*)	280.2	14.2	0.000	0.714
habitat state	266.0	0.0	0.066	0.792
habitat state + temperature	264.6	1.4	0.076	0.798
Midge larva mass				
(random effect only: *station*)	7383.7	170.9	0.000	0.289
habitat state	7376.2	163.4	0.003	0.263
habitat state + midge density	7380.0	167.2	0.006	0.332
habitat state + temperature	7233.5	20.7	0.232	0.584
habitat state + temperature + habitat state × temperature	7212.8	0.0	0.199	0.487

The models were evaluated using deviance information criterion (DIC). Each covariate was added sequentially using stepwise forward selection. DIC = deviance information criterion; ΔDIC was recalculated as a difference in a DIC value from the most supported model. $R^2{}_m$ = phsedo-R^2 for fixed effects only; and $R^2{}_c$ = phsedo-R^2 for both fixed and random effects

including the interaction term, habitat state × temperature, did not improve the model fit (ΔDIC = 4.8). Perch–midge mass ratios were also positively correlated with midge density in the sediment (Table 5). Further, including the interaction term, habitat state × midge density, improved the model fit (ΔDIC = 22.1; Table 4), revealing that mean mass ratios were negatively correlated with midge density under hypoxia, whereas mean mass ratios were positively correlated with midge density under normoxia (Fig. 4c). Including the perch biomass term did not improve the model fit (ΔDIC = 0.01, Table 5).

Discussion

Our study based on individual-level field observations revealed that Lake Erie yellow perch largely maintained their trophic relationships with non-biting midge larvae in contracted benthic habitats through modified size-mediated interactions after bottom-water dissolved oxygen depletion during summer (Table 6). Bottom-water hypoxia may directly and indirectly enhance or restrict foraging by demersal predators (Pihl et al. 1992; Rahel and Nutzman 1994; Taylor and Eggleston 2000), modulating trophic interactions and transfer efficiencies in lake ecosystems (Schindler and Scheuerell 2002). In Lake Erie, midge populations remained productive in thermally stratified, hypoxic waters, becoming a dominant prey base (midge larvae comprised up to ~70% of zoobenthos biomass) for perch. Despite their high densities, midge larvae also maintained their body size in hypoxic water. In contrast, perch on average ingested relatively smaller midges (but in higher numbers) in hypoxic water, while prey size ingested by perch shrunk less in areas with higher midge density. These findings indicate that higher hypoxia tolerance of midge larvae may allow them to maintain an abundant food supply to perch, sustaining the perch–midge size-based link (albeit temporarily modified) in thermally stratified, hypoxic water during summer.

Body size variation of Lake Erie midge larvae in the sediment may be more strongly regulated by size-based predation (indirectly) by demersal fishes including yellow perch responding to variable bottom water habitat conditions. When bottom water was well-oxygenated, midge larvae in the sediment attained larger body size in unstratified (warmer) water than stratified (cooler) water, independent of their density; however, their body size variation was negatively correlated with thermal variation in bottom water (Table 6). These seemingly contradictory patterns may have resulted from an indirect temperature effect, size-based predation by perch and likely other demersal predators, on midge body size. Top-down regulation of prey body size structure can occur in systems with high size-mediated predation rates, as demonstrated in a whole-lake experiment by Blumenshine et al. (2000). In Lake Erie, perch ingested larger midge larvae (lower PPMRs) in stratified, normoxic water than unstratified water (Table 6). Further, PPMR variation was also positively correlated with thermal variation in bottom water. Thermal stratification may allow cool-water (and perhaps cold-water) predators such as yellow perch to conserve energy (lower metabolic cost) and forage more efficiently in bottom water (Levy 1990; Mehner 2012), ultimately promoting size-biased predation effects on zoobenthos (Blumenshine et al. 2000).

The size-based perch–midge link appears to persist in oxygen-depleted bottom water. Despite severe hypoxia, perch continued to consume large amounts (~85% of the diet) of midges, likely through brief, frequent diving (a ‘foraging foray’) into bottom waters documented in hydroacoustic surveys (Roberts et al. 2012). However, relative prey size ingested by perch was up to ~64%

Table 4 Model selection results for linear mixed-effects models with body mass ratios of central Lake Erie yellow perch (*Perca flavescens*): non-biting midge (chironomid) larvae (predator–prey mass ratio or PPMR) as a response variable

Model	DIC	ΔDIC	R^2_m	R^2_c
(random effects only: *station/ fish ID*)	4448.0	106.1	0.000	0.532
habitat state	4433.3	91.4	0.028	0.526
habitat state + temperature	4388.6	46.7	0.293	0.716
habitat state + temperature + temperature × habitat state	4383.8	41.9	0.148	0.565
habitat state + temperature + midge density	4354.4	12.5	0.194	0.579
habitat state + temperature + midge density + perch biomass	4354.4	12.5	0.194	0.583
habitat state + temperature + midge density + temperature × midge density	4355.8	13.9	0.204	0.587
habitat state + temperature + midge density + habitat state × midge density	4341.9	0.0	0.213	0.609

Fixed effects tested include bottom-water habitat states, water temperature, midge biomass density, and perch biomass with hierarchically structured random intercepts, *station* and *fish ID*. The models were evaluated using deviance information criterion (DIC). Each covariate was added sequentially using stepwise forward selection. DIC = deviance information criterion; ΔDIC was recalculated as a difference in a DIC value from the most supported model. $R^2{}_m$ = pseudo-R^2 for fixed effects only; and $R^2{}_c$ = pseudo-R^2 for both fixed and random effects

smaller (higher PPMRs) in stratified, hypoxic water than stratified, normoxic water, whereas body size of midge larvae in the sediment was 37% larger in hypoxic water (Table 6). These reversed patterns may indicate less efficient foraging by perch (Brante and Hughes 2001; Shin et al. 2005) such as brief forays into hypoxic water, allowing them to capture only prey near the sediment surface. Severe hypoxia can restrict behaviors including foraging (Kramer 1987; Rahel and Nutzman 1994). Possible mechanisms involved in modified foraging by diving predators in hypoxic water may include; 1) reduced foraging duration–hypoxia can reduce the time spent by predators (with increased swimming speeds) in bottom water (Taylor et al. 2007; Neuenfeldt et al. 2009); and 2) reduced foraging efficiency–hypoxia may force predators to forage less selectively (e.g., lower net energy gain, Taylor et al. 2007). Such alternative foraging behaviors also have been documented for benthic and pelagic predators in other aquatic systems (Rahel and Nutzman 1994; Mistri 2004; Seibel 2011). Predatory marine crabs (*Carcinus maenas* and *Thalamita danae*), for example, spent more time in handling and selected smaller bivalve prey when temporarily exposed to hypoxia (Brante and Hughes 2001; Shin et al. 2005). Further studies on explicit mechanisms underlying foraging in hypoxic water (e.g., the number of and duration of dives by diving predators) would help understand energetic

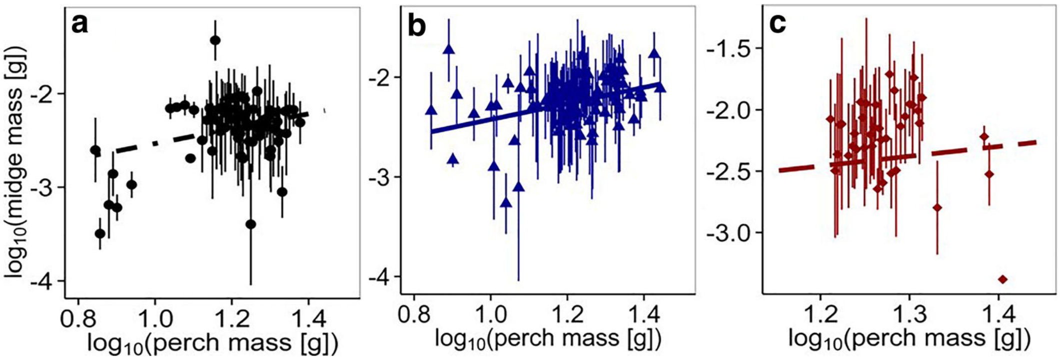

Fig. 3 Relationships between $\log_{10}$-transformed body mass of central Lake Erie yellow perch (*Perca flavescens*) and non-biting midge (chironomid) larvae consumed by perch. Triangles, circles, and diamonds indicate observed mean midge mass ± standard deviation in each fish stomach under different bottom-water habitat states. Dash-dotted, solid, and dashed lines indicate the selected linear mixed-effects model with habitat state (unstratified normoxia, stratified normoxia, and stratified hypoxia, respectively) as a fixed effect and *station* and *fish ID* as random intercepts: (**a**) $y = 0.76\times - 2.36$; (**b**) $y = 0.76\times - 2.25$; and (**c**) $y = 0.76\times - 2.44$

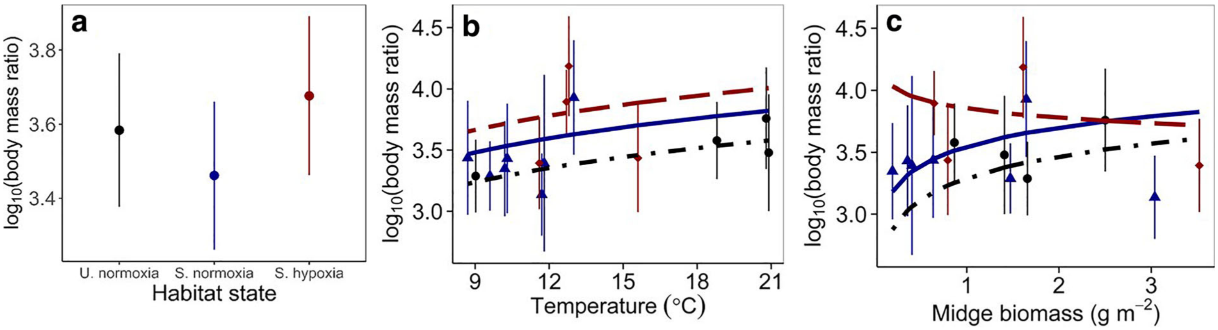

Fig. 4 Body mass ratios ($\log_{10}$-transformed) of central Lake Erie yellow perch (*Perca flavescens*): non-biting midge (chironomid) larvae ingested by perch under varying bottom-water habitat states (unstratified normoxia, stratified normoxia, and stratified hypoxia), water temperature and midge biomass density. In a, circles and error bars indicate mean ± 95% confidence intervals estimated by the selected linear mixed-effects model. In (**b**) and (**c**), triangles, circles, and diamonds indicate observed mean ± standard deviation for survey-averaged fish under varying bottom-water habitat states. In (**b**) and (**c**), dash-dotted black, solid blue, and dashed red lines indicate the selected linear mixed-effects model with habitat state (unstratified normoxia, stratified normoxia, and stratified hypoxia, respectively), water temperature, and midge biomass density as fixed effects and *station* and *fish ID* as random intercepts (Table 4). In (**b**), the midge density effect in the model is controlled by fixing at mean values across all surveys; and in (**c**), the temperature effect is controlled by fixing at mean values across all surveys

tradeoffs in foraging in food-rich, but potentially lethal waters (Scarbro 2014).

Density dependence may have played an indirect role in a size-based perch–midge interaction in stratified, hypoxic water. Although body size of midges in the sediment varied independently of their density, body size of midges ingested by perch varied with midge density in the sediment (Table 6). Further, this prey density-dependent predation by perch in hypoxic water differed from perch in normoxic water; body size of midges ingested by perch was positively correlated with midge density in hypoxic water, whereas ingested midge body size was negatively correlated with midge density in normoxic water. These contrasting patterns in size-mediated trophic interactions may be shaped by spatial distributions of size-structured prey populations under variable habitat conditions (Macciusi and Baker 1991; Pihl et al. 1992; Kornijów 1997). Transient hypoxia may promote production of resilient zoobenthos such as midges by releasing them from resource competition and predation in eutrophic systems (Brodersen and Quinlan 2006), allowing them to grow, survive, and reproduce at higher rates (a ~ 10–20-fold increase in biomass density in central Lake Erie). However, an experimental study also has demonstrated that hypoxia can induce upward movement within the sediment and heightened activities at the sediment–water column interface by larger midge larvae (Irving et al. 2004), which normally reside in deeper layers of the sediment (Panis et al. 1996). Although our sampling method prevented us from examining midge vertical distribution in the sediment (and thus midge size ranges encountered by perch), a positive density dependence in size-based predation of midges by perch indicate greater density (crowding) may have 'promoted' upward migration of larger midges in hypoxic water. Such prey aggregation forced by habitat contraction could increase their detectability by predators

Table 5 Parameter estimates and associated statistics for the selected linear mixed-effects model with body mass ratios of central Lake Erie yellow perch (*Perca flavescens*): non-biting midge (chironomid) larvae (predator–prey mass ratio or PPMR) as a response variable

Fixed effects	Estimate	SE	*t* value
habitat state (normoxia)	3.552	0.128	27.83
habitat state (unstratified)	3.301	0.127	25.92
habitat state (hypoxia)	3.822	0.127	30.08
temperature	0.124	0.062	2.00
midge density	0.178	0.025	7.05
habitat state (hypoxia) × midge density	−0.265	0.073	−3.62
habitat state (unstratified) × midge density	0.025	0.215	0.12

Bottom-water habitat states, water temperature, and midge biomass density were selected as fixed effects (see Table 4 for model structure)

Table 6 Summary of expected and observed responses by central Lake Erie non-biting midge (chironomid) larvae and yellow perch (*Perca flavescens*) (midge biomass density, midge body mass, and perch: midge predator–prey mass ratio or PPMR) to drivers tested with linear mixed-effects models. Up triangles (▲) indicate an increase in a response variable; down triangles (▼) indicate a decrease in a response variable; and right triangles (▶) indicate no effect on a response variable

Response	Driver	Expected effect	Observed effect
midge density	thermal stratification	▶	▲
	hypoxia	▼	▲
	temperature	▲	▶
midge body mass	thermal stratification	▶	▼
	hypoxia	▼	▲
	midge density	▼	▶
	temperature	▲	▼
perch: midge PPMR	thermal stratification	▼	▼
	hypoxia	▲	▲
	temperature	▲	▲
	midge density	▼	▲
	perch biomass	▲	▶

and reduce search time in a stressful environment (Rahel and Nutzman 1994; Aday et al. 2000). Prey behavioral responses to hypoxia may thus partially compensate for compromised foraging opportunities of predators by migrating between microhabitats (Rahel and Kolar 1990; Kolar and Rahel 1993). In Lake Erie, increased vulnerability of productive midge populations to perch predation (via vertical shifts) may have maintained a predator–prey link in stratified, hypoxic water, revealing plasticity of this predator–prey system.

A hypoxia-driven increase in vulnerability to predation is shared by other zoobenthos (Pihl et al. 1992; Kolar and Rahel 1993), zooplankton (Taylor and Rand 2003), and larval fish (Keister et al. 2000). Because of limited mobility and obligate benthic life history stages, zoobenthos often remain in hypoxic areas (Pihl et al. 1992; Rabalais et al. 2002; Craig et al. 2005) and become more vulnerable to predation (Pihl et al. 1992; Aday et al. 2000). Marine bivalves, for example, respond to hypoxia by protruding their siphon above the sediment surface (Seitz et al. 2003), increasing consumption of their siphons by predators. Although pelagic prey such as zooplankton and larval fish may escape from hypoxia as dissolved oxygen concentration progressively declines (Eby and Crowder 2002; Ludsin et al. 2009), some may become more exposed to pelagic predators (Costantini et al. 2008; Brandt et al. 2011). Because bottom-water hypoxia forces sensitive prey out of their dark bottom-water refugia into more illuminated and oxygenated waters (Goto et al. 2012), pelagic predators (piscivores and planktivores) that feed by sight may experience a short-term increase in prey encounter rates and thus consumption rates (Taylor and Rand 2003; Vanderploeg et al. 2009).

Amplified predator–prey interactions in contracted habitats also have been documented for other sources of natural and human-induced disturbances in aquatic ecosystems (Holt 1977; Domenici et al. 2007), including dry seasons in tropical river floodplains (Willis et al. 2005), droughts in temperate streams (Dewson et al. 2007; Goto et al. 2015), and fragmentation in tidal creeks (Layman et al. 2007). Under such disturbances, predators, prey, or both may modify their behaviors to minimize the risk of exposure to stressors (e.g., excessive heat), which can ultimately increase predator–prey encounter rates (Dewson et al. 2007; Domenici et al. 2007). Resulting changes in their interactions may thus modulate top-down or bottom-up effects in food webs and ultimately how an ecosystem operates (Ives et al. 2005; Heithaus et al. 2008; Frank et al. 2011).

Continued access to zoobenthos, abundant and energy-rich food sources, during summer is vital for growth and survival of demersal predators (Wu and Culver 1992; Gopalan et al. 1998; Goto and Wallace 2010). Resilient trophic coupling in the perch–midge system may further suggest perch's critical role as a benthic–pelagic coupler (Schindler and Scheuerell 2002; Vander Zanden and Vadeboncoeur 2002), sustaining productive fisheries in frequently perturbed systems such as Lake Erie (Kraus et al. 2015). Modified benthic–pelagic coupling may however have additional management implications. Altered trait-mediated predator–prey interactions can cascade through food webs, potentially effecting further consequences (e.g., alternative energy pathways) in perturbed ecosystems (Schmitz et al. 2004). Many trophic interactions disrupted by transient disturbances such as summer bottom-water hypoxia may modify nutrient recycling and alter ecosystem productivity regimes (Österblom et al. 2007; Diaz and Rosenberg 2008; Scavia et al. 2014). With large-scale environmental changes such as climate warming and excessive land use, we may expect further increases in spatial and temporal variation in bottom-water oxygen depletion that may ultimately reshape benthic–pelagic coupling (Baird et al. 2004; Long and Seitz 2008). Monitoring transient size-mediated predator–prey interactions may therefore help the assessment of long-term implications for ecosystem productivity and resource sustainability in nutrient-enriched systems.

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Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflict of interest.

Human participants and animal study This article does not contain any studies with human participants or animals performed by any of the authors.

Informed consent For this type of study formal consent is not required.

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