POPULATION DYNAMICS OF SPAWNING WALLEYE IN OTSEGO LAKE, NY

A Thesis

by

Hayley B. Dower

Submitted in partial fulfillment

for the requirements for the degree of

Masters of Science in Biology

State University College at Oneonta

Oneonta, New York

2020

Approved by:

____

Dr. Daniel Stich (Committee chair)

____

Paul H. Lord (Committee member)

____

Holly Waterfield (Committee member)

Abstract

Walleye (*Sander vitreus*) are recreationally and ecologically important throughout New York State waterbodies. The species has been stocked throughout the state for purposes of establishing and enhancing recreational fisheries and biological control of landlocked alewife populations and milfoil management in the state. In populations supported by large-scale stocking efforts, we rarely collect information about natural reproduction. Walleye were stocked from 2000-2014 in Otsego Lake, New York for biological control of alewife (*Alosa pseudoharengus*) with a secondary purpose of re-establishing a recreational fishery. Following the functional elimination of alewife from the lake, walleye stocking ceased and their population has been supported only by natural reproduction. With the collapse of the alewife population and the increased popularity of a harvest-orientation for walleye, the status of the population and the ability to sustain a fishery into the future is currently uncertain. The purpose of this thesis was to characterize baseline population dynamics of spawning walleye in Otsego Lake, NY following successful re-introduction of the species and establishment of wild reproduction. To achieve this, the specific objectives of my thesis were to: 1) characterize spawning walleye demographics (age, growth, sex ratio, and size distribution), 2) estimate annual survival and population abundance of stream-spawning walleye in the lake, and 3) quantify variability in reproductive phenology as related to environmental cues to inform future sampling efforts. Sex ratios of spawning fish were heavily skewed toward males, but the proportion of females in spawning tributaries has increased in recent years. We found that mean size and age of spawning walleye varied between males and females but increased across sexes during the study period. Additionally, estimated population abundance decreased markedly from about 6,428 individuals in 2008 to 1,724 individuals in 2017 before stabilizing at about 868 individuals in 2018 and 748 individuals in 2019. Taken as a whole, these changes suggest that the naturally reproducing walleye population may be stabilizing at numbers lower than were sustained during years of active stocking, which may affect how harvest influences the population in the future. Finally, I was able to create predictive relationships between environmental variables of interest (date, photoperiod, and degree days) that were useful for predicting the initiation of spawning accurately and, with a precision of about one week, to facilitate more efficient sampling of this population in the future. The information provided by this study will facilitate future management of Otsego Lake. Continued monitoring of this population will help resolve or confirm some of the outstanding uncertainties related to current stock status and trends observed.

Acknowledgements

I would like to thank numerous organizations and groups for helping successfully complete this intensive thesis research. First, I would like to acknowledge all of the people who helped with field research, laboratory research, and other aspects of this thesis. Dr. Daniel Stich, Paul H. Lord, and Holly Waterfield were all major contributors to the completion of this project. A large number of undergraduate, graduate, and other volunteers helped complete the intensive fieldwork during the time of this study. Some organizations I would like to acknowledge are the SUNY Oneonta Biological Field Station, NYS Parks and Recreation and Historic Preservation, NYSDEC Region 4 Fisheries, SUNY Cobleskill, SUNY Oneonta Student Research Grant Program, and National Science Foundation Field Station and Marine Laboratories Grant. This research would not have been possible without the help of all of these contributing groups.

Table of Contents

Preface **1**
INTRODUCTION **1**
Walleye life-history 1
Fate of stocked walleye 3
STUDY SYSTEM **4**
OBJECTIVES **7**

Chapter 1 .... **8**

Population Dynamics of Spawning Walleye (*Sander vitreus*) in Otsego Lake, NY **8**
Introduction **8**
Material and Methods **10**
Sex Ratio 11
Size structure 11
Age and growth 12
Population Abundance 13
Results **13**
Size Distribution 14
Age and growth 14
Population Abundance 15
Discussion **15**
Sex Ratio 16
Size distribution 16

Chapter 2 .... **26**

Spawning Phenology of Walleye (*Sander vitreus*) in Otsego Lake, New York **26**
Introduction **26**
Materials and Methods **27**
Results **30**
Discussion **31**

References **37**

Preface

INTRODUCTION

Recreational fisheries in New York State are an important part of the economy. The net economic value of these fisheries was last estimated to be USD $284 million before the turn of the century (Connelly and Brown 2007). By 2007, the economic contribution of recreational fisheries in New York State was second in the country only to Florida, with an estimated value of more than $2.2 billion (United States Fish and Wildlife Service [USFWS] 2011). Among these fisheries, walleye (*Sander vitreus* Mitchell 1818) is a popular sport fish found in many lakes throughout North America and in New York. Approximately 188 million walleye have been stocked in 35 waters across New York State since the early 1990s (NYSDEC unpublished stocking data). The fish is stocked for purposes that include establishing and enhancing recreational fisheries, biological control of landlocked alewife (*Alosa pseudoharengus*) populations, and milfoil management in the state (Cornwell 2001; Rudstam et al. 2011).

Walleye life-history

Walleye are a cool-water species of fish in the Percidae family. The dorsal coloration of the fish ranges from olive to golden brown while the ventral coloration ranges from yellow to white. The fish has two dorsal fins, one with spines and one without, two spines in the anal fin, and an operculum with a razor-like edge. Walleye also have a large terminal mouth with prominent canine teeth (Froese and Pauly 2019). The eyes of walleye have a reflective layer called the *tapetum lucidum*, which allows the fish to see in low-light conditions. The average length of adult walleye ranges from 330 mm to more than 500 mm with females being larger than males (Froese and Pauly 2019).

Annual spawning occurs in early spring, usually after ice out, when water temperature is 4-11°C (Wolfert et al. 1969). Spawning occurs over gravel substrate where water depth is less than 3 meters and sufficient dissolved oxygen is present, in rivers, along lake shorelines, and in shallow bays (Johnson 1961, Colby et al. 1979). Females and males travel to these areas for spawning at night, from dusk until dawn. Egg production varies with body weight, therefore egg abundance is positively correlated to body size. Larger females produce more eggs than smaller females in the same waterbody (Baccante and Colby 1996). Proper maturation of gonads is dependent on winter water temperature; temperature less than 10 °C are ideal (Schueller and Hansen 2005). The release of eggs can occur on a single night or over the course of multiple nights; the reproductive behavior may vary (Ellis and Giles 1965). Once the eggs and milt have been released, there is no parental care of developing embryos (Balon et al. 1977, Barton and Barry 2011).

Walleye eggs, varying in size from 1.4 to 2.1 mm diameter (Wolfert 1969, Manny et al. 2007), settle in crevices in the substrate where they incubate (Colby et al 1979). The incubation period is temperature-dependent; eggs hatch approximately 12-18 days after fertilization, depending on temperature (Scott and Crossman 1973, Kerr et al. 2004, Manny et al. 2007). Rapid embryo development and short incubation period are associated with higher water temperatures. Survival to hatch varies based on abiotic conditions such as water levels and bottom substrate quality. Lower water levels and smooth or mucky substrate may lead to decreased survival (Johnson 1961). Survival to hatch is also related to egg quality (Moodie et al. 1989) and maternal characteristics (Shaw et al 2018). Larval walleye range in size from 6.0 to 8.6 mm and are weak swimmers that are moved primarily by the current (Scott and Crossman

1973). One to two weeks after hatching, the walleye are strong enough swimmers to distribute themselves in the water column (Colby et al 1979).

Juvenile growth and survival are size dependent, meaning important mechanisms for growth and survival vary with size (Hoxmeier et al. 2006). Survival through the first growing season varies widely, from 0.07% to 0.008% (Serns 1982). Juveniles smaller than 100 mm in length are influenced differently by the factors of predation, prey abundance, temperature, and egg quality (Johnston 1997). Prey abundance and composition are important determinants of survival during the first growing season (Johnston and Mathias 1994). Predation mostly affects larval walleye because they cannot swim on their own; they move with the currents. Predation rates on young walleye vary with walleye size, abundance, size distribution of the predator population and if there is a presence of alternative prey (Hoxmeier et al. 2006). Warmer water temperatures in early summer generally increase growth of juvenile walleye (Hoxmeier et al. 2006). Age of maturation in walleye varies with gender. Females typically reach maturity after three to six years and males reach maturity more quickly in two to four years (Scott and Crossman 1973).

Fate of stocked walleye

Stocking of walleye fry and fingerlings has occurred extensively in New York State, but there is still little information available about the successful establishment of reproducing populations in recipient waters. There is uncertainty about recruitment and population dynamics of stocked walleye, such as timing and location of spawning, their growth and development, and long-term changes in stock productivity (Jones and Bence 2009). There are multiple reasons for the lack of information about stocking success in these systems. First, it is difficult to study the many lakes walleye are stocked into each year due to logistical constraints. Second, interactions of the abiotic and biotic factors are complex and difficult to study, so they are poorly understood (Johnson et al. 1996). Many of the factors involved in establishing reproductive walleye populations are beyond the control of biologists and are unpredictable from year-to-year (Rutherford et al. 2016), and from system to system (Moodie et al. 1989). Knowledge of the population dynamics of stocked walleye is virtually absent in many waters as a result of the uncertainty regarding the initial success of the stocking efforts (Johnson et al. 1996).

STUDY SYSTEM

Otsego Lake is the largest natural lake in New York State Department of Environmental Conservation (NYSDEC) Region 4, and supports multiple recreational fisheries including walleye. The abundance of walleye and other popular game fish in Otsego Lake brings many anglers to the area, providing support to the local economy (Tufts et al. 2015). In 2007, more than $2.2 million was spent on recreational angling by Otsego County residents (Connelly and Brown 2007). Notably, this was during a period of walleye reintroduction in Otsego Lake, when population numbers were unknown during early stocking efforts (Cornwell 2001).

Walleye were historically present in Otsego Lake (Harman et al. 1997), although it is uncertain whether they were native or introduced. The population underwent declines in the mid-1900s, due to a host of factors, likely including unchecked recreational harvest; reduced water quality due to agricultural, residential and urban development; and the introduction of numerous non-native fishes such as common carp (*Cyprinus carpio*) and cisco (*Coregonus artedi*). Walleye likely persisted in small remnant populations through the 1970s and 1980s (Foster 1989).

Prior to 1986, Otsego Lake had high water transparency and high dissolved oxygen. It also contained an open-water algae community that was controlled by large zooplankton (Harman and Sohacki 1980). The ecosystem of Otsego Lake changed when alewife were introduced in the 1980s (Harman et al. 2002). Alewife are efficient predators of grazing zooplankton such as *Daphnia* spp. (Park and Post 2018) and so, have the ability to change zooplankton communities following their establishment in lake systems (Brodersen et al. 2015, Huss et al. 2014). In general, alewife tend to feed on the largest, most efficient grazers in zooplankton communities, which can cause a decrease in the consumption of algae. The introduction of alewife, particularly their direct influence on zooplankton through predation, had effects that permeate through all trophic levels; these changes can cause shifts in both predator and prey fishes through competition and predation on larval fish (Rudstam et al. 2011).

By the time that alewife abundance peaked during 2002, mean cladoceran size in Otsego Lake had decreased, algal biomass increased, water transparency decreased, and deep-water (hypolimnetic) dissolved oxygen decreased (Harman et al. 2002). Along with disrupting zooplankton communities through intensive predation and affecting water quality parameters, alewife are efficient predators of walleye eggs and larvae (Brooking et al. 1998), making it even more difficult for walleye to persist following decades of stress incurred through other vectors. During a socio-economic review that detailed the impact that alewife introduction had on the community, the near absence of walleye was noted as a major issue concerning anglers during this time (Foster et al. 2000), offset only partially by the boon to productivity of cold-water salmonids, such as lake trout (*Salvelinus namaycusch,* Walbaum 1792), provided by alewife.

From 2000 through 2014, NYSDEC in collaboration with SUNY Cobleskill, SUNY Oneonta Biological Field Station, the Otsego Lake Association, Otsego County Conservation

Association, Otsego 2000 and local conservation organizations funded and effectively stocked approximately 0.6 million Oneida Lake walleye in Otsego Lake. Spawning behaviors were first observed in 2006 (Golding et al. 2006). However, at that time it was widely held that alewife predation on larval walleye prevented recruitment (Brooking et al. 1998). Following the stocking period, the alewife population was reduced below detection in targeted gill net and hydroacoustic monitoring by 2011 (Waterfield and Cornwell 2013). Although not measured empirically, it is thought that the presence of a robust lake trout population and increased water clarity following zebra mussel (*Dreissena polymorpha*, Pallas 1771) introduction in 2007 (Horvath 2008) contributed to alewife decline. Routine cold-water fisheries assessments documented a decline in lake trout fitness and abundance in the years following the alewife population decline (NYSDEC Region 4, unpublished data), implying that alewife had been an important component of lake trout diet (Waterfield, SUNY Oneonta BFS, personal communication). Water quality indicators and zooplankton communities also returned to pre-alewife levels in the lake (Albright et al. 2016). As a result of the successful control of alewife in the lake, walleye stocking was ceased in favor of natural reproduction (Van Maaren, NYSDEC Region 4, personal communication).

During the summer of 2016, the first wild-spawned, juvenile walleye were collected from a tributary to Otsego Lake (Dower, personal observation), two years after the last stocking event. Larger, presumably juvenile walleye were collected in the years preceding, but could be identified only through the absence of fin clips and were not thought to be definitive evidence of wild recruitment. The species is currently managed based on a state-wide minimum length (380 mm) and bag limits (3 fish per day) (NYSDEC, fishing regulations, New York Freshwater Fishing Statewide Regulations). Little is known about the population dynamics of historical populations of natural spawning walleye in Otsego Lake prior to alewife introduction. At this time, it is unclear to what degree the fishery is exploited, and how this might influence population characteristics of a newly established, self-sustaining population of walleye in the lake. Basic information about growth rates, sex ratios, survival, and recruitment of young to adulthood would provide useful benchmarks for future management and angling regulations in continued support of what has once again become a popular sport fishery.

OBJECTIVES

The goal of my project is to characterize baseline population dynamics of spawning walleye in Otsego Lake, NY following successful re-introduction of the species and establishment of wild reproduction. To achieve this, the specific objectives of my thesis are to: 1) characterize spawning walleye demographics (age, growth, sex ratio, and size distributions), 2) quantify variability in reproductive phenology as related to environmental cues to inform future sampling efforts, and 3) estimate annual survival, spawning site fidelity, and population abundance of stream-spawning walleye in the lake.

Chapter 1
Population Dynamics of Spawning Walleye (*Sander vitreus*) in Otsego Lake, NY

Introduction

Walleye (*Sander vitreus* Mitchill 1818) are popular sport fish found in many lakes throughout North America. Approximately 188 million walleye have been stocked in 35 waters across New York State since the early 1990s (NYSDEC unpublished stocking data). This fish is stocked for the purposes of establishing and enhancing recreational fisheries and biological control of landlocked alewife (*Alosa pseudoharengus* Wilson 1811), and Eurasian milfoil (*Myriophyllum spicatum*) populations in New York (Cornwell 2001). Alewife control was the primary reason for walleye stocking in Otsego Lake, NY. Otsego Lake, which supports multiple recreational fisheries in addition to walleye, is the largest natural lake in New York State Department of Environmental Conservation (NYSDEC) Region 4. The abundance of walleye in Otsego Lake also brings many anglers to the area, providing support to the local economy (Tufts et al. 2015).

Walleye were historically present in Otsego Lake (Harman et al. 1997), but the population declined in the mid-1900s following the introduction of cisco (*Coregonus artedi* Lesueur 1818). Walleye likely persisted in small remnant populations following these introductions (Foster 1989). Prior to 1986, Otsego Lake had high water transparency, high dissolved oxygen, and an open-water algal community that was controlled by large zooplankton (Harman and Sohacki 1980). The ecosystem of Otsego Lake changed when alewife were introduced. Algal biomass increased, water transparency decreased, and hypolimnetic dissolved oxygen was limiting. These changes jeopardized the cold-water fishery (Harman et al. 2002). Along with disrupting zooplankton communities through intensive predation and affecting water quality parameters, alewife are efficient predators of walleye eggs and larvae (Brooking et al.

1998), making it even more difficult for walleye to persist following alewife introduction in the 1986.

Between 2000 and 2014, NYSDEC, in collaboration with SUNY Cobleskill, SUNY Oneonta Biological Field Station, the Otsego Lake Association, Otsego County Conservation Association, Otsego 2000 and other local conservation organizations, funded and stocked approximately 0.6 million Oneida Lake walleye in Otsego Lake. Following a period of intensive management, the alewife population was reduced below detection in routine sampling by 2011 (Waterfield and Cornwell 2013). Water quality indicators also returned to pre-alewife levels in the lake (Albright et al. 2016). During the summer of 2016, the first wild-reared juvenile walleye was collected (Dower, personal observation). As a result of these successes, stocking was ceased to allow for a population maintained by natural reproduction (Van Maaren, NYSDEC Region 4, personal communication). The species is currently managed based on state-wide minimum length (380 mm) and daily bag limits (3 fish per day) (NYSDEC unpublished data). Little is known about the population dynamics of natural spawning walleye in Otsego Lake due to lack of data prior to alewife introduction. Basic information about growth rates, sex ratios, survival, and recruitment of young to adulthood would facilitate future management efforts.

In recognition of these needs, the goal of this study was to characterize the demographics of stream spawning walleye in Otsego Lake, NY. To do this, we conducted intensive sampling in tributaries used for spawning from 2017 through 2019. Specifically, my objectives were to 1) quantify sex ratios of spawning walleye in multiple tributaries and understand any underlying differences between spawning groups, 2) characterize age and growth of spawning walleye to understand interannual variability and differences in fish using different spawning tributaries, and 3) determine the population abundance of spawning walleye in Otsego Lake.

Material and Methods

The sites used for this study included three tributaries where walleye were known to spawn: Shadow Brook, Hayden Creek, and Cripple Creek (Lydon et al. 2008). All three streams are located at the north end of the lake (Figure 1.1). These tributaries were chosen because they were well known spawning locations for walleye in Otsego Lake. However, concurrent spawning surveys for rainbow smelt (*Osmerus mordax* Mitchill 1814) and white sucker (*Catostomus commersoni* Lacepede 1803) confirmed that these streams hosted the majority of stream spawning by fish during the study period (Decker et al. 2007).

Spotlighting surveys began on April 1, 2017, and the first spawning walleye were caught on April 10, 2017. The spawning run lasted until April 20, 2017, when no more walleye were captured for two consecutive nights of sampling. In 2018, spotlighting began April 1 and the spawning run began on April 10. The spawning run lasted until April 30, 2018 when no more walleye were captured for two consecutive nights of sampling. In 2019, spotlighting began April 1 and the first spawning fish were collected on April 8. The spawning run lasted until April 24, 2019 when no more walleye were captured for two consecutive nights of sampling.

Backpack electrofishing was used to sample walleye at night in each tributary. We began sampling at 2000 hours and continued until 0300 hours or until we were only collecting recaptures from that night. Sampling started at the downstream end of pre-determined sampling reaches and progressed upstream slowly from side to side of the stream using 300 volts at 30 hz. Walleye were placed in plastic totes filled with stream water, without anesthetic, for processing. For each fish, sex was determined, total length was measured in mm, and scales were collected from the left side ventral to the dorsal fin. A uniquely encoded passive integrated transponder (PIT) tag was injected into walleye using a syringe. In 2017, PIT tags were injected in the dorsal musculature, but they were injected into the peritoneal cavity during 2018 and 2019. All fish were released back into the stream alive.

Sex Ratio

We analyzed sex ratio of spawning walleye using generalized linear models. The base model was a binomial logistic regression model where the response variable was “Sex” (0 = female, 1 = male). We used four models to characterize differences in sex ratios between years, tributaries, or both relative to the global mean. These included a “null” model with no explanatory variables that represented lake-wide sex ratio of spawners, an “annual” model with categorical fixed effect of year, a “site-specific” model with categorical fixed effects of stream, and a “year-site” model that included additive fixed effects of year and site as categorical explanatory variables. We used the Akaike Information Criterion corrected for sample size (AICc) to determine the relative support for each of these hypotheses and to select a “best” model (Burnham and Anderson 2002). The difference in scores (ΔAICc) is the difference in AICc between the best model and each of the other models. In general, a model with a lower AICc is a better model. Models with ΔAICc of less than 2.0 are considered to have similar support as the best model. Models with ΔAICc from 2.0 to 4.0 have some support, and models with delta AICc greater than 4.0 are not well supported (Burnham and Anderson 2002).

Size structure

We analyzed size structure of spawning walleye to assess differences between sexes and years. The base model was a generalized linear model with a Gaussian (normal) error structure, where the response variable was total length (TL). We used four models to characterize differences in total length between years, sex, or both relative to the global mean. These included a "null" model with no explanatory variables that represented lake-wide mean of the TL of spawners, an "annual" model with categorical fixed effect of year, a "gender" model with categorical fixed effect of sex, and a "year-sex" model that included additive fixed effects of year and sex as categorical explanatory variables. We used AICc model selection to determine the relative support for each of these hypotheses and to select a best model (Burnham and Anderson 2002).

Age and growth

We modeled growth of spawning walleye using the von Bertalanffy growth function (VBGF; von Bertalanffy 1938). We began by fitting separate growth curves for male and female walleye and used a likelihood ratio test to determine if growth differed significantly between males and females. We failed to detect a difference in the fitted models, so we used a sex-aggregated growth curve to estimate VBGF parameters for the spawning population. We used bootstrap methods to construct confidence intervals for all parameters. To do this, we used a subset of 40% of the data to estimate growth parameters (L_∞, K, t_0), and repeated the process 1,000 times, calculating 95% confidence intervals from the distribution of 1,000 estimates for each parameter. Using these parameters and their 95% CI, we estimated natural mortality (M) using the method recommended by Then et al. (2015):

$$M = 4.118K^{0.73}L_\infty^{-0.33}$$

Survival was then determined as $S = 1 - (1 - e^{-M})$ (Ricker 1975).

Population Abundance

We used mark-recapture data from 750 PIT tagged walleye from 2017-2019 to estimate population size of stream-spawning walleye in each year of study using the closed population estimator of Schnabel (1938). Analyses for 2018 and 2019 spawning runs incorporated recapture data from previous years. The Schnabel (1938) method uses mark and recapture data to estimate population size from marked and unmarked individuals. It relies on repeated observations of previously marked individuals to estimate abundance (*N*) as:

$$\widehat{N} = \frac{\sum_{t=1}^{n} C_t M_t}{\sum_{t=1}^{n} R_t}$$

where M_t is the number of individuals marked and released before sample t, C_t is the total number of individuals caught in sample t, and R_t is the number of previously marked individuals captured in sample t (Schnabel 1938). Important assumptions of this method include that population is closed, meaning there is no emigration or immigration during the time of sampling, each fish (marked or unmarked) has the same probability of being captured in each sample, all marks are recorded correctly, and marks are not lost between sampling events (Schnabel 1938).

Results

A total of 750 unique walleye were collected during three spawning seasons. The greatest number of fish was caught in Shadow Brook each year (Table 1.1). The sex ratio of spawners was heavily skewed toward males in all years and streams. Sex ratios varied significantly between years and sites; however, the best model included only the variable year (Table 1.2). Although we only estimated categorical differences between years, there was a general increase in the proportional representation of females in the population from 2017 to 2019. The mean proportion of females was 11.3% (8.4-15.0% CI) in 2017, 14.9% (11.0-20.0% CI) in 2018, and 20.2% (15.2-26.4% CI) in 2019, indicating an overall increase of nearly 100% in recent years.

Size Distribution

Total length (TL) of spawning walleye ranged from 390 mm to 660 mm (Figure 1.2). The size distribution varied between years and between males and females, as indicated by the inclusion of both year and sex in the best model (Table 1.3). Females (mean = 546 mm, SD = 49 mm) were significantly longer than males across years (mean = 496 mm, SD = 35 mm). However, TL of females increased from 530 mm (SD = 55) in 2017 to 566 mm (SD = 27) in 2019, and TL of males increased from 486 mm (SD = 38) in 2017 to 509 mm (SD = 27) in 2019 (Figure 1.2).

Age and growth

The von Bertalanffy growth models for females and males showed no significant difference in size between males and females according to the likelihood ratio test, so the aggregate growth curve was used to estimate growth parameters and 95% CI (Table 1.4). The estimated parameters were then used to determine the instantaneous natural mortality, M = 0.34 (95%CI = 0.30-0.39), which corresponded to annual survival of S = 0.71 (95%CI = 0.68-0.74) for the spawning walleye population. Using the bootstrapped parameter estimates for L_{∞}, K, t_0, we estimated mean length at age and plotted the resulting growth curves against the raw data (Figure 1.3).

Population Abundance

Abundance of stream spawning walleye was variable between years. Overall, it appears that abundance has decreased during the time of study. Population abundance decreased from an estimated 1,724 spawners in 2017 (95% CI = 1,335 – 2,434) to 868 (95% CI = 604 – 1,295) in 2018. Abundance appeared to stabilize thereafter with a mean of 748 and a 95% CI of 513-1,132 in 2019 (Figure 1.4).

Discussion

Walleye were stocked in Otsego Lake, NY, for biological control of invasive landlocked alewife, which had dramatic effects on lake ecology after they were introduced (Harman et al. 2002). After the termination of a 14-year walleye stocking effort, little was known about the population dynamics, of the now naturally spawning walleye, due to lack of data prior to alewife introduction. The information gathered about sex ratios, size distribution, age and growth structures and population abundance will facilitate future management efforts. The sex ratio of spawners was heavily skewed towards males in Otsego Lake, although this appears to be changing. Likewise, size distributions varied between years and between males and females, and walleye size appeared to have increased from 2017 to 2019, with females being significantly larger than males. After characterizing baseline growth rates and estimating natural mortality of spawning walleyes, we also noted apparent decreases in population abundance of spawners during the past several years.

Sex Ratio

The sex ratio of spawners varied significantly between years and streams, however it is strongly skewed towards males, which is common for walleye populations in other North American waterbodies (Haglund 2016). From 2017 to 2019, there was a general increase in the proportional representation of females. At this time, the reason for this change is not fully understood, possible factors may be the mortality of stocked walleye cohorts, which may have been skewed toward males (Bartron 2018), or selective harvest of large females by anglers (Myers 2014) could contribute to a change in demographics. In Otsego Lake, males reach legal harvest size (380 mm) by age 4, but growth slows thereafter. By contrast, females reach legal harvest size sooner, at age 3, and they reach larger sizes during their lifetime, which might lead to higher rates of exploitation both earlier and later in life.

Size distribution

The size distribution of walleye varied between years and between sexes (Table 1.2). Females were significantly longer than males, which is common for fishes (Pauly 2019); however, we also observed increases in the total length of both males and females from 2017 to 2019 (Figure 1.2). The increase in size each year indicates that the walleye population may be an aging population, with new cohorts not recruiting at a rate typical of stocked fish (Mathias et al. 1992). Alternatively, this could indicate that walleye are incurring high mortality through non-selective harvest (VanDeValk et al. 2005), or that walleye are simply growing to reproductive sizes more slowly in the absence of alewife as an abundant prey base (Cade et al. 2008). The age and growth analysis showed that walleye reach harvestable size at about 3 years of age in Otsego Lake (Figure 1.3), whereas most fish were not sexually mature until about age 4 in this study.

Growth to these ages corresponds with state-wide averages for length-at-age (Wang et al. 2009), but appears to slow thereafter, with maximum ages that are younger than other populations in the state (He et al. 2005; Wang et al. 2009).

The abundance of spawning walleye in Otsego Lake appears to have decreased throughout the study, with a large decrease from 2017 to 2018, and then stabilized, but with a reduced population abundance from 2018 to 2019. While this may otherwise be attributed to estimation error or violations of statistical assumptions (Schnabel 1938), these trends are consistent with analysis of other population demographics considered here. Furthermore, the decreases within this study are also in line with reductions in spawner abundance from 2009 to 2017 (Lydon et al. 2008; Willson et al. 2012). The large decrease from 2008 to 2017, followed by slower rates of decrease in recent years may indicate that the walleye population is beginning to stabilize around the natural carrying capacity for the lake. This would be consistent with historically low abundances of walleye prior to the introduction of alewife (Harman et al. 1997).

The goal of this study was to provide information about the demographics of stream spawning walleye in Otsego Lake, NY. The information provided in this study will facilitate future management of Otsego Lake. Continued monitoring of this population will help resolve or confirm some of the outstanding uncertainties related to current stock status and apparent trends. For example, the estimates derived through this study provide the ability to understand potential outcomes of harvest regulations through use of common fishery management tools such as yield-per-recruit curves (Beverton and Holt 1957) moving forward.

Table 1.1. Total number of walleye caught each year and the number of walleye caught in each Otsego Lake spawning tributary sampled in each year.

Year	Total	Shadow Brook	Cripple Creek	Hayden Creek
2017	530	244	60	116
2018	268	254	0	14
2019	225	195	23	7
Total	1,023	693	83	137

Table 1.2. Model selection statistics for Otsego Lake walleye sex ratio models showing model, number of parameters (K), Akaike information criterion corrected for sample size (AICc), the difference in AICc between the best model and each of the others (ΔAICc), the probability that a given model is the best among those considered (w), and the negative log likelihood (LL) of each model.

Model	K	AICc	ΔAICc	w	LL
Annual	3	653.070	0.000	0.539	-323.520
Year-Site	5	654.282	1.212	0.294	-322.103
Site	3	656.611	3.541	0.092	-325.290
Null (mean)	1	656.991	3.920	0.076	-327.493

Table 1.3. Model selection statistics for size distribution models showing model, number of parameters (K), Akaike information criterion corrected for sample size (AICc), the difference in AICc between the best model and each of the others (ΔAICc), the probability that a given model was the best among those considered (w), and the negative log likelihood (LL) for each model.

Models	K	AICc	ΔAICc	w	LL
Year-sex	5	8925.373	0.000	1.000	-4457.65
Sex	3	9000.544	75.171	0.000	-4497.26
Annual	4	9122.759	197.386	0.000	-4557.36
Null (mean)	2	9190.992	265.619	0.000	-4593.49

Table 1.4. Otsego Lake walleye sex-specific and sex-aggregate parameters of the von Bertalanffy growth function showing means and standard deviations.

Model	L_∞	K	t_0
Female	624 (23)	0.34 (0.04)	0.07 (0.19)
Male	512 (5)	0.62 (0.04)	-0.58 (0.11)
Aggregate	523 (6)	0.57 (0.04)	-0.65 (0.12)

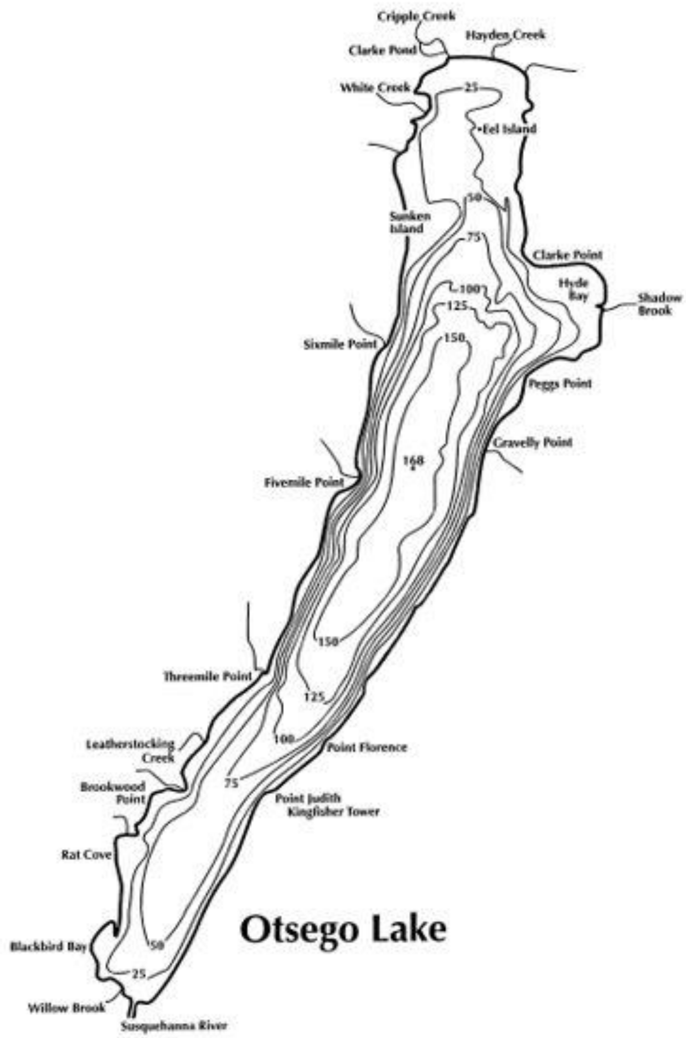

Figure 1.1. Map of Otsego Lake, NY showing electrofishing sites: Hayden Creek, Cripple Creek, and Shadow Brook, at the north end of the lake. Contour lines represent depth (in feet) (SUNY Oneonta Biological Field Station, unpublished data).

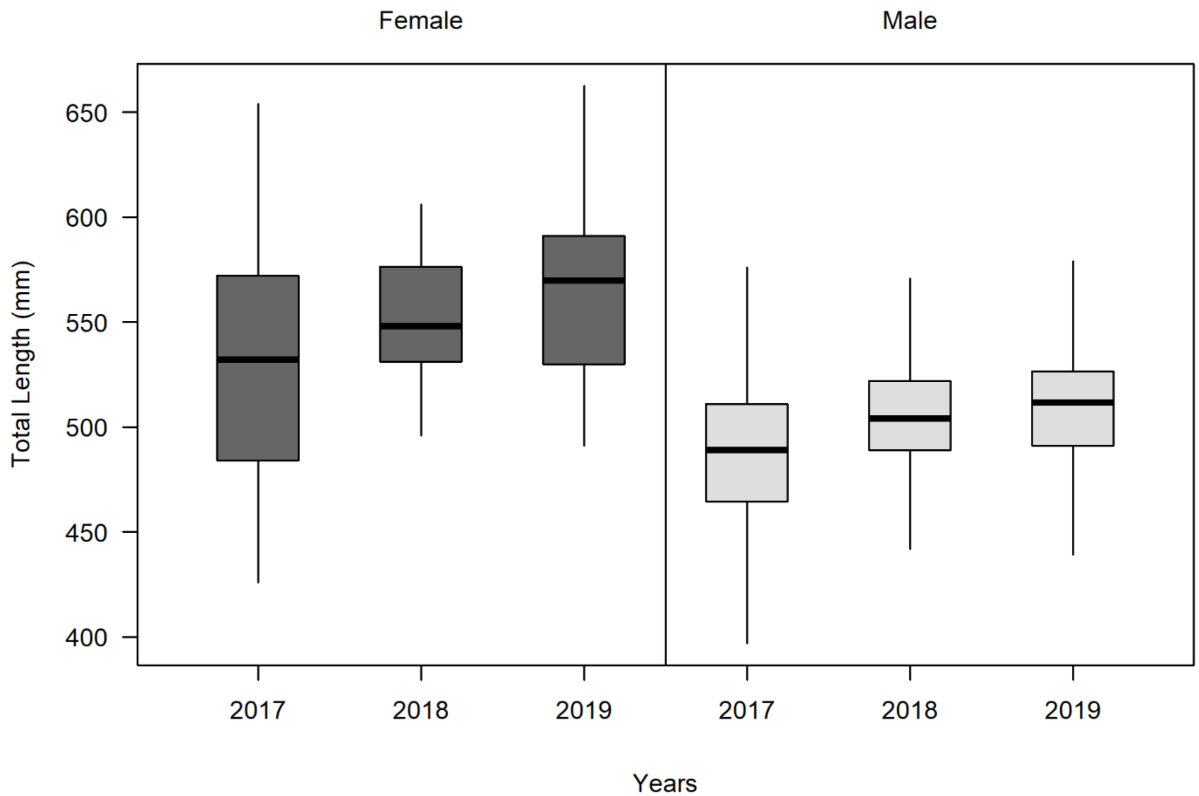

Figure 1.2. Size distribution of Otsego Lake walleye from 2017 to 2019, showing the increase in size for females (left, dark gray) and males (right, light gray) and differences in total length between females and males. The thick, black line represents the median, the box ends represent the inner quartile range, and whiskers correspond to first and ninety-ninth percentiles.

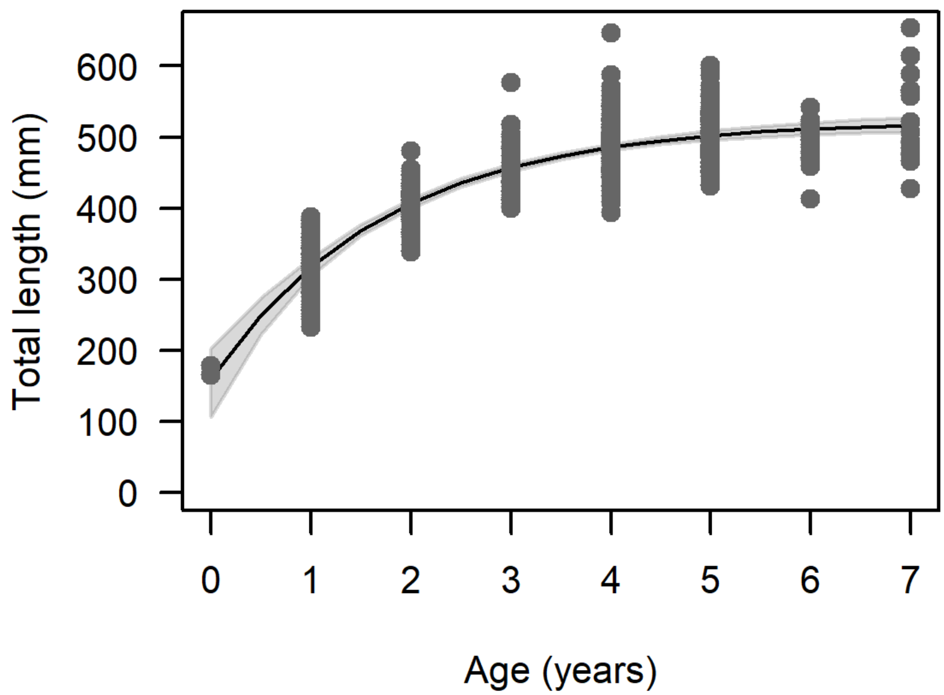

Figure 1.3. Estimated length at age for walleye in Otsego Lake, NY 2017-2019 using von Bertalanffy model. Raw data are shown as gray points, mean predicted length at age is indicated by the solid, black line, and the 95% confidence interval is represented by the gray polygon.

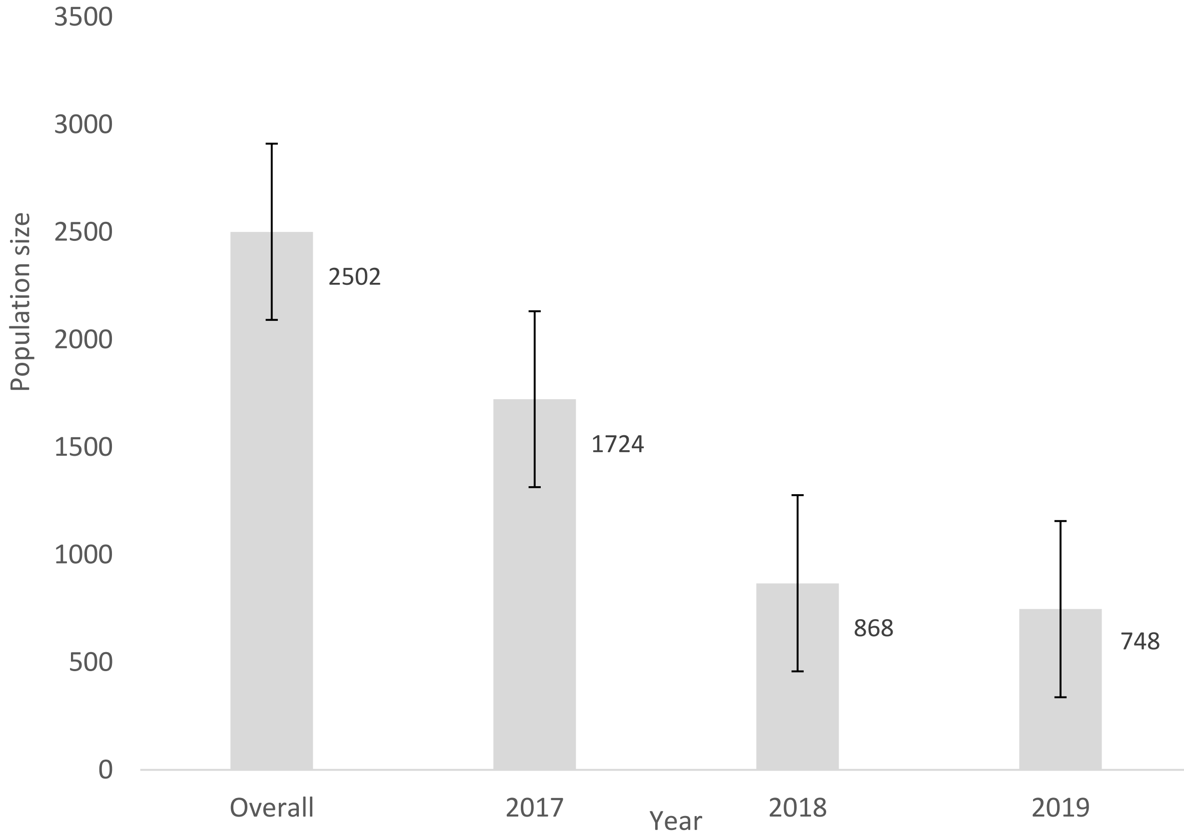

Figure 1.4. Population abundance of spawning walleye in Otsego Lake, NY 2017-2019 using the method of Schnabel (1938).

Chapter 2
Spawning Phenology of Walleye (*Sander vitreus*) in Otsego Lake, New York

Introduction

Walleye (*Sander vitreus*) are popular sportfish throughout North America, and New York State. However, the fate and reproductive ecology of self-sustaining populations following successful establishment through stocking, and subsequent cessation of stocking programs, is poorly understood. Basic information about the timing of reproductive behaviors, including timing of spawning events would be useful in helping biologists plan sampling activities for studies of behavior and population dynamics. In general, spawning events in fish are driven by circannual rhythms entrained by photoperiod (Stark 2007), but temperature may also be a trigger for releasing behaviors related to spawning. Walleye spawn in water temperatures ranging from 4°C to 11°C (Schneider et al. 2010). Environmental cues such as air and water temperature (Lester et al. 2004), photoperiod (Harder et al. 2012), and degree days may all influence when seasonal walleye spawning migrations to tributaries occur (Binder et al. 2010).

Walleye stocking occurred in Otsego Lake, NY from 2000 until 2014 for the primary purpose of controlling alewife (*Alosa pseudoharengus*), and a secondary goal of re-establishing a recreational fishery. Walleye spawning behavior was first documented in Cripple Creek in 2006 (Golding et al. 2006) and was later confirmed in additional tributaries (Decker et al. 2007, Lydon et al. 2008). Stocking was ended in 2014 in favor of natural reproduction following successful control of alewife (Van Maaren NYSDEC Region 4, personal communication). In 2016, the first wild-reared, juvenile walleye was caught in a tributary to Otsego Lake (Dower personal observation).

Initial studies of wild spawning walleye in Otsego Lake have focused on habitat use and behavior (Golding et al. 2006, Decker et al. 2007), estimating abundance and site fidelity (Lydon et al. 2008), and understanding interannual population dynamics (Chapter 1). To effectively and efficiently study the population of walleye, it is necessary to know when their spawning run begins. The spawning run is when most fish will be in tributaries and available for study. Knowledge about the spawning patterns also provides a baseline for monitoring changes over time and varying climate conditions. This is beneficial when trying to identify possible shifts associated with variations in recruitment and stock abundance (Ciannelli et al. 2013).

Walleye were studied in Otsego Lake, NY during the 2017, 2018, and 2019 spawning runs to establish a predictive relationship between environmental variables and the timing of the spawning run in combination with historical data. The purpose of this investigation was primarily to maximize field sampling efficiency and was thus focused on predicting the initiation of spawning based on readily available environmental information. We used Bayesian hierarchical models to predict the number of walleye in each spawning tributary on each day of the run based on day of year, photoperiod, air temperature, and degree days. These relationships were used to predict the start of the spawning run based on readily available environmental data while accounting for variability between streams.

Materials and Methods

The study systems used for this project included three tributaries located at the north end of Otsego Lake, NY (Figure 1.1). All are known spawning sites for walleye: Shadow Brook, Hayden Creek, and Cripple Creek (Lydon et al. 2008). We used a combination of historical trap-netting data (2008 and 2012) and contemporary mark-recapture data to quantify arrival timing as a function of environmental variables (date, photoperiod, temperature, or degree days). Methods for trap-net surveys are detailed in Lydon et al. (2008) and Willson et al. (2012). In 2008, trap nets were deployed in each tributary used for spawning immediately after ice-out on 9 April 2008 and checked daily until 25 April. Fish were later recaptured on the nights of May 9, 10, 15, and 31 using an electrofishing boat (Lydon et al. 2008). In 2012, walleye were collected in the spawning tributaries using electrofishing Smith-Root and Halltech backpacks each night from 20 March to 11 April 2012 (Willson et al. 2012).

We began spotlighting surveys for walleye in each of the spawning streams on 1 April during three consecutive years (2017, 2018, and 2019). We used backpack electrofishing units, Smith-Root and Halltech (300 volts at 30 hz), to collect spawning walleye in streams. Sampling began at 2000 hours and continued until 0300 hours or until we only collected recaptures from that night. We started sampling at the downstream end of pre-determined sampling reaches and slowly progressed upstream moving from side to side of the stream until depth or velocity barriers to sampling were encountered, or all walleye were collected. Walleye were placed in totes filled with stream water, without anesthetic, for processing. For each walleye, sex was determined, total length was measured in mm, and scales were collected from the left side ventral to the dorsal fin. A passive integrated transponder (PIT) tag was injected into each fish with a syringe. Tags were injected into the dorsal musculature in 2017, but they were injected into the peritoneal cavity during the 2018 and 2019 seasons. All fish were released back into the stream alive when data collection was completed.

We used Bayesian hierarchical models to predict counts of walleye in streams during each day and determine the best supported predictor. All models used a negative binomial likelihood for daily counts (Y) because of overdispersion in the data:

$$Y_i = \text{Negative Binomial}(p_i, r),$$

where p was the success parameter (count), and r was the overdispersion parameter. To account for correlation between these parameters during estimation, we parameterized p as:

$$p_i = \frac{r}{(r + \lambda_i)},$$

where λ was the expectation of a log-scale linear predictor with stream-specific intercepts (β_{0ij}), and a shared slope (β_X) and second-order polynomial term (β_{X2}) corresponding to the predictor of interest for each fish (X_i):

$$\log(\lambda_i) = \beta_{0ij} + \beta_X X_i + \beta_{X2} X_i^2.$$

Each stream-specific intercept was drawn from a shared prior with a grand mean of μ_{β_0} and a pooled variance (σ^2). We used a diffuse, normal prior on μ_{β_0}, with a mean of zero and a variance of 100, and we specified a uniform prior on σ^2 between zero and 100. Priors on β_X and β_{X2} were specified as diffuse, normal distributions with a mean of zero and a precision of 100. We used Markov Chain Monte Carlo methods to estimate models in JAGS (Plummer 2003) using the R2jags package (Su and Masanao 2015) in R (R Core Team 2019). For each model, we used three Markov Chains with a total of 30,000 samples, of which the first 15,000 were discarded as burn-in and every tenth sample was retained. The same base model was used with all of the different environmental predictors considered, including day of year, photoperiod, air temperature, and degree days (sum of non-zero Celsius air temperature from January 1 to date of observation). The best model was determined using deviance information criterion (DIC) model selection. Predictions were made from the results of the best model and used to predict the number of walleye in the tributaries on a given day. To test predictive ability, we re-fit the best model using only those data from years prior to 2019, and then predicted the first day on which fish were expected to enter streams in 2019.

Results

The spawning run was characterized by an initial increase in walleye counts, followed by a gradual decrease as the spawning run ended each year. This general trend was observed for all three tributaries, lasting about 15 days each year, and was variable between streams. The earliest fish collection occurred on April 5 during 2008 and the latest occurred on April 30 in 2018. The greatest number of walleye were observed in Shadow Brook each year, and, in general, the spawning run in that stream began earlier and ended later than in the other tributaries. The spawning population in Hayden Creek was second most abundant but was more variable between years. Cripple Creek was the most variable of the three spawning runs and generally the lowest in abundance, with no fish collected there in 2012.

To better understand variability in the timing of walleye spawning, environmental cues (degree days, temperature, photoperiod, and day of year) were incorporated in count models to determine which was the best predictor for walleye spawning in Otsego Lake, NY. Degree days was the best supported predictor, with a DIC of 738.4 (Table 2.1). Photoperiod was the next best supported variable, with ΔDIC of 0.7 (Table 2.1). Neither day of year nor air temperature were as well supported as these two predictors, but the relationship between walleye counts and day of year was statistically significant. We failed to detect a statistically significant relationship between air temperature and counts of walleye in streams. The correlations between each of the environmental predictors and the counts all tended to follow the same patterns. Therefore, predications were made using only the degree day model (Figure 2.1).

The degree day model appeared to be useful for predicting spawning initiation and peak numbers across years, with uncertainty associated with the termination of spawn. According to the degree day model, the maximum number of fish predicted per stream in a given night was about 100 fish based on the upper 95% CRI (Critical Interval). This aligned well with the observed maximum of 111 walleye on April 18 2013 in Shadow Brook. When the 2019 spawning data were omitted from fitting the model, the mean predicted start date for the spawn in 2019 was April 8 (95% CRI = April 2 – April 16) based on degree days calculated from spring 2019 air temperatures prior to the spawn. Incidentally, the first walleye were collected that year on April 8, the same as the predicted start of the spawning run. The run was predicted to terminate on April 30 2019 based on the lower 95% CRI from degree day model predictions. However, mean and upper 95% CRI predictions extended into mid-May 2019. The last day spawning walleye were observed in 2019 was April 25, well before the last predicted spawning dates, indicating considerable uncertainty in prediction of terminal spawning dates.

Discussion

Ecological monitoring, in general, is expensive. A standardized fishery survey can cost from $500 to $3,000 USD (Baldigo et al. 2017). This has led to the conclusion that poorly designed monitoring is wasteful of resources (Legg and Nagy 2006, McDonald-Madden et al. 2010). The ability to better predict biological events of interest, and understand changes in biological parameters, can increase the efficiency of monitoring and reduce waste where limited resources are available for competing monitoring needs (George et al. 2019). Additionally, improved knowledge of biological events can be useful for conservation and management of exploited species.

Understanding the timing of the walleye spawning run in Otsego Lake, NY is important for multiple reasons. This information will be useful when planning field studies, and this can save money and resources that could be reallocated. Understanding the spawning phenology is also important for setting harvest regulations, especially as timing varies between streams and years based on environmental conditions. With knowledge of when the spawning begins and ends, fishing seasons can be adjusted to prevent harvest before and during this spawn. Throughout this study, we were able to quantify relationships between known correlates of spawning behavior including degree days, temperature, photoperiod, and day of year. We established predictive relationships between the environmental cues and the count of walleye and tested these to determine the accuracy and precision of the tool. The predictive models that were created will facilitate planning future studies and determining harvest seasons for this locally important walleye fishery, and the approach is easily extended to other systems.

The best predictor of spawning walleye counts during this study was degree days (accumulated thermal experience) prior to the spawn. Interestingly, daily temperature was a poor predictor of spawning behavior. This inconsistency aligns well with the wide ranges of temperatures (4 – 11°C) that have been reported for spawning in this species (Schneider et al. 2010). Photoperiod also was a useful predictor of walleye spawning behavior during the time period studied, as has been observed elsewhere (Stark 2007), as was day of year (Table 2.1). However, these variables are static, and many not provide robust prediction of phenological events with changes to global climate, and reported shifts in timing of migrations have become increasingly common in recent years (e.g., Otero et al. 2013). Likewise, air temperatures, while readily available through local weather stations, are an indirect indicator of water temperatures, and are inherently more variable during spring at Otsego Lake. Collection of daily water temperature data from tributaries to the lake may provide further improvements to predictive capabilities of the tools developed here.

These findings are important in the fields of fisheries science and management because they can be used to predict spawning initiation and duration. The current walleye fishing season in New York State spans from the first Saturday in May through March 15 in the following spring. Based on observed counts, and on predictions from the degree day model, this season excludes most or all walleye spawning activity in Otsego Lake. Knowing the timing of the spawn will also be useful when planning field activities and will allow biologists to allocate monitoring resources more judiciously. In recent years, multiple field teams monitored streams at night for as many as three weeks before observing the first spawning walleye in Otsego Lake. Our results suggest that this can be reduced to just several days or a week. For example, the lower 95% CRI from the degree day predictions suggested that walleye spawning would initiate on April 2 at the earliest in 2019, just one week before the first walleye were predicted to (and did) spawn that year. Continued refinement of these predictive tools through ongoing data collection has the potential to provide improvements to biological knowledge, survey efficiency, and fisheries management and conservation.

Table 2.1. Model selection statistics for Otsego Lake walleye spawning phenology variable models showing model, number of parameters (K), deviance information criterion (DIC), and the difference in DIC between the best model and each of the others (ΔDIC).

Model variable	**K**	**DIC**	**ΔDIC**
Degree Day + $(\text{Degree Day})^2$	10	738.4	0
Photoperiod + $(\text{Photoperiod})^2$	10	739.1	0.7
Day of Year + $(\text{Day of Year})^2$	10	745.7	7.3
Air Temperature + Air $(\text{Temperature})^2$	10	757.4	19

Table 2.2. Otsego Lake walleye spawning parameter estimates and diagnostic indicators from the best model, including the name of each parameter, log-scale mean, standard deviation, lower and upper bounds to 95% credible intervals (CRI), the Gelman-Rubin (1992) convergence diagnostic $\hat{r}$, and bulk effective sample size (N_{EFF}, number of independent posterior samples) for each parameter. Standardized regression coefficients are based on mean (140.745) and standard deviation (51.587) of degree day observed in the data set. Precision parameters for each parameter are not shown.

Parameter	Mean	SD	Lower 95% CRI	Upper 95% CRI	$\hat{r}$	N_{EFF}
$\beta_{0,\ Cripple}$	2.712	0.300	2.138	3.319	1.002	1700
$\beta_{0,\ Hayden}$	3.146	0.198	2.771	3.552	1.002	1300
$\beta_{0,\ Shadow}$	3.566	0.182	3.214	3.930	1.001	4500
β_X	0.516	0.127	0.268	0.765	1.001	4500
β_{X2}	-0.510	0.100	-0.701	-0.306	1.001	4500
μ_{β_0}	2.852	1.101	-0.212	4.465	1.004	2100

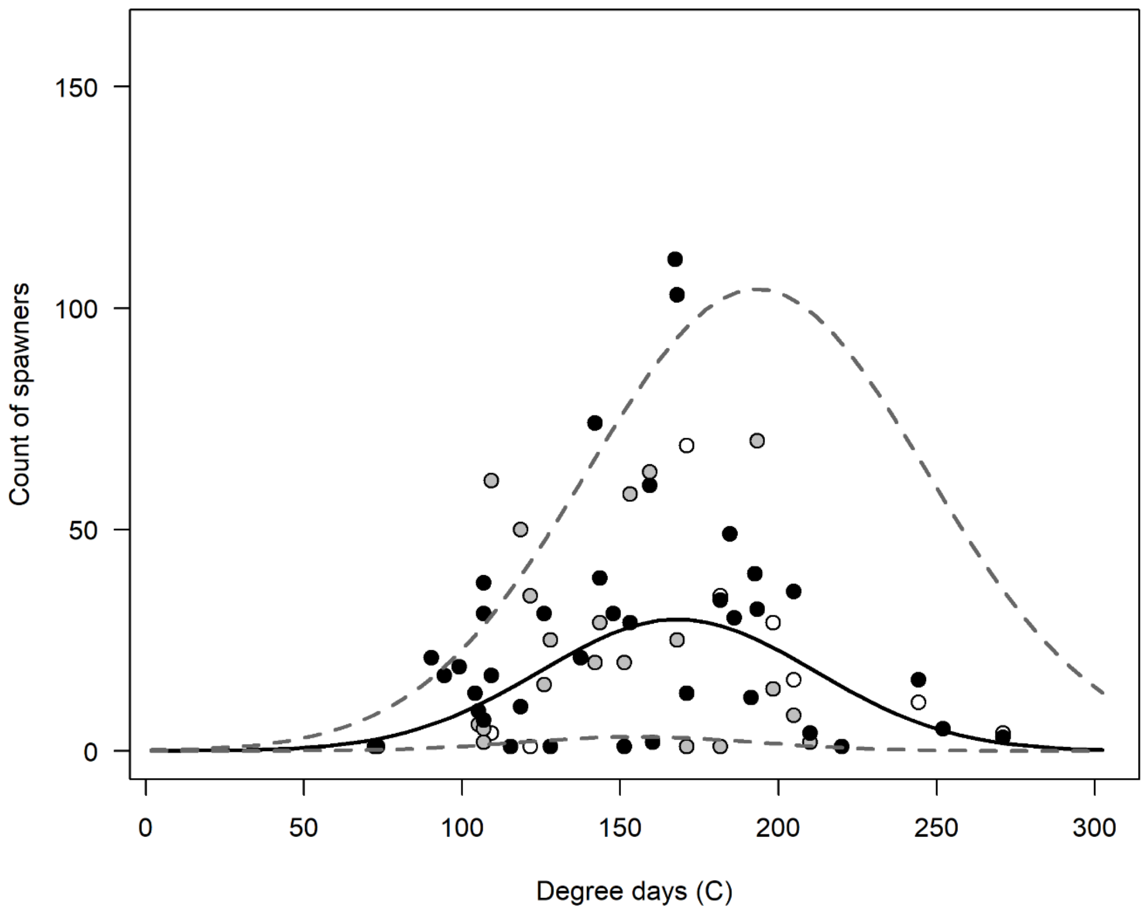

Figure 2.1. Predicted number of walleye in tributaries to Otsego Lake, NY by degree day across years. The solid, black line represents the mean and the gray dashed lines represent the upper and lower confidence intervals. White dots correspond to nightly counts in Cripple Creek across all years, gray dots are Hayden Creek, and black dots represent nightly counts in Shadow Brook.

References

Albright, M. F., C. Murch, and K. Johnson. 2016. A survey of Otsego Lake's zooplankton community. Pages 22—33 W. N. Harman, editor, 49th Annual Report of the State University of New York at Oneonta Biological Field Station, Cooperstown, NY.

Baldigo, B. P., L. A. Sporn, S. D. George, and J. A. Ball. 2017. Efficacy of environmental DNA to detect and quantify brook trout populations in headwater streams of the Adirondack Mountains, New York. Transactions of the American Fisheries Society 146:99-111.

Balon, E. K., Momot, W. T, Regier, H. A. 1977. Reproductive guilds of percids: results of the paleogeographical history and ecological succession. Canadian Journal of Fisheries and Aquatic Sciences 34: 1910-1921.

Barton, B. A., T. P. Barry. 2011. Biology, management, and culture of walleye and sauger. American Fisheries Society 26: 199-232.

Bartron, M. L., N. M. Sard, and K. T. Scribner. 2018. Evaulation of effective number of breeders and coancestry among progeny produced using common hatchery mating strategies. Transactions of the American Fisheries Society 147:185-194.

Baccante, D. A., P. J. Colby. 1996. Harvest, density and reproductive characteristics of North American walleye populations. Annales Zoologici Fennici 33: 601-615.

Beverton, R. J. H., and S. J. Holt, 1957. On the dynamics of exploited fish populations. Fisheries Investigations 19: 1-533.

Binder, T. R., R. L. McLaughlin, D. G. McDonald. 2010. Relative importance of water temperature, water level, and lunar cycle to migratory activity in spawning-phase sea lampreys in Lake Ontario. Transactions of the American Fisheries Society 139: 700-712.

Brodersen, J., J. G. Howeth, D. M. Post. 2015. Emergence of a novel prey life history promotes contemporary sympatric diversification in a top predator. *Nature Communications 6:*1-9.

Brooking, T. E., L. G. Rudstam, M. H. Olson, and A. J. Vandevalk. 1998. Size-dependent alewife predation on larval walleyes in laboratory experiments. North American Journal of Fisheries Management 18:960-965.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. New York, Springer.

Cade, B. S., J. W. Terrell, and M. T. Porath. 2008. Estimating fish body condition with quantile regression. North American Journal of Fisheries Management 28:349-359.

Ciannelli, L., J. A. D. Fisher, M. Skern-Mauritzen, M. E. Hunsicker, M. Hidalgo, K. T. Frank, K. K. M. Bailey. 2013. Theory, consequences and evidence of eroding population spatial structure in harvested marine fishes: a review. Marine Ecology Progress Series 480: 227-243.

Cornwell, M. D. 2001. Walleye reintroduction update: Walleye stocking and electrofishing summary 2000-1. Pages 135—139 in W. N. Harman, editor, 34th Annual Report of the State University of New York at Oneonta Biological Field Station, Cooperstown, NY.

Connelly, N. A., T. L. Brown. 2007. Estimated angler effort and expenditures in New York State Counties. New York statewide angler survey 3: 1-64.

Colby, P., J., R. E. McNicol, R. A. Ryder. 1979. Synopsis of biological data on the walleye. Food and Agricultural Organization Fish Synopsis 119: 1-139.

Decker, B. F., D. S. Stich, M. A. DiSarno, J. R. Foster. 2007. Walleye spawning movements in Otsego Lake, NY. Pages 190—212 in 40th Annual Report of the State University of New York at Oneonta Biological Field Station, Cooperstown, NY.

Ellis, D., V., M. A. Giles. 1965. Spawning behavior of the walleye, *Stizostedion vitreum*. American Fisheries Society 94:358-362.

Foster, J. R., M. S. Gray, M. D. Cornwell. 2000. The impact of alewife introduction on the socio-economic value of the Otsego Lake ice fishery. Pages 84—91 in 33rd Annual Report of the State University of New York at Oneonta Biological Field Station, Cooperstown, NY.

Foster, I. R. 1989. Zooplankton community structure as an ecological indicator of the coldwater fish community of Otsego Lake. Pages 112—116 in 22nd Annual Report of the State University of New York at Oneonta Biological Field Station, Cooperstown, NY.

Froese, R. and D. Pauly. 2019. FishBase. World Wide Web electronic publication. www.fishbase.org.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7: 457-472. https://projecteuclid.org/euclid.ss/1177011136.

George, S.D., B. P. Baldigo, D. S. Stich. 2019. Temporal variability in stream fish assemblage metrics and implications for long-term monitoring. Ecological Indicators 101: 661-669.

Golding, I. T., E. Reinicke, F. R. Foster. 2006. Distribution and movements of walleye (*Sander vitreum*) in Otsego Lake, New York. Pages 66—80 in W. N. Harman, editor, 39th Annual Report of the State University of New York at Oneonta Biological Field Station, Cooperstown, NY.

Haglund, J. M., D. A. Isermann, and G. G. Sass. 2016. Walleye population and fishery responses after elimination of legal harvest on Escanaba Lake, Wisonsin. North American Journal of Fisheries Management 36:1315-1324.

Harder, T. M., G. G. Gotsch, R. C. Summerfelt. 2012. Effect of photoperiod on growth and feed efficiency of fingerling walleye. North American Journal of Aquaculture 74: 547-552.

Harman, W. N., M. F. Albright, D. M. Warner. 2002. Trophic changes in Otsego Lake, NY following the introduction of the alewife (*Alosa psuedoharengus*). Lake and Reservoir Management 18: 215-226.

Harman, W. N., and L. P. Sohacki. 1980. The limnology of Otsego Lake (Glimmerglass). In Bloomfield, J.A. ed. Lakes of New York State. Vol III Ecology of the Lakes of EastCentral New York. Pages 1-129. Academic Press, Inc. New York.

Harman W. N., L. P. Sohacki, M. F. Albright, and D. L. Rosen. 1997. The State of Otsego Lake 1936-1996. State University of New York Biological Field Station, Cooperstown, NY.

He, J. X., L. G. Rudstam, J. L. Forney, A. J. VanDeValk, and D. J. Stewart. 2005. Long-term patterns in growth of Oneida Lake walleye: a multivariate and stage-explicit approach for applying the von Bertalanffy growth function. Journal of Fish Biology 66:1459-1470.

Horvath, T. 2008. Economically viable strategy for prevention of invasive species introduction: case study of Otsego Lake, New York. Aquatic Invasions 3: 3-9.

Hoxmeier, R. J., H., Wahl, D. H., Brooks, R. C., Heidinger. 2006. Growth and survival of age-0 walleye (*Sander vitreus*): interactions among walleye size, prey availability, predation, and abiotic factors. Canadian Journal of Fisheries & Aquatic Sciences, 63: 2173–2182.

Huss, M., J. G. Howeth, J. Osterman, D. M. Post. 2014. Intraspecific phenotypic variation among alewife populations drives parallel phenotypic shifts in bluegill. *Proceedings of the Royal Society B. 281: 2-7.*

Johnson, B. M., M. Vogelsang, R. S. Stewart. 1996. Enhancing a walleye population by stocking: effectiveness and constraints on recruitment. Annales Zoologici Fennici 33: 577-588.

Johnson, F. H. 1961. Walleye egg survival during incubation on several types of bottom in Lake Winnibigoshish, Minnesota, and Connecting Waters. Transactions of the American Fisheries Society 90:3, 312-322.

Johnston, T. A. 1997. Within-population variability in egg characteristics of walleye (*Stizostedion vitreum*) and white sucker (*Catostomus commersoni*). Canadian Journal of Fisheries and Aquatic Sciences 54: 1006-1014.

Johnston, T. A., and J. A. Mathias. 1994. Feeding ecology of walleye, *Stizostedion vitreum*, larvae: effects of body size, zooplankton abundance, and zooplankton community composition. Canadian Journals of Fisheries and Aquatic Sciences 51: 2077-2089.

Jones, M. L. and J. R. Bence. 2009. Uncertainty and fishery management in the North American Great Lakes: Lessons from applications of decision analysis. American Fisheries Society Symposium 70: 1-21.

Kerr, S. J., A. J. Dextrase, N. P. Lester, and C. A. Lewis. 2004. Strategies for managing walleye, Ontario Ministry of Natural Resources, Petersborough, Ontario 1-79.

Legg, C. J. and L. Nagy. 2006. Why most conservation monitoring is, but need not be, a waste of time. Journal of Environmental Management 78: 194-199.

Lester, N. P., A. J. Dextrase, R. S. Kushneriuk, M. R. Rawson, and P. A. Ryan. 2004. Light and temperature: key factors affecting walleye abundance and production. Transactions of the American Fisheries Society 133: 588-605.

Lydon, J. C., M. D. Cornwell, J. R., Foster, T. E. Brooking, and S. Cavaliere. 2008. Mark-recapture and catch per unit effort measures of walleye (*Sander vitreus*) abundance in Otsego Lake, NY. Pages 137-146 in W. N. Harman, editor, 41st Annual Report of the State University of New York at Oneonta Biological Field Station, Cooperstown, NY.

Manny, B. A., G. W. Kennedy, J. D. Allen, and J. R. P. French. 2007. First evidence of egg deposition by walleye (*Sander vitreus*) in the Detroit River. Journal of Great Lakes Research 33: 512-516.

Mathias, J. A., W. G. Granzin, J. F. Craig, J. A. Babaluk, and J. F. Flannagan. 1992. Evaluation of stocking walleye fry to enhance a commercial fishery in a large, Canadian prairie lake. North American Journal of Fisheries Management 12:299-306.

McDonald-Madden, E., P. W. Baxter, R. A. Fuller, T. G. Martin, E. T. Game, J. Montambault, and H. P. Possingham. 2010. Monitoring does not always count. Trends in Ecology and Evolution 25: 547-550.

Moodie, G. E. E., N. L. Loadman, M. D. Wiegand, and J. A. Mathias. 1989. Influence of egg characteristics on survival, growth and feeding in larval walleye (*Stizostedion vitreum*). Canadian Journal of Fisheries and Aquatic Sciences 46: 516-521.

Myers, R. A., M. W. Smith, J. M. Hoenig, N. Kmiecik, M. A. Luehring, M. T. Drake, P. J. Schmalz, and G. G. Sass. 2014. Size- and sex-specific capture and harvest selectivity of walleyes from tagging studies. Transaction of the American Fisheries Society 143:438-450.

Otero, J., J. H. L'Abee-Lund, T. Castro-Santos, K. Leonardsson, G. O. Storvik, B. Jonsson, B. Dempson, I. C. Russel, A. J. Jensen, J. Bagliniere, M. Dionne, J. D. Armstrong, A. Romakkaneimi, B. H. Letcher, J. F. Kocik, J. Erkinaro, R. Poole, G. Rogan, H. Lundqvist, J. C. MacLean, E. Jokikokko, J. V. Arnekleiv, R. J. Kennedy, E. Niemela, P. Caballero, P. A. Music, T. Antonsson, S. Gudjonsson, A. E. Ceselov, A. Lamberg, S. Groom, B. H. Taylor, M. Taverner, M. Dillane, F. Arnason, G. Horton, N. A. Hvidsten, I. R. Jonsson, N. Jonsson, S. McKelvey, T. F. Næsje, Ø. Skaala, G. W. Smith, H. Sægrov, N. C. Stenseth, L. A. Vøllestad. 2013. Basin-scale phenology and effects of climate variability on global timing and initial seaward migration of Atlantic salmon (*Salmo salar*). Global Change Biology 20: 61-75.

Pauly, D. 2019. Female fish grow bigger—let's deal with it. Trends in Ecology and Evolution 34:181-182.

Park, J. S., and D. M. Post. 2018. Evolutionary history of *Daphnia* drives divergence in consumption preference and alters temporal community dynamics of producers. *Ecology and Evolution* 8: 859–865.

Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *In* K. Hornik, F. Leisch, and A. Zeileis, editors. Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003), March 20–22, Vienna, Austria.

R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada 191:29-73.

Rudstam, L. G., T. E. Brooking, S. D. Krueger, J. R. Jackson, and L. Witherbee. 2011. Analysis of compensatory responses in land-locked alewives to walleye predation: a tale of two lakes. Transactions of the American Fisheries Society 140: 1587-1603.

Rutherford, E. S., J. Allison, C. R. Ruetz III, J. R. Elliott, J. K. Nohner, M. R. DuFour, R. P. O’Neal, D. J. Jude, and S. R. Hensler. 2016. Density and survival of walleye eggs and larvae in a Great Lakes tributary. Transactions of the American Fisheries Society 145: 563-577.

Schnabel, Z. E. (1938). The estimation of the total fish population of a lake. American Mathematical Monthly 45, 348-352.

Schneider, K. N., R. M. Newman, V. Card, S. Weisberg, and D. L. Pereira. 2010. Timing of Walleye spawning as an indicator of climate change. Transaction of the American Fisheries Society 139: 1198-1210.

Schueller, A. M., and M. Hansen, 2005. Density Dependence of walleye maturity and fecundity in Big Crooked Lake, Wisconsin, 1997-2003. North American Journal of Fisheries Management 25: 841-847.

Shaw, S. L., G. G. Sass, and J. A. VanDeHey. 2018. Maternal effects better predict walleye recruitment in Escanaba Lake, Wisconsin, 1957-2015; implications for regulations. Canadian Journal of Fisheries and Aquatic Sciences 75: 2320-2331.

Scott, W., B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada 184: 1-96.

Serns, S. L. 1982. Walleye fecundity, potential egg deposition, and survival from egg to fall young-of-year in Ecanaba Lake, Wisconsin, 1979-1981. North American Journal of Fisheries Management 2: 388-394.

Stark, J. W. 2007. Geographic and seasonal variations in maturation and growth of female Pacific cod (*Gadus macrocephalus*) in the Gulf of Alaska and Bering Sea. Fishery Bulletin 105: 396-407.

Su, Yu-Sung and Masanao Yajima. 2015. R2jags: Using R to run 'JAGS'. R package version 0.5-7. URL: https://CRAN.R-project.org/package=R2jags

Then, A. Y., J. M. Hoenig, N. G. Hall, D. A. Hewitt, and E. Jardim. 2015. Evaluating the predictive performances of empirical estimators of natural mortality rate using information on over 200 fish species. ICES Journal of Marine Sciences 72:82-92.

Tufts, B. L., J. Holden, and M. Demille. 2015. Benefits arising from sustainable use of North America's fishery resources: economic and conservation impacts of recreational angling. International Journal of Environmental Studies 72:850-868.

U.S. Department of the Interior, U.S. Fish and Wildlife Services, and U.S Department of commerce, U.S. Census Bureau. 2011 National Survey of Fishing, Hunting, and Wildlife-Associated Recreation.

VanDeValk, A. J., J. L. Forney, J. R. Jackson, L. G. Rudstam, T. E. Brooking, and S. D. Krueger. 2005. Angler catch rates and catchability of walleyes in Oneida Lake, New York. North American Journal of Fisheries Management 25:1441-1447.

von Bertalanffy, L., 1938. A quantitative theory of organic growth (inquiries on growth laws. II). Human Biology 10:182-213.

Wang, H., H. A. Cook, D. W. Einhouse, D. G. Fielder, K. A. Kayle, L. G. Rudstam, and T. O. Hook. 2009. Maturation schedules of walleye populations in the Great Lakes Region: comparison of maturation indices and evaluation of sampling-induced biases. North American Journal of Fisheries Management 29:1540-1554.

Waterfield, H. A., and M. Cornwell. 2013. Hydroacoustic survey of Otsego Lake's pelagic fish community, spring 2013. Pages 213-220 in W. N. Harman, editor, 46th Annual Report of the State University of New York at Oneonta Biological Field Station, Cooperstown, NY.

Willson, J., J. R. Foster, and M. D. Cornwell. 2012. 2012 population estimate of walleye (*Sander vitreus*) in Otsego Lake. Pages 195-200 in W. N. Harman, editor, 45th Annual Report of the State University of New York at Oneonta Biological Field Station, Cooperstown, NY.

Wolfert, D. R. 1969. Maturity and fecundity of walleyes from the eastern and western basins of Lake Erie. Journal of the Fisheries Research Board of Canada 26: 1877-1888.