

Intraspecific Niche Partitioning and Ecosystem State Drive Carbon Pathways Supporting Lake Food Webs

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ABSTRACT

Individual behavior drives population-level patterns, yet few studies have integrated how intraspecific niche partitioning influences energy pathways that support consumer production across multiple ecosystem states. We used stable isotope analyses to assess the individual foraging behavior of a dominant consumer, yellow perch (*Perca flavescens*), in a single lake (Oneida Lake, NY) under both eutrophic (1960s) and mesotrophic (2000s) conditions and at different yellow perch densities. We then integrated this data with intensive population surveys to assess how variation in foraging behavior between individuals and lake trophic status interacts to drive energy pathways supporting consumer production. Stable isotope analyses highlight that individual yellow perch varied greatly in their reliance on benthic and pelagic energy pathways even within a given year. At the population-level, benthic reliance increased from 2 to 20% under eutrophic conditions to 30–70%

under mesotrophic conditions. At low densities, individual fish primarily selected inshore habitats and were reliant on benthic carbon, increasing population-level reliance on benthic carbon. This pattern was present during both trophic states, but was more pronounced during mesotrophic conditions. Our results highlight that variation in foraging behavior between individuals can affect the integration of benthic and pelagic energy pathways at the population-level, and that this integration is dependent on ecosystem state and consumer population density. We propose that models that incorporate variation between individual consumers across multiple habitats can more accurately represent energy flows within ecosystems.

Key words: Intraspecific niche partitioning; Carbon niche breadth; Dreissenid mussels; Context dependency; Stable isotope.

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INTRODUCTION

Understanding extrinsic and intrinsic drivers of niche breadth and resource use is a central challenge in ecology (Elton 1927; Schoener 1974) and can have important implications for the transfer of energy to higher trophic levels. However, nearly all

studies of the energy sources supporting consumer production evaluate individual organisms and average their resource use to describe the population-level niche (Vander Zanden and Vadeboncoeur 2002; Pace and others 2004; Vadeboncoeur and others 2008; Weidel and others 2008; Solomon and others 2011; Vander Zanden and others 2011). This approach assumes that consumers are mobile and able to integrate resources across a variety of habitats (Vander Zanden and Vadeboncoeur 2002) such that individual resource use is representative of the total population. Growing empirical evidence suggests many species exhibit high levels of individual specialization, where individual niche breadth only overlaps with a subset of the total population niche breadth (Bolnick and others 2003). This specialization reduces food web connectivity (Quevedo and others 2009) and requires an understanding of the relative distribution of specialists within the population to accurately describe population reliance on multiple energy pathways. Food web models that fail to address this challenge may misrepresent a population's resource use and niche breadth, and their sensitivity to ecosystem perturbations.

The degree of specialization within a population is often closely linked to population density (Bolnick and others 2003; Svanbäck and Persson 2009; Jones and Post 2013), although other ecological conditions may also be important (for example, water clarity, presence of zebra mussels (*Dreissena polymorpha*); Hirsch and others 2013). At low densities, intraspecific competition is weak, per capita resources are abundant, and the benefits of specialization and consequent morphological differentiation are low. At high densities, however, intraspecific competition is strong, and the enhanced feeding performance of trophic specialists increases their frequency in the population, leading to a high degree of individual specialization and disruptive selection for morphological divergence (Svanbäck and Persson 2009). Furthermore, at high densities, some individuals may switch from preferred to secondary prey, increasing individual specialization while expanding the total population niche (Araújo and others 2008). Because population density can influence individual and population niche breadth, it can be expected that energy pathways supporting production at higher trophic levels will also change at different densities.

Support of higher trophic levels may also be driven by the relative magnitude of different energy pathways within ecosystems. In lake ecosystems, primary production comes from both autochthonous (benthic and pelagic) and al-

lochthonous (terrestrial) sources (Forbes 1887; Lindeman 1942; Pace and others 2004). Historically, the dominant paradigm has been that fish production is driven by pelagic-phytoplankton-based food chains. However, there is growing evidence that benthic (Vander Zanden and Vadeboncoeur 2002; Vadeboncoeur and others 2008; Vander Zanden and others 2011) and terrestrial energy pathways (Pace and others 2004; Weidel and others 2008; Solomon and others 2011) are substantial contributors to production at higher trophic levels. Environmental conditions are thought to drive the relative importance of pelagic, benthic, and terrestrial energy pathways. For instance, shallow lakes can transition between clear or turbid states, leading to differences in the relative distributions of inshore (littoral) and offshore (limnetic and demersal) habitats, and altering the importance of production from benthic and pelagic energy pathways (Scheffer and others 1993). The amount of terrestrial carbon inputs can also modify the relative importance of allochthonous and autochthonous carbon sources (Weidel and others 2008; Solomon and others 2011). In both cases, environmental conditions (for example, water clarity, terrestrial carbon inputs) drive the distribution of available resources and modify energy pathways supporting higher trophic levels, including fish.

Despite the clear implications of individual specialization on ecosystem-level processes, including energy transfer through food webs, few studies have integrated these two research areas. This has limited our ability to provide an integrated understanding of how energy pathways leading to higher trophic levels vary over time and space and across different ecosystem states. Given the strong effect of population density on individual specialization and the importance of environmental conditions on the magnitude of energy fluxes among different carbon pathways, it seems likely that ecosystem state and population density may interact to drive carbon pathways supporting consumer production at higher trophic levels. However, empirical studies designed to test the strength of this interaction are rare, likely due to the scarcity of datasets with the requisite resolution across habitats and the duration necessary to determine the degree of specialization within a population and the abundance of different specialists across a range of environmental conditions and population densities.

Here, we integrate individual variation in stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) with catch statistics from inshore and offshore habitats to describe population-level benthic reliance of a generalist

fish population, yellow perch (*Perca flavescens*). We assess how population density and ecosystem state interact to drive energy pathways supporting fish production. We hypothesized that (1) individual fish reliance on pelagic and benthic energy pathways will differ across inshore and offshore habitats, (2) ecosystem state and density will influence how individuals within the population are distributed among inshore and offshore habitats, and (3) ecosystem state and population density will interact to define the degree of benthic energy reliance by fish.

METHODS

Study Site and Species

Oneida Lake, New York is a large, shallow lake (area 207 km², maximum depth 16.6 m, mean

depth 6.8 m; Figure 1) located in the fertile plain of Lake Ontario, and is the site of a long-term monitoring program conducted by the Cornell Biological Field Station. During ice-free months, the lake is well mixed and isothermal, though brief periods of stratification and hypolimnetic anoxia occur in some years. During the 1970s, the lake was eutrophic with July and August total phosphorus (TP) levels averaging 41.0 µg L⁻¹. The lake is currently mesotrophic with TP averaging 22.6 µg L⁻¹ (Rudstam 2015). The shift in trophic state was primarily driven by reductions in nutrient loading beginning in the 1980s and the introduction of zebra mussels in 1991. Changes in trophic state led to widespread ecological changes and shifts in resource availability across inshore and offshore habitats in the lake, including increases in water clarity, elevated benthic primary production, and an expansion of the

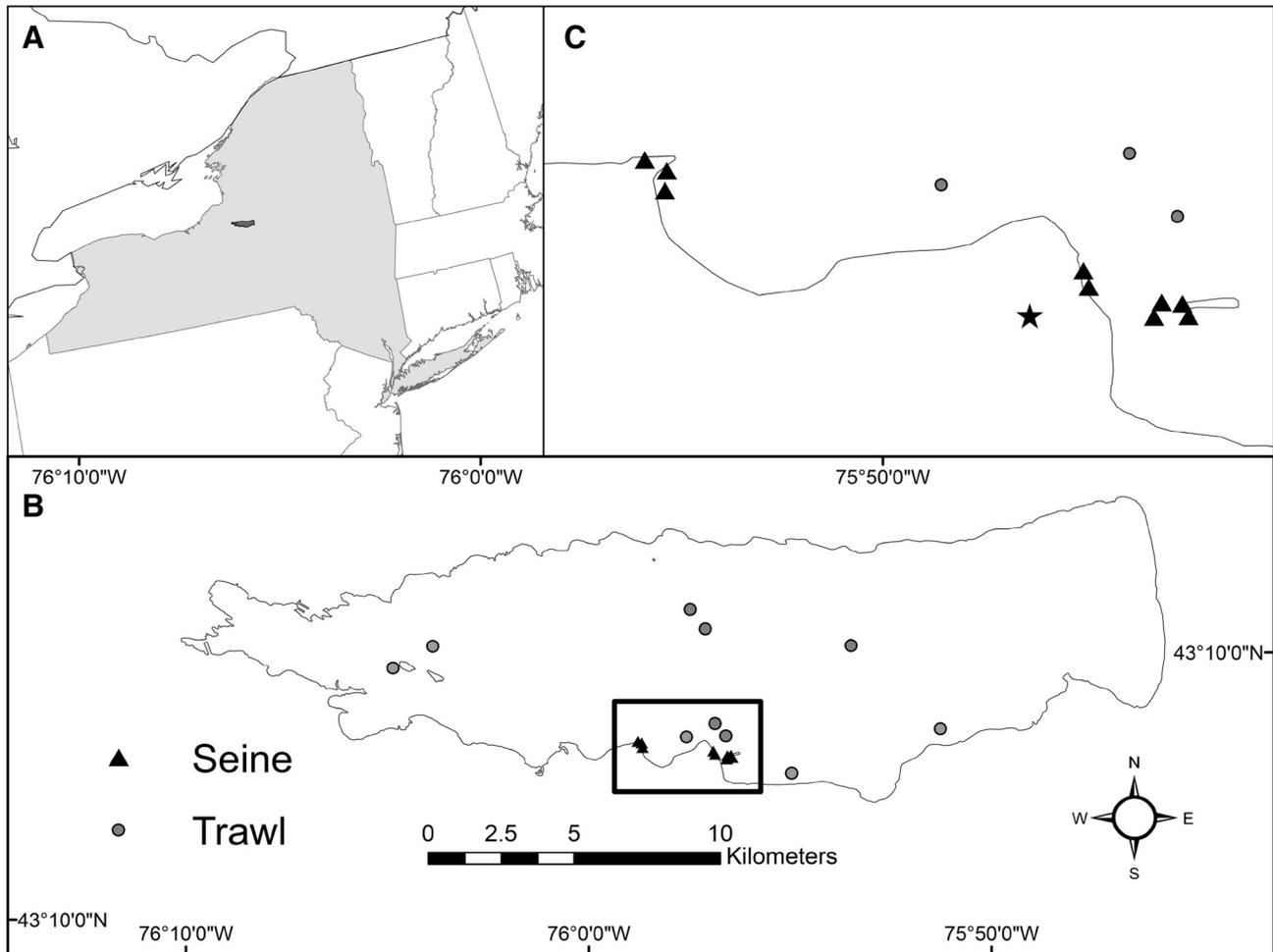


Figure 1. Map of Oneida Lake indicating long-term seine and trawl sampling locations. (A) Location of Oneida Lake within New York State. (B) Oneida Lake with seine and trawl sampling locations indicated. (C) Sampling location near Shackleton Point and the Cornell Biological Field Station (indicated with *star*).

littoral zone (Zhu and others 2006; Mayer and others in press). The fish community of Oneida Lake is dominated by walleye (*Sander vitreus*) and yellow perch, though species composition has changed over time resulting in a diversification of both prey and predator communities.

Yellow perch are generalists that exhibit a complex ontogeny, occupying all habitats of Oneida Lake (Clady 1976; Irwin and others 2009). Age-0 yellow perch are the dominant forage fish in the lake in most years, representing a critical link between lower and higher trophic levels (Forney 1974). Adult yellow perch spawn in inshore habitats during mid-May, laying egg strands onto macrophytes and other structures. Following hatching, fry are transported via water currents to offshore pelagic (limnetic) habitats where they feed primarily on zooplankton for 1–2 months (Mills and Forney 1981). At approximately 1.0 g (mid-July), age-0 yellow perch transition to inshore (littoral) and offshore benthic (demersal) habitats, and continue to occupy these habitats throughout the summer and fall, consuming zooplankton and macroinvertebrates (Mayer and others 2000). In Oneida Lake, little is known about the importance of inshore habitats and benthic energy pathways to age-0 yellow perch production and population dynamics, as most previous research has focused on offshore habitats (Irwin and others 2009; but see Clady 1976).

Field Collections and Archived Samples

Age-0 yellow perch population dynamics have been monitored in Oneida Lake for over 50 years. Sampling began each year in early June and continued throughout the growing season using a variety of gears across life stages and habitats (see Irwin and others 2009 for more details). The first estimates of age-0 yellow perch abundance were obtained in offshore habitats when the fish were approximately 18 mm (Figure 2). Samples were collected at multiple depth strata and locations using high-speed Miller samplers (0.1 m diameter, 0.68 m length, 540 or 760 μm mesh net). Since 1961, offshore benthic age-0 yellow perch have been sampled with a bottom trawl (5.5 m footrope, 13 mm cod end) weekly from July through October at 10 standard sites (Figure 1) at depths of 6 m (4 sites), 8 m (2 sites), and 12 m (4 sites). Inshore age-0 yellow perch were sampled using a beach seine (23 m by 1.5-m, 6-mm mesh) at 9 standard sites (Figure 1) during a subset of the years when trawling was conducted (~20 years). Sampling locations were consistent across all years in both

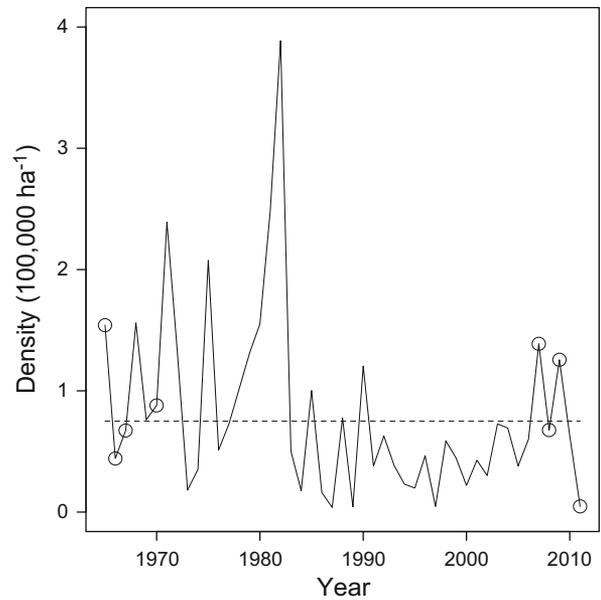


Figure 2. Temporal trend in age-0 yellow perch densities. Annual estimates are based on 18 mm survey conducted during early June. Densities scaled by 100,000 fish. Horizontal line indicates cut-off of low and high densities at 75,000 fish per hectare used to highlight results in Figures 4, 5, and 7. Years included in analyses are indicated with a circle.

surveys. In all surveys, catch was identified to species, counted, and a subsample measured for total length. A subsample of the catch from each survey date was archived and either preserved in formaldehyde or frozen (Table S1). Formaldehyde preserved samples were fixed in 1:10 formaldehyde:water solution immediately after collection.

Stomach Contents and Stable Isotope analysis

Diet composition and stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of age-0 yellow perch were analyzed to provide short- and long-term indicators of individual variation in niche breadth and reliance on pelagic and benthic energy pathways. Reliance on terrestrial carbon was not accounted for and assumed to be low due to Oneida Lake's large size and trophic state (Wilkinson and others 2013). Analyses were conducted on samples from eight years that represented two distinct ecosystem states (Zhu and others 2006; Mayer and others in press): pre-dreissenid introduction (eutrophic: 1965, 1966, 1967, 1970) and post-dreissenid introduction (mesotrophic: 2007, 2008, 2009, 2011). Individual years were selected to cover the range of densities observed within each ecosystem state (Table S1, Figure 2) based on density estimates of age-0

yellow perch at 18 mm (Rudstam and Jackson 2012). Within each year, analyses focused on age-0 yellow perch collected during July and August to evaluate individual variability in the use of benthic and pelagic energy pathways during and after the transition from offshore pelagic to inshore and offshore benthic habitats. Within each month, 20 fish from each habitat were analyzed.

Diet composition was used to determine short-term foraging behavior for individual yellow perch in inshore and offshore habitats and to provide context to understand stable isotope results. Stomach contents were defined as diet items from the esophagus to the pylorus and enumerated based on broad taxonomic groups including cladocerans, copepods, amphipods, chironomids, isopods, trichopterans, and other macroinvertebrates. For a subsample of stomachs, zooplankton were grouped within a single zooplankton category; typically if diet items were highly digested and difficult to distinguish. We used permutation multivariate analyses of variance (PERMANOVA; Anderson 2001) to test for foraging differences across habitat, time period, and a habitat \times time period interaction. PERMANOVA uses permutation methods in an analysis of variance (ANOVA) experimental design to test for differences in the centroid of the distance matrix for major diet items. Non-metric multidimensional scaling (NMDS) was used to visualize foraging differences between habitats and time period in two dimensions. All analyses were done using the 'vegan' package in R (Oksanen and others 2003; R Development Core Team 2013).

Stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were used to complement diet analyses by providing an integrated picture of long-term foraging patterns to determine (1) individual reliance on benthic and pelagic energy pathways, and (2) potential movement patterns between habitats. Primary consumers collected during the diet analyses were used to provide time-integrated values of benthic and pelagic carbon end-members at the base of the food web (Post 2002; Table S1). Diet items from inshore fish were used to estimate benthic end-members, while diet items from offshore fish were used to estimate pelagic end-members. Diet items with a $\delta^{13}\text{C}$ that did not accurately reflect the appropriate carbon pathway for the habitat where a fish was captured in were removed (for example, cladocerans with $\delta^{13}\text{C}$ of -31.28 from an inshore fish diet were not used to calculate benthic end-member); however, these were rare (<5%). For each month and year combination, dorsal muscle was dissected from approximately 20 inshore and 20 offshore age-0 yellow perch (40 total) used in the diet

composition analyses. Lipid extraction performed on 5 fish indicated no significant effect of lipids on $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ ratios (paired t test; $\Delta \delta^{13}\text{C} = -0.13$, $t_4 = 0.77$, p value 0.48; $\Delta \delta^{15}\text{N} = 0.31$, $t_4 = 0.12$, p value = 0.12); therefore, lipids were not removed from samples used in the analyses. Invertebrate and fish tissue samples were dried for at least 48 h at 60°C.

Dried samples ($1 \pm 0.1 \mu\text{g}$) were packed into tin capsules for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses. Analyses were performed using a Thermo Delta V isotope ratio mass spectrometer interfaced to a NC2500 elemental analyzer at the Cornell Isotope Laboratory (Ithaca, New York, USA). Stable isotope ratios were expressed as parts per thousand deviations from a chemical methionine standard. A subsample was analyzed in duplicate, and the analytical error was 0.27‰ for $\delta^{13}\text{C}$ and 0.12‰ for $\delta^{15}\text{N}$. Proportion of benthic reliance for each individual was estimated from the isotopic ratios of muscle tissue with a two end-member mixing model parameterized with the major diet items (Post 2002). Though differences in preservation techniques could confound differences observed between time periods, we suspect this effect was minimal. Previous estimates of formaldehyde preservation effects to carbon isotopic signatures observed consistent negative shifts of approximately 0.5 to 1.0 parts per thousand for fish, benthic invertebrates, and zooplankton (Sarakinis and others 2002; Rennie and others 2012).

Population and Carbon Source Estimation

Catch statistics and stable isotope samples were integrated to provide an estimate of the benthic reliance of the entire age-0 yellow perch population. Catch-per-unit-effort in offshore and inshore habitats was determined from trawl and seine surveys, and converted to density using the average area sampled by each gear. Points were considered outliers if their residuals from first fit regressions exceeded three times the interquartile range and were thus excluded. For each year, catch curves were modeled assuming a linear mortality rate using a Bayesian approach in the programs R and JAGS and the package 'R2jags' (Plummer 2003; R Core Team 2013; Su and Yajima 2015). We chose this approach to characterize uncertainty in our habitat-specific density estimates and to generate a distribution of density estimates to draw from during the error propagation procedure described below. We used independent, diffuse priors for the slope and intercept of the catch curves (for

example, a normal distribution with a mean and standard deviation of 0.0 and 0.1, respectively, for each model parameter). We ran three chains of length 1500 after a burn in of 500 and thinned the posterior chains by two. We used the median value of the generated density estimates on July 15 and August 15 to estimate the percent benthic support of the population, which corresponded to sampling dates used for stable isotope analysis. Percent benthic support of the population was determined using the following equation:

$$\% \text{ Benthic}_{\text{pop}} = \frac{\alpha_{\text{in}} \times \text{Density}_{\text{in}} \times \% \text{ Benthic}_{\text{in}} + (1 - \alpha_{\text{in}}) \times \text{Density}_{\text{off}} \times \% \text{ Benthic}_{\text{off}}}{\alpha_{\text{in}} \times \text{Density}_{\text{in}} + (1 - \alpha_{\text{in}}) \times \text{Density}_{\text{off}}}$$

where α_{in} represented the estimated proportion of lake area that was defined as inshore habitats, Density_x represented the habitat-specific density (so that the product of these terms produced abundance in given habitat), and $\% \text{ Benthic}_x$ represented the average benthic reliance of age-0 yellow perch captured in the seine ($x = \text{in}$) or trawl ($x = \text{off}$) based on stable isotopes. α_{in} was set at 0.25 and 0.43 based on observed changes in the area of inshore habitats before and after dreissenid mussel establishment (Fitzgerald and others in press). This equation weights the estimate of percent benthic reliance of the population by habitat availability and density, rather than sample size to give an unbiased estimate of carbon pathways supporting consumer production.

To incorporate error propagation into our calculation of population-level benthic reliance, we developed a resampling procedure that draws from the distributions of habitat-specific densities, stable isotope ratios of benthic and pelagic end-members, and age-0 yellow perch stable isotope ratios. For each iteration, one benthic and one pelagic end-member signature were drawn and used to convert individual age-0 yellow perch stable isotope ratios to percent benthic reliance. Inshore and offshore density estimates were then drawn from the distributions of habitat-specific densities, and used to determine the number of draws (with replacement) to take from the pool of individual age-0 yellow perch benthic reliance estimates for each habitat. These values were averaged to determine percent benthic reliance of the total population for that iteration. Each resampling procedure was performed 1000 times for each month/year combination to develop a distribution of population-level percent benthic reliance for each scenario of in-

shore-offshore habitat distributions ($\alpha_{\text{in}} = 0.25, 0.43$). We also included scenarios where $\alpha_{\text{in}} = 0.0$ and 1.0 to determine how including only offshore or inshore samples, respectively, affected our estimates of population-level benthic reliance.

Statistical Analyses and Model Selection

We used linear mixed effects models to test for the significance of fixed effects (that is, habitat, time period, density, and their interactions), while

incorporating random effects (month; repeat measures), on benthic and pelagic end-members, individual age-0 yellow perch benthic reliance, and benthic reliance of the age-0 yellow perch population (at $\alpha_{\text{in}} = 0.25$ and 0.43). Habitat and time period were discrete predictors, while density was continuous. Benthic reliance of the age-0 yellow perch population was transformed using the logit function because estimates during the eutrophic period were clustered near zero. In all analyses, the best fitting, most parsimonious model from all candidate models was selected using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). All analyses were conducted using the 'nlme' package in R (Pinheiro and others 2015; R Core Team 2013).

RESULTS

Diet Analyses

Diet composition of age-0 yellow perch consistently indicated habitat-specific foraging patterns during both time periods (Table S2; Table 1; Figure 3). The PERMANOVA test found a significant effect of time period, habitat, and a time period \times habitat interaction on diet composition of age-0 yellow perch (Table 1). Zooplankton, such as cladocerans and copepods, were the dominant diet items in offshore-caught age-0 yellow perch, while diet composition in inshore habitats was dominated by benthic invertebrates, such as amphipods, chironomids, and trichopterans (Table S2; Figure 3). The significant time period \times habitat interaction indicates stronger foraging divergence between habitats during the 2000s, as foraging on zooplankton decreased in inshore habitats during mesotrophic conditions (NMDS plot; Figure 3).

Table 1. Summary of PERMANOVA Results

	DF	SS	F stat	P value
Time period	1	3.17	9.35	<0.001
Habitat	1	26.26	77.41	<0.001
Time period × habitat	1	1.12	3.3	<0.003
Residuals	52	187.307		
Total	555	217.87		

PERMANOVA table based on Bray–Curtis dissimilarity of major diet items in stomachs of age-0 yellow perch across time periods, habitats, and a habitat × time period interaction.

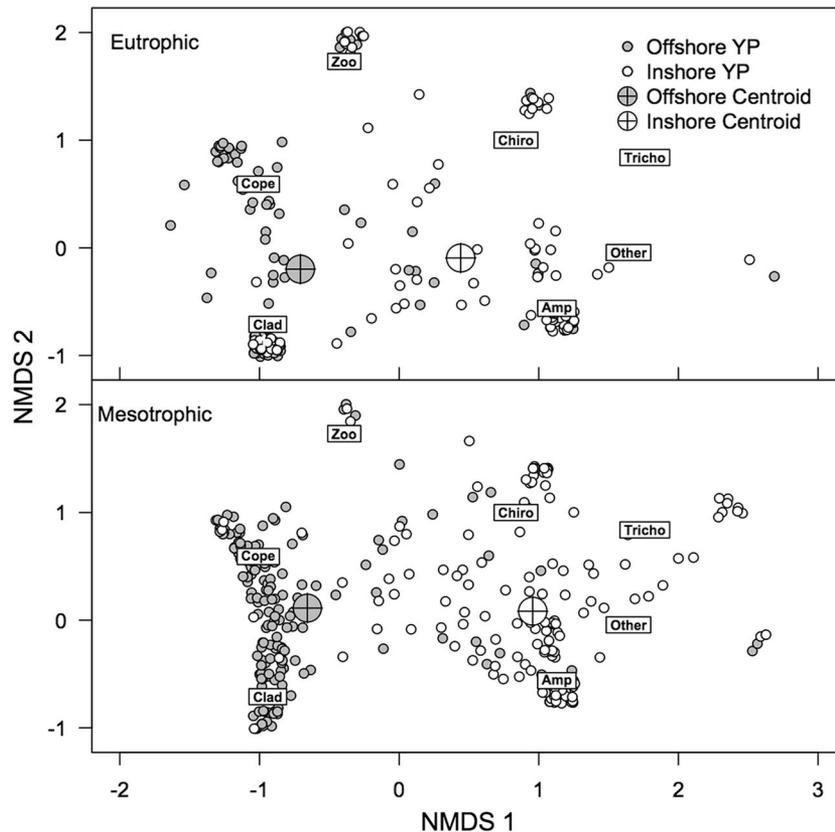


Figure 3. NMDS plot of major diet items. NMDS of major diet items in age-0 yellow perch from inshore and offshore habitats during eutrophic and mesotrophic conditions. NMDS was derived using a Bray–Curtis distance matrix, and resulted in a low final stress of 0.08. Each point represents the diet of an individual age-0 yellow perch. Empty stomachs were more common during eutrophic conditions, resulting in fewer points being plotted. Locations of diet items within NMDS space are indicated and include amphipods (Amp), chironomids (Chiro), cladocerans (Clad), copepods (Cope), Trichoptera (Tricho), zooplankton (Zoo), and other (Other).

Stable Isotope Analysis

End-member $\delta^{13}\text{C}$ stable isotope ratios showed clear separation of benthic and pelagic energy pathways (Figure 4), with a mean $\delta^{13}\text{C}$ of -31.32 (SD = 1.10) for pelagic carbon and a mean of -24.39 (SD = 1.28) for benthic carbon. Divergence between pelagic and benthic end-members increased slightly during the 2000s, but there were

no differences between high- and low-density years (Figure 4; Table 2). Age-0 yellow perch $\delta^{13}\text{C}$ stable isotope ratios exhibited a similar pelagic–benthic divergence during 15 out of 16 month/year combinations (Figure 4). In all years, $\delta^{13}\text{C}$ stable isotope ratios of offshore fish clustered near pelagic end-members. Inshore fish exhibited more complicated patterns, clustering near benthic

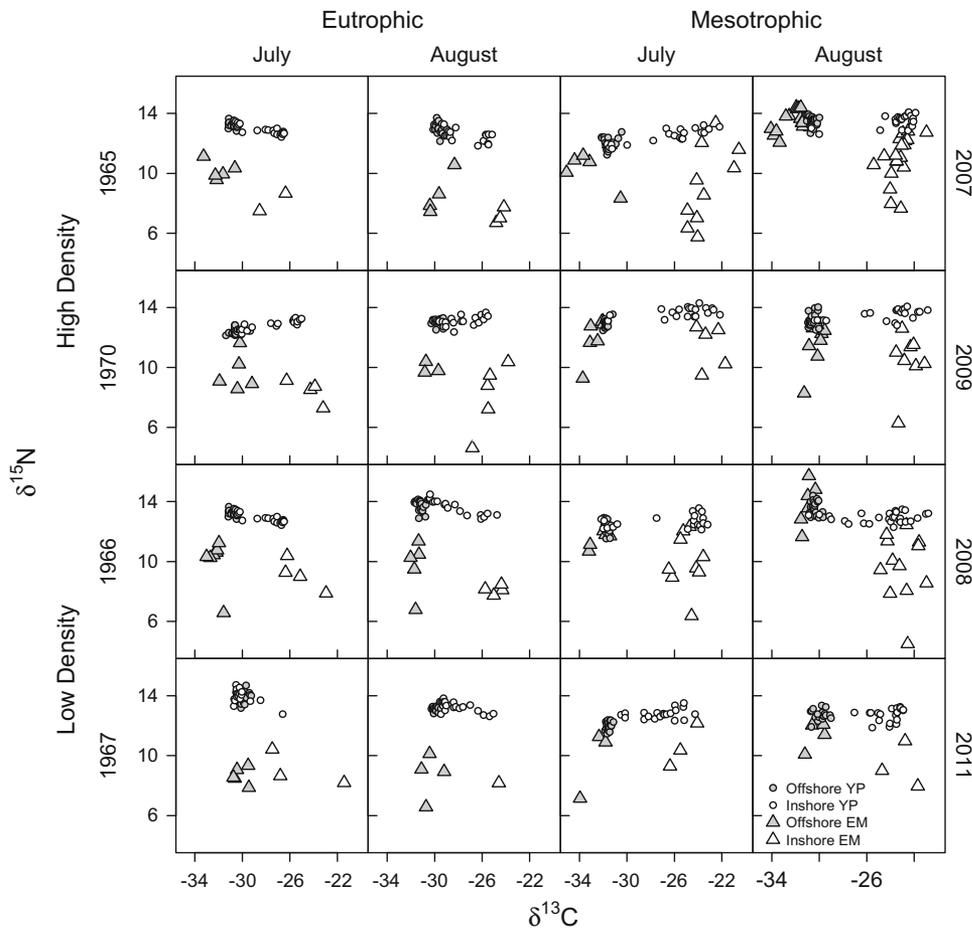


Figure 4. Dual isotope plots of age-0 yellow perch and their prey. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope ratios for age-0 yellow perch (YP) and their primary diet items from offshore and inshore habitats. Diet items plotted are those used to establish benthic and pelagic end-members (EM).

end-members in some years, and spanning the entire pelagic-benthic continuum in others (Figure 4). Individual age-0 yellow perch benthic reliance differed across habitats during both time periods, but increased during mesotrophic conditions (Table 2). These differences were driven by variation in inshore habitats, as benthic reliance of offshore fish was low in all years (Table S1).

Habitat-Specific Population Densities

During the 1960s, age-0 yellow perch were 1.5–7.5 times denser in offshore habitats than inshore habitats. During the 2000s, this pattern switched, as inshore densities ranged from approximately equal to 10 times the densities in offshore habitats (Table S1). Offshore densities varied by two orders of magnitude (range 165–40,025 fish/ha) and declined on average from approximately 20,000 fish in the 1960s to 4000 fish per hectare in the 2000s (Table S1). Inshore densities varied by one order of magnitude (range 1115–20,923 fish/ha) and in all but two month/year combinations ranged from 1000 to 10,000 fish per hectare. Inshore density

showed little change between the 1960s and 2000s, at approximately 5704 and 7653 fish per hectare, respectively (Table S1).

Population-Level Benthic Reliance

Integration of stable isotope signatures and habitat-specific catch statistics indicated that time period and density drove energy pathways supporting age-0 yellow perch production (Table 2; Figure 5). During the 2000s, age-0 yellow perch benthic reliance was highest, and the strength of the density effect increased as densities became higher in inshore relative to offshore habitats (Table S1; Table 2; Figures 5 and 6). These results were consistent regardless of whether the proportion of the lake defined as inshore habitat (α_{in}) was set at 0.25 or 0.43 (Table 1; Figure 7). This pattern was supported by the results of the resampling procedure designed to incorporate uncertainty in our estimates of habitat-specific densities, stable isotope ratios of benthic and pelagic end-members, and age-0 yellow perch stable isotope ratios (Figure 7).

Table 2. Model Selection and Coefficients Summary Table

Candidate model	Intercept	Inshore	Eutrophic	Density	Eutrophic: density	Eutrophic: inshore	Inshore: density	Eutrophic: inshore: Density	ΔAIC_c	w_i	w_i/w_1
Carbon end members											
Habitat × time period	-31.78	8.21	0.91			-2.55			-	0.69	1.00
Habitat × time period + density	-31.83	8.21	0.91	0.00		-2.55			3.60	0.11	6.04
Percent benthic reliance											
Habitat × time period	8.00	70.73	-2.75			-32.25			-	0.85	1.00
Habitat × time period + density	4.94	70.73	-2.90	4.0×10^5		-32.35			2.91	0.19	4.28
Benthic production ($\alpha = 0.25$)											
Time period + DENSITY	0.50		-2.15	-9.1×10^{-6}					-	1.00	1.00
Time period × Density	0.49		-2.12	-9.0×10^{-6}	-3.0×10^{-7}				3.074	0.17	4.65
Benthic production ($\alpha = 0.43$)											
Time period + density	0.81		-2.20	-6.8×10^{-6}					-	0.69	1.00
Time period × density	0.90		-2.45	-7.9×10^{-6}	2.9×10^6				2.78	0.17	4.01
Time period	0.23		-2.23						3.30	0.13	5.20

Candidate models testing the effects of habitat, time period, density, and their interactions on benthic and pelagic end-members, individual age-0 yellow perch benthic reliance, and benthic reliance of the age-0 yellow perch population (based on logit transformation of percent benthic reliance of the population at $\alpha_{in} = 0.25$ and 0.43). AIC_c , Akaike weights (w_i), and evidence ratios (w_i/w_1) are included for candidate models with evidence ratios < 10. Significant model coefficients ($\alpha = 0.05$) are indicated in bold. Intercepts correspond to offshore habitats, high densities, and mesotrophic conditions; therefore, coefficients correspond to inshore habitats, low densities, and eutrophic conditions, when applicable.

DISCUSSION

Intraspecific Specialization, Density, and Ecosystem State

Nearly all individuals in our dataset specialize on either benthic or pelagic energy pathways in all years, regardless of population density. Theory predicts that individual specialization should increase at higher population densities through either exploitative or interference competition (Svanbäck and Persson 2009), but not always (Jones and Post 2013). At high densities, intraspecific competition for limited resources is stronger and requires individuals to specialize on a subset of the total niche (that is, exploitative). Similarly, a subset of individuals may occupy optimal habitats, displacing other individuals to suboptimal habitats where resources are not as good (that is, interference; Post and others 1997). At low densities, specialization is unnecessary due to low intraspecific competition for abundant resources (Svanbäck and Persson 2009), or a lack of saturation in optimal habitats (Post and others 1997).

Our results show that intraspecific niche partitioning drives segregation of the energy pathways supporting consumer production in Oneida Lake. Across multiple decades and months, diet data demonstrate that inshore yellow perch (that is, fish captured with seine) consume benthic invertebrates, while offshore yellow perch (that is, fish captured with trawl) consume zooplankton. Stable isotope analyses of yellow perch tissues that integrate foraging patterns over multiple weeks, moreover, demonstrate that our diet samples reflect consistent segregation of the diet items consumed by fish in these two habitats. Further understanding of specialization on specific prey items might be improved by incorporating multiple tissue types that vary in their turnover rates (Martínez del Rio and others 2009); however, our intent was not to demonstrate that individual fish specialize on a specific diet item, but rather a specific energy pathway.

This intraspecific partitioning of diet items decouples benthic and pelagic energy pathways, a result that would not be expected by merely looking at the aggregate diets and tissue stable isotopes of all yellow perch in Oneida Lake. Assuming no intraspecific niche partitioning would suggest that yellow perch are moving between habitats and foraging haphazardly from both benthic and pelagic energy pathways, leading to yellow perch with tissue isotopic composition near the middle of the carbon continuum in any habitat. Our study,

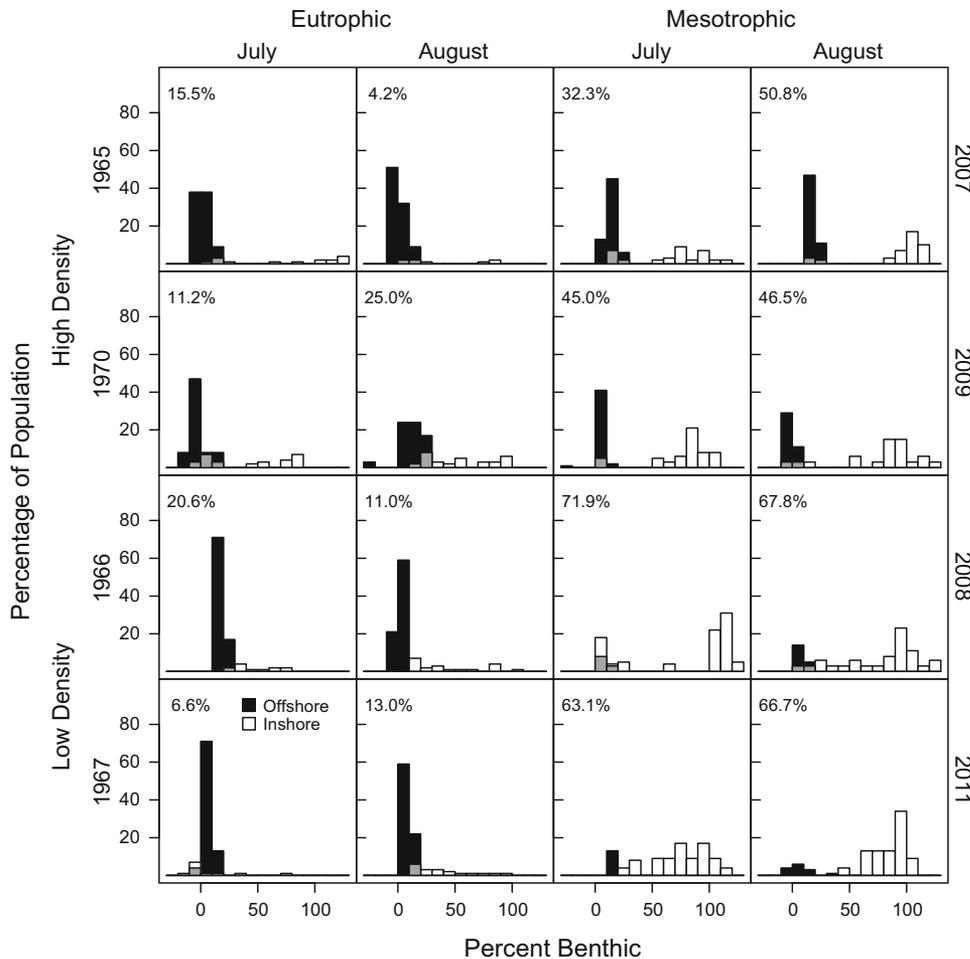


Figure 5. Percent benthic reliance of inshore and offshore age-0 yellow perch. Histogram of benthic reliance for age-0 yellow perch presented as a percentage of the total population for inshore and offshore habitats by month and year. Measured benthic reliance of individual age-0 yellow perch is scaled based on the observed densities in each habitat and the assumption that inshore habitats occupy 43% of total lake surface area ($\alpha_{in} = 0.43$). Total population-level benthic reliance presented in the upper left of each month/year combination. Gray bars indicate overlap in percent benthic reliance across offshore and inshore habitats.

however, found no evidence of bidirectional movement between inshore and offshore habitats, because every offshore yellow perch collected had a strong pelagic carbon signature. The most likely interpretation is that offshore fish do migrate into inshore habitats and stay there. Therefore, based on agreement between diet data and carbon isotopes, we conclude nearly all age-0 yellow perch are specializing on either benthic or pelagic energy pathways during summer and only a small subset of the population switch from offshore to inshore habitats. Interestingly, a previous stable isotope study conducted on Oneida Lake observed a similar range of $\delta^{13}\text{C}$ ratios in adult yellow perch (-29.80 to -23.01), suggesting decoupling of pelagic and benthic energy pathways is maintained at later life stages (Bowman 2005).

In Oneida Lake, the effect of total population density on benthic reliance of individuals in inshore and offshore habitats was minimal compared to its effect on the distribution of age-0 yellow perch across habitats. We suspect the weak relationship between density and benthic-pelagic

divergence is driven by the fact that these metrics do not take into consideration how total population density influences the distribution of yellow perch across inshore and offshore habitats. In species where specialization occurs in all years, understanding population density effects on individual specialization requires knowledge of the relative abundance of each specialist type. At low densities, a larger proportion of individuals within the population occupied inshore habitats, elevating the importance of benthic energy pathways (Table S1; Figure 5). At high densities, more individuals within the population occupied offshore habitats, elevating the importance of pelagic energy pathways (Table S1; Figure 5). By incorporating density, the patterns observed for age-0 yellow perch follow theoretical predictions about interactions between individual specialization and density (Svanbäck and Persson 2009), especially during mesotrophic conditions. These results suggest that benthic specialization in inshore habitats is likely the most optimal foraging strategy to balance growth and predation risk, but pelagic

specialization dominates at high total population densities due to stronger intraspecific competition in inshore and offshore habitats, as evidenced by density-dependent growth rates and a reduction in predation risk in offshore habitats (Irwin and others 2009). Interestingly, switching from pelagic to benthic specialization is most common at low densities (Figure 4), and is likely due to a combination of less exploitative and interference competition between conspecifics (Post and others 1997; Svanbäck and Persson 2009).

Ecosystem state had a strong effect on the extent of separation between benthic and pelagic energy pathways leading up to age-0 yellow perch, and was driven by increased benthic reliance in inshore habitats during mesotrophic conditions. We suspect this was primarily driven by shifts in fish behavior, such as foraging and habitat selection, that take advantage of increased benthic productivity in inshore habitats (Zhu and others 2006; Mayer and others in press). During eutrophic conditions, $\delta^{13}\text{C}$ ratios of inshore age-0 yellow perch consistently spanned across the entire carbon continuum as fish foraged on both benthic invertebrates and zooplankton (Table S1; Figure 3), and/or continuously moved from offshore to inshore habitats (Figure 4). In contrast, during mesotrophic conditions, inshore age-0 yellow perch foraging was dominated by benthic invertebrates (Table S1; Figure 3), and inshore age-0 yellow perch $\delta^{13}\text{C}$ values appeared more clustered near benthic end-members in most years, but not all (Figure 4). Though increased interspecific competition due to changes in the Oneida Lake fish community may have influenced these patterns, we suspect the effect is weak as age-0 yellow perch growth rates have increased over time (Irwin and others 2009). Previous research has failed to document strong competitive interactions between age-0 yellow perch and other fish in the lake (Hall and Rudstam 1999), including detailed studies of competitive interactions between age-0 white perch (*Morone americana*; Prout and others 1990) and age-0 gizzard shad (*Dorosoma cepedianum*; Roseman and others 1996).

Preservation differences between time periods may contribute to differences observed across ecosystems states, but we suspect the effect is minimal and does not influence our conclusions for several reasons. First, literature estimates of preservation effects on end-members and fish carbon isotopic signature shifts are within the same range and in a consistent direction toward more negative (Sarakinis and others 2002; Rennie and others 2012). Second, the scale of estimated carbon isotopic shifts (0.5–1.0 parts per thousand) is relatively small

compared to the separation of pelagic and benthic end-member signatures observed in this study (6.94 parts per thousand). Third, age-0 yellow perch $\delta^{13}\text{C}$ ratios span up to but rarely past end-member $\delta^{13}\text{C}$ ratios, suggesting similar effects of formaldehyde on fish and invertebrates $\delta^{13}\text{C}$ ratios.

Use of Multiple Energy Pathways

Variation in the distribution and degree of specialization across habitats changes how species interact with their environment, ultimately driving which energy pathways support production at higher trophic levels. Benthic reliance of age-0 yellow perch illustrates this point and demonstrates that energy pathways supporting production of consumers can vary on both short- and long-term time scales (Carpenter and Turner 2001). Over the long-term, ecosystem state dictates the magnitude of different energy pathways available to consumers (that is, lake trophic status and the presence/absence of zebra mussels). At shorter time scales, patterns of habitat use change based on abundance, altering the relative importance of different energy pathways to consumers.

In Oneida Lake, eutrophic conditions drove increased importance of pelagic energy pathways for age-0 yellow perch and reduced differentiation between inshore and offshore habitats. During mesotrophic conditions, higher light penetration and concomitant increases in benthic primary production accentuated the importance of benthic energy pathways to age-0 yellow perch production (Table S1; Figure 5). In both time periods, variation in yellow perch population density drove inter-annual variability in the energy pathways supporting production (as reflected by carbon isotopes). This density effect on population-level carbon pathway use was largely driven by the relationship between perch density and habitat use. At high densities, a greater proportion of the population used offshore habitats, and benthic reliance of the whole population decreased. Conversely, at low densities, age-0 yellow perch used inshore habitats, increasing the population-level reliance on benthic energy pathways. Though important in both time periods, density has a stronger effect on population-level benthic reliance during mesotrophic conditions (Figures 6, 7). We propose that ecosystem state defines the range of benthic support of fish populations, while population density determines where along the potential range a fish population will occur during a specific year.

In our analyses, we explored effects of ecosystem state and density under two scenarios of habitat

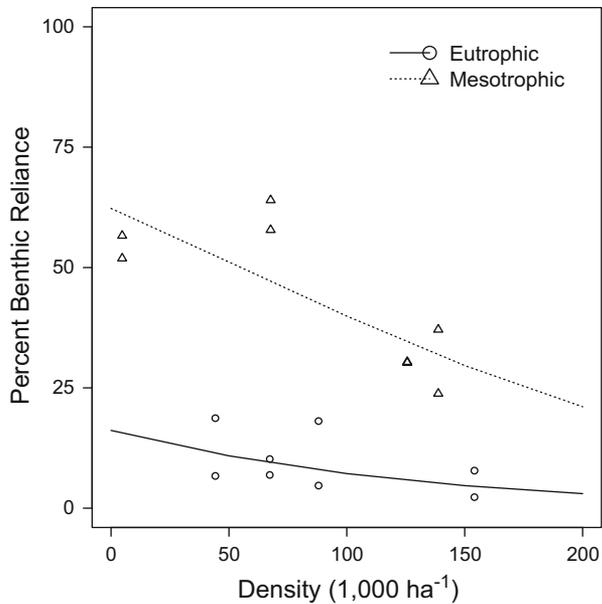


Figure 6. Effect of density and ecosystem state on percent benthic reliance. Relationships based on best fitting, most parsimonious model with time period and density as predictors under the scenario where $\alpha_{in} = 0.25$.

distributions ($\alpha_{in} = 0.25$ and 0.43 ; Fitzgerald and others in press), and assumed that distributions did not change over time. This assumption leads to conservative estimates of the effect of environmental conditions on the importance of different energy pathways to age-0 yellow perch production. In Oneida Lake, increases in water clarity led to an expansion of the littoral zone (inshore) from 25 to 43% of lake surface area as the photic zone expanded to include more benthic surface area (Fitzgerald and others in press). Under this assumption, age-0 yellow perch benthic reliance increased from approximately 2–20% (eutrophic) to 30–70% (mesotrophic), with lower reliance associated with higher densities (Table S1; Figure 7). Failure to incorporate information on density and resource use from both offshore and inshore habitats would have either led us to overestimate age-0 yellow perch benthic reliance (Figure 7 inshore-only) or inaccurately conclude that benthic energy reliance did not shift with changing ecological conditions (Figure 7 offshore-only).

These results represent a step forward toward understanding short- and long-term drivers of en-

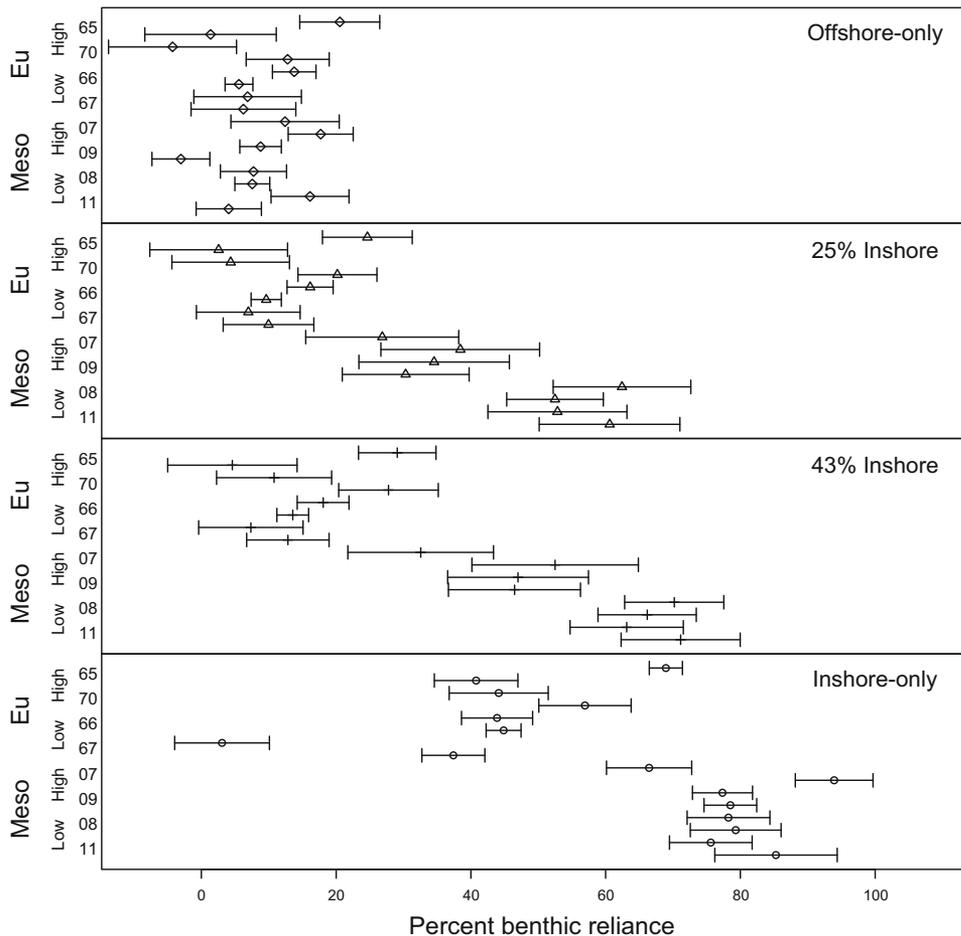


Figure 7. Uncertainty of percent benthic reliance estimates across habitat distribution scenarios. Population-level benthic reliance of age-0 yellow perch obtained from variance propagation procedure presented across scenarios of inshore and offshore habitat availability ($\alpha_{in} = 0.25$ and 0.43). Offshore-only and Inshore-only represent population-level benthic reliance estimates if age-0 yellow perch samples were only collected in those habitats, respectively.

ergy pathways supporting consumer production (Weidel and others 2008), and shed light on underlying mechanisms of inconsistent and mixed responses of higher trophic levels (that is, fish foraging, population, and community dynamics) to introductions of dreissenid mussels (Higgins and Vander Zanden 2010). Much previous research on these topics has assumed fish are mobile, utilize multiple habitats, and integrate both benthic and pelagic production and, therefore, that lake wide changes could be evaluated by monitoring a single habitat. Though this may be true for some species, our results provide additional evidence that individuals often specialize on only a subset of available resources or energy pathways (see also Bolnick and others 2003). Within these populations, individuals may show inconsistent or even contradictory responses to ecological perturbations, making it difficult to make accurate conclusions about population-level responses to perturbations without information from multiple habitats.

Niche Diversity and Resilience

Across species and systems, the ability of a population to adapt or change their behavior in response to changes in habitat and resource distributions is likely context dependent (Agrawal and others 2007), and may explain inconsistencies of species responses to ecosystem changes across diverse systems (Higgins and Vander Zanden 2010). To address these inconsistencies and aid our understanding of ecological response to perturbations, further appreciation of the effect of individual decisions on consumer-resource dynamics is needed. In particular, the ability of individuals and populations to adapt their behavior to changing ecological conditions, and the importance of a multiple habitat approach to studying ecological dynamics should be considered. Populations able to utilize multiple habitats (for example, inshore and offshore) and energy pathways (for example, benthic and pelagic) are likely to be more resilient to ecosystem perturbations (for example, portfolio effect; Schindler and others 2010). For instance, in Oneida Lake, yellow perch densities in offshore habitats have decreased across all age-0 life stages; however, age-1 densities have not decreased (Irwin and others 2009). We suspect the increasing importance of inshore habitats to age-0 yellow perch, illustrated here, is an important factor contributing to recruitment stability observed at age-1 (Fitzgerald and others 2006). Conversely, habitat and resource specialists are likely to be either positively or negatively impacted by ecological

perturbations, depending on the specific habitat they occupy, because they exhibit less plasticity in resource use under different ecological conditions.

The physical characteristics of a specific ecosystem should also influence the resiliency of a population to ecosystem perturbations. For instance, populations that occur in very shallow or deep lakes are unlikely to show as much resilience to ecosystem changes that cause declines in one habitat type because habitats will tend to be homogenous in lakes with these types of bathymetry. However, generalist populations should be more resilient in intermediate lakes that are not dominated by one habitat, because reduced profitability of one habitat can be compensated by increased profitability of another habitat, as was observed in Oneida Lake. Therefore, not surprisingly, a higher diversity of resource use by a population should increase resiliency to ecosystem changes. Conservation objectives should be established to maintain the diversity of individual specialist and resource use strategies within populations to allow adaptation to changing ecological conditions.

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