

Year-class variation drives interactions between warm-water predators and yellow perch

William W. Fetzer, Collin J. Farrell, James R. Jackson, and Lars G. Rudstam

Abstract: Walleye (*Sander vitreus*), smallmouth bass (*Micropterus dolomieu*), and largemouth bass (*Micropterus salmoides*) are common top predators across many north temperate lakes, but no previous analyses have assessed factors driving their combined impact on mortality of a shared prey, yellow perch (*Perca flavescens*). We estimated consumption dynamics of walleye, smallmouth bass, and largemouth bass during 3 years that differed in age-0 yellow perch year-class strength and evaluated the relative contribution of each predator to age-0 yellow perch mortality, in Oneida Lake, New York, USA. Habitat-specific diet composition and population densities were integrated with temperature and growth rates to parameterize a bioenergetics model and estimate annual consumption of major diet items. Walleye were the dominant predator in both offshore and inshore habitats, while smallmouth bass and largemouth bass were also important inshore predators. Consumption of age-0 yellow perch by all three predators was positively correlated to age-0 yellow perch year-class strength, but our ability to account for age-0 yellow perch mortality decreased during years when year-class strength was strong. Within each year, predation by the three species accounted for all observed age-0 yellow perch mortality in late summer and fall, but not in the early summer, suggesting other predators in the lake likely predate on the youngest, most vulnerable yellow perch. These results are important for understanding how diverse predator communities can alter the spatial and temporal availability of prey refuges and influence mortality of a shared prey.

Résumé : Si le doré jaune (*Sander vitreus*), l'achigan à petite bouche (*Micropterus dolomieu*) et l'achigan à grande bouche (*Micropterus salmoides*) sont des prédateurs de niveau trophique supérieur répandus dans de nombreux lacs tempérés du Nord, aucune analyse antérieure n'a évalué les facteurs qui modulent leur incidence combinée sur la mortalité d'une proie commune, la perchaude (*Perca flavescens*). Nous avons estimé la dynamique de la consommation des dorés jaunes, achigans à petite bouche et achigans à grande bouche durant 3 années caractérisées par différentes forces de la classe d'âge 0 des perchaudes et évalué la contribution relative de chaque prédateur à la mortalité des perchaudes de cette classe d'âge dans le lac Oneida (État de New York, États-Unis). La composition des régimes alimentaires et les densités de population propres à l'habitat ont été intégrées à la température et aux taux de croissance pour paramétrer un modèle bioénergétique et estimer la consommation annuelle d'éléments importants du régime alimentaire. Le doré jaune était le prédateur dominant dans les habitats tant littoraux qu'extracôtiers, alors que l'achigan à petite bouche et l'achigan à grande bouche étaient également des prédateurs importants dans les zones littorales. La consommation de perchaudes d'âge 0 par les trois prédateurs était positivement corrélée à la force de la classe d'âge 0 des perchaudes, mais la capacité d'expliquer la mortalité des perchaudes d'âge 0 diminuait durant les années où la force de cette classe d'âge était grande. Pour chaque année, la prédation par les trois espèces expliquait toute la mortalité observée de perchaudes d'âge 0 à la fin de l'été et à l'automne, mais pas au début de l'été, donnant à penser que d'autres prédateurs dans le lac se nourrissent vraisemblablement de perchaudes les plus jeunes et vulnérables. Ces résultats sont importants pour la compréhension de l'incidence de communautés de prédateurs variées sur la disponibilité spatiale et temporelle de refuges pour les proies et sur la mortalité d'une proie commune. [Traduit par la Rédaction]

Introduction

Predation is an important source of mortality for fish during their early life stages, and considerable effort has been focused on understanding the factors driving variation in predator–prey dynamics. This research often focuses on describing predator foraging habits (Liao et al. 2004), diet overlap between potential competitors (VanDeValk et al. 2002; Olson and Young 2003; Wuellner et al. 2011), and responses to changing forage availability (Forney 1974). Ultimately, an underlying objective is to understand how predation influences ecosystem structure and function by altering prey demographics and population dynamics (Forney 1977a; Dembkowski et al. 2015), community composition (Brooks and Dodson 1965), and cross-

trophic interactions (Carpenter et al. 1985) within food webs. However, it is often challenging to directly quantify the relative impact of individual or multiple predators on a population or community of prey species. These analyses are data intensive, requiring estimates of predator and prey abundance, predator and prey growth rates, predator foraging dynamics, and other environmental data, such as temperature (Forney 1977a; Tsehaye et al. 2014; Dembkowski et al. 2015). As such, our understanding of predator–prey interactions is often based on assumptions or correlations, while establishing causal relationships remains difficult.

Several recent publications have documented shifts in predator populations in north temperate lakes from walleye (*Sander vitreus*)

Received 26 May 2015. Accepted 31 December 2015.

W.W. Fetzer,* C.J. Farrell, J.R. Jackson, and L.G. Rudstam. Cornell Biological Field Station, Department of Natural Resources, Cornell University, 900 Shackelton Point Road, Bridgeport, NY 13030, USA.

Corresponding author: William W. Fetzer (email: William.Fetzer@wisconsin.gov).

*Present address: Wisconsin Department of Natural Resources, 101 S. Webster St., Madison, WI 53703, USA.

Copyright remains with the author(s) or their institution(s). Permission for reuse (free in most cases) can be obtained from RightsLink.

to black bass (i.e., smallmouth bass (*Micropterus dolomieu*) and largemouth bass (*Micropterus salmoides*)) (Robillard and Fox 2006; Irwin et al. 2016), leading to speculation about the potential effects of these changes to food web dynamics. Walleye and black bass are considered top predators across many temperate lakes in North America, and substantial literature has focused on evaluating their foraging dynamics. Several studies have documented dietary overlap between smallmouth bass and walleye, but did not observe evidence of competition, such as decreased growth rates, lower condition, or reduced abundances, between species (Fayram et al. 2005; Wuellner et al. 2010, 2011). Wuellner et al. (2011) found that generalist feeding by smallmouth bass limits the intensity of competition between these species and concluded inverse abundance relationships are likely driven by environmental factors and not direct interspecific interactions. Less is understood about the degree of dietary overlap between largemouth bass and walleye. Both walleye and largemouth bass are more piscivorous than smallmouth bass (Santucci and Wahl 1993; Hodgson et al. 1997; Fayram et al. 2005), indicating the potential for more intense competition than between walleye and largemouth bass. Previous research on these three predators is primarily limited to assessment of dietary overlap, and little is known about their food web interactions and combined consumptive effects on temporal and spatial patterns of mortality for a shared prey.

Yellow perch (*Perca flavescens*) are one of the most common species in north temperate lakes. As a generalist, yellow perch occupy inshore and offshore habitats and serve as an important prey species for many predators, including walleye, smallmouth bass, largemouth bass, and other species (Forney 1977a; Liao et al. 2004; Dembkowski et al. 2015). Yellow perch year-class strength can vary by several orders of magnitude across years (Irwin et al. 2009), which can influence food web dynamics and community composition by altering predator foraging and buffering alternative prey species from predation (Forney 1974; Hall and Rudstam 1999). Previous attempts to reconstruct yellow perch mortality from predation have been limited to analyses of a single predator and habitat (Forney 1977a; Dembkowski et al. 2015) or have not directly accounted for the effect of year-class strength variation on predator-prey interactions (Dembkowski et al. 2015). Liao et al. (2004) provides one of the only comparisons of consumption of yellow perch by multiple predators, but are unable to relate this directly to its effect on yellow perch mortality. Quantifying the extent and variation of predator-prey interactions between walleye, smallmouth bass, and largemouth bass and yellow perch across habitats, predators, and years could improve management of these four important sport fish.

This study focuses on the relative effect of walleye, smallmouth bass, and largemouth bass predation on mortality of a shared prey species, yellow perch, in Oneida Lake, New York. We parameterized bioenergetic simulations with species-specific growth rates, diet composition, abundance, and temperature to estimate population-level consumption by all species, focusing on age-0 and age-1 yellow perch. We then compared consumption estimates with independent abundance estimates of age-0 yellow perch available for Oneida Lake, which allowed us to explore the individual and combined importance of all three predators in driving age-0 yellow perch mortality across inshore and offshore habitats and a range of age-0 yellow perch densities.

Methods

Study site

Oneida Lake, New York, USA, is a large, shallow, mesotrophic lake (area: 207 km²; mean depth: 6.8 m; maximum depth: 16.8 m)

that contains a diverse fish community (>80 species), dominated by yellow perch, white perch (*Morone americana*), and walleye. The Cornell Biological Field Station (CBFS) has maintained a long-term fisheries and limnological monitoring program on the lake since 1956, providing data across trophic levels and life history stages of multiple fish species. Oneida Lake has gone through a number of changes in recent years, including increasing summer water temperatures (Jackson et al. 2008) and the introduction of dreissenid mussels (zebra mussels (*Dreissena polymorpha*) in the early 1990s and quagga mussels (*Dreissena rostriformis bugensis*) in the mid-2000s). Increasing water clarity associated with dreissenid mussels shifted productivity from pelagic to benthic habitats, increased the abundance of aquatic macrophytes, and subsequently increased the extent of the littoral zone (Zhu et al. 2006). The expansion of the littoral zone increased the amount of suitable habitat for black bass in Oneida Lake and, combined with increasing water temperatures, may explain increases in black bass catches across multiple standardized datasets (Jackson et al. 2012; Irwin et al. 2016). Concurrently, abundance across all age-0 life stages of yellow perch decreased (Irwin et al. 2009), and the population became increasingly driven by production from littoral habitats (Fetzer et al. 2015). These changes suggested that predation by inshore predators could be accounting for a greater proportion of age-0 yellow perch mortality relative to earlier time periods, which were dominated by walleye in offshore habitats (Forney 1977a).

Predator population estimation, age structure, and growth

To determine walleye, smallmouth bass, and largemouth bass abundances, age structure, and growth patterns, we used multiple long-term datasets available through the CBFS long-term monitoring program and complemented these with additional field surveys during 2006–2009. Abundance, age structure, and growth rates were estimated for walleye via a long-term gillnet survey complemented with mark-recapture studies every 2–3 years and available through previously published data and the Knowledge Network for Biocomplexity (see Rudstam and Jackson 2012a for more details). Walleye abundance, age, and length-at-age estimates greater than age-6 were grouped because previous work demonstrated that age estimates from scales were unreliable at ages beyond age-7 (J.L. Forney, CBFS, Bridgeport, New York, unpublished data, 2013). Additional assessment of walleye length-at-age analyses from a subsample of otoliths collected via the long-term monitoring program suggests this is likely due to slow growth past age-7 (Table S1[†]; Fig. S1[†]).

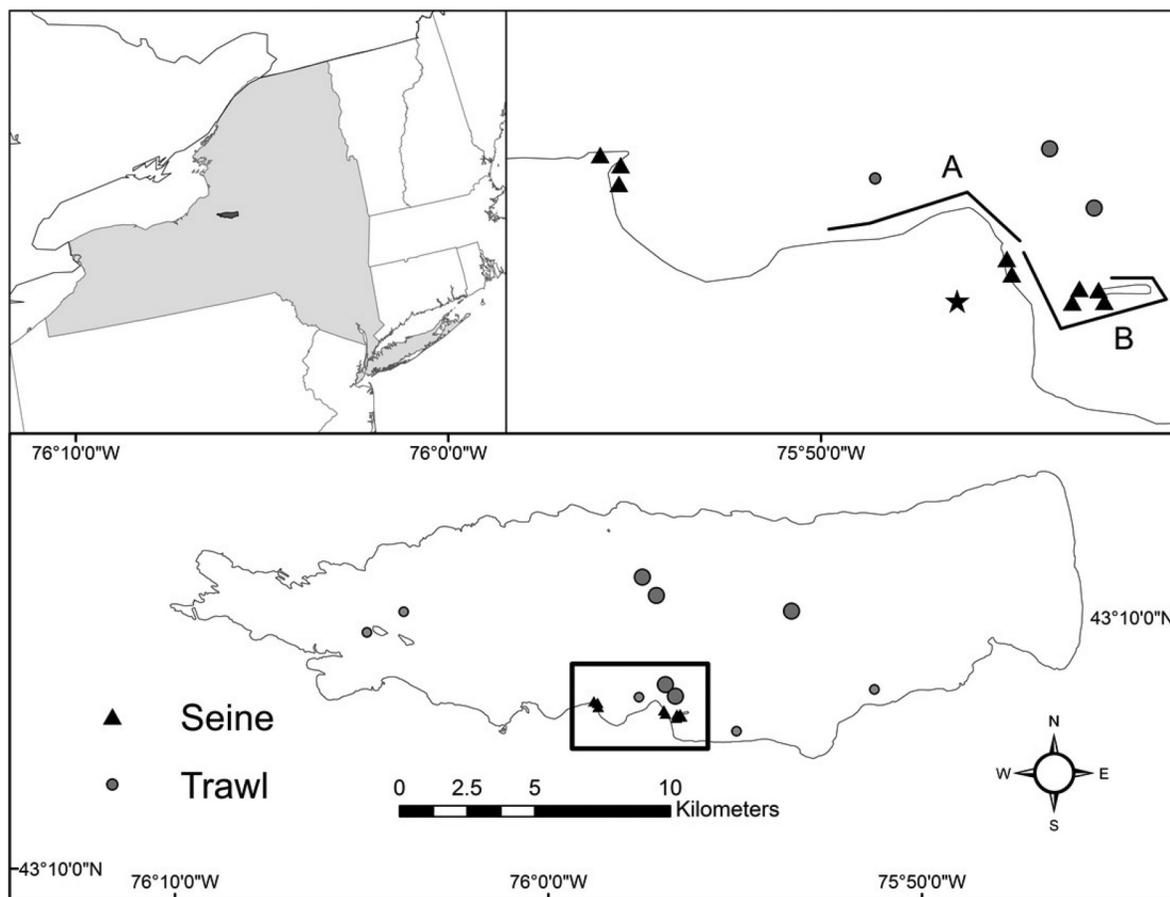
Smallmouth bass and largemouth bass were not as well studied as walleye in Oneida Lake; therefore, we estimated their relative abundance using walleye as a benchmark. A mark-recapture study was conducted on smallmouth bass in the 1960s (Forney 1972), but was limited to Shackleton Point (Fig. 1). Smallmouth bass were regularly captured in the standardized long-term gillnet survey, but no relationship exists between gillnet catch and population size for smallmouth bass in Oneida Lake. To overcome this limitation, an established relationship among population size, gillnet catch per unit effort (CPUE), and gillnet catchability for age-4 and older walleye in Oneida Lake ($R^2 = 0.60$; J. Jackson, unpublished data), developed following the general approach of Peterman and Steer (1981), was applied to the gillnet catch of smallmouth bass to estimate the population of age-3 and older smallmouth bass in Oneida Lake, New York.

$$(1) \quad \text{Abundance} = 1.05 \times e^{10.114 + [0.592 \times \ln(\text{Catch})]}$$

It was assumed that age-3 and older smallmouth bass and age-4 and older walleye have similar catchabilities and that catchability

[†]Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2015-0275>.

Fig. 1. Map of Oneida Lake and sampling locations used to collect predator diets. Electrofishing transects (A–B) were located near Shackleton Point, indicated with a star. Trawling sites are indicated with filled circles and include walleye diet trawls (large circles) and yellow perch abundance trawls (large and small circles). Seine sites are indicated with filled triangles.



does not change across ages for smallmouth bass (similar to walleye; Irwin et al. 2008). Largemouth bass were not consistently caught in any of the long-term monitoring of Oneida Lake, making population estimates difficult. However, angler CPUE of largemouth bass was approximately half of smallmouth bass CPUE (Jackson et al. 2012); therefore, it was assumed that largemouth bass were half as abundant as smallmouth bass in Oneida Lake.

To obtain age and growth estimates for largemouth bass and smallmouth bass, scales were collected via electrofishing (see section on Predator foraging dynamics below), dried, and pressed into a cellulose acetate plastic slide to increase the ease of aging and measuring annuli. Two readers compared independently determined annuli until a consensus was reached, after which each annuli radius and the total scale radius were measured from the focus along the anterolateral axis (Pierce et al. 1996). Scales that showed regeneration were not included in the analysis. Back-calculated lengths-at-age were determined using the Fraser–Lee model with biological intercept (Maceina et al. 2007; biological intercept = c ; smallmouth bass: $c = 21$ mm; largemouth bass: $c = 26$ mm; obtained from Carlander 1950). Length-at-age was converted to mass using standard length–mass relationships for smallmouth bass and largemouth bass in lakes across New York State (smallmouth bass: $\ln(\text{mass (g)}) = -11.78 + 3.09 \cdot \ln(\text{length (mm)})$, $R^2 = 0.97$; largemouth bass: $\ln(\text{mass (g)}) = -12.51 + 3.23 \cdot \ln(\text{length (mm)})$, $R^2 = 0.98$; P.C. Perry, Cornell University, Ithaca, New York, personal communication, 2012). Annual growth in mass was determined as the difference between mass at age i and mass at age $i + 1$.

Weighted catch-curve analyses were used to estimate the proportion of smallmouth bass and largemouth bass in each age-class

from age-1 to age-8+ (Maceina and Bettoli 1998). Weighted catch-curve analyses weigh each observation by the amount of information it contains, reducing the influence of older, rarer age-classes. For each species, catch-at-age data from diet surveys were pooled across years of sampling and used to fit the weighted catch-curve analyses, which provided an estimate of the age structure for smallmouth bass and largemouth bass. The ratio of age-1 and age-2 smallmouth bass and largemouth bass relative to age-3 and older fish, from the weighted catch-curve analyses, was combined with the age-3+ abundance estimates to determine the total abundance of age-1 and older smallmouth bass and largemouth bass in the lake. Age-specific abundances were determined by multiplying the total population estimate by the proportion of fish in each age-class predicted by the catch-curve analysis. These population and age-structure estimates provided the best available information to evaluate consumption dynamics of walleye and black bass and to estimate the relative contribution of black bass and walleye predation to mortality of age-0 yellow perch and allowed us to discuss how large black bass populations would need to be to have a similar impact on yellow perch as walleye.

Predator foraging dynamics

To obtain seasonal predator diets, walleye, smallmouth bass, and largemouth bass were collected monthly from June through October in 2007–2009 via electrofishing or trawling. Inshore habitats were sampled during two nights and two mornings each month using an electrofishing boat (Smith-Root electronics, 354 V pulsed DC current, pulse rate of 60 Hz, 8 A of current into water). Evening sampling consisted of two runs of approximately 45 min

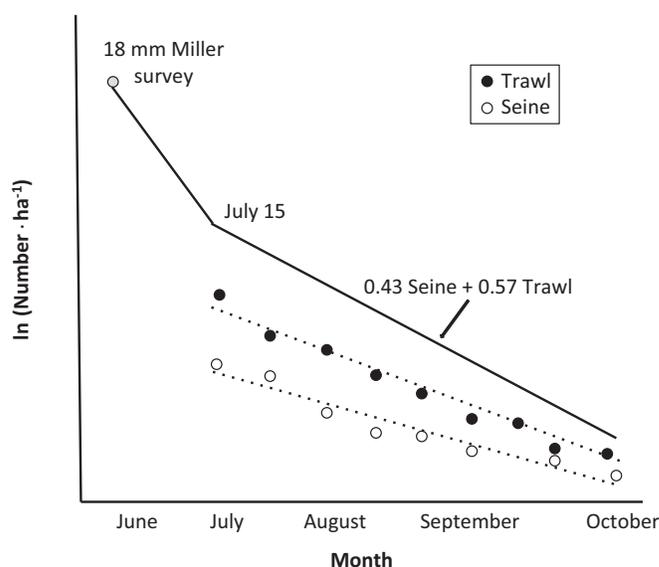
to 1 h, starting at sunset and continuing until both runs were completed and all fish were processed. Morning sampling consisted of one run starting 1.5 h before sunrise. Sampling was focused near Shackleton Point on the south-central shoreline of Oneida Lake and consisted of approximately equal distributions of rocky and weedy sites to efficiently capture both black bass species (Olson et al. 2003; Fig. 1). Offshore habitats were sampled two mornings each month with a 12.2 m bottom trawl that was fished at depths between 5 and 12 m for 15 min at five sites (see Lantry et al. 2008 for more details; Fig. 1). During each morning, two sites were sampled immediately following sunrise: one near Shackleton Point and one offshore. The bottom trawl diet survey was also conducted in 2006 to aid in the differentiation of the walleye population between inshore and offshore habitats. Upon capture, all fish were processed immediately to minimize digestion of stomach contents. Fish from both electrofishing and trawling were anesthetized with MS-222, measured for length, and a scale sample collected to age fish and back-calculate length-at-age to determine growth rates. Stomach contents were initially removed via acrylic tubes and supplemented with gastric lavage and (or) dissection if additional diet items were detected but unable to be removed through acrylic tubes. Diet samples were preserved in 10% formaldehyde and brought back to the laboratory for processing.

Stomach contents were analyzed in the laboratory. All diet items, which were sufficiently undigested, were identified to species, enumerated, and measured for length. Age-0 and age-1 fish were separated into two categories based on length distributions when possible. Unidentified fish diet items were assigned to species based on the observed species composition of identifiable fish for each sampling date. Biomasses of individual prey items were determined from length–mass relationships available for Oneida Lake (J.L. Forney, Cornell Biological Field Station, Bridgeport, New York, unpublished data, 2012). To calculate the percentage composition of total biomass comprised by each diet item, we used the following equation:

$$(2) \quad \text{Percentage}_i = \frac{n_i \cdot B_i}{n_1 \cdot B_1 + n_2 \cdot B_2 \dots + n_x \cdot B_x}$$

where i represents a unique diet category (e.g., age-0 yellow perch), x is the total number of diet categories in the diet, n_i is the number of diet item i in the diet, and B_i is the mean biomass of diet item i in the diet. On dates when diet items were too digested to obtain length estimates, an estimated length was assigned based on length estimates from diets collected on proximate sampling dates (within a week) or length distributions in the lake available through additional datasets (e.g., seine or trawl surveys). These diet items were composed of uncommon age-0 fish species with narrow length distributions. For benthic invertebrates, specifically crayfish, published length–mass relationships were used to estimate biomass of individual prey items based on the observed length in diets (Benke et al. 1999). To avoid over-representation of dates when few diets were collected, percent composition by biomass for each sampling date within a monthly survey (e.g., two evenings and two mornings electrofishing) was converted into a monthly weighted average based on the number of diets collected on each specific date. Diet composition for walleye was separated into inshore and offshore diets based on samples collected through electrofishing and trawling, respectively. Diet composition was not broken up into predator size classes because sample sizes were not sufficient in some months. In general, variation in diet composition was greater across months than across age-classes within a month, changing seasonally with prey availability.

Fig. 2. Schematic of age-0 yellow perch abundance estimation. Visualization of how density estimates ($\ln(\text{number} \cdot \text{ha}^{-1})$) from the 18 mm Miller survey, bottom trawl, and beach seine were integrated to estimate age-0 yellow perch abundance during the limnetic and littoral–demersal stages within a year.



Yellow perch population dynamics

Age-0 yellow perch abundance and growth rates were tracked throughout the growing season throughout all habitats of Oneida Lake. Pelagic and demersal habitats (offshore) were sampled using a combination of high-speed Miller sampling for larvae in June (Rudstam et al. 2002) and standardized bottom trawl surveys for juveniles in July through October (Irwin et al. 2009; Rudstam and Jackson 2012b), while littoral habitats (inshore) were sampled for juveniles in July through October using a beach seine. The first estimates of age-0 yellow perch abundance were obtained in offshore habitats when the fish were approximately 18 mm (Fig. 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). Offshore benthic age-0 yellow perch were sampled with a bottom trawl (5.5 m footrope, 13 mm cod end) weekly from July through October at 10 standard sites (Fig. 1) at depths of 6 m (four sites), 8 m (two sites), and 12 m (four sites). Inshore age-0 yellow perch were sampled using a beach seine (23 m by 1.5 m, 6 mm mesh) at nine standard sites (Fig. 1). Sampling locations were consistent across all years in the trawl and seine surveys.

To account for ontogenetic changes in habitat use by age-0 yellow perch, abundance estimates were divided into two stages (Fig. 2). During the limnetic stage, defined as the interval of growth between 18 mm and 15 July (when age-0 yellow perch are approximately 1.0 g), it was assumed that age-0 yellow perch were homogeneously distributed across Oneida Lake. Density estimates during the limnetic stage were based on the 18 mm Miller survey (Rudstam and Jackson 2012b). During the littoral–demersal stage, defined as the interval of growth from 15 July through the fall, it was assumed that age-0 yellow perch were heterogeneously distributed across inshore and offshore habitats (bottom trawl and seine). During this time period, inshore and offshore catch-curves were calculated independently based on the natural log of density estimates available from the seine and trawl surveys, respectively. Inshore and offshore catch-curves were then combined using a weighted average of density ($\text{number} \cdot \text{ha}^{-1}$) based on current projections of inshore–offshore spatial coverage in the lake (inshore = 43%; offshore = 57%; Fig. 2; Fitzgerald et al. 2016). During the limnetic period, a constant instantaneous mortality was as-

sumed from the timing of the 18 mm survey to 15 July (start of littoral–demersal stage) and calculated based on observed decreases in abundance. To accurately reflect a gradual transition from the limnetic and littoral–demersal stages, daily instantaneous mortality throughout the growing season was based on a 20-day moving average across dates. This prevented an abrupt decrease in daily mortality as fish transitioned from the limnetic to the littoral–demersal stage and did not affect mortality at the beginning or end of the growing season.

Bioenergetic simulations and consumption estimation

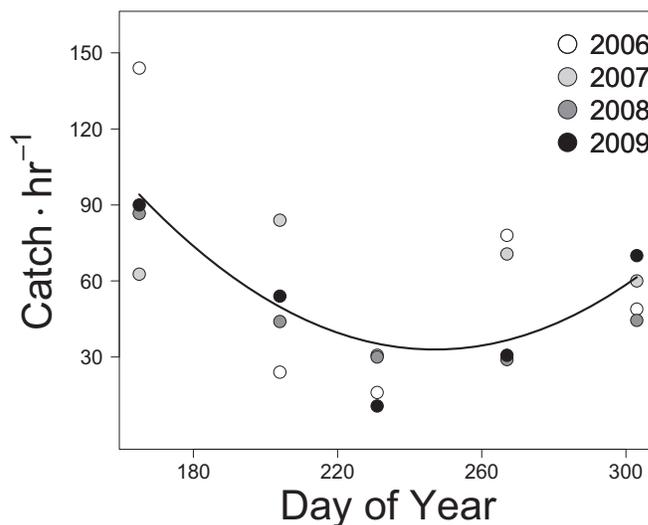
We used a bioenergetics modeling approach (Hanson et al. 1997) to estimate consumption dynamics of walleye, smallmouth bass, and largemouth bass and to assess their relative contribution to mortality of age-0 yellow perch. Bioenergetics models are mass-balance equations that can be used to estimate consumption or growth by balancing the following equation:

$$(3) \quad C = G + R + F + U$$

where C is consumption, G is growth, R is respiration, F is egestion, and U is excretion. To perform bioenergetics simulations, species-specific abundance estimates, growth rates, and diet composition were integrated with water temperature to fit bioenergetics models parameterized with energy densities of predators (Lantry et al. 2008) and prey items (Table S1[†]; Wuellner et al. 2010) and species-specific physiological parameters (Table S2[†]; Wisconsin bioenergetics model; Hanson et al. 1997). Growth rates within a year were based on back-calculated lengths-at-age from scales collected in the immediate subsequent year (e.g., 2007 growth based on scales collected in 2008). No scales were collected from black bass during 2010 to assess growth rates during 2009; therefore, black bass growth rates for 2009 were based on a von Bertalanffy growth equation fit separately for each species to all length-at-age data to determine the mean age-specific annual growth for both black bass species. Water temperature was continuously recorded throughout the year at depths of 2 and 10 m with a HOBO temperature recorder in 12 m of water at Shackleton Point (Onset Computer Corporation, Bourne, Massachusetts, USA; Fig. 1). Water temperature in the model was based on the mean measurement at 2 and 10 m depth.

Simulations were run for a single individual from each age-class of walleye, smallmouth bass, and largemouth bass to estimate daily consumption over the course of the growing season. Individual daily consumption was then scaled up to the population level using population estimates and age structure for each species, assuming no mortality. Population estimates and age structure for walleye differed across years, but were assumed to be the same for black bass because of data limitations. To separate the walleye population into offshore and inshore components and to account for seasonal changes in habitat use, a second-order polynomial function was fit to observed changes in CPUE in the 12.2 m bottom trawl survey during 2006–2009 (Fig. 3). Though 2006 diet data were not used to estimate consumption, we included the CPUE trends in these analyses to improve our ability to model seasonal habitat use by walleye. We assumed that seasonal trends in trawl CPUE reflected habitat switching between offshore and inshore habitats and not seasonal changes in trawl catchability or changes in population size due to mortality. Daily CPUE was scaled to the percentage of the walleye population offshore under the assumption that 90% of the population was offshore on the first day of simulations. This assumption was supported by seasonal CPUE trends in the trawl and electrofishing surveys, which suggested walleye were uncommon in inshore habitats during early summer, but not entirely absent. All age-classes were assumed to follow the same seasonal trend in inshore–offshore distribution.

Fig. 3. Seasonal trends in walleye catch per hour in offshore trawls. Monthly catch rates of walleye in the offshore trawl during 2006–2009, with polynomial best-fit line used to assign proportions of walleye population in inshore and offshore habitats, are indicated.



To assess the effect of uncertainty in our population estimates on consumption estimates, we performed additional simulations by developing upper and lower bounds for predator abundance and scaling up individual consumption to these population estimates. Confidence intervals for the walleye population were only available for years when mark–recapture studies were conducted (e.g., 2007 in our study). To overcome this, we calculated the mean percent difference of the lower and upper bounds of the 95% confidence interval from the calculated population estimate from all years when walleye mark–recapture studies were conducted on Oneida Lake (25 years). The lower (mean = 17.7%, SD = 2.9%, range = 14.3%–24.8%) and upper (mean = 21.7%, SD = 4.4%, range = 16.7%–32.9%) percent differences were then applied to the estimated population sizes in all years of our study to estimate upper and lower bounds of the population size. For black bass, no data were available to evaluate the level of uncertainty in our population estimates. Because of this data limitation, we performed additional simulations at double and half our point estimates of black bass population size to establish high and low estimates for the range of potential black bass consumption.

For all simulations, estimates of walleye, smallmouth bass, and largemouth bass consumption of age-0 and age-1 yellow perch from bioenergetics simulations were converted to number of individuals consumed per day by dividing biomass consumed per day by observed age-0 and age-1 yellow perch individual masses on each day. For age-0 yellow perch, daily consumption estimates were compared with abundance estimates to determine the proportion of total age-0 yellow perch mortality that could be accounted for by each predator and to assess the potential importance of additional predators in the lake based on differences between observed total mortality and mortality due to walleye and black bass.

Results

Population estimates and age structure

Walleye were the most abundant predator during the study, ranging in density from 32.1 to 40.5 fish per hectare (Table 1). The proportion of the walleye population in offshore habitats was highest in early summer, declined during late summer, and increased throughout the fall (Fig. 3; $CPUE = 0.0091 \cdot (\text{date})^2 - 1.51 \cdot (\text{date}) + 95.60$; $R^2 = 0.48$). Smallmouth bass density was estimated at 17.5 fish per hectare, while largemouth bass density was estimated at

Table 1. Density estimates (number·ha⁻¹) for different age groups of walleye (WE), smallmouth bass (SMB), and largemouth bass (LMB).

Species	Year	Age-specific abundance (no.·ha ⁻¹)								Total (no.·ha ⁻¹)
		Age-1	Age-2	Age-3	Age-4	Age-5	Age-6	Age-7	Age-8	
LMB	2006–2009	2.4	1.7	1.3	0.9	0.7	0.5	0.4	0.9	8.8 (4.4, 17.5)
SMB	2006–2009	3.5	2.8	2.3	1.9	1.6	1.3	1.1	3.0	17.5 (8.8, 35)
WE	2007	9.5	6.9	4.5	1.3	1.0	16.4	—	—	39.6 (32.6, 48.2)
	2008	4.9	4.2	1.7	4.8	1.1	15.4	—	—	32.1 (26.4, 39.0)
	2009	9.8	5.8	2.7	3.3	4.2	14.6	—	—	40.5 (33.3, 49.3)

Note: All age-8 and older smallmouth bass and largemouth bass are included in the age-8 column; all age-6 and older walleye are included in the age-6 column. Density ranges used in uncertainty analyses are presented in parentheses in the Total column.

8.8 fish per hectare (Table 1). Age structure for all species generally followed a typical catch-at-age curve, illustrating decreasing abundance in each age-class as age increased. Some imprecision was present in our estimates of age-specific walleye abundance, as cohorts did not always decrease in abundance in subsequent years, and was likely due to the difficulties associated with estimating fish densities in natural systems. Overall, these inconsistencies were small and cohort abundance only increased by greater than one fish per hectare for one cohort in one year. Abundance in the oldest age-class increased for all species because all fish older than that cutoff were grouped into that age-class (Table 1). This was especially noticeable in walleye and was primarily driven by the strong 2001 year-class, which was age-6 during the first year of our study (Table S4¹).

Diet composition and consumption estimates

During 2007–2009, diets were collected from 1052 inshore and 779 offshore walleye, 294 largemouth bass, and 287 smallmouth bass in Oneida Lake, New York (Table 2). Age-0 yellow perch, age-1 yellow perch, age-0 gizzard shad (*Dorosoma cepedianum*), and crayfish dominated consumption dynamics of all three predators (Table 2; Table 3; Fig. 4); however, the composition of predator diets differed across predators, seasons, and years based on the availability of age-0 yellow perch. When age-0 yellow perch were abundant, consumption by all predators was dominated by age-0 yellow perch. When age-0 yellow perch were less abundant, each predator switched to alternative prey, while maintaining fairly constant total consumption (Table 2; Table 3).

Offshore and inshore walleye diets were fairly consistent across years. Offshore walleye primarily consumed age-0 yellow perch during early summer but shifted to age-0 gizzard shad by late fall (Table 2; Table 3; Fig. 4). Age-1 yellow perch were the only other major diet item consistently observed in offshore walleye diets (Table 2; Table 3). Inshore walleye diets were dominated by age-0 and age-1 yellow perch in early summer, shifting to gizzard shad by late October (Table 2; Table 3; Fig. 4). When age-0 yellow perch year classes were weak, offshore and inshore walleye subsidized energetic needs by switching to age-0 gizzard shad earlier in the summer and consuming a greater biomass of age-0 gizzard shad throughout the year (Table 3; Fig. 4). Population-level consumption by walleye across inshore and offshore habitats was strongly influenced by seasonal patterns in habitat use. In early summer, walleye consumption was dominated by fish in the offshore habitats, but transitioned to inshore habitats by midsummer (Fig. 4). As a result, consumption of age-0 yellow perch was dominated by offshore habitats in early summer, while inshore consumption was highest in mid- to late summer. Additional species consumed by walleye included emerald shiners (*Notropis atherinoides*), age-0 and age-1 pumpkinseed (*Lepomis gibbosus*), banded killifish (*Fundulus diaphanus*), age-0 and age-1 brown bullhead (*Ameiurus nebulosus*), age-0 walleye, age-0 smallmouth bass, age-0 white perch, and trout-perch (*Percopsis omiscomaycus*).

Crayfish consistently dominated smallmouth bass diets at all times, but age-0 yellow perch were also an important diet item (Table 2; Table 3; Fig. 4). Smallmouth bass also consumed age-1

pumpkinseed, banded killifish, age-0 white perch, age-0 tessellated darter (*Etheostoma olmstedii*), age-0 brown bullhead, and age-0 white sucker (*Catostomus commersonii*). Largemouth bass diets were dominated by age-1 yellow perch in early summer but shifted to age-0 yellow perch, crayfish, and age-0 gizzard shad through midsummer and into the fall (Table 2; Table 3; Fig. 4). Other diet items included emerald shiners, age-0 and age-1 pumpkinseed, banded killifish, age-0 and age-1 brown bullhead, and benthic invertebrates. Less common prey species typically accounted for less than 10% of total diet biomass for both smallmouth bass and largemouth bass, but were occasionally important. During weak year classes of age-0 yellow perch, smallmouth bass and largemouth bass subsidized consumption by primarily switching to crayfish, but age-0 gizzard shad and age-0 brown bullhead were also important.

Predation on yellow perch

The relative importance of age-0 yellow perch as a percentage of total consumption varied across years and was highest in 2007 and lowest in 2008 (Table 3; Fig. 4). Predation also varied seasonally. In early summer, consumption of age-0 yellow perch by biomass and numbers was primarily driven by offshore walleye (Table 3; Fig. 4; Fig. 5). Inshore walleye and largemouth bass tended to consume the greatest biomass and numbers of age-0 yellow perch during mid- to late summer, while smallmouth bass tended to consume age-0 yellow perch throughout the growing season, except in 2008 (Fig. 4; Fig. 5). Consumption of age-1 yellow perch tended to occur during early to midsummer (Fig. 4; Fig. 6), but the magnitude of consumption did not show consistent patterns across years (Table 3).

Walleye, smallmouth bass, and largemouth bass consumption of age-0 yellow perch accounted for a significant proportion of yellow perch mortality (Table 4; Fig. 5). Comparisons of observed age-0 yellow perch mortality and consumption estimates showed that the largest gap between consumption and total mortality was in early summer, but declined to near zero by midsummer (Fig. 5). Mortality unaccounted for by the three predators was highest in 2007, when age-0 yellow perch were the most abundant. During 2008 and 2009, walleye, smallmouth bass, and largemouth bass consumed approximately 40% (range 30.8%–55.0%) of the total density of age-0 yellow perch available at the start of the bioenergetics simulations, but only 29% (range 21.8%–40.1%) in 2007 (Table 4). Across all years, offshore walleye consumed the highest percentage of the age-0 yellow perch population (mean: 24.3%), followed by inshore walleye (mean: 7.6%), smallmouth bass (mean: 3.4%), and largemouth bass (mean: 1.4%). Numerically, walleye consumption of age-0 yellow perch was, on average, 10 and 27 times higher than smallmouth bass and largemouth bass, respectively, despite having a population size of only two times smallmouth bass and approximately four times largemouth bass. These patterns were consistent across our simulations using high and low population estimates for all predators (Table 4; Fig. 5).

Table 2. Percent composition by biomass of major prey items in walleye (WE), smallmouth bass (SMB), and largemouth bass (LMB) diets used to inform bioenergetics simulations.

Year	Habitat	Species	Month	n	Age-0 YP	Age-1 YP	Age-0 GIZZ	CRAY	PS	BBH	Other			
2007	Inshore	LMB	June	41	1	95						4		
			July	36	52	29		14	5	<1				
			August	8	100									
			September	8	85			15						
		October	20	64		25	10				<1			
		SMB	June	25	32	24		23					21 ^c	
			July	17	21			74					5	
			August	14	15			85						
	September		15	52			36					11 ^e		
	October	33	32		27	41					<1			
	WE	June	29	64	34							1		
		July	52	81	15			2	<1	0		<1		
		August	92	98					<1	<1		2		
		September	67	92	5			2	<1	<1		<1		
	Offshore	WE	June	126	18	2	77				<1	3	1	
			July	47	96	4							<1	
August			63	88	8	3						1		
September			23	29	28	30			<1			13 ^d		
October		53	70		30									
Inshore		LMB	June	45	5	1	93						1	
			July	15	8	61			18	14			<1	
			August	15	5	41			52			1		
	September		6					67		33				
October	27	23	32	12		10			18		5			
SMB	June	34			70				2	11				
	July	30	10	4							<1			
	August	13	16								<1			
	September	3					1							
October	17			56		25	7	12						
WE	June	16			60		12	18				10 ^f		
	July	35	59	36								5		
	August	58	43	55				<1	<1			2		
	September	52	18	32	34				6			9		
October	47	24	3	60							13 ^b			
Offshore	WE	June	98	9	<1	90				<1		<1		
		July	65	99								<1		
		August	44	36		48				<1		15 ^e		
		September	30	10		84						5		
October	29			100										
2009	Inshore	LMB	June	100	6	2	89					3		
			July	16					12	12	12			
			August	29	20	52			10			4		
			September	4	50	66			50					
		October	21	33				64						
		SMB	June	12	36	18	18		23	5				
			July	19	14	20			58					5
			August	23	13	6			81					
	September		17	11		27		49					13 ^c	
	October	35	4	17	51		28							
	WE	June	10	38	12	28		22						
		July	38	25	24							37	14 ^a	
		August	56	24	55					16	5			
		September	30	37	19	35				2			7	
	October	68	68	10	4				11			7		
	Offshore	WE	June	204	35	13	52						0	
July			90	96	1			2					1	
August			54	68	28	0							4	
September			8	6	23	69							2	
October		23	4		89							7		
Inshore		LMB	June	105	5	6	69						19 ^{a,e}	
			July											
			August											
	September													
October								1						

Note: Major diet items include yellow perch (YP), gizzard shad (GIZZ), crayfish (CRAY), pumpkinseed (PS), and brown bullhead (BBH). Footnotes indicate major species when "other" category exceeds 10% of diet and include the following:

^aEmerald shiner.

^bAge-0 smallmouth bass.

^cAge-0 tessellated darter.

^dTrout-perch.

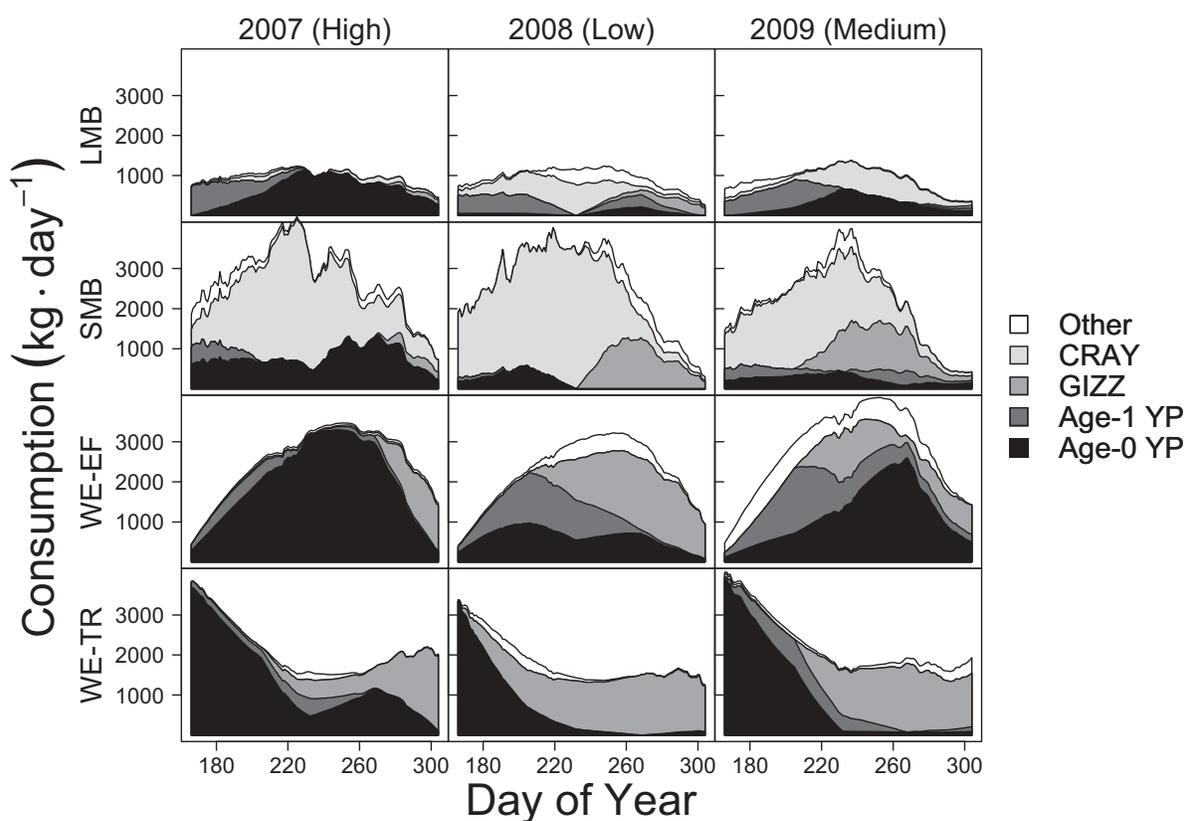
^eAge-0 white perch.

^fAge-0 white sucker.

Table 3. Year- and species-specific consumption estimates ($\text{kg}\cdot\text{ha}^{-1}$) of major diet items for walleye (WE), smallmouth bass (SMB), and largemouth bass (LMB).

Habitat	Species	Year	<i>n</i>	Age-0 YP	Age-1 YP	CRAY	Age-0 GIZZ	BBH	Other	Total
Inshore	LMB	2007	113	4.37 (67.2)	1.31 (20.1)	0.53 (8.1)	0.15 (2.4)	0.02 (0.4)	0.12 (1.8)	6.50
		2008	97	0.52 (8.2)	1.70 (26.8)	2.45 (38.7)	0.52 (8.2)	0.94 (14.9)	0.20 (3.2)	6.33
		2009	84	1.91 (30.9)	1.54 (24.8)	2.27 (36.6)	0.07 (1.1)	0.16 (2.5)	0.25 (4.1)	6.20
	SMB	2007	104	5.35 (29.0)	0.58 (3.1)	10.94 (59.3)	0.35 (1.9)	—	1.24 (6.7)	18.47
		2008	79	1.04 (6.0)	0.11 (0.7)	12.60 (72.5)	2.65 (15.3)	0.47 (2.7)	0.49 (2.8)	17.37
		2009	104	1.67 (11.4)	1.22 (8.3)	7.84 (53.4)	3.15 (21.5)	—	0.80 (5.4)	14.70
	WE	2007	366	13.77 (80.6)	1.26 (7.4)	0.18 (1.1)	1.55 (9.1)	0.10 (0.5)	0.23 (1.3)	17.09
		2008	290	4.16 (27.2)	3.86 (25.2)	—	5.82 (38.1)	0.31 (2.0)	1.15 (7.5)	15.30
		2009	396	8.05 (42.7)	4.55 (24.1)	—	3.12 (16.6)	0.72 (3.7)	2.43 (12.9)	18.86
Offshore	WE	2007	231	9.32 (65.5)	1.16 (8.2)	—	3.45 (24.2)	—	0.31 (2.1)	14.24
		2008	268	4.29 (34.8)	0.03 (0.2)	—	7.27 (59.1)	—	0.72 (5.9)	12.31
		2009	280	6.59 (43.6)	1.95 (12.9)	0.07 (0.5)	5.71 (37.8)	—	0.79 (5.2)	15.11

Note: Major diet items include age-0 yellow perch (Age-0 YP), age-1 yellow perch (Age-1 YP), crayfish (CRAY), age-0 gizzard shad (Age-0 GIZZ), brown bullhead (BBH), and all other diet items (Other) based on estimates from bioenergetics simulations. Percentage of total annual consumption accounted for by each diet item is presented in parentheses.

Fig. 4. Population-level consumption of major diet items by walleye (WE), smallmouth bass (SMB), and largemouth bass (LMB). Seasonal trends in the consumption ($\text{kg}\cdot\text{day}^{-1}$) of age-0 yellow perch (Age-0 YP), age-1 yellow perch (Age-1 YP), age-0 gizzard shad (GIZZ), crayfish (CRAY), and other (Other) diet items by LMB, SMB, inshore walleye (WE-EF), and offshore walleye (WE-TR) during years with high (2007), low (2008), and medium (2009) population abundances of age-0 yellow perch.

Discussion

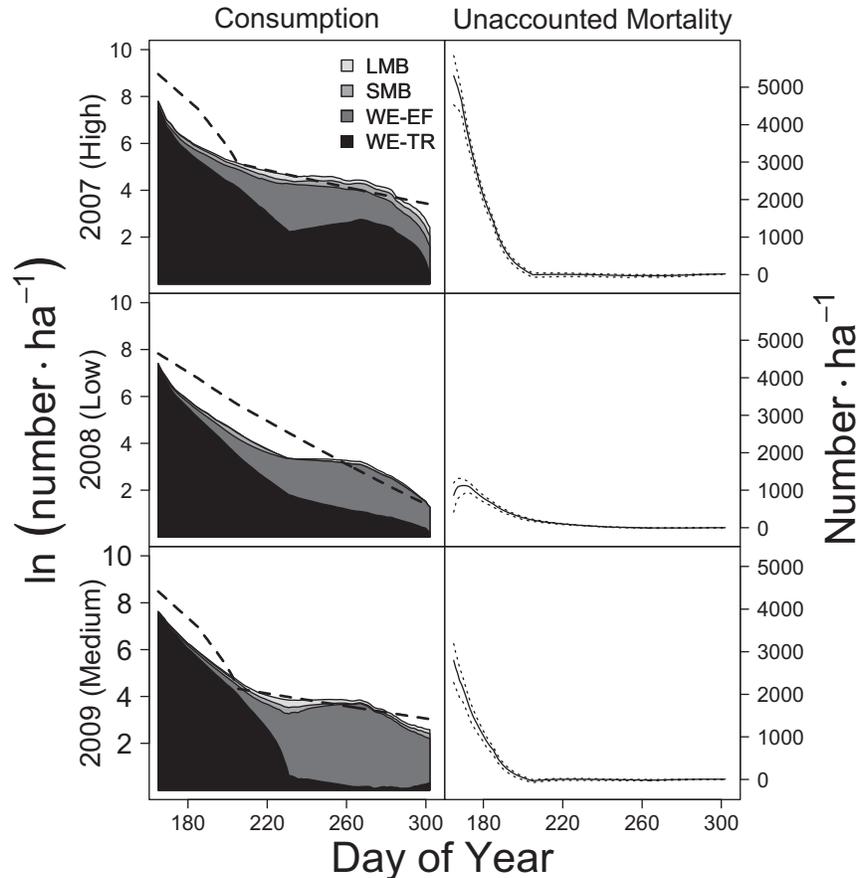
Walleye, smallmouth bass, largemouth bass, and yellow perch are four of the most common sport fish in temperate lakes of North America, yet this study represents the first attempt to quantify the relative contribution of walleye, smallmouth bass, and largemouth bass predation to yellow perch mortality. We show that the importance of each predator on yellow perch mortality varies across space and time, but is disproportionately dominated by walleye in Oneida Lake. By looking at predation dynamics across a range of yellow perch densities, we demonstrate that all predators increase consumption of alternative prey at low yellow

perch densities, while the importance of additional predators on yellow perch increases at high age-0 yellow perch densities.

Walleye and black bass impacts on yellow perch population dynamics

Walleye, smallmouth bass, and largemouth bass are all important predators on age-0 and age-1 yellow perch, but the relative importance of each predator varies across yellow perch life history stage and across habitats. Walleye in offshore habitats primarily consumed yellow perch as larvae, while inshore walleye, smallmouth bass, and largemouth bass primarily consumed yellow

Fig. 5. Comparison of observed age-0 yellow perch mortality and number consumed by walleye (WE), smallmouth bass (SMB), and largemouth bass (LMB). Seasonal trends in the number of age-0 yellow perch ($\ln(\text{number} \cdot \text{ha}^{-1})$) consumed by offshore walleye (WE-TR), inshore walleye (WE-EF), SMB, and LMB during high (2007), low (2008), and medium (2009) population abundances of age-0 yellow perch are indicated. Total loss of age-0 yellow perch based on population estimates from 18 mm, trawl, and seine surveys is indicated with dashed line. Also shown is the difference between age-0 yellow perch mortality from population estimates and WE, SMB, and LMB predation ($\text{number} \cdot \text{ha}^{-1}$) for 2007, 2008, and 2009. Dashed lines indicate upper and lower estimates of unaccounted mortality-based uncertainty in WE, SMB, and LMB population estimates.



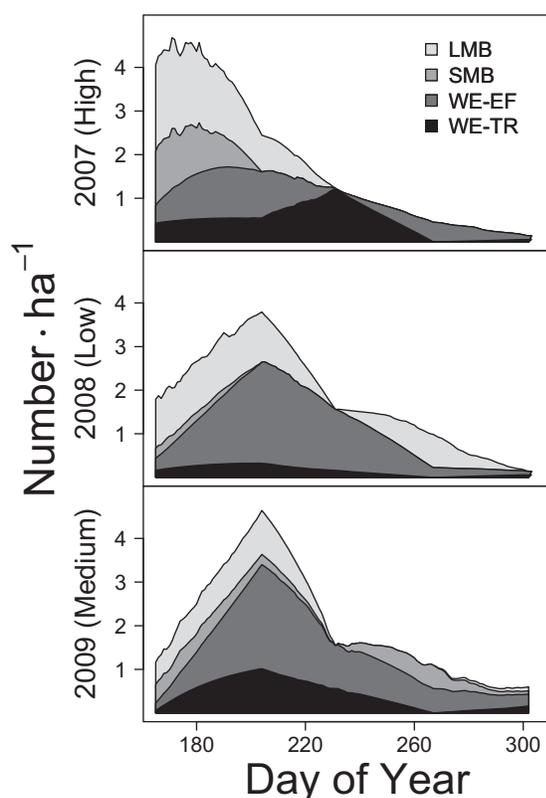
perch as juveniles during late summer and throughout their second year of life. Across all predators in this study, walleye were the dominant consumers of age-0 yellow perch in both habitats, and their effect on age-0 yellow perch population dynamics was disproportionately high relative to their abundance. The timing of walleye predation on age-0 yellow perch drives the disproportionate effect of walleye, occurring in offshore habitats during early summer when age-0 yellow perch are small, abundant, and highly vulnerable.

The disproportionate effect of walleye on yellow perch suggests the uncertainty associated with our estimates of black bass abundances should have little effect on our ability to assess the relative importance of these predators on yellow perch population dynamics. In Oneida Lake, walleye are approximately two to four times as abundant as smallmouth bass and largemouth bass, but they consume on average 10 times and 27 times as many age-0 yellow perch, respectively (range 5–45 times as many). Black bass would have to be several times more abundant than walleye to have a similar effect on yellow perch population dynamics. To date, all sampling indicates that this is not the case. Similarly, uncertainty in our estimates of walleye abundance and age structure are unlikely to influence our ability to draw conclusions from our results. Simulations with high and low abundances for all predators (Table 4; Fig. 5) showed similar patterns across all years

and highlighted the dominant role of walleye as a source of mortality of age-0 yellow perch. Grouping all walleye greater than age-6 into a single age-class is also unlikely to influence our results for several reasons: (i) most of fish in the age-6+ cohort come from a single year class that would have been age-6 through age-8 during the duration of our study (Table S4¹); (ii) walleye length changes less than 10 mm per year after age-7 in Oneida Lake (Table S1¹; Fig. S1¹); and (iii) as a result of this slowing growth, yearly consumption rates are very similar across age-classes after age-4 (Table S5¹).

High consumption of yellow perch by walleye and black bass is not limited to age-0 yellow perch, but continues with age-1 yellow perch and likely plays an important role in determining the number of yellow perch that recruit into the fishery (Nielsen 1980). Our results provide evidence that predation by inshore predators may be one factor contributing to the lack of recovery by the yellow perch population to double-crested cormorant (*Phalacrocorax auritus*) hazing on Oneida Lake (VanDeValk et al. 2002; Rudstam et al. 2004; DeBruyne 2014) and highlight the importance of monitoring multiple habitats and predator species when assessing sources of mortality. Changes in the distribution of juvenile yellow perch from offshore to inshore habitats in Oneida Lake (Fetzer et al. 2015) is also likely contributing to the importance of inshore predators as a source of juvenile and age-1 yellow perch mortality.

Fig. 6. Daily consumption of age-1 yellow perch by walleye (WE), smallmouth bass (SMB), and largemouth bass (LMB). Seasonal trends are shown in the total number of age-1 yellow perch (number·ha⁻¹) consumed by offshore walleye (WE-TR), inshore walleye (WE-EF), SMB, and LMB during 2007 (high), 2008 (low), and 2009 (medium).



Yellow perch abundance, alternative predators, and prey buffering

Age-0 yellow perch abundances directly affected foraging by all predators and influenced our ability to account for age-0 yellow perch mortality from walleye and black bass predation. At high age-0 yellow perch densities, consumption by walleye and black bass was dominated by age-0 yellow perch, but our ability to account for age-0 yellow perch mortality decreased. Conversely, at low yellow perch densities, alternative prey made up a greater proportion of walleye and black bass consumption estimates, but our ability to account for age-0 yellow perch mortality increased. This suggests consumption of age-0 yellow perch by predators not assessed in this study is density-dependent, increasing during years with strong year classes. Similarly, these results suggest strong year classes of age-0 yellow perch may buffer some alternative prey from predation, but not all, depending on the spatial and temporal overlap of age-0 yellow perch and alternative prey species (*sensu* Hall and Rudstam 1999).

The proportion of age-0 yellow perch mortality that could be attributed to walleye and black bass was lowest when age-0 yellow perch were abundant (e.g., 2007), despite the highest consumption of age-0 yellow perch across all predators. This suggests alternative predators, not sampled in this study, increase their consumption when age-0 yellow perch are abundant. High yellow perch densities will increase encounter rates and provide more opportunities for predators to develop search images for age-0 yellow perch. Increasing predator diversity and predation pressure during strong year classes of age-0 yellow perch has also switched age-0 yellow perch mortality from depensatory to compensatory in Oneida Lake. In the 1960s, walleye and yellow perch were the dominant fish species in the lake, and age-0 yellow perch

mortality was depensatory (Forney 1971), because strong year classes could satiate walleye. However, in recent years, strong year classes of age-0 yellow perch no longer satiate the more diverse predator community in the lake, and age-0 yellow perch mortality is no longer depensatory (Irwin et al. 2009). As predator diversity has increased, interannual fluctuations in age-0 yellow perch population dynamics and recruitment have decreased, becoming more stable from year to year (Irwin et al. 2009).

In all years, our inability to account for age-0 yellow perch mortality via walleye and black bass predation was highest in early summer. Interestingly, early mortality of yellow perch has increased in Oneida Lake since the 1990s (Irwin et al. 2009) and is likely driven by white perch. White perch are likely an important contributor for several reasons: (i) white perch catches in the gillnet survey have increased over the last 30 years (Jackson et al. 2012), (ii) their ability to capture larval yellow perch may have increased with higher water clarity, and (iii) large numbers of larval yellow perch are commonly observed in white perch diets collected through the CBFS's long-term gillnet surveys during early summer. We suspect predation by white perch and other species, including age-0 walleye, likely explains the large differences between observed mortality and consumption estimates during early summer. Surprisingly, cannibalism by adult yellow perch does not appear to be a likely source of age-0 yellow perch mortality during early summer, as yellow perch cannibalism in Oneida Lake occurs during mid- to late summer (Tarby 1974) and has declined in recent years (Fetzer 2013).

For each predator in this study, foraging appears to be opportunistic, taking advantage of the most abundant prey species in the lake. Diets of all predators were dominated by age-0 yellow perch during strong yellow perch year classes, but shifted to alternative prey during weak year classes. Walleye shifted consumption to age-0 gizzard shad and other fish species, while smallmouth bass and largemouth bass shifted consumption to age-0 gizzard shad and crayfish. This supports previous observations from Oneida Lake that strong year classes of age-0 yellow perch and gizzard shad buffer other species from predation (Forney 1974, 1977b; Nielsen 1980; Hall and Rudstam 1999; Fitzgerald et al. 2006). By using multiple forage species within the lake, total consumption of these predators was not dependent on availability of age-0 yellow perch, and the total forage base was able to meet the consumptive demands of all predators. Opportunistic foraging by walleye and black bass is consistent with results from other systems (Fayram et al. 2005; Wuellner et al. 2010; Wuellner et al. 2011) and likely explains why negative competitive interactions between walleye and black bass are rarely documented in the literature (Wuellner et al. 2011). However, in systems with a limited forage base, competition between these predators could be more intense. As black bass continue to expand their northern range into systems with lower species diversity, competition between native predators and black bass may increase in intensity and lead to negative population-level consequences for walleye and other native predators (e.g., Vander Zanden et al. 1999).

Age-1 consumption estimates were similar in all years, despite large differences in age-0 yellow perch year-class strength. This suggests age-0 yellow perch no longer buffer age-1 yellow perch from predation as was observed in the 1970s (Nielsen 1980). Consumption of age-1 yellow perch is primarily driven by walleye and black bass in inshore habitats during June and July. During this time period, age-0 yellow perch are still primarily in pelagic, offshore habitats, and other inshore prey fish are too small or rare to be frequently consumed by predators. Therefore, until there is spatial overlap between age-0 yellow perch and age-1 yellow perch in midsummer, age-0 yellow perch do not act as a predation buffer for age-1 yellow perch. However, very strong year classes may reduce the period of high age-1 yellow perch predation to only early summer (Fig. 6; 2007).

Table 4. Walleye (WE), smallmouth bass (SMB), and largemouth bass (LMB) numerical consumption of age-0 yellow perch (YP) and impacts on age-0 YP population dynamics.

Year	Habitat	Species	Age-0 YP density (no.·ha ⁻¹)	Age-0 YP consumption (no.·ha ⁻¹)	Percentage of age-0 YP consumed
2007	Inshore	LMB	109 034	2 109 (1 054, 4 217)	1.9 (1.0, 3.9)
		SMB	—	4 667 (2 333, 9 333)	4.3 (2.1, 8.6)
		WE	—	8 003 (6 586, 9 740)	7.3 (6.0, 8.9)
	Offshore	WE	—	16 816 (13 839, 20 465)	15.4 (12.7, 18.8)
		Total	—	31 594 (23 813, 43 755)	29.0 (21.8, 40.1)
2008	Inshore	LMB	49 178	387 (194, 775)	0.8 (0.4, 1.6)
		SMB	—	1 424 (712, 2 847)	2.9 (1.4, 5.8)
		WE	—	4 232 (3 483, 5 150)	8.6 (7.1, 10.5)
	Offshore	WE	—	13 061 (10 749, 15 896)	26.6 (21.9, 32.3)
		Total	—	19 104 (15 138, 24 668)	38.8 (30.8, 50.2)
2009	Inshore	LMB	66 340	977 (289, 1 954)	1.5 (0.7, 2.9)
		SMB	—	2 030 (1 015, 4 060)	3.1 (1.5, 6.1)
		WE	—	4 507 (3 709, 5 485)	6.8 (5.6, 8.3)
	Offshore	WE	—	20 523 (16 890, 24 977)	30.9 (25.5, 37.6)
	Total	—	28 037 (22 103, 36 476)	42.3 (33.3, 55.0)	

Note: Age-0 yellow perch densities are based on estimated abundances on 15 June. Range of age-0 yellow perch consumption under different scenarios of predator abundance is presented in parentheses.

Research on consumption of yellow perch in Oneida Lake has primarily been limited to studying a single habitat (offshore) and a single predator, such as walleye (Forney 1977a; Lantry et al. 2008), yellow perch (Tarby 1974), and double-crested cormorants (VanDeValk et al. 2002). We employed an approach that addresses foraging by diverse predators on multiple life history stages of yellow perch in both inshore and offshore habitats. Our results clearly demonstrate that predation by inshore walleye and black bass is an important contributor to age-0 and age-1 yellow perch mortality, and greater emphasis should be placed on characterizing predator-prey dynamics across multiple habitats. High foraging plasticity of walleye, smallmouth bass, and largemouth bass allows them to take advantage of changes in prey availability to meet their consumptive demands. This likely contributes to the lack of evidence for direct competition between these species (Fayram et al. 2005; Wuellner et al. 2010, 2011) and suggests that shifts in sport fish populations from walleye to smallmouth bass and largemouth bass observed across north temperate lakes (Robillard and Fox 2006; Hansen et al. 2015; Irwin et al. 2016) are likely driven by alternative drivers, such as poor survival of juvenile walleye (Venturelli et al. 2014). Given walleye and yellow perch early life histories are similar (Craig 1987), our results suggest future research should assess walleye cannibalism during the limnetic stage and consumption of juvenile and subadult walleye by inshore predators. As the relative importance of black bass continues to increase in north temperate lakes, it will be important to understand how predator-prey dynamics change over time and space and how those changes affect population dynamics of ecologically and economically important prey species.

Acknowledgements

We thank the staff and students of the CBFS for assisting with field and laboratory work. The manuscript was improved by suggestions from Joel Nohner, Brian Roth, Derek West, and two anonymous reviewers. Kyle Herreman helped make the map. This study was funded by the New York State Department of Environmental Conservation through Federal Aid in Sport Fish Restoration Project F-48-R to the Cornell Warmwater Fisheries Unit. All sampling was conducted under Cornell University IACUC protocol No. 2006-0088.

References

Benke, A.C., Huryn, A.D., Smock, L.A., and Wallace, J.B. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particu-

lar reference to the southeastern United States. *J. N. Am. Benthol. Soc.* **18**(3): 308–343. doi:10.2307/1468447.

Brooks, J.L., and Dodson, S.I. 1965. Predation, body size, and composition of plankton. *Science*, **150**(3692): 28–35. doi:10.1126/science.150.3692.28. PMID: 17829740.

Carlander, K.D. 1950. Handbook of freshwater fish biology. Wm. C. Brown Company, Dubuque, Iowa.

Carpenter, S.R., Kitchell, J.F., and Hodgson, J.R. 1985. Cascading trophic interactions and lake productivity. *Bioscience*, **35**(10): 634–639. doi:10.2307/1309989.

Craig, J.F. 1987. The biology of perch and related fish. Croom Helm, London.

DeBruyne, R.L. 2014. Evaluating the efficacy of predator management concurrent with changes in prey communities. Ph.D. dissertation, Department of Natural Resources, Cornell University, Ithaca, New York.

Dembkowski, D.J., Willis, D.W., Blackwell, B.G., Chipps, S.R., Bacula, T.D., and Wuellner, M.R. 2015. Influence of smallmouth bass predation on recruitment of age-0 yellow perch in South Dakota glacial lakes. *N. Am. J. Fish. Manage.* **35**(4): 736–747. doi:10.1080/02755947.2015.1044629.

Fayram, A., Hansen, M., and Ehlinger, T. 2005. Interactions between walleyes and four fish species with implications for walleye stocking. *N. Am. J. Fish. Manage.* **25**(4): 1321–1330. doi:10.1577/M04-203.1.

Fetzer, W.W. 2013. Disentangling the effects of multiple ecosystem changes on fish population and community dynamics. Ph.D. dissertation, Department of Natural Resources, Cornell University, Ithaca, New York.

Fetzer, W.W., Luebs, M.M., Jackson, J.R., and Rudstam, L.G. 2015. Intraspecific niche partitioning and ecosystem state drive carbon pathways supporting lake food webs. *Ecosystems*, **18**: 1440–1454. doi:10.1007/s10021-015-9910-9.

Fitzgerald, D.G., Forney, J.L., Rudstam, L.G., Irwin, B.J., and VanDeValk, A.J. 2006. Gizzard shad put a freeze on winter mortality of age-0 yellow perch but not white perch: analysis of age-0 winter survival. *Ecol. Appl.* **16**(4): 1487–1501. doi:10.1890/1051-0761(2006)016[1487:GSPAFO]2.0.CO;2. PMID:16937813.

Fitzgerald, D.G., Zhu, B., Mills, E.L., Rudstam, L.G., Hoskins, S.B., Haddad, D.E., Burch, N.R., Coleman, J.T., and Crabtree, D.L. 2016. Dynamics of aquatic vegetation in Oneida Lake, 1915–2005: a response to ecosystem change. *In Oneida Lake: long-term dynamics of a managed ecosystem and its fisheries.* Edited by L.G. Rudstam, E.L. Mills, J.R. Jackson, and D.J. Stewart. American Fisheries Society, Bethesda, Md. pp. 181–199.

Forney, J.L. 1971. Development of dominant year classes in a yellow perch population. *Trans. Am. Fish. Soc.* **100**(4): 739–749. doi:10.1577/1548-8659(1971)100<739:DODYCI>2.0.CO;2.

Forney, J.L. 1972. Biology and management of smallmouth bass in Oneida Lake, New York. *New York Fish Game J.* **19**: 132–154.

Forney, J.L. 1974. Interactions between yellow perch abundance, walleye predation, and survival of alternate prey in Oneida Lake, New York. *Trans. Am. Fish. Soc.* **103**(1): 15–24. doi:10.1577/1548-8659(1974)103<15:IBYPAW>2.0.CO;2.

Forney, J.L. 1977a. Reconstruction of yellow perch (*Perca flavescens*) cohorts from examination of walleye (*Stizostedion vitreum vitreum*) stomachs. *J. Fish. Res. Board Can.* **34**(7): 925–932. doi:10.1139/f77-144.

Forney, J.L. 1977b. Evidence of inter- and intraspecific competition as factors regulating walleye (*Stizostedion vitreum vitreum*) biomass in Oneida Lake, New York. *J. Fish. Res. Board Can.* **34**(10): 1812–1820. doi:10.1139/f77-247.

Hall, S.R., and Rudstam, L.G. 1999. Habitat use and recruitment: a comparison of long-term recruitment patterns among fish species in a shallow eutrophic lake, Oneida Lake, NY, U.S.A. *Hydrobiologia*, **408**: 101–113. doi:10.1023/A:1017062022447.

- Hansen, G.J.A., Gaeta, J.W., Hansen, J.F., and Carpenter, S.R. 2015. Learning to manage and managing to learn: sustaining freshwater recreational fisheries in a changing environment. *Fisheries*, **40**(2): 56–64. doi:10.1080/03632415.2014.996804.
- Hanson, P.C., Johnson, T.B., Schindler, D.E., and Kitchell, J.F. 1997. Fish bioenergetics 3.0. University of Wisconsin, Sea Grant Institute, WISCU-T-97-001, Madison, Wisc.
- Hodgson, J.R., He, X., Schindler, D.E., and Kitchell, J.F. 1997. Diet overlap in a piscivore community. *Ecol. Freshw. Fish*, **6**(3): 144–149. doi:10.1111/j.1600-0633.1997.TB00156.x.
- Irwin, B.J., Treska, T.J., Rudstam, L.G., Sullivan, P.J., Jackson, J.R., VanDeValk, A.J., and Forney, J.L. 2008. Estimating walleye (*Sander vitreus*) density, gear catchability, and mortality using three fishery-independent data sets for Oneida Lake, New York. *Can. J. Fish. Aquat. Sci.* **65**(7): 1366–1378. doi:10.1139/F08-062.
- Irwin, B.J., Rudstam, L.G., Jackson, J.R., VanDeValk, A.J., Forney, J.L., and Fitzgerald, D.G. 2009. Depensatory mortality, density-dependent growth, and delayed compensation: disentangling the interplay of mortality, growth, and density during early life stages of yellow perch. *Trans. Am. Fish. Soc.* **138**(1): 99–110. doi:10.1577/T07-256.1.
- Irwin, B.J., Rudstam, L.G., Jackson, J.R., VanDeValk, A.J., and Forney, J.L. 2016. Long-term trends in the fish community of Oneida Lake: analysis of the effect of zebra mussel introduction. In *Oneida Lake: long-term dynamics of a managed ecosystem and its fisheries*. Edited by L.G. Rudstam, E.L. Mills, J.R. Jackson, and D.J. Stewart. American Fisheries Society, Bethesda, Md. pp. 375–396.
- Jackson, J.R., VanDeValk, A.J., Forney, J.L., Lantry, B.F., Brooking, T.E., and Rudstam, L.G. 2008. Long-term dynamics of burbot in Oneida Lake, New York: life at the southern edge of the range in an era of climate change. In *Burbot: ecology, management, culture*. Edited by J.L. Paragamian and D.H. Bennett. American Fisheries Society Symposium, Bethesda, Md. pp. 131–152.
- Jackson, J.R., Rudstam, L.G., Brooking, T.E., Krueger, S.D., Holeck, K.T., Hotaling, C., and Forney, J.L. 2012. The fisheries and limnology of Oneida Lake 2000–2011. New York State Department of Environmental Conservation, Albany, New York.
- Lantry, B.F., Rudstam, L.G., Forney, J.L., VanDeValk, A.J., Mills, E.L., Stewart, D.J., and Adams, J.V. 2008. Comparisons between consumption estimates from bioenergetics simulations and field measurements for walleyes from Oneida Lake, New York. *Trans. Am. Fish. Soc.* **137**(5): 1406–1421. doi:10.1577/T07-051.1.
- Liao, H., Pierce, C.L., and Larscheid, J.G. 2004. Consumption dynamics of the adult piscivorous fish community in Spirit Lake, Iowa. *N. Am. J. Fish. Manage.* **24**(3): 890–902. doi:10.1577/M02-178.1.
- Maceina, M.J., and Bettoli, P.W. 1998. Variation in largemouth bass recruitment in four mainstream impoundments of the Tennessee River. *N. Am. J. Fish. Manage.* **18**(4): 998–1003. doi:10.1577/1548-8675(1998)018<0998:VILBRI>2.0.CO;2.
- Maceina, M.J., Boxrucker, J., Buckmeier, D.L., Gangl, R.S., Lucchesi, D.O., Isermann, D.A., Jackson, J.R., and Martinez, P.J. 2007. Current status and review of freshwater fish aging procedures used by state and provincial fisheries agencies with recommendations for future directions. *Fisheries*, **32**(7): 329–340. doi:10.1577/1548-8446(2007)32[329:CSAROF]2.0.CO;2.
- Nielsen, L.A. 1980. Effect of walleye (*Stizostedion vitreum vitreum*) predation on juvenile mortality and recruitment of yellow perch (*Perca flavescens*) in Oneida Lake, New York. *Can. J. Fish. Aquat. Sci.* **37**(1): 11–19. doi:10.1139/f80-002.
- Olson, M.H., and Young, B.P. 2003. Patterns of diet and growth in co-occurring populations of largemouth bass and smallmouth bass. *Trans. Am. Fish. Soc.* **132**(6): 1207–1213. doi:10.1577/T02-146.
- Olson, M.H., Young, B.P., and Blinkoff, K.D. 2003. Mechanisms underlying habitat use of juvenile largemouth bass and smallmouth bass. *Trans. Am. Fish. Soc.* **132**(2): 398–405. doi:10.1577/1548-8659(2003)132<0398:MUHUO>2.0.CO;2.
- Peterman, R.M., and Steer, G.J. 1981. Relation between sport-fishing catchability coefficients and salmon abundance. *Trans. Am. Fish. Soc.* **110**(5): 585–593. doi:10.1577/1548-8659(1981)110<585:RBSCCA>2.0.CO;2.
- Pierce, C.L., Rasmussen, J.B., and Leggett, W.C. 1996. Back-calculation of fish length from scales: empirical comparison of proportional methods. *Trans. Am. Fish. Soc.* **125**(6): 889–898. doi:10.1577/1548-8659(1996)125<0889:BCOFLF>2.3.CO;2.
- Robillard, M.M., and Fox, M.G. 2006. Historical changes in abundance and community structure of warmwater piscivore communities associated with changes in water clarity, nutrients, and temperature. *Can. J. Fish. Aquat. Sci.* **63**(4): 798–809. doi:10.1139/f05-259.
- Rudstam, L.G., and Jackson, J.R. 2012a. Walleye abundance and length at age in Oneida Lake, NY (1957–2011) [online]. Knowledge Network for Biocomplexity. Available from <http://knb.ecoinformatics.org/knb/metacat/datastar.14.49/knb> [accessed 24 March 2015].
- Rudstam, L.G., and Jackson, J.R. 2012b. Yellow perch abundance and length at age in Oneida Lake, NY (1957–2011) [online]. Knowledge Network for Biocomplexity. Available from <http://knb.ecoinformatics.org/knb/metacat/cbfs.127.12/knb> [accessed 24 March 2015].
- Rudstam, L.G., VanDeValk, A.J., and Scheuerell, M.D. 2002. Comparison of acoustic and Miller high-speed sampler estimates of larval fish abundance in Oneida Lake, New York. *Fish. Res.* **57**(2): 145–154. doi:10.1016/S0165-7836(01)00347-2.
- Rudstam, L.G., VanDeValk, A.J., Adams, C.M., Coleman, J.T.H., Forney, J.L., and Richmond, M.E. 2004. Cormorant predation and the population dynamics of walleye and yellow perch in Oneida Lake. *Ecol. Appl.* **14**(1): 149–163. doi:10.1890/03-5010.
- Santucci, V.J., Jr., and Wahl, D.H. 1993. Factors influencing survival and growth of stocked walleye (*Stizostedion vitreum*) in a centrarchid-dominated impoundment. *Can. J. Fish. Aquat. Sci.* **50**(7): 1548–1558. doi:10.1139/f93-176.
- Tarby, M.J. 1974. Characteristics of yellow perch cannibalism in Oneida Lake and the relation to first year survival. *Trans. Am. Fish. Soc.* **103**(3): 462–471. doi:10.1577/1548-8659(1974)103<462:COYPCI>2.0.CO;2.
- Tsehaye, I., Jones, M.L., Bence, J.R., Brenden, T.O., Madenjian, C.P., and Warner, D.M. 2014. A multispecies statistical age-structured model to assess predator–prey balance: application to an intensively managed Lake Michigan pelagic fish community. *Can. J. Fish. Aquat. Sci.* **71**(4): 627–644. doi:10.1139/cjfas-2013-0313.
- Vander Zanden, M.J., Casselman, J.M., and Rasmussen, J.B. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature*, **401**(6752): 464–467. doi:10.1038/46762.
- VanDeValk, A.J., Adams, C.M., Rudstam, L.G., Forney, J.L., Brooking, T.E., Gerken, M., Young, B., and Hooper, J. 2002. Comparison of angler and cormorant harvest of walleye and yellow perch in Oneida Lake, New York. *Trans. Am. Fish. Soc.* **131**(1): 27–39. doi:10.1577/1548-8659(2002)131<0027:COAACH>2.0.CO;2.
- Venturelli, P., Bence, J., Brenden, T., Lester, N., and Rudstam, L. 2014. Mille Lacs Lake walleye blue ribbon panel data review and recommendations for future data collection and management. Report to Minnesota Department of Natural Resources, St. Paul, Minn.
- Wuellner, M.R., Chipps, S.R., Willis, D.W., and Adams, W.E., Jr. 2010. Interactions between walleyes and smallmouth bass in a Missouri River reservoir with consideration of the influence of temperature and prey. *N. Am. J. Fish. Manage.* **30**(2): 445–463. doi:10.1577/M09-066.1.
- Wuellner, M.R., Willis, D.W., Blackwell, B.G., and Lott, J.P. 2011. Empirical assessment of potential interactions between walleye and smallmouth bass. *J. Appl. Ichthyol.* **27**(5): 1173–1180. doi:10.1111/j.1439-0426.2011.01789.x.
- Zhu, B., Fitzgerald, D.G., Mayer, C.M., Rudstam, L.G., and Mills, E.L. 2006. Alteration of ecosystem function by zebra mussels in Oneida Lake: impacts on submerged macrophytes. *Ecosystems*, **9**(6): 1017–1028. doi:10.1007/s10021-005-0049-y.