

# Spatio-temporal, ontogenetic and interindividual variation of age-0 diets in a population of yellow perch

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**Abstract** – Dietary niches of fishes have traditionally been evaluated at the population level, with diet pattern central tendencies compared spatio-temporally among habitats and populations. More recently, however, studies have emphasised the importance of within-population diet variation and niche partitioning. Several studies have examined diets of young yellow perch (*Perca flavescens*) at the population level and have described an ontogenetic transition from zooplankton to benthic prey during the first year of life. However, independent of ontogenetic diet shifts, intrapopulation variation of young yellow perch diets remains largely unexplored. We quantified patterns of diet composition in age-0 yellow perch collected from Saginaw Bay, Lake Huron, USA during July–October, 2009 and 2010. We observed substantial variation in diet composition among individuals across and within sites, but found relatively weak evidence indicating an ontogenetic diet shift. Zooplankton were the dominant prey for age-0 yellow perch on most occasions, and individual diets were composed primarily of either zooplankton (e.g. *Daphnia* spp., Calanoida) or benthic (i.e. Chironomidae larvae, Chydoridae) prey. These patterns were not simply attributable to differences in prey availability and ontogenetic diet shifts, because a) not only diet composition, but also prey selectivity (Chesson's  $\alpha$ ) varied among sites and b) individual and spatial diet differences were evident independent of ontogeny. Within-cohort differences in diet composition may be an important, but often overlooked, phenomenon with implications for cumulative trophic interactions and intracohort growth and survival among young fish.

**Key words:** perch; ontogenetic shift; niche; diet selection; specialization

## Introduction

Knowledge of the trophic niches of fishes is key to understanding energy pathways in aquatic ecosystems (Lindeman 1942; Carpenter et al. 1987), and can inform fisheries management (e.g. Pauly et al. 1998) and elucidate consequences of ecosystem stressors (e.g. Madenjian et al. 2010). Thus, foraging habits of many fishes have been studied extensively, with a focus on describing population-level and ecosystem-specific diet niches (e.g. Forney 1974; Sampson et al. 2009; Specziár & Rezsú 2009). Within-population niche partitioning or individual specialisation, how-

ever, is an often overlooked aspect of foraging ecology (Bolnick et al. 2003; Bolnick 2004). In large aquatic ecosystems, trophic niches are often generalised at the species (e.g. Madenjian et al. 2002) or age-class (e.g. Schaeffer et al. 2000) level and within-species diet differences, their causes, and implications are often ignored. In particular, within-cohort diet differences of fish during early-life stages have rarely been quantified (but see Post et al. 1997; Grey 2001). Such differences may be important as intrapopulation variation in foraging patterns may affect trophic interactions (Quevedo et al. 2009) and contribute to differential growth and survival among young fish.

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Rapid growth of fish during early life is often vital for survival to later-life stages (Miller et al. 1988; Post & Evans 1989). Predation pressure (e.g. Fitzgerald et al. 2006) and starvation (Hurst 2007) can be important causes of mortality, but usually decrease with size of young fish (Sogard 1997; Lundvall et al. 1999). Thus, young fish tend to select prey that maximise net energetic gains (e.g. Graeb et al. 2006) based upon factors such as energy content, handling time (Schoener 1971) and prey availability (e.g. Roberts et al. 2009). Prey types that optimise growth of young fish may change through ontogeny as foraging efficiency and the ability to ingest larger prey increases with fish size (Graeb et al. 2006); hence, many young fish undergo ontogenetic transitions in prey consumed. Moreover, behaviours to minimise predation risk may affect diets of young fish via differences in prey availability among habitats and increased competition in areas with low predation risk (Diehl & Eklöv 1995). Shifts in habitat occupancy and diets through ontogeny characterise early-life stages of many fish (Werner & Gilliam 1984; Olson 1996) and may be a mechanism to maximise growth while minimising mortality risks (e.g. Werner et al. 1983).

During ontogeny, diets of yellow perch (*Perca flavescens*), an omnivorous eurythermal fish species, often transition from zooplankton to benthic invertebrates to fish (Graeb et al. 2006). This change in prey consumption has been postulated to reflect a trade-off between predation risks and energetic gains (Post & McQueen 1988). However, diets and diet shifts of young perch are variable across systems and among years, and environmental conditions and prey availability may strongly influence yellow perch diets and ontogenetic transitions (Post & McQueen 1994; Roseman et al. 1995). For example, several studies (e.g. Mills & Forney 1981; Wu & Culver 1992) have demonstrated a shift by yellow perch from planktonic to benthic prey (e.g. Chironomidae larvae) that coincides with seasonal declines of *Daphnia* spp. (hereafter *Daphnia*). Yet, despite the importance of early-life prey consumption, important aspects of age-0 yellow perch diet patterns and prey selection remain relatively unexplored, and with the exception of ontogenetic effects, interindividual variation is rarely included in studies of age-0 yellow perch feeding dynamics.

Yellow perch comprise an important fishery and a large component of the fish community in inner Saginaw Bay (Fielder & Thomas 2006), a shallow, productive ecosystem in Lake Huron, North America (Nalepa et al. 1996). Various environmental conditions that could potentially influence prey consumption by young yellow perch have recently changed in Saginaw Bay. Increased production of age-0 yellow

perch since 2003 has been linked with a drastic decline in abundances of exotic alewife throughout Lake Huron, including Saginaw Bay (Fielder & Thomas 2006; Fielder et al. 2007; Ivan et al. 2011). Other exotic species, such as benthivorous round goby (*Neogobius melanostomus*), *Bythotrephes longimanus* and *Dreissena* spp. mussels, are currently abundant in inner Saginaw Bay (S.A. Pothoven & T.O. Höök, unpublished data) and may influence foraging behaviour of yellow perch. Current poor survival by young Saginaw Bay yellow perch has led to poor recruitment success (Fielder & Thomas 2006) and may be related to low growth rates during early life (Ivan et al. 2011; Roswell 2011), suggesting diets of age-0 yellow perch may play a role in population dynamics.

The objectives of this study were to evaluate: (i) spatial, temporal and ontogenetic variation in prey composition of age-0 yellow perch in inner Saginaw Bay, (ii) the role of individual diet specialisation in contributing to population-level diet patterns and (iii) the role of prey availability in determining prey composition and selection. Because *Daphnia* and Chironomidae larvae are preferred prey of yellow perch in other systems, we predicted yellow perch diet composition would change concurrent with changes in availability of these prey in the environment. Moreover, given anticipated diet transitions, we hypothesised that temporal (ontogenetic) diet variation would exceed spatial and among-individual diet variation.

## Methods

We collected zooplankton, macroinvertebrates and age-0 yellow perch approximately monthly (July–October) at four stations in inner Saginaw Bay, Lake Huron during 2009 and 2010 (Fig. 1). Sites were selected to provide overlap with locations of historical (e.g. Nalepa et al. 1996) and concurrent sampling conducted by other researchers as part of a larger study. To index available planktonic prey for young yellow perch, on each sampling occasion, we collected zooplankton with duplicate vertical tows of a plankton net (64- $\mu\text{m}$  mesh net, 0.3 m opening, towed through entire water column at 0.5  $\text{m}\cdot\text{s}^{-1}$ ). We preserved zooplankton samples with 10% sugar-buffered formalin following anaesthesia with bicarbonate. In the laboratory, we subsampled zooplankton samples using a Hensen–Stempel pipette and identified and counted a minimum of 600 individual organisms per sample. All predatory zooplankton (*B. longimanus* and *Leptodora kindtii*) collected in each tow were counted, except in cases when numbers were exceedingly high, in which case we split samples one to three times before counting. We calculated densities on a volumetric ( $\text{no}\cdot\text{m}^{-3}$ ) and areal ( $\text{no}\cdot\text{m}^{-2}$ ,

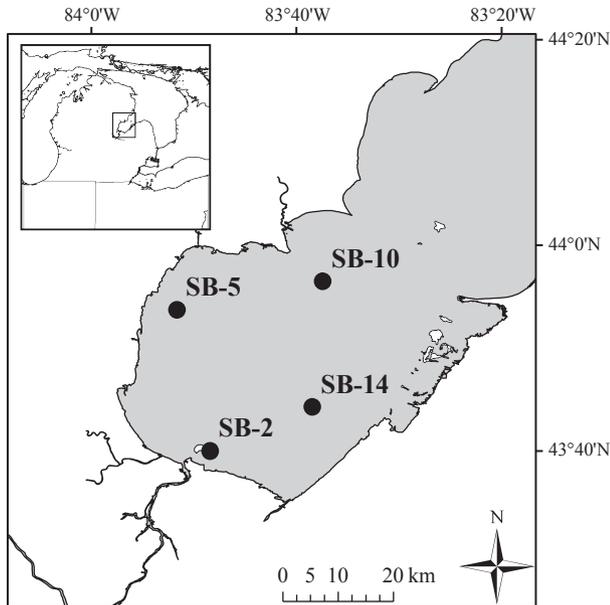


Fig. 1. Location of Saginaw Bay, Lake Huron and sampling locations for this study.

calculated by multiplying volumetric density by depth) basis.

On each sampling occasion, we collected macroinvertebrates with duplicate sediment grabs with a standard Ponar dredge (0.052 m<sup>2</sup>, 500 µm mesh). We concentrated samples through a 500-µm mesh screen and preserved them with 10% formalin, with Rose Bengal. In the laboratory, we examined preserved benthic samples in a tray under magnification (1.5×) and removed, identified and enumerated all animals in a sample. We did not enumerate individual Oligochaeta because these animals broke apart into small pieces in our samples; because this prey type is rarely

consumed by yellow perch, we felt justified in excluding these counts.

We collected fish with a 7.6-m semi-balloon bottom trawl with a 13-mm stretched-mesh cod-end, which was towed for 10 min at approximately 1.29 m·s<sup>-1</sup> (1- to 5- trawl tows per site-date). We collected age-0 yellow perch at each of our sites four times between day 188 (July 7) and day 279 (October 6) in 2009 and three times between day 187 (July 6) and day 266 (September 23) in 2010. During each sampling event, all sites were sampled within a 3-day period, and to facilitate time-specific comparisons across sites, we represent sampling as the mean sampling date for a given week. We sorted fish by species, stored specimens on ice and after arrival on shore, we stored fish at -20 °C. In the laboratory, we enumerated age-0 yellow perch and measured total lengths of up to 30 fish per trawl. We randomly selected up to 20 fish for diet analysis from samples collected each month at each site. When multiple trawls were conducted at a site, we divided these 20 fish among trawls based on the proportion each trawl contributed to the total catch at that site. We analysed diets from at least three fish (when available) from each trawl. Thus, when some trawl samples constituted small proportions of total catch for a site-date combination, we analysed diets of more than 20 fish. In total, we analysed diets of 526 age-0 yellow perch, which spanned a broad range of sizes (31–101 mm total length, 0.2–12.1 g wet weight).

We removed stomach contents from yellow perch and replaced empty stomachs in the fish. Then, we quantified wet and dry (after drying for 48–72 h. at 70 °C) mass of individual fish. We identified and enumerated stomach contents under a dissecting

Table 1. Prey categories of age-0 yellow perch diets and per cent of diet (by counts and dry biomass) comprised of each category.

Taxonomic group	Per cent by counts	Per cent by biomass
Calanoid	23.8	23.5
Calanoida*		
Chydoridae	8.6	6.6
Chydoridae*		
<i>Daphnia</i>	37.4	33.5
<i>Daphnia</i> spp.*		
Predatory Zooplankton	3.1	9.4
<i>Bythotrephes</i> spp.*, <i>Leptodora</i> spp.*		
Other zooplankton	16.2	7.2
Cyclopoida*, Cladocera (excl. <i>Daphnia</i> and predatory zooplankton)*†, <i>Dreissena</i> spp. veligers*, Copepod nauplii†		
Chironomidae larvae	7.7	11.8
Chironomidae larvae*		
Other	3.1	8.1
Amphipoda*, <i>Chironomidae pupae</i> *, <i>Dreissena</i> spp. Adults*, Harpacticoida*, <i>Hemimysis</i> spp.†, Hydracarina†, Insects (excl. Chironomidae)*, Isopoda*, Larval fish*, Nematoda*, Oligochaeta*, Ostracoda†, Sphaeriidae*		

\*Mass estimated with length-mass regressions (Dumont et al. 1975; Smock 1980; Culver et al. 1985; Soetaert et al. 2009, Sprung 1993; Pepin 1995; Rahkola et al. 1998, Benke et al. 1999; Lemke & Benke 2004; Conroy et al. 2005).

†Mass estimated with published values for mean dry mass (Hawkins & Evans 1979; Nalepa & Quigley 1980; Meyer 1994; Stockwell & Johannsson 1997).

microscope equipped with a digital camera and image analysis software (Image J). We counted whole organisms and partial organisms with heads attached and measured lengths of whole organisms. Depending on prey type, we used published length-mass regressions or published dry mass means to estimate biomass of prey (Table 1). Based on the calculated dry mass of prey, we estimated the proportion each prey type contributed to total diet biomass for each fish. Then, we multiplied the estimated proportions by measured total diet dry mass to estimate total mass of each prey type in diets of each fish.

### Data analyses

To facilitate diet analyses, we grouped prey items into seven categories (Table 1). We included common prey items (i.e. *Daphnia*, calanoid copepods, epibenthic Chydoridae, Chironomidae larvae and large, predatory zooplankton [i.e. *B. longimanus* and *L. kindtii*]) as five of the categories. We grouped other zooplankton taxa (e.g. cyclopoid copepods, *Bosmina*) into one category and combined other benthic macroinvertebrates (aside from Chironomidae larvae) and rare prey items (i.e. found in <5 fish) into a category labelled 'Other.' We used a two-factor MANCOVA to evaluate the association among the diet biomass of seven prey categories (response variables) and explanatory variables: site and date (factors), and total length of individual yellow perch (covariate). In addition, based upon the seven diet item categories (Table 1), we used nonmetric multidimensional scaling (NMDS) to ordinate spatio-temporal (site and sampling date) patterns of overall diet biomass composition. NMDS is a dimension-reducing technique that uses the orders of distances of observations (we used Euclidean distance) and is not bound by the assumption of normality required for many other multivariate methods.

We evaluated diet specialisation on the seven prey categories by comparing the prey biomass consumed by individual perch with: (i) the prey consumed by all age-0 yellow perch collected at the same site and date and (ii) the prey consumed by all age-0 yellow perch evaluated for this study (i.e. across sites, dates, and years). To this end, we first quantified an index of proportional similarity (Feinsinger et al. 1981):

$$PS_i = 1 - 0.5 \sum_j |p_{ij} - q_j| \quad (1)$$

where  $p_{ij}$  is the proportion of prey type  $j$  in the diet of individual  $i$ , and  $q_j$  is the proportion of prey type  $j$  in the population of diets (either all fish from the same site and date, or all from the study). Although this metric was developed to evaluate niche breadth, it can also be used to index individual specialisation

(IS; Bolnick et al. 2002). The site- and date-specific mean PS value represents the IS value for each site ( $k$ ) and date ( $l$ ):

$$IS_{k,l} = \frac{1}{N} \sum PS_i \quad (2)$$

Values of IS range from near 0 to 1, with values closer to 0 indicating specialisation and values closer to 1 indicating similar diets across the population (no specialisation; Bolnick et al. 2002). Again, we quantified two IS values for each site-date combination, (i) based on comparison among diets from the specific site and date ( $IS_s$ ) and (ii) based on comparison with diets across all sites and dates ( $IS_a$ ). To evaluate differences in specialisation within sites and dates, we used a two-way ANOVA and Tukey's HSD *post hoc* test to compare mean  $IS_s$  values (arcsine square root transformed for normality) across sites and times. We compared mean  $IS_a$  values for each site across dates to determine the contribution of spatial differences to individual niche partitioning.

Finally, to evaluate the influence of prey availability on diets of age-0 yellow perch we a) calculated selectivity indices and b) related proportional diet biomass and selection of primary prey (*Daphnia* and Chironomidae larvae) to availability of prey. We quantified site- and time-specific selectivity indices,  $\alpha$  (Chesson 1983), as

$$\alpha = \frac{r_i/p_i}{\sum_i r_i/p_i} \quad (3)$$

where  $r_i$  is the proportion of prey type  $i$  in diets (by count), and  $p_i$  is the proportion of prey type  $i$  in the environment (based on areal density). Chesson's  $\alpha$  ranges from 0 to 1, with larger values indicating a prey item is more preferred. Using ANCOVA, we related proportional composition and selection ( $\alpha$ ) of *Daphnia* and Chironomidae larvae (arcsine square root transformed values) to site (as a factor) and density estimates of these prey items (as a covariate). We used SPSS 19 (SPSS Inc., Chicago, IL, USA) for all statistical analyses, except NMDS, for which we used SAS 9.2 (SAS Institute Inc., Cary, NC, USA).

### Results

Across a wide range of prey abundances and environmental conditions, age-0 yellow perch in Saginaw Bay exhibited gradual, inconsistent shifts in prey consumption through ontogeny. However, substantial spatial variation and specialisation were evident. Specifically, individual yellow perch tended to target either zooplankton (e.g. *Daphnia*) or benthic (e.g. Chironomidae larvae) prey, and these patterns of consumption were

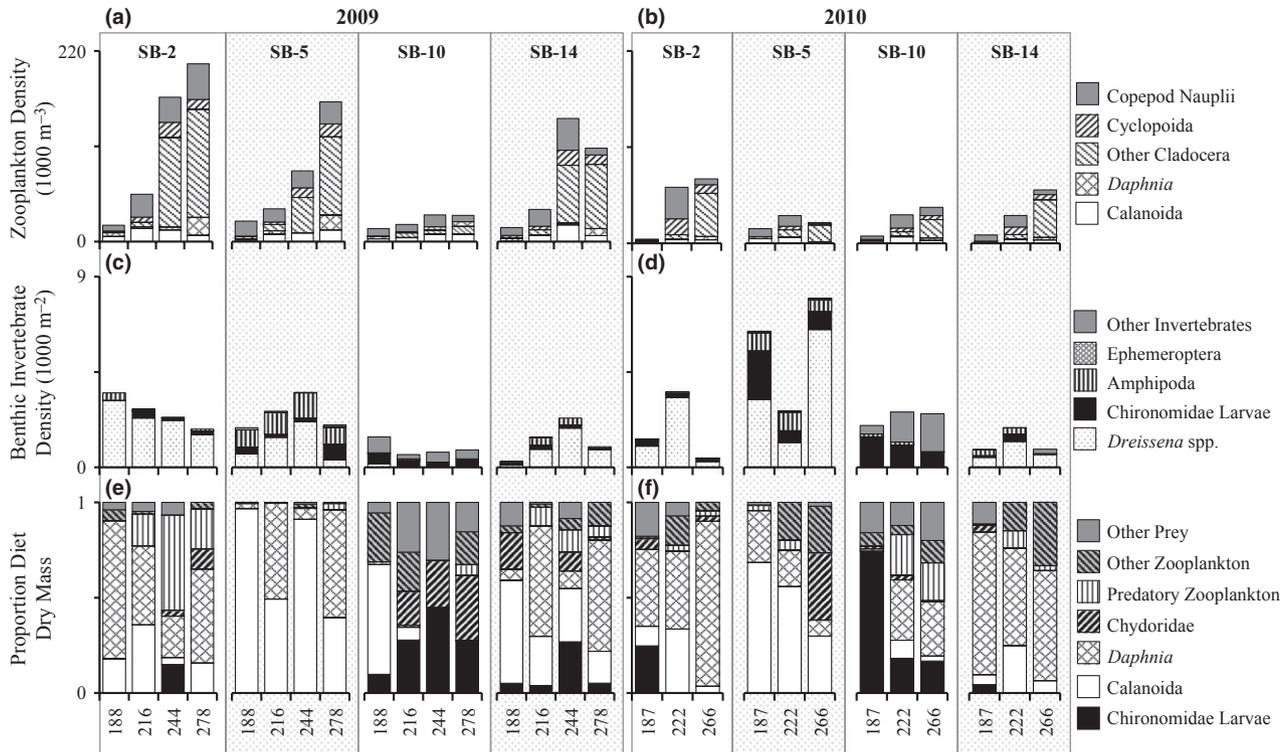


Fig. 2. Monthly (day of year displayed) mean volumetric densities of crustacean zooplankton estimated from vertical tows with a zooplankton net (a, b), monthly mean benthic invertebrate densities estimated from Ponar samples (c, d) and mean monthly proportional composition of age-0 yellow perch diets by biomass of diet types, plotted by site during 2009 and 2010. 'Other Cladocera' (a, b) include *Bosmina* and other relatively small Cladocera; and 'other invertebrates' (c, d) include Chironomidae pupae, Gastropoda, Hirudinea, Isopoda, Sphaeriidae, Trichoptera and Turbellaria. For details on prey categories (e, f) see Table 1.

related to the availability of prey items at specific sites and site-specific selectivity preferences.

Densities of potential yellow perch prey varied over time and across sites (Fig. 2a–d). High intra- and interannual variation in total crustacean zooplankton abundance and zooplankton community composition was evident from monthly zooplankton tows. Composition of the zooplankton community also varied within and between years. Densities of crustacean zooplankton, especially *Bosmina* (included as 'other Cladocera' in Fig. 2a,b), increased from summer to fall, leading to peak total abundances in the fall (particularly apparent during 2009). Numerically, large-bodied cladocerans such as *Daphnia* were never proportionally abundant; however, unlike some other ecosystems, *Daphnia* never declined to zero abundance in Saginaw Bay.

Amphipoda, Chironomidae larvae and *Dreissena* spp. (primarily *Dreissena bugensis*) were dominant components of macroinvertebrate communities at our study sites (Fig. 2c,d). Unlike zooplankton, site-specific densities and composition of benthic macroinvertebrates changed little within years. However, total benthic macroinvertebrate densities, especially Chironomidae larvae densities, were somewhat higher in 2010 than in 2009. Moreover, we

observed consistent differences in composition of the benthic invertebrate community across sites. For example, while *Dreissena* spp. were consistently present at most sites, they were usually rare or absent at SB-10.

Yellow perch catch per unit effort (CPUE; number caught per minute of trawling) varied by more than two orders of magnitude across sites and dates, and mean sizes of age-0 yellow perch generally increased for each cohort as the year progressed (Table 2). Age-0 yellow perch diet composition (by dry biomass) was highly variable across sites and among months and years (Fig. 2e,f). Large numbers of *Daphnia* were present in diets at most sites during most dates, and this prey category comprised the largest portion of overall diet dry mass (33.5%, Table 1). Calanoid copepods and other zooplankton were also important prey at many sites, and Chironomidae larvae were important on a few occasions. Predatory zooplankton, Chydoridae and other diet items were present, but contributed less to overall diet biomass (Table 1). After accounting for the effect of total length (MANCOVA: Pillai's Trace = 0.27,  $F_{7, 489} = 26.14$ ,  $P < 0.01$ ), diet composition was significantly related to sampling date (MANCOVA: Pillai's Trace = 0.63,  $F_{42, 2964} = 8.32$ ,  $P < 0.01$ ) and site

Table 2. Site characteristics and date-specific CPUE (catch per unit of effort; number per minute trawling) and mean ( $\pm$  SD) total length (mm) of yellow perch captured at each site.

Site	Depth (m)	Substrate*	Year	Day of Year	Age-0 yellow perch CPUE (#/min.)	Age-0 yellow perch mean ( $\pm$ SD) total length (mm)
SB-2	3.9	Rocky/large cobble	2009	188	9.9	39.4 $\pm$ 3.7
				216	38.6	60.6 $\pm$ 4.3
				244	21.8	75.6 $\pm$ 7.8
			2010	278	1.7	75.5 $\pm$ 5.4
				187	13.4	49.5 $\pm$ 4.5
				222	41.7	65.0 $\pm$ 3.8
				266	37.9	77.8 $\pm$ 6.8
SB-5	3.6	Small cobble/ gravel/sand	2009	188	36.4	39.2 $\pm$ 2.6
				216	71.9	54.5 $\pm$ 4.0
				244	30.3	64.8 $\pm$ 4.9
			2010	278	75.7	70.8 $\pm$ 4.5
				187	62.5	45.8 $\pm$ 3.7
				222	17.2	60.8 $\pm$ 4.2
				266	3.3	75.7 $\pm$ 4.5
SB-10	12.2	Silt/muck	2009	188	7.9	38.1 $\pm$ 3.2
				216	5.9	61.0 $\pm$ 5.0
				244	10.8	71.4 $\pm$ 6.5
			2010	278	2.5	78.1 $\pm$ 7.6
				187	2.5	51.5 $\pm$ 2.9
				222	42.9	73.9 $\pm$ 5.7
				266	14.0	84.5 $\pm$ 7.0
SB-14	3.8	Sand	2009	188	20.4	38.1 $\pm$ 3.9
				216	141.0	59.2 $\pm$ 4.6
				244	21.4	69.5 $\pm$ 5.1
			2010	278	1.4	76.9 $\pm$ 5.0
				187	75.4	47.2 $\pm$ 3.8
				222	10.2	63.3 $\pm$ 3.8
				266	0.8	80.0 $\pm$ 4.0

\*Substrate was visually categorised from contents of Ponar samples.

(MANCOVA: Pillai's Trace = 0.68,  $F_{21, 1473} = 20.70$ ,  $P < 0.01$ ), as well as the interaction between date and site (MANCOVA: Pillai's Trace = 1.14,  $F_{126, 3465} = 5.37$ ,  $P < 0.01$ ).

The NMDS model resulted in two axes and a stress of 0.09 (Fig. 3). Axis 1 was negatively correlated (Spearman's rank correlation coefficient,  $\rho$ ) with diet mass of *Daphnia* ( $\rho = -0.97$ ,  $P < 0.01$ ) and predatory zooplankton ( $\rho = -0.49$ ,  $P < 0.01$ ) and positively correlated with the 'other prey' category ( $\rho = +0.57$ ,  $P < 0.01$ ), Chironomidae larvae ( $\rho = +0.47$ ,  $P < 0.05$ ), and Chydoridae ( $\rho = +0.39$ ,  $P < 0.05$ ). Axis 2 was positively correlated with Calanoida ( $\rho = +0.82$ ,  $P < 0.01$ ) and negatively correlated with Chironomidae larvae ( $\rho = -0.63$ ,  $P < 0.01$ ), the 'other prey' category ( $\rho = -0.49$ ,  $P < 0.01$ ), Chydoridae ( $\rho = -0.47$ ,  $P < 0.05$ ) and predatory zooplankton ( $\rho = -0.39$ ,  $P < 0.05$ ). Thus, variation along axis 1 generally represents a contrast between high diet biomass of *Daphnia* and predatory zooplankton (low values) and high diet biomass of nonzooplankton prey (high values), while variation along axis 2 indicates relative diet biomass of calanoid copepods (high values). Diet composition consistently differed among some sites, and diet com-

position at SB-10 and SB-5 was most distinct. Few consistent temporal trends were observed, although spatial differences were more apparent during fall (Days 244, 266, and 278) than during summer.

We did not observe a sharp, size-related ontogenetic shift in prey importance from zooplankton to benthic prey during 2009 and 2010 (Fig. 4a,b). While larger age-0 yellow perch tended to eat more benthic macroinvertebrates than smaller individuals, benthic organisms (Chironomidae larvae and other clearly benthic taxa) comprised less diet biomass than zooplankton across all lengths. Given the smaller mean size of zooplankton relative to benthic invertebrates, the disparity in consumption of these two diet categories is even more dramatic if one considers the relative number of diet items consumed (146,609 zooplankters, as compared with 2957 benthic organisms). Moreover, greater than half (60.5%) of all yellow perch diets examined contained exclusively zooplankton prey (Fig. 4c,d).

Individual yellow perch rarely simultaneously consumed high levels of zooplankton prey and benthic prey, suggesting a high degree of specialisation was common (Fig. 4c,d). The site at which fish were collected often corresponded to whether diets contained

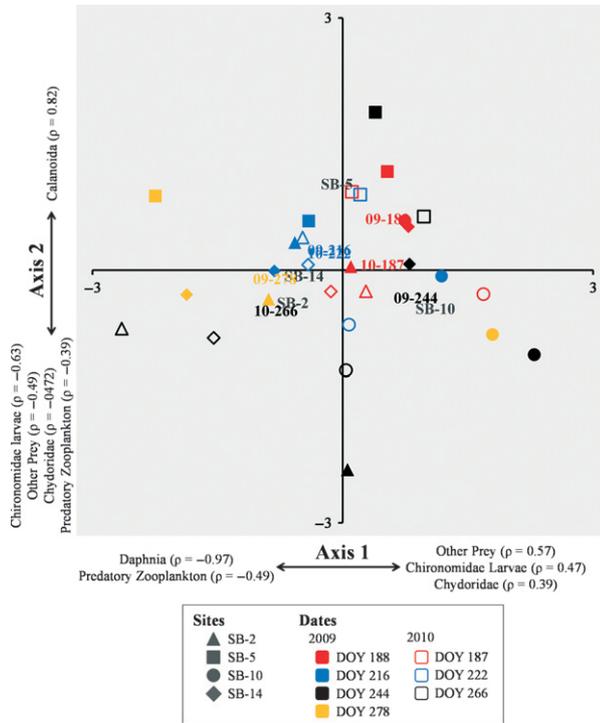


Fig. 3. Nonmetric multidimensional scaling of diet data using diet dry mass of seven prey categories at each combination of site and date. Site and date means are also plotted. Spearman's rank correlations ( $\rho$ ) are shown for prey types significantly correlated with each axis.

zooplankton or nonzooplankton prey; for example, most individuals from SB-5 contained exclusively zooplankton, while most individuals from SB-10 contained nonzooplankton prey. Moreover, we observed substantial variability in individual diet specialisation (Fig. 5). When the diet niche was defined separately for each sampling occasion, the degree of specialisation varied broadly across site and date (Fig. 5a,b), with the largest across-site differences observed in July (day 188) 2009. Results of a two-way ANOVA indicated within-site and date specialisation was significantly related to both site ( $F_{3, 498} = 66.28, P < 0.01$ ) and date ( $F_{6, 498} = 2.70, P = 0.01$ ).  $IS_s$  values were significantly higher at SB-5 and significantly lower at SB-10 than at other sites (Tukey's HSD *post hoc* test). Thus, within-site diet composition at SB-5 was most similar among individuals, diets at SB-10 were most specialised (i.e. the mean overlap of SB-10 individuals' diets with all others at SB-10 was low on most dates), and diet overlap was intermediate at SB-2 and SB-14. The only significant difference in  $IS_s$  values among dates was between day 216 (2009) and day 222 (2010; Tukey's HSD *post hoc* test).

Defining niche breadth as the entire diet composition data set from our study led to reduced  $IS$  values ( $IS_a < IS_s$ ; less overlap between individual diets and the broader overall diet niche; Fig. 5c,d). Diets at SB-10 consistently showed the least overlap with the

overall niche breadth on all dates except day 266 in 2010, when SB-5 diets were most dissimilar to diets across all sites. This pattern is reflected in the mean  $IS_a$  values for each site (across seven sampling dates: SB-2 = 0.44, SB-5 = 0.42, SB-10 = 0.28, SB-14 = 0.42).

Selectivity patterns of juvenile yellow perch varied substantially across sites and dates (Fig. 6), and prey abundance therefore was not the sole factor determining diet patterns. Across 28 combinations of site and date, all prey types were positively selected by age-0 perch at least twice. However, *Daphnia* (18 occasions) and Chironomidae larvae (five occasions) were generally the most strongly selected prey items. Calanoid copepods (two occasions), Chydoridae (2) and predatory zooplankton (1) were less frequently the most strongly selected prey. Selectivity indices varied by site, with *Daphnia* being the preferred prey item on the majority of sampling occasions at SB-2, SB-5 and SB-14, and Chironomidae larvae being the preferred prey item during the majority of sampling events at SB-10.

To consider the role of prey densities on prey consumption and selectivity, we focused on proportional composition and selectivity of preferred prey items, *Daphnia* and Chironomidae larvae. Initial analyses failed to reject the assumption of homogeneity of slopes relating prey density and diet proportional composition and selection ( $F_{3, 20}$  range: 0.08–2.40,  $P$  range: 0.10–0.97). While consumption and selection of *Daphnia* and Chironomidae larvae varied by site, these diet patterns were not strongly related to site- and date-specific abundance of *Daphnia* and Chironomidae larvae in the environment independent of site (Fig. 7). That is, across eight separate ANCOVAs selection (Chesson's  $\alpha$ ) and proportion of diet dry mass comprised of *Daphnia* and Chironomidae larvae showed insignificant associations with the environmental abundance of *Daphnia* and Chironomidae larvae ( $F_{1, 23}$  range: 0.07 – 2.93;  $P$  range: 0.10–0.80), while the effect of site was significant ( $F_{3, 23}$  range: 3.56–10.81,  $P$  range: < 0.01–0.03).

## Discussion

Patterns of central tendency (e.g. date-specific means) provide incomplete descriptions of diets of age-0 yellow perch in Saginaw Bay due to consistent spatial differences and individual specialisation. In many systems, young yellow perch sharply transition from zooplanktivory to benthivory during the first year of life (e.g. Wu & Culver 1992). Although time and individual size played a role in diet variation, we did not observe a sharp ontogenetic shift in diet composition and instead documented consistent spatial variation. While some studies have focused on diet

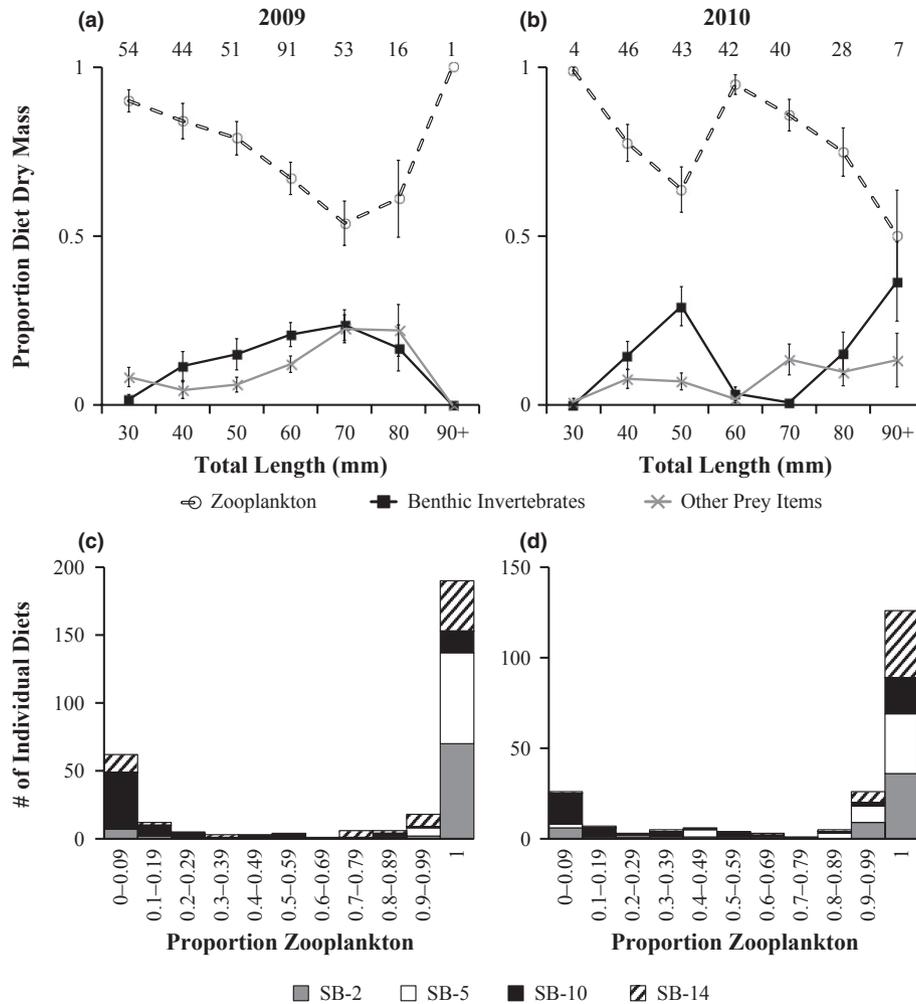


Fig. 4. Panels (a, b): Length-specific proportion ( $\pm$  SE) of yellow perch diet biomass composed of zooplankton, benthic invertebrates, and other prey items (e.g. *Chironomidae* pupae, Chydoridae), by 10 mm total length bins (90 + includes two fish >99 mm in 2010) for 2009 and 2010. Numbers above each bin indicate sample size. Panels c, d: Histogram of proportion zooplankton comprising diet biomass of individual yellow perch (sites stacked) for 2009 and 2010. The bimodal distributions indicate foraging strategies are dominated by foraging on either zooplankton or other prey types, but rarely both.

differences across lakes (e.g. Post & McQueen 1994), spatial variation in diets of young perch within ecosystems has rarely been described. Diet data summarised across multiple sites potentially mask spatial patterns, and specialisation among individuals (within sites) further complicates interpretation of diet patterns. We found that diet composition differed among individuals caught at the same sites and dates (and therefore likely experiencing similar environmental conditions), indicating relationships between mean diet composition and environmental variables may oversimplify the factors structuring foraging patterns of young yellow perch.

As evidenced by this and other studies, patterns of ontogenetic diet shifts by young yellow perch are not consistent across systems. Wu & Culver (1992) found juvenile perch consuming almost entirely benthic prey at 30 mm, while others found shifts to benthic prey to occur at sizes greater than the size of

age-0 yellow perch collected in this study. For example, delayed ontogenetic transitions to benthic prey are evident for some populations of Eurasian perch (*Perca fluviatilis*), which are ecologically and morphologically similar to yellow perch (e.g. Estlander et al. 2010). In fact, some populations of Eurasian perch may consume primarily zooplankton at all sizes (Persson 1986). It is plausible that yellow perch in Saginaw Bay switch away from zooplankton prey at much larger sizes (Fielder & Thomas 2006). Note that we did not collect many age-0 yellow perch larger than 90 mm and hence our description of diets of such large individuals is less informative. Nonetheless, it is clear that ontogenetic diet shifts by age-0 yellow perch in Saginaw Bay did not occur at as small sizes as for other Laurentian Great Lakes populations (Wu & Culver 1992; Pothoven et al. 2000).

Diets of young yellow perch may be structured by prey availability and other environmental factors,

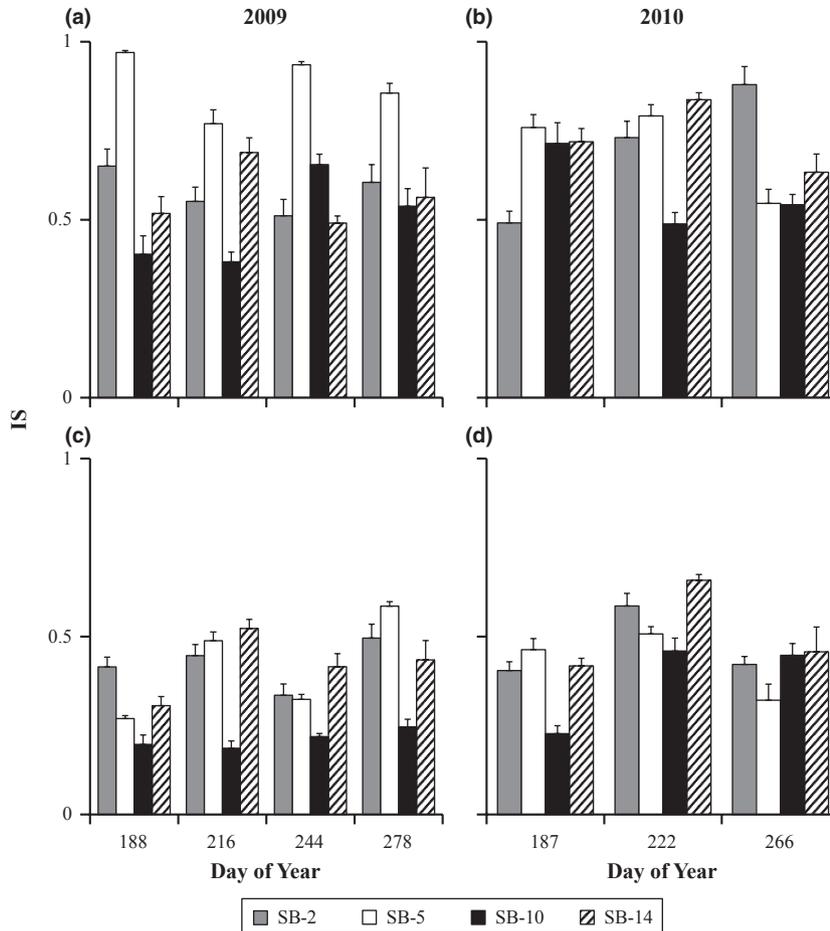


Fig. 5. Panels (a, b): mean proportional similarity of individual age-0 yellow perch diet composition relative to site- and date-specific niche breadths (i.e. all diets from the site and date of capture;  $IS_s$ ) during 2009 and 2010. Panels (c, d): mean proportional similarity of individual age-0 yellow perch diet composition relative to overall niche breadth (i.e. individual diets compared with all diets in this study; across sites, dates and years;  $IS_a$ ). All IS values range from 0 to 1, where 0 represents a high degree of specialisation, and 1 indicates similar diet composition across all individuals. Error bars indicate standard error.

and authors report perch switching to benthic prey as *Daphnia* abundance declines (Mills & Forney 1981; Wu & Culver 1992). However, we did not observe strong relationships between consumption patterns and abundance of *Daphnia* and Chironomidae larvae. Additional environmental factors such as turbidity (Wellington et al. 2010), interspecific competition (Persson 1986; Bergman & Greenberg 1994), predation risk (Mikheev et al. 2006), size-structure of the prey base (Mills et al. 1984, 1989) and impediments to benthic foraging (Post & McQueen 1994; Mayer et al. 2001; Roberts et al. 2009) can all influence prey consumption. Our sites differed in some physical characteristics, especially depth and substrate, and these differences may have contributed to patterns of diet composition and prey selection observed for age-0 yellow perch in Saginaw Bay. Spatial diet differences could also feasibly reflect asynchronous seasonal progression of prey populations, but we observed temporally consistent differences in abundance of some prey groups across

sites, suggesting this phenomenon played a small role in structuring spatial diet variation. Furthermore, consistent differences in diet composition were evident after accounting for prey abundances with Chesson's  $\alpha$ , suggesting spatial patterns in diets were not driven solely by prey availability.

Despite the relatively weak ontogenetic diet shift from zooplankton to benthic invertebrate prey, the types of prey consumed by age-0 yellow perch in Saginaw Bay were similar to observations in other ecosystems. Many authors have reported that *Daphnia*, often of intermediate size, are preferred prey of young yellow perch (Mills et al. 1984; Prout et al. 1990; Wu & Culver 1994). Chironomidae larvae are commonly preferred by larger-sized juvenile perch, especially later in the growing season after *Daphnia* abundance declines (Mills & Forney 1981; Wu & Culver 1992). Mayfly larvae, particularly *Hexagenia* spp., have also been shown to be important prey items of young perch (Tyson & Knight 2001). While there is now evidence of a limited presence of

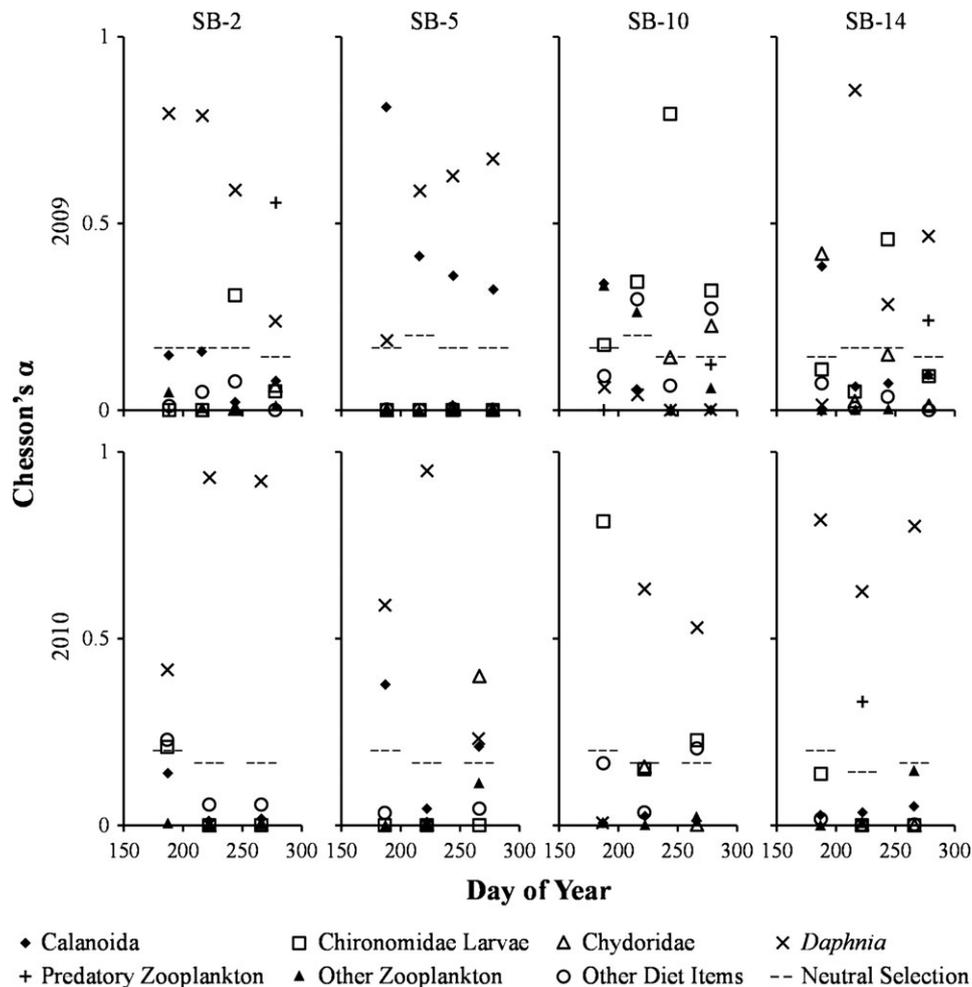


Fig. 6. Mean selectivity (indexed as Chesson's  $\alpha$ ) for each prey category for each site–date combination during 2009 (top) and 2010 (bottom). Values range from 0 to 1, where 0 indicates a prey type not selected, and 1 indicates a highly selected prey type. Neutral selection threshold indicates the  $\alpha$  value corresponding to neutral selection for that particular site and date.

*Hexagenia* spp. in Saginaw Bay after they were essentially extirpated through habitat degradation (Nalepa et al. 2003), we did not document *Hexagenia* spp. in diets of age-0 yellow perch.

Interestingly, cladocerans of the family Chydoridae, especially *Eurycercus* spp., were often important components in diets of Saginaw Bay juvenile perch. While these benthic cladocerans have been documented in diets of a few populations of yellow perch (e.g. Hanson & Leggett 1986), many studies did not indicate Chydoridae were present in diets of young perch (e.g. Roseman et al. 1995). Chydoridae are similar in size and may represent an alternative to *Daphnia*. However, Chydoridae are currently poorly sampled in many ecosystems due to their small size and benthic habits (Balcer et al. 1984) and were not quantified in our Ponar samples.

As a whole, we observed age-0 yellow perch consuming a high frequency of intermediate-sized and relatively small prey items. High consumption of small diet items could suggest that availability of lar-

ger prey is limited, forcing perch to spend additional time searching and attacking smaller prey. Hayward & Margraf (1987) showed that yellow perch consumed larger prey where they were available in Lake Erie. However, yellow perch may not always select the largest available prey items; Mills et al. (1984) found that juvenile yellow perch selected intermediate-sized *Daphnia* despite the presence of larger zooplankton. Consumption of such intermediate-sized prey may increase efficiency of digestion (i.e. higher egestion rates, allowing increased total consumption and assimilation) and can be important for growth of young perch when total consumption is low (Mills et al. 1989). We did not directly evaluate size-selective predation by age-0 yellow perch in Saginaw Bay, but perch often did not strongly select the largest available prey items (e.g. zooplankton prey such as *Daphnia* are smaller than most Chironomidae larvae).

While others have documented ontogenetic diet variation and reported consumption of similar types

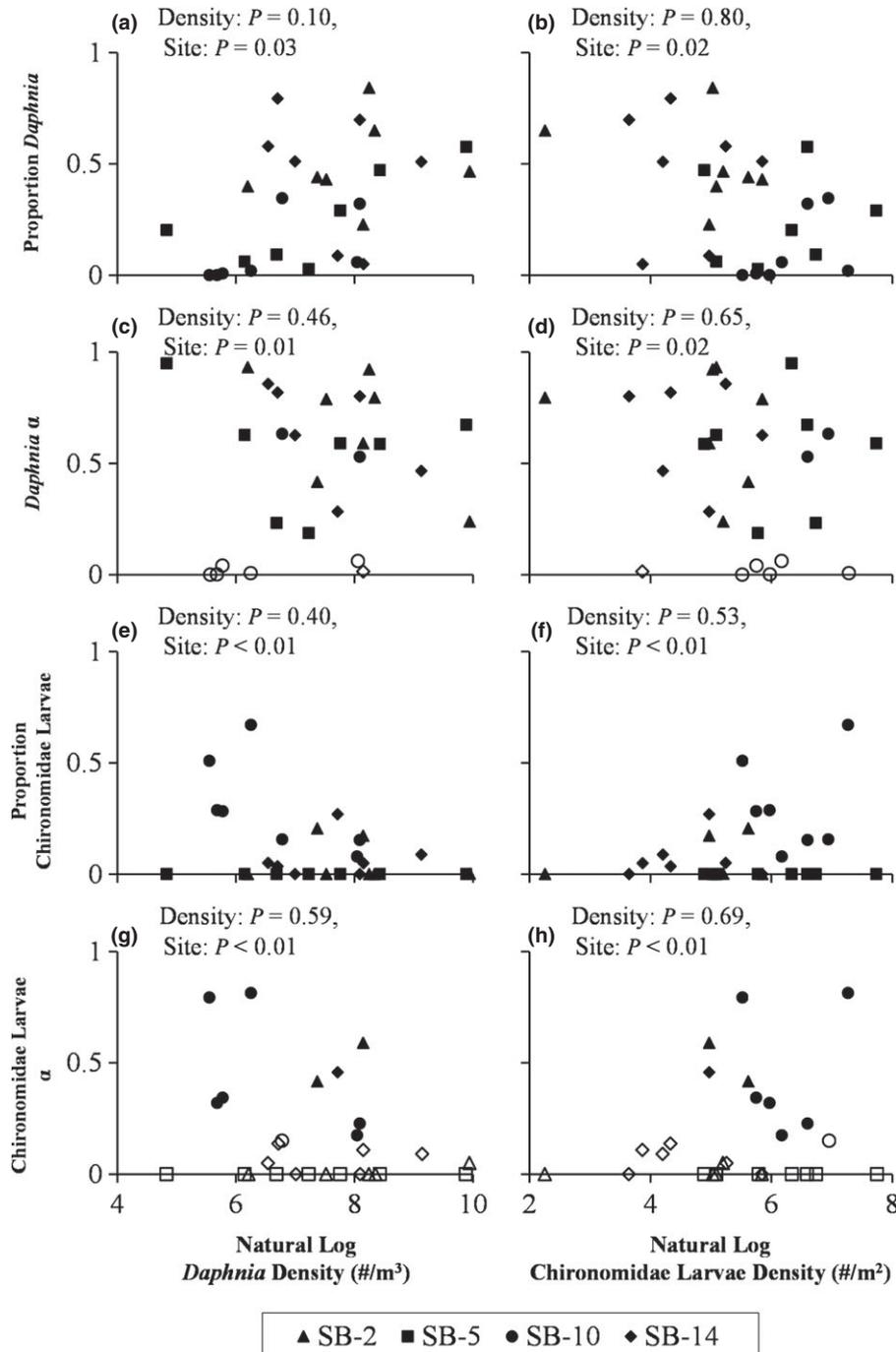


Fig. 7. Proportion *Daphnia* in diets (a, b), values of Chesson's  $\alpha$  for *Daphnia* (c, d), proportion of Chironomidae larvae in diets (e, f) and values of Chesson's  $\alpha$  for Chironomidae larvae (g, h) versus the natural log of *Daphnia* (left column) and Chironomidae larvae (right column) densities in the environment. Points represent the mean value for each site and date combination ( $N = 28$ ). Filled symbols in plots of Chesson's  $\alpha$  values indicate positive selection, while open symbols indicate values of  $\alpha$  below neutral selection. ANCOVA significance values of covariate (*Daphnia* or Chironomidae larvae densities) and factor (site) are shown above each graph (see text).

of prey as we observed in Saginaw Bay, interindividual diet variation of age-0 yellow perch has previously not been fully evaluated. We observed consistent spatial differences in diet composition and prey selection among relatively homogeneous open-water locations in Saginaw Bay (e.g. no nearshore marsh or beach habitats). Spatial variation in diets

plausibly would be even more pronounced if we would have included more dissimilar sites. For example, age-0 yellow perch collected in nearshore wetlands of Saginaw Bay consumed prey items not documented in this study (Parker et al. 2009b; C.R. Roswell, unpublished data). Further, we found that prey selectivities varied among our open-water loca-

tions, indicating diet strategies were structured differently across sites. Some differences in selectivities may be related to our methods. To allow for comparisons between pelagic and benthic prey, we collapsed numbers of zooplankton per cubic metre into numbers per square metre (e.g. Hondorp et al. 2011), thereby assuming zooplankton prey throughout the water column were available to young perch and potentially overestimating availability of zooplankton. However, this assumption may be reasonable because inner Saginaw Bay is relatively shallow and is likely well-mixed. The highly localised nature of zooplankton net and Ponar samples may have also biased selectivity measures by excluding aggregations of some prey (e.g. schools of *Daphnia*) that were available to perch caught in trawls, which covered a larger area than invertebrate samples. Nonetheless, we observed consistent spatial differences in prey densities and selectivity, suggesting this effect had a minimal impact.

Both within- and among-site interindividual diet variance contributed to overall diet patterns. Available evidence suggests that yellow perch in Saginaw Bay are of the same genetic stock (Parker et al. 2009a); thus, our data suggest niche discrimination within a population, rather than among populations. Specialisation by yellow perch has been reported by Post et al. (1997) and was attributed to high densities of yellow perch and resulting competitive interactions. Bolnick et al. (2003) suggested within-population specialisation was a widespread, often important and understudied component of niche variation among many animal groups. Our methods did not include a long-term measure of resource use (e.g. stable isotopes), which is important for discerning the temporal consistency of among-individual differences found in the ‘snapshot’ provided by stomach content analyses (Bolnick et al. 2002). Thus, these data are not optimal for evaluating the role of long-term individual specialisation. However, individual and spatial differences (especially targeting zooplankton versus other prey) seemed to be a constant feature through time among Saginaw Bay age-0 yellow perch diets. Persson (1979) found that less than 20% of diet items consumed by Eurasian perch remained in stomachs after 24 h at temperatures similar to our study. While movement patterns of age-0 yellow perch in Saginaw Bay are largely unknown, it is likely that prey we found in yellow perch stomachs were consumed in close proximity to capture location (for comparison, study sites were all >15 km apart). If young perch remain in a confined area, then the spatial diet discrimination we documented would translate to consistent individual specialisation. Nonetheless, future studies could evaluate movement patterns and the consistency of specialisation among age-0 yellow perch in Saginaw Bay.

Within-population niche partitioning may be driven by trade-offs in morphology or other factors that create differences in optimal resource use among individuals (Bolnick et al. 2003; Svanbäck & Eklöv 2003). We did not undertake analysis of morphological differences of age-0 yellow perch, although we did observe some consistent differences in mean lengths of yellow perch across sites (mean lengths of age-0 yellow perch at SB-5 were consistently smaller than at other sites). These differences in size across sites may have influenced the mean diet patterns at each site, but due to substantial overlap in the ranges of sizes across sites in each month, it is unlikely these differences were the primary drivers of the patterns we observed. Parker et al. (2009a) compared morphology of young yellow perch across Lake Michigan and Saginaw Bay habitats and found morphological differences between zooplanktivorous and insectivorous fish (e.g. longer pectoral fins and gill rakers in zooplanktivores), but no significant differences in yellow perch morphology were apparent within Saginaw Bay. Parker et al.’s (2009a) analyses were based on mostly larger yellow perch (age-1) and a small sample of insectivorous fish, and thus, these analyses may not have had sufficient power to detect morphological differences among small Saginaw Bay yellow perch.

Distinct partitions in foraging patterns within populations may affect linkages in food webs (Quevedo et al. 2009). The occurrence of strong interindividual differences in prey consumption by young yellow perch has potential to not only confound interpretation of mean diet patterns, but also may have implications for our understanding of early-life stage dynamics of yellow perch and their role in aquatic foodwebs. Roswell (2011) found that age-0 yellow perch in Saginaw Bay are subject to strong size-selective predation by walleye (*Sander vitreus*), which tend to selectively consume smaller age-0 yellow perch. Differential mortality rates between zooplankton and benthic specialists could lead to disproportionate contributions of each group to adult life stages. If these differences were pronounced, diet data from field studies indicating an ontogenetic shift in prey type could simply reflect a difference in relative survival rates. On the other hand, the persistent occurrence of two groups of specialists may suggest that long-term selection does not favour one or the other. Perhaps some annual conditions support the survival of zooplankton specialists, while conditions during other years favour benthic specialists, in which case within-cohort differences in diets may increase stability of population-level mean survival of young perch.

To conclude, foraging strategies of young yellow perch were highly variable and complex in Saginaw

Bay. We observed a relatively weak ontogenetic dietary shift from zooplankton to benthic prey, but documented a high degree of spatial variability, suggesting local conditions strongly influence young perch consumption patterns. While *Daphnia* abundance may contribute to diet variability, other factors also likely play a role as prey selection patterns were inconsistent, and individual differences were important within some sites and dates. Foraging strategies of age-0 yellow perch, which influence growth and recruitment success, exhibit substantial variation that may not be captured with measures of central tendency commonly used to describe diet patterns.

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