

EVALUATING EFFECTS OF ECOLOGICAL CHANGE ON IMPORTANT SPORT
FISHES IN ONEIDA LAKE, NEW YORK

A Dissertation

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Brian James Irwin

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Brian James Irwin, Ph.D.

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Aquatic ecosystems provide numerous resources to diverse user groups. As a result, these systems are often targets of planned management actions but are also sensitive to uncontrolled biological invasions. Oneida Lake has a rich history of ecological study across multiple trophic levels and has experienced notable perturbations to its food web during the past half-century. To evaluate large-scale ecological changes, I used multiple approaches to examine dynamics in several long-term data series. In Chapter 1, I quantified age-0 yellow perch density at four early life stages and calculated mortality and growth rates. At all stages, densities have declined over time. Mortality rates from egg to 18mm showed no time trend, increased for 18mm – 1 Aug., and decreased from 1 Aug. – 15 Oct. Depensatory mortality, prevalent in the 1960s to early 1970s, was not seen in recent years. Growth has increased, was density dependent, and was significantly correlated with increased Secchi depth. The combined effect has been a decline in abundance and an increase in individual size by the end of the first year. In Chapter 2, I combined three long-term data sets for walleye to simultaneously estimate mortality, catchability in gillnets and trawls, and density using a non-linear minimization routine. A multi-mortality model with two time periods suggested decreased fishing mortality but increased sub-adult mortality during recent years when more restrictive size limits were in place and double-crested cormorants were abundant. In Chapter 3, I used gillnet and bottom trawl catches to identify changes in fish abundance after zebra mussel colonization. Based on *a priori* expectations, I evaluated changes between pre- and post-zebra mussel periods and compared observed values with projections from 30-year

population trajectories. Between periods, gillnet catches of Pelagic fishes declined while catches of Littoral and Benthic fishes increased. Population trajectories indicated declining percids; however, gillnet catches of smallmouth bass and pumpkinseed sunfish remained high throughout much of the zebra mussel period. Changing ecological conditions (increased water clarity, temperature, and macrophytes; altered nutrient pathways; and variable top predators) appear to favor a fish community shift away from percids and towards centrarchids.

BIOGRAPHICAL SKETCH

Brian was born in Charleston, IL on 5 June 1976. He attended Mattoon High School, graduating in 1994. He graduated in 1998 with a Bachelor's of Science from the University of Illinois. While at Illinois, he worked as an undergraduate laboratory assistant for Dr. David H. Wahl and Dr. Lawrence Page, and he also completed an internship with the Illinois Natural History Survey. Following graduation, he enrolled in the Department of Fisheries and Allied Aquacultures at Auburn University. In 2000, he married Rachel L. (Hawley) Irwin. He completed a Master's of Science with a focus on Fish Ecology in 2001, under the guidance of Dr. Dennis R. DeVries. In 2001, he moved to Syracuse, NY and enrolled in the Department of Natural Resources at Cornell University.

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PREFACE

Causes and Consequences of Ecological Changes in Freshwater Ecosystems

Human-induced global change is accelerating (Vitousek et al. 1997). Although terrestrial developments, such as urbanization and clear-cutting of forests, provide vivid visual evidence of the effects of human pursuits, aquatic natural resources are similarly sensitive to anthropogenic actions (Schindler 1997, 2001). Recent estimates suggest that humans use more than half of all accessible freshwater runoff (Postel et al. 1996). Currently, anthropogenic modifications of aquatic ecosystems continue at unprecedented scales (e.g., Wu et al. 2004), transportation of exotic organisms continues to be ineffectively controlled (Holeck et al. 2004), and human activities increasingly affect fresh waters through a variety of indirect pathways (e.g., Kaushal et al. 2005). Of additional concern, is that these human-induced influences can be irreversible once set into motion, and they can impose positive-feedback loops that would exacerbate their future effects. Unfortunately, societal uses of freshwater resources are often incongruous with ecological needs (Baron et al. 2002). In fact, implementation of viable short-term management targets can still yield long-term ecological disasters (e.g., the Aral Sea; Postel 2000). Ultimately, fresh water is a critical resource that is only available as a finite supply – a limitation that is already felt in many parts of the world and will become more pronounced in the future as the availability of clean, fresh water to natural processes will likely be reduced by increased societal demands due to the rapid increase in human population size (e.g., the diversion of freshwater supplies to urban areas), increased pollution, the spread of invasive species, and other ecological changes (Naiman et al. 1995; Naiman and Turner 2000; Postel 2000; Jackson et al. 2001). Simply put, we are approaching, or have possibly passed, the point at which there will not be enough fresh water to go around.

The survival of aquatic organisms is related to a variety of environmental factors and anthropogenic influences, and shifts in these relationships are common under conditions of ecological change. Both planned management actions and unplanned introductions of nonindigenous organisms can cause shifts in aquatic food web structure through a combination of direct and indirect effects (Mills et al. 1994). For instance, nutrient reductions can strongly influence aquatic communities, even on large scales (Stockner et al. 2000; Ludsin et al. 2001; Mills et al. 2003). Likewise, the invasion and rapid colonization of exotic organisms, such as the zebra mussel *Dreissena polymorpha*, have disrupted trophic interactions in many freshwater systems throughout much of North America (Nalepa and Schloesser 1993; MacIsaac 1996; Mayer et al. 2000). Additionally, overexploitation of aquatic organisms has contributed to alteration of food web structure (Pauly et al. 2000). Fishes are generally the targets of heavy exploitation (i.e., they provide substantial economic, recreational, and nutritional resources), while also being influenced by a variety of climatic and less-direct anthropogenic effects (Meisner et al. 1987; Mills et al. 2003). Preservation of fishes, both in terms of yield and biodiversity, will rely on improved understanding of fish community responses to ecological changes.

Increased Understanding Through Analysis of Long-term Data

The analysis of ecological information often reflects either a predetermined experimental design or retrospective examination of available data. A well-constructed experimental design can have many advantages over retrospective studies, including an increased level of control and the ability for repeatability. However, freshwater ecosystems are often unavailable for controlled manipulation to test ecological theories (due to economical, ethical, or purely physical constraints). Even so, it is becoming increasingly apparent that important freshwater ecosystems are

experiencing increased demands and can be sensitive to both sudden perturbation (e.g. invasive species) and long-term changes (e.g. global warming). In order to ascertain the consequences of perturbations, it is usually necessary to identify the baseline conditions that preceded ecological change. Long-term monitoring programs can provide such information (e.g., Schindler 1997), and retrospective analyses of monitoring data should not be undervalued. Recently, ecosystem-level studies and ecosystem-based management have risen to the forefront of applied ecology (Carpenter et al. 1995; Link 2002; Pikitch et al. 2004). This movement has been driven by the need to understand the complex mechanisms operating in freshwater ecosystems combined with the recognition that more holistic and adaptive management approaches are valuable steps toward sustainable use of aquatic resources.

Oneida Lake as a Study System

Oneida Lake has become one of the most studied freshwater ecosystems in North America due, in part, to its recreational and economic importance. Long-term monitoring programs have produced data series on multiple trophic levels ranging from algae to top predators (Adams and Hankinson 1928; Harman and Forney 1970; Greeson 1971; Mills et al. 1978; Forney 1980; Mills and Forney 1988; Hall and Rudstam 1999; Rudstam et al. 2004). Walleye *Sander vitreus* and yellow perch *Perca flavescens* are the most sought after sport fishes and have remained important components of the Oneida Lake food web since studies of the population dynamics of these two species were initiated by researchers at the Cornell Biological Field Station in 1957 (Forney 1980; Mills and Forney 1988). As a result, Oneida Lake has become a textbook example for percid interactions (Diana 1995; Craig 2000). Since the early 1960s, Oneida Lake has experienced several notable ecological changes, including

declines in phosphorus levels and phytoplankton abundance (Idrisi et al. 2001; Zhu et al. *in press*). During the 1980s, alternative forage species, such as white perch *Morone americana* and gizzard shad *Dorosoma cepedianum*, occasionally produced abundant young of the year. The exotic zebra mussel was found in high abundance in 1992 (Mayer et al. 2002). During this same period, a resident population of double-crested cormorants *Phalacrocorax auritus* increased rapidly, triggering management efforts to reduce their numbers (Coleman 2003). Recently, other fishes have gained attention, including the successful reintroduction efforts for lake sturgeon *Acipenser fulvescens* (a threatened species in NY state; Jackson et al. 2002) and an increase in high-profile angling tournaments targeting black bass *Micropterus* spp. (e.g., B.A.S.S., CITGO Bassmaster).

Summary of Thesis Chapters: Results, Synthesis, & Implications

The objective of my dissertation was to evaluate the effects of large-scale ecological changes on important sport fishes. To achieve this objective, I used multiple approaches to examine several long-term data series from Oneida Lake. Because fish recruitment remains an area of great interest to fisheries ecology (Fuiman and Werner 2002) and early life stages of fishes may be particularly sensitive to ecological change, I evaluated a suite of environmental and biological variables against observed mortality and growth rates of age-0 yellow perch for a >40 year period (see Chapter 1). Several of the included potential explanatory variables (e.g., temperature, and water clarity) would be expected to respond to ecological changes. Mortality and growth rates were calculated for intervals that occurred between four early life stages of age-0 yellow perch. Across time, age-0 yellow perch density has declined at each of these early life stages. Mortality rates were variable across early-life-stage intervals, with no time trend present from egg to 18mm (interval 1), an

increase during the 18mm – 1 Aug. (interval 2), and a decrease during 1 Aug. – 15 Oct. (interval 3). Predation-driven compensatory mortality was prevalent for age-0 yellow perch during the 1960s and early 1970s (Forney 1971, 1980), but was not seen in recent years. During both interval 2 and interval 3, growth rates increased and were density dependent. Increased water clarity was identified as an important variable related to the successful transition through the first year of life for age-0 yellow perch. Variation in environmental factors can strongly influence early-life-stage survival through both short (e.g., high wind events) and long terms (e.g., changes in foraging arenas and accumulation of predator biomass).

In Chapter 2, I constructed a baseline model using three long-term data sets for walleye and simultaneously estimated mortality, gear catchability, and density using a non-linear minimization routine. Additionally, I hypothesized that sub-adult mortality had increased during a period of increased numbers of double-crested cormorants (e.g., VanDeValk et al. 2002; Rudstam et al. 2004). Using a multi-mortality model with two time periods produced decreased fishing mortality (due to imposed vulnerabilities and more restrictive harvest regulations) but increased estimates of sub-adult mortality during recent years when double-crested cormorants were abundant.

In Chapter 3, I evaluated long-term patterns in the Oneida Lake fish community using data from both gillnet and bottom trawl catches. The primary objective for this chapter was to identify changes in fish abundance after zebra mussel colonization. Because zebra mussels can have strong and multiple effects on aquatic food webs and cause corresponding cascades through multiple trophic levels, I expected to observed fish community changes between pre- and post-zebra mussel periods. Between periods, gillnet catches of Pelagic fishes declined while catches of Littoral and Benthic fishes increased. For each species and grouping, I also compared observed values for both gears with projections from 30-year population trajectories.

These population trajectories indicated a strong decline of percids over time. However, gillnet catches of both smallmouth bass and pumpkinseed sunfish remained high throughout much of the zebra mussel period. Overall, the Oneida Lake fish community has experienced increases in water clarity, temperature, and macrophytes, as well as altered nutrient pathways and variable top predators. Combined, these changes will likely favor a fish community shift away from percids and towards centrarchids.

Review of Related Contributions

Many of the long-term data presented here have also contributed to a large-scale comparative project between Oneida Lake and the Bay of Quinte, Ontario. These two systems were especially well suited for comparative study because both systems have experienced similar ecological changes over the past three decades and can provide detailed data for multiple trophic groups. It is our belief that such large-scale comparative work can produce insights that would not have been otherwise attainable (Koops et al. 2006). Ongoing comparative work includes evaluating climate patterns and dynamics of catch-per-unit-effort indices from both Oneida Lake and the Bay of Quinte (Casselman et al. *in prep.*) as well as an assessment of the relative catches across additional aquatic ecosystems (Fitzgerald et al. *in prep.*)

One of the primary objectives for this comparative study was to construct Ecopath with Ecosim models (Christensen et al. 2004) for each of three ecologically-distinct periods for both systems (Irwin et al. *in prep.*; Koops et al. *in prep.*). For these models, annual parameters (1972 to 2002) were compiled for 42 trophic groups, including 23 fish groups in Oneida Lake. For each included species or group, input parameters for biomass, a production to biomass ratio, a consumption to biomass ratio, and diet composition estimates are required. Based on these inputs, the Ecopath

software was then used to estimate ecotrophic efficiency, which Christensen et al. (2004) define as the production utilized within the system. When data were available, a time-series of annual data were generated for each of the required input parameters in order to also evaluate variability over time. Input values were summarized into three ecologically distinct time stanzas (for Oneida Lake: Stanza 1 = 1972-1985, Stanza 2 = 1986-1991, Stanza 3 = 1992-2002). Definitions of the Oneida Lake Ecopath periods are:

Stanza 1: Pre-introduction of zebra mussels and pre-control of phosphorous,

Stanza 2: Pre-introduction of zebra mussels and post-control of phosphorous,
and

Stanza 3: Post-introduction of zebra mussels and post-control of phosphorous.

These ecosystem models will allow for simulations to gauge system responses to perturbations and explore additional scenarios that would be intractable to otherwise implement (e.g., removing zebra mussels). Such scenarios can help reveal system sensitivities to various stressors and aid understanding of the effects of exotic species. Overall, the use of multiple approaches and interdisciplinary collaboration to evaluate “similar symptoms in separate systems” through comparative study has produced several unique insights, increased confidence in conclusions, and identified potential avenues for future research (Koops et al. 2006).

Concluding Remarks

Human influence on the global condition is unique both in its magnitude and number of pathways, and one end result is an irreplaceable loss of biodiversity (Ehrlich and Wilson 1991). Because climate change, species invasions, and other anthropogenic effects will likely continue to occur at different temporal and spatial scales, disentangling the effects of these stressors will be challenging. I suggest the

application of multiple approaches to long-term monitoring data as an avenue to aid understanding of large-scale perturbations. Increased understanding of the effects of ecological changes can help reduce unwanted regime shifts and will assist future attempts of ecosystem forecasting. Many ecological changes are currently in motion or primed for initiation and will be experienced by future generations. The availability of clean, fresh water will likely continue to decline in the future (while needs will not), increasing social pressures and the stakes of management decisions. Rapid, responsive management of aquatic systems will be increasingly complicated by the dynamic behavior of user groups and unexpected ecological changes. During such periods, the importance of quantitative assessment will increase so that risk-sensitive information can be distributed to stakeholders and managers.

In the following chapters, I reviewed several ecological changes experienced by the Oneida Lake food web and used multiple long-term data series to evaluate the effects. I documented a prolonged period of sustained low densities of multiple early life stages of yellow perch and quantified changes in mortality and growth rates. During recent years of reduced densities, yellow perch have typically reached a size of 18mm earlier in the year, but mortality after 18mm to 1 August has increased. Increased growth rates have promoted a larger end-of-year size, which reduced subsequent mortality during the first winter (Fitzgerald et al. *in press*). In this sense, growth and mortality rates operate through a process of delayed compensation, such that the benefits of increased growth are experienced during a later life stage. Estimates of sub-adult walleye mortality were also higher, although the cause is likely different from those affecting early life stages of yellow perch. The increased mortality of sub-adult walleye corresponded with the increased presence of double-crested cormorants. Even after a noticeable decline in walleye abundance, numbers of age-0 yellow perch did not increase as would have been previously expected.

Ecological changes, such as increased water temperature, increased water clarity, habitat alternations, and shifts in the food web structure of Oneida Lake have contributed to fish community dynamics. For example, smallmouth bass are increasingly captured in sampling gears and are likely benefiting from warmer waters and an increased extent of aquatic macrophytes. Zebra mussels have also become an important component of the Oneida Lake food web given their potential to dominate benthic biomass and indirectly influence the environment experienced by multiple life stages of fish. Combined, the periods of ecological changes have produced direct and indirect influences that are unfavorable for a rapid return to a tightly-coupled predator-prey relationship between walleye and yellow perch. As a result, fish community dynamics in Oneida Lake will likely be less dominated by percid interactions in the future than was seen prior to the occurrences of large-scale ecological changes discussed here.

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CHAPTER ONE

Factors Affecting the Success of Early Life Stages of Yellow Perch in Oneida Lake, New York

ABSTRACT

Identifying the determinants of year-class success is complex, given the numerous biological and physical factors that can influence growth and mortality rates of early life stages of fishes. We quantified long-term (>40 years) patterns in age-0 yellow perch *Perca flavescens* density in Oneida Lake at four early life stages (egg, at 18mm, on 1 August, and on 15 October) and calculated mortality and growth rates during the three intervals between these early life stages. First, we tested for density dependent effects on mortality and growth using the whole data set. Second, we investigated the effects of several variables suggested in the literature to affect mortality and growth of young fish using separate general linear models for each interval in a more restricted data set (1970-2003). Explanatory variables included water temperature, Secchi depth, an index of high-wind events, *Daphnia* spp. biomass, measures of prey buffering and competition, and ratios of predator biomass to age-0 yellow perch densities. Predator biomass was summarized as a ratio relative to density of young yellow perch and included measures of walleye *Sander vitreus*, white perch *Morone americana*, and yellow perch. We considered the role of age-0 white perch and age-0 gizzard shad *Dorosoma cepedianum* as both alternative forage for predators and potential competitors in the age-0 fish community. Age-0 yellow perch densities have declined over time at each of the early life stages examined. Mortality rates from egg to 18mm (interval 1) showed no time trend, increased for 18mm – 1

Aug. (interval 2), and decreased from 1 Aug. – 15 Oct. (interval 3). Mortality was significantly correlated with water temperature during interval 1, but none of the included variables were significantly related to mortality during intervals 2 or 3. Contrary to expectations from the 1960s, mortality rates of age-0 yellow perch in Oneida Lake are no longer depensatory. Overall, growth of age-0 yellow perch has increased, was density dependent, and was significantly correlated with increased Secchi depth. The combined effect has been a decline in age-0 yellow perch abundance and an increase in individual size by the end of their first year. Implications for future survival are also discussed.

INTRODUCTION

Fish recruitment has long been the subject of inquiry, including studies focused on the processes affecting survival during early life stages and potential spawner-recruit relationships (Chambers and Trippel 1997; Fuiman and Werner 2002). Because the condition and size of the mature fish stock should at least partially determine the production of young, the relation between spawning stocks and numbers of recruits has been examined for numerous species and system types, but results have not revealed consistent patterns (Ricker 1954; Myers and Barrowman 1996; Hinrichsen 2001). The variability in these relationships implies that recruitment is also influenced by factors other than the reproductive potential of the parental stock. Additional factors that have been identified as important for at least some freshwater fish include hatch dates (Garvey and Stein 1998; Gopalan et al. 1998), temperature and climate (Clapp et al. 1997; Casselman 2002), changes in habitat and hydrology (Sammons et al. 2002), food supply and competition (DeVries and Stein 1992), and predation (Rice 2002). These factors can sometimes act independently or in

association to affect recruitment (Paukert et al. 2002) and can regulate the number of age-0 fish that successfully transition through early life stages by inducing mortality events that either dramatically reduce year class strength in a short episode or act subtly to remove individuals over longer periods of time (Houde 1989).

Growth rates are often considered in analyses of recruitment because achieving an increased size through rapid growth is usually believed to reduce mortality of young fishes. Achieving an increased size through rapid growth reduces the time spent in vulnerable early life stages (Houde 1994), decreases the sensitivity of young fish to the physical environment (Roseman et al. 1999), allows for consumption of larger and potentially more energetically profitable prey (Schael et al. 1991), and reduces vulnerability to smaller and potentially more abundant predators (Miller et al. 1988). Growth rates of age-0 fish can also determine the timing of habitat shifts (Noble 1968, 1975; Wahl et al. 1993), which can be accompanied by changes in food availability and temperature regimes that then can influence subsequent growth. In general, a “bigger is better” hypothesis is assumed to be the best survival strategy for young fishes. However, increased foraging activities that produce more rapid growth can also lead to increased exposure to predators and therefore increased mortality (Walters 2000).

For young fishes, the interplay of mechanisms that affect mortality and growth can determine if the transition through the first year of life is successful. These mechanisms can be density dependent and either decrease mortality at low densities (compensatory) or increase mortality at low densities (depensatory). As an example, predation-driven depensatory mortality can disproportionately reduce the density of prey during a weak year class (Forney 1971). Conversely, compensation can alleviate the effects of early-life-stage mortality, if remaining individuals experience decreased subsequent mortality, potentially through increased growth. In this regard, some

factors that increase mortality during one life stage may reciprocally act to increase survival during a later life stage (Pepin 1991). As such, early mortality events are not always catastrophic for eventual cohort success, and the stage at which year-class strength is set can vary among species and across systems (Houde 1994). Due to the complexities associated with identifying the determinants of year-class success, recruitment variability may be best understood by evaluating patterns in both mortality and growth rates (e.g., Houde 1987) as they relate to various biological and physical factors because these rates are critical for successful transitions across early life stages.

Consideration of multiple factors relative to both mortality and growth rates within several early-life-stage intervals is possible for young yellow perch *Perca flavescens* in Oneida Lake, NY, given the rich history of ecological study across multiple trophic levels for this system (e.g., Forney 1977; McQueen et al. 1986; Mills and Forney 1988; Rudstam et al. 2004). Located northeast of Syracuse, NY, Oneida Lake is relatively shallow (mean depth 6.8m) but has the largest surface area (207 km²) of any lake entirely in New York State. These characteristics combined with a long fetch facilitate mixing by wind-driven currents, even to the point of affecting the distribution of larval fishes (Houde 1969; Forney 1980). The lake is moderately eutrophic but phosphorus levels and phytoplankton abundance have declined since the 1960s (Idrisi et al. 2001; Zhu et al. *in press*). Additional physical properties of the system are described in Mills et al. (1978). Recreational anglers heavily target walleye *Sander vitreus* and yellow perch, and studies of the population dynamics of these two species were initiated by the Cornell Biological Field Station in 1957. By the early 1970s, limnological studies were incorporated to provide an improved assessment of interactions across multiple trophic levels. As a result of these long-term studies, Oneida Lake has become a textbook example for percid interactions (Diana 1995; Craig 2000).

Herein, we examine long-term trends (>40 years) in density of age-0 yellow perch at multiple early life stages (see Figure 1-1) as well as variability in growth and mortality rates during the intervals between these stages (see Figure 1-2). Based on earlier analyses of portions of this data set, we used estimated density at the egg stage, 18mm larvae, 1 August, and 15 October (e.g., Forney 1980; Mills and Forney 1988; Rose et al. 1999). First, we present trends in density, mortality, and growth rates over time for each early-life-stage interval. Second, we test *a priori* expectations, based on findings of Forney (1980) and Mayer et al. (2000), that both mortality and growth rates would be negatively related to density of age-0 yellow perch in each interval. Third, we used multiple regression analyses to evaluate the relative importance of several environmental and biotic measures as explanatory variables for mortality and growth rates during early-life-stage intervals of age-0 yellow perch. For each included explanatory variable, we had an *a priori* expectation of the directional correlation shared with the response variables of interest. Due to various limits on data availability, multiple regression models did not include data before 1970. When possible, measures of a particular explanatory variable were averaged within an early-life-stage interval for use in multiple regression analyses for that interval's response rates. For models attempting to explain variability in mortality, we considered the following variables: average individual size of age-0 yellow perch, Secchi depth, water temperature, an index of high-wind events, a ratio of predator biomass to age-0 yellow perch density, density of age-0 gizzard shad *Dorosoma cepedianum*, and density of age-0 white perch *Morone americana*. For the models attempting to explain variability in growth, explanatory variables included: density of age-0 yellow perch, Secchi depth, water temperature, *Daphnia* spp. biomass, and the densities of both age-0 white perch and age-0 gizzard shad. A background to previous studies in

Oneida Lake and the expected directional relationship for each of the included explanatory variable is reviewed below.

Physical Conditions

For young fishes, abiotic factors that are often density-independent can be important for the successful transition among early life stages. In Oneida Lake, high-wind events can destroy yellow perch eggs and produce a severe pulse of early-life-stage mortality (Clady and Hutchinson 1975). We expected that high-wind events will be detrimental to yellow perch during interval 1. Over a large spatial scale, temperature can also influence the production of strong year classes (Koonce et al 1977; Casselman 2002). Temperature can play a particularly important role during early life stages of fish because the time spent in these vulnerable periods can be reduced when thermal conditions are optimal. Temperature can also influence growth by affecting consumption rates or the temporal overlap between a predator and its prey (e.g., Winder and Schindler 2004). We expected mortality of young perch to be negatively related to temperature and growth to be positively related to temperature.

The establishment of zebra mussels *Dreissena polymorpha* in 1992 has altered the food web of Oneida Lake. Grazing by zebra mussels can redirect energy pathways of freshwater lakes by filtering particulate matter, thus increasing water clarity, the depth of the photic zone (Idrisi et al. 2001), and benthic production (Mayer et al. 2002). We expected increased Secchi depth to lead to increased mortality during interval 1 because clearer foraging conditions likely benefit ichthyoplanktivores' detection of prey more than young yellow perch's detection of predators. The effects of increased water clarity on growth rates are more difficult to predict. For young zooplanktivores with short reactive distances, turbid water conditions may enhance the contrast between zooplankton and the surrounding water and therefore lead to

increased prey detection and growth rates (Utne-Palm 2002). For more developed fishes in later life stages (e.g., interval 3), clear-water conditions may be more favorable if they produce a corresponding increase in the range of suitable foraging habitats.

Zooplankton

Zooplankton are a primary food resource for young yellow perch in Oneida Lake, and previous studies have indicated the importance of *Daphnia* spp. for yellow perch growth (Noble 1975; Mills and Forney 1983, 1988). While young yellow perch do not select for the largest available size of *Daphnia* (Noble 1975; Hansen and Wahl 1981), the abundance of the larger species (*Daphnia pulicaria*, previously *D. pulex*) was previously related to yellow perch growth through the season in Oneida Lake (Mills and Forney 1983, 1988). Thus, we expected that biomass of *Daphnia* is positively related to age-0 yellow perch growth rates, and we tested both total *Daphnia* spp. biomass (sum of three species: *D. pulicaria*, *D. galeata*, and *D. retrocurva*, see Methods for additional details) and *D. pulicaria* density alone.

A strong correlation between yellow perch growth and *Daphnia* spp. density suggests that yellow perch could be food limited, but neither Noble (1975) nor Mills et al. (1989) found growth rates of age-0 yellow perch to be density dependent. More recent analyses have suggested that growth of age-0 yellow perch can be density dependent during at least some intervals (Mayer et al. 2000). Growth of age-0 yellow perch could be density dependent for reasons other than exploitative competition for food resources (Boisclair and Leggett 1989), potentially if increased activity at high densities incurs higher energy costs and limits growth. Therefore, we also include yellow perch density in the analyses of growth rates and expect density to be negatively related to growth.

Predation

During the 1960s and 1970s, walleye and yellow perch formed a tightly coupled predator-prey system in Oneida Lake (Forney 1966, 1980; Rose et al. 1999). Most of the mortality of young perch after they achieved a length of 18mm could be attributed to walleye predation (Forney 1977). Depensatory mortality of age-0 yellow perch caused weak year classes to suffer a disproportional amount of mortality and increased the differences between strong and weak cohorts through the first summer (Forney 1971, 1980). Cannibalism by yellow perch in Oneida Lake was previously shown to be size-dependent and positively associated with prey density but only contributed about 25% of the total mortality of young yellow perch (Tarby 1974). In addition to walleye and yellow perch, Oneida Lake has an abundant population of white perch, a known predator of young fish in Oneida Lake (Aslop and Forney 1962). In terms of total predation, we expect high levels of predator biomass to be detrimental to survival of age-0 yellow perch in Oneida Lake. Further, we expect that larger individuals would have an increased ability to successfully transition through an early-life-stage interval.

Alternative Forage and Age-0 Competition

Although walleye and yellow perch were the most important species (both recreationally and ecologically) in Oneida Lake over the past 50 years, both populations have declined, contributing to shifts in the composition of the fish community over time (Hall and Rudstam 1999; Chapter 3). In some years, the abundance of age-0 white perch and gizzard shad was high. Both of these species could provide alternative forage to top predators, such as walleye, as well as compete with age-0 yellow perch for food resources (Aslop and Forney 1962; Mills and Forney

1988), although subsequent evidence for competition is weak (Prout et al. 1990; Roseman et al. 1996). Therefore, we expect that high densities of these species to decrease mortality and growth rates of age-0 yellow perch

METHODS

Age-0 yellow perch surveys

Spawning by yellow perch occurs in inshore areas of Oneida Lake, and their eggs typically hatch during May (Forney 1971; Mills and Forney 1988). Annual egg deposition estimates were based on an equation relating fecundity to perch weight, estimates of weight and abundance at age, and the proportion of mature females per age class (for additional details see Clady 1976). For most of the data series, adult yellow perch were age 3 and older, but in the 1990s-2000s, some age-2 yellow perch were also included due to increased growth rates during these more recent years.

Each spring, a larval yellow perch survey was conducted when pilot sampling indicated the larval yellow perch cohort had reached a mean total length of approximately 18mm (usually mid June). Larval yellow perch were collected at multiple depth strata from 46-52 sites that include both inshore and offshore areas of Oneida Lake using four high-speed Miller samplers, each of which are constructed out of a 68mm long Plexiglas tube with a 10cm mouth opening and a 540µm mesh net (for additional details see Rudstam et al. 2002). Larvae were enumerated and measured (nearest 0.1mm) in the laboratory. Density estimates were adjusted for daytime gear avoidance (Noble 1970). Estimates of larval yellow perch abundance were based on samples taken from the surface to 6m depths.

Because the timing of Miller sampling varied somewhat from the time larval yellow perch achieved a mean size of 18mm, we standardized these collections to a

uniform size to compare abundance over time (Jackson and Noble 2000). To standardize annual larval density estimates to 18mm achievement, we calculated daily larval growth and mortality rates from a subset of years when Miller-sampling surveys were used to collect larval yellow perch at approximately 8mm (N = 11 years; 1968-1977, 1998, 2001). For these years, we estimated daily growth ($N = 11$, $\bar{x} \pm 1 \text{ SE} = 0.48\text{mm} / \text{day} \pm 0.02$) and instantaneous mortality ($N = 9$, $\bar{x} \pm 1 \text{ SE} = -0.042 \pm 0.005$) rates from the 8mm survey to the 18mm survey (Appendix 1-1) and used these increments to adjust the abundance estimates to the time a cohort reached 18mm for each year (henceforth called the standardized 18mm survey). Because a direct measure of yellow perch hatch dates was not available for most years, this estimated daily growth rate from 8mm to 18mm was also used to estimate the length of the period between hatching (assumed to occur at 4mm because larval yellow perch < 5mm have been captured in Oneida Lake; Clady 1976) and 18mm achievement to be 29 days. This time period was used so that the calculated mortality during interval 1 would be an instantaneous daily rate on a comparable scale as estimates for both intervals 2 and 3. The estimated hatch dates indicated that hatching of yellow perch occurs during May, which is consistent with earlier observations for Oneida Lake (Forney 1971).

Densities and mean length of age-0 yellow perch on both 1 August and 15 October were calculated from weekly bottom trawl collections at 10 standardized sites. The bottom trawl has a 5.5m footrope with a 13mm mesh cod end, and each trawl haul covered approximately 0.1 ha of bottom surface area with a transect length of approximately 280m (for additional details see Forney 1976; VanDeValk et al. 2002). Year-specific catch curves were developed from trawl catches through the growing season, assuming a constant instantaneous mortality rate for that year, and used to estimate abundance on 1 August and 15 October of each year. Occasionally,

dates with low catches (associated with low oxygen levels in deep waters) were excluded. A sub-sample of yellow perch collected in bottom trawls were measured for total length (nearest mm). Each year, the average sizes of age-0 yellow perch were plotted across the trawl collection dates to create annual growth curves from which mean size of age-0 yellow perch on both 1 August and 15 October was estimated.

We used the long-term data series of age-0 yellow perch density at four early life stages (egg, at 18mm, on 1 August, and on 15 October; Figure 1-1) to calculate mortality and growth rates for specific early-life-stage intervals (interval 1: egg to 18mm achievement; interval 2: 18mm achievement to 1 August; and interval 3: 1 August to 15 October; see Figure 1-2). Because growth measures were not directly available for interval 1 (egg to 18mm), we summarized larval growth rates from the 8mm survey to the 18mm survey for 11 years when these data were available. For both interval 2 and interval 3, a measure of average individual size was calculated as the average of age-0 yellow perch total length at the start and end of the interval.

Physical Conditions

When possible, we calculated averages of explanatory variables within each of the three early-life-stage intervals established for age-0 yellow perch. Water clarity has been routinely measured in Oneida Lake using a Secchi disk. Average Secchi depth was calculated within each early-life-stage interval, but May estimates of water clarity were not available for 1970-1972. Therefore, average Secchi depth values during interval 1 for these three years were based on observed data from June only. Average Secchi depths from late May (May 15 or later) are correlated with average Secchi depths during June in Oneida Lake (Pearson Correlation; $N = 31$, $r = 0.513$, $P = 0.003$). We elected to retain these years in the multiple regression analyses for interval 1 because data on all other variables were available for these three additional

years. For most years, a temperature logger at a station near the Cornell Biological Field Station (CBFS) measured water temperature daily at a depth of 2m. In a few cases, when daily values were not available throughout the interval of interest (due to equipment malfunction or late deployment), we interpolated between weekly estimates to obtain daily values prior to calculating interval-specific averages.

Average daily wind speed was taken from National Weather Service readings at Hancock International Airport (local climatological data), located 19 kilometers southwest of Oneida Lake. Because high-wind events may be more important than average wind speed as an indicator of detrimental conditions for eggs, we developed an index of high-wind events for use as an explanatory variable during interval 1. Based on available daily average wind speed data from 1970 through September 2004 ($N = 12,691$), the upper 75% quantile was 4.96 m/s. We considered this an indicator of a day with high winds and calculated the number of days when average wind speed exceeded 4.96 m/s as a measure of high-wind events. For this index, we included wind speed measures for interval 1 as the time from three weeks prior to each year's estimated hatch date to the day of 18mm.

Zooplankton

To estimate food availability for age-0 yellow perch during intervals 2 and 3, we included data on three daphnid species: *Daphnia pulicaria*, *Daphnia galeata*, and *Daphnia retrocurva*. For each of the three included zooplankton species, density data were available as weekly averages, and these data were then summarized within each of the three early-life-stage intervals of age-0 yellow perch. In Oneida Lake, *Daphnia* densities can be highly correlated among species (e.g., Mills and Forney et al. 1988), leading to multicollinearity problems if more than one species is included in the analysis. Therefore, we converted each species to biomass and summed across species

for an index of *Daphnia* spp. for each early-life-stage interval. Biomass was calculated using average of weekly species-specific individual weights available from 1975 to 2003 in the Cornell Biological Field Station database (*D. pulicaria*: N = 2937, mean = 21.4 µg, 1 SE = 0.2; *D. galeata*: N = 3219, mean = 11.8 µg, 1 SE = 0.1; and *D. retrocurva*: N = 1032, mean = 7.6 µg, 1 SE = 0.2). These conversions were necessary due to a lack of biomass data for early years. For the interval spanning from the 8 to 18mm larval survey, we included the density of cyclopoid copepods (*Acanthocyclops vernalis*, *Diacyclops thomasi*, *Ergasilus* sp., and *Mesocyclops edax*) as an index of food availability rather than *Daphnia* spp. because small copepods can be important first prey to small larval yellow perch before they are able to consume larger *Daphnia* (e.g., Whiteside et al. 1985). Clady (1977) found that copepod nauplii were more common than cyclopoid or calanoids in the stomachs of small larval yellow perch (mean total length = 8.6mm), but measures of nauplii density were not available for all years of the current study.

Predation

For both adult walleye and adult yellow perch in Oneida Lake, gillnet catches are a good indicator of adult abundance (Jackson et al. *in review*). However, direct abundance estimates of adult walleye (age-4 and older) and adult yellow perch (age-3 and older) are also available for several years when mark-recapture population estimates were conducted (for additional details on mark-recapture methods see Forney 1980; Jackson et al. *in review*). Therefore, abundance estimates for both adult walleye and adult yellow perch were obtained using mark-recapture population estimates when available, extrapolation between biannual mark-recapture years for years between estimates, and species-specific relationships between annual total catch of adults in gillnets and the mark-recapture estimates for all other years (for additional

details on the gillnet sampling see Jackson et al. *in review*, Irwin et al. *in review*). A correction factor (CF; walleye = 1.04; yellow perch = 1.06) was applied to the gillnet-based estimates of percid abundance to account for the bias of the \log_{10} - \log_{10} transformation (Sprugel 1983). These gillnet-based annual estimates of adult population abundance were then separated into adult age groups based on the annual age distributions of walleye and yellow perch captured in gillnets and converted to number per hectare.

Age-specific abundances of adult percids were converted to biomass using annual estimates of length-at-age and a length-to-weight regression developed using all available data (1957-1973; 1975-2003) for walleye and yellow perch collected in multifilament gillnets set during June. For both species, length-at-age estimates were back-calculated using scales. Length-at-age estimates were obtained for female and male walleye separately; therefore, these values were averaged assuming a 50:50 of male and female walleye in Oneida Lake. The length-weight regression for walleye was ($N = 2271$, $F = 98825$, $R^2 = 0.978$, $P < 0.0001$):

$$(1) \quad \text{Log}_e \text{ Weight (g)} = -12.29 + 3.11(\text{Log}_e \text{ Total Length (mm)}).$$

Likewise, the length-weight regression for yellow perch was estimated as ($N = 8453$, $F = 176665$, $R^2 = 0.954$, $P < 0.0001$):

$$(2) \quad \text{Log}_e \text{ Weight (g)} = -12.36 + 3.22(\text{Log}_e \text{ Total Length (mm)}).$$

Because mark-recapture data were only available for adult walleye and adult yellow perch, annual abundance of sub-adults was estimated using a combination of trawl and gillnet data. Annual estimates of age-1 walleye and age-1 yellow perch were based on summer catches in bottom trawls. Age-2 walleye abundance was based on the total catch of age-2s in gillnets adjusted for gear selectivity (Irwin et al. *in review*). For adult walleye, the average total annual mortality based on mark-recapture years (from 1970 to 2003) was 35% ($N = 9$, Range 0.15-0.65, SE = 0.06).

Annual age-3 walleye abundance was backcast from age-4 abundance based on an assumed annual natural mortality rate (5%; Forney 1967) combined with one half of the fishing mortality of adult fish ($30\% / 2$) so that the estimated mortality rate applied from age-3 to 4 was 20%. Annual abundances of age-2 yellow perch were estimated from catches in gillnets adjusted for gear selectivity (Forney et al. 1994). Average length-at-age values for age-1 walleye and age-1 yellow perch captured in summer trawls were used in total length to weight regressions to convert these abundance estimates to biomass using the same methods as for adult fish (see above).

We also used gillnet data to estimate abundance of white perch. In order to represent white perch on the same unit scale as walleye and yellow perch, we estimated annual population abundance of white perch from the total catch of white perch in gillnets using a generalized (walleye and yellow perch combined) regression and a correction factor (for additional details see Irwin et al. *in prep.*; CF = 1.05). The annual average weight of white perch collected in gillnets was used to convert abundance estimates to biomass. For a few years during the 1970s, weights of white perch were not available; therefore, we applied the mean of the annual average weights to the abundance estimates to calculate biomass for those years.

These combined methods provided a metric of annual predator biomass for each of five groups: white perch, age-1 walleye, age-2 and older walleye, age-1 yellow perch, and age-2 and older yellow perch. To represent predator biomass relative to the age-0 yellow perch population, predator-to-prey ratios were calculated using the above estimate of combined predator biomass and the estimate of age-0 yellow perch density at the start of each of the three early-life-stage intervals.

Alternate Forage and Age-0 Competition

For models predicting mortality rates of age-0 yellow perch, we expected that large cohorts of age-0 gizzard shad and age-0 white perch could buffer age-0 yellow perch from predation during intervals 2 and 3 (buffering was not expected during interval 1 because gizzard shad and white perch hatch late in interval 1 or in interval 2 in Oneida Lake). In models predicting growth rates, we expected that age-0 gizzard shad and age-0 white perch could compete with age-0 yellow perch for food resources. For an index of gizzard shad abundance during interval 2, we used the sum of larval density estimates for 8-14mm gizzard shad obtained with Miller survey conducted at approximately 10-day intervals through the summer. For interval 3, we used the number of age-0 gizzard shad in the diet of walleye caught in October (expressed as # of gizzard shad per gram of walleye) as a relative index of age-0 gizzard shad abundance (for additional details see Fitzgerald et al. *in press*). To represent age-0 white perch abundance during both intervals 2 and 3, we calculated the density (# / ha) of age-0 white perch based on annual bottom trawl collections conducted from August through October.

Statistical Analyses

We used simple linear regression to test for density-dependent mortality and growth and to determine if temporal trends were present in mortality and growth rates as well as many of the included explanatory variables. Second, we used multiple regression analyses to evaluate the relationships between a suite of explanatory variables and five response variables of interest (3 mortality and 2 growth rates). Estimates of larval yellow perch density were not available prior to 1965 or for 1978; therefore, mortality and growth rates during intervals 1 and 2 were calculated for fewer years than for interval 3 (which includes data from 1961 – 1964 and 1978). For

each response variable, we began by constructing a “full” model that included all variables for which we had both available data and directional *a priori* hypotheses relating the explanatory variable to the response. Fitzgerald et al. (*in press*) recently used a similar approach to evaluate over-winter mortality of yellow perch in Oneida Lake. Because it is necessary for the regression analysis to have a complete set of observations across variables, multiple regression analyses used data from 1970 through 2003. However, larval collections were not available for 1978, so this year was not considered for either interval 1 or interval 2. Before performing multiple regression analyses, the correlation structure of the explanatory variables was examined. We did not include interaction or higher-order terms in the multivariate regression models. Regression procedures were performed using the REG procedure in SAS (V. 9.1).

RESULTS

Temporal Trends & the Role of Density

Long-term data suggests a decline in abundance of young yellow perch in Oneida Lake at all early life stages included in this study (egg deposition: $N = 43$, $R^2 = 0.378$, $P < 0.001$; larval abundance at 18mm: $N = 38$, $R^2 = 0.145$, $P = 0.018$; abundance on 1 August: $N = 43$, $R^2 = 0.519$, $P < 0.001$; and abundance on 15 October: $N = 43$, $R^2 = 0.248$, $P < 0.001$; Table 1-1; Figure 1-1). The decline in age-0 yellow perch coincides with a general increase over time in age-0 yellow perch mortality during interval 2 ($N = 38$, $R^2 = 0.232$, $P = 0.002$; Figure 1-2), but mortality rates have decreased later in the year ($N = 43$, $R^2 = 0.122$, $P = 0.022$; Figure 1-2). No temporal trend was evident for mortality during interval 1 ($N = 38$, $R^2 < 0.001$, $P = 0.956$; Figure 1-2). Daily growth rates (in mm) of age-0 yellow perch have increased

Table 1-1. Measures of age-0 yellow perch density (# / ha) at five early life stages in Oneida Lake and size on 1 Aug. and 15 Oct. The presented larval densities at 8mm and 18mm were standardized each year to these sizes. The calculated day of 18mm achievement (Day18mm) is also provided.

Year	Egg (millions)	8mm	18mm	Day18mm	1 Aug. (mm)	(mm)	15 Oct. (mm)	(mm)
1961	2.07	.	.	.	27720	40.0	2850	60.0
1962	2.24	.	.	.	21080	51.5	4260	73.0
1963	2.58	.	.	.	17730	47.0	780	61.0
1964	2.60	.	.	.	25590	49.0	4960	71.0
1965	3.00	.	140100	168	21670	41.0	2610	60.0
1966	2.68	.	40200	171	11970	49.0	160	73.0
1967	2.93	.	61200	168	24500	47.5	2100	72.0
1968	3.02	.	141800	167	35170	49.0	6700	65.5
1969	2.84	151000	68600	166	7170	44.0	210	65.0
1970	2.83	197900	70700	163	13510	51.0	860	78.0
1971	2.16	215600	181300	173	36240	38.0	3520	58.5
1972	2.63	152900	89400	167	2530	44.2	100	66.0
1973	3.26	38900	18700	169	1200	48.2	510	87.0
1974	3.28	77900	29900	167	3150	50.5	320	72.0
1975	2.46	362300	151300	163	21370	43.6	450	66.0
1976	2.33	126700	41200	171	6540	48.0	180	72.0
1977	2.08	219900	59100	159	14430	54.3	4140	69.5
1978	2.25	.	.	.	6060	51.5	180	73.0
1979	3.13	.	83500	169	13400	48.5	360	74.5
1980	4.99	.	114200	163	8580	50.0	500	82.0
1981	4.52	.	194200	163	21170	39.0	2590	57.5
1982	3.25	.	300400	169	16720	41.0	980	62.0
1983	2.42	.	43600	170	9620	50.5	710	79.5
1984	2.84	.	16200	168	5030	50.0	900	70.0
1985	1.32	.	76000	162	8360	50.5	2720	71.0
1986	2.09	.	14900	157	470	55.0	70	82.0
1987	2.54	.	4000	156	960	57.5	220	68.0
1988	2.20	.	66900	163	4000	52.5	220	82.0
1989	1.66	.	3300	162	150	52.5	20	80.5
1990	1.73	.	114400	168	2620	50.5	460	73.0
1991	1.50	.	32400	151	900	60.0	340	81.5
1992	1.15	.	60300	160	1780	50.5	100	73.5
1993	1.54	.	30400	170	2820	51.0	320	85.0
1994	0.66	.	19800	169	3830	55.0	280	83.5
1995	0.99	.	16900	161	1440	60.5	90	91.5
1996	0.96	.	40700	167	1250	51.0	80	80.0
1997	0.76	.	5300	167	110	53.5	20	80.0
1998	0.60	52700	70800	155	1320	60.5	700	82.0
1999	0.65	.	38500	155	1550	65.5	360	81.5
2000	0.76	.	20300	164	1080	53.0	140	77.0
2001	0.84	103700	35300	164	3200	60.0	270	84.0
2002	2.71	.	24200	168	5100	54.0	1660	75.5
2003	1.24	.	63300	167	1130	54.5	600	85.0
Mean	2.2	154500	67982	165	9633	50.6	1153	74.1
CV	45.8	60.0	91.7	3.1	104.0	11.9	135.5	11.5

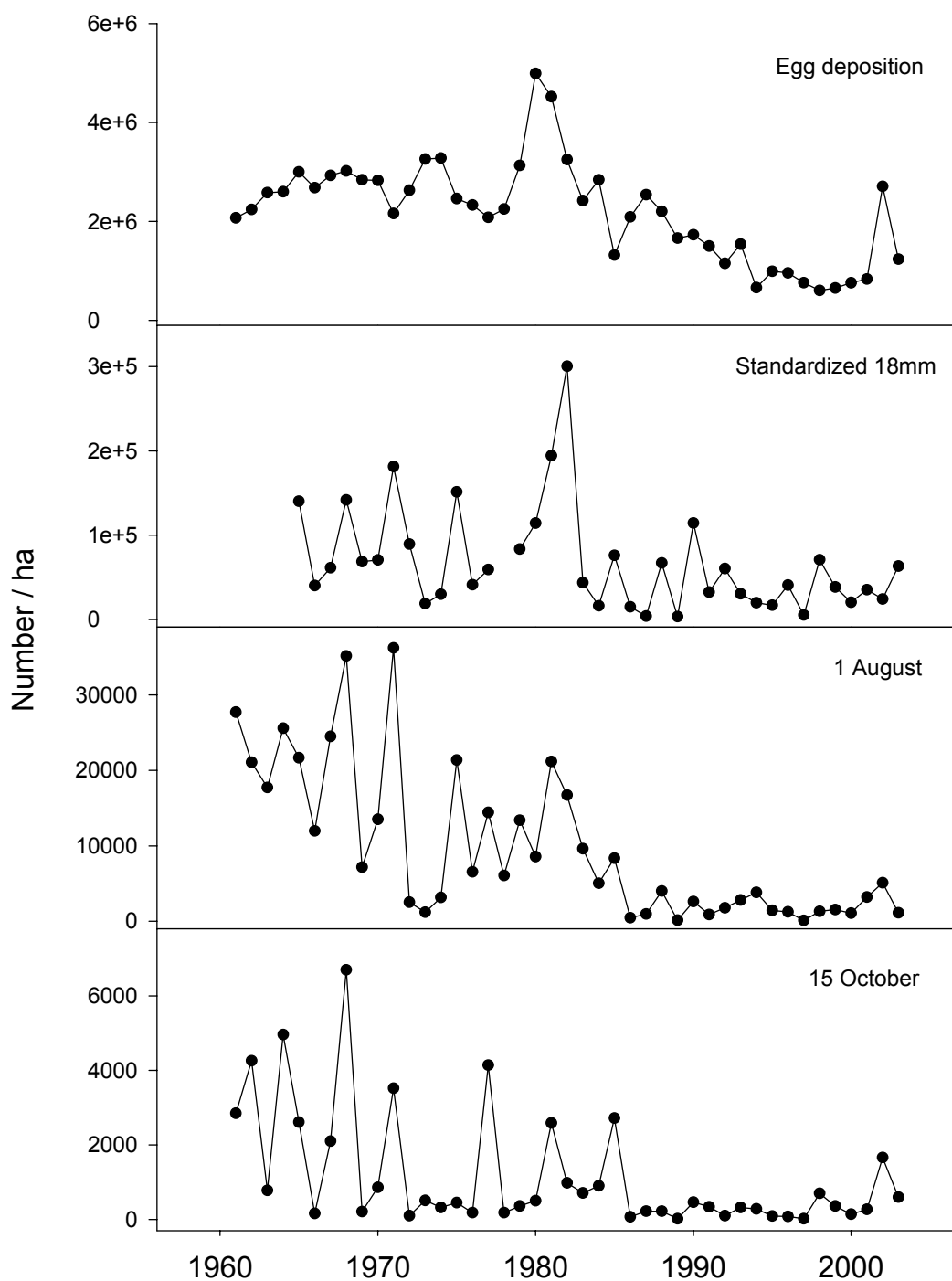


Figure 1-1. Estimated annual age-0 yellow perch density in Oneida Lake during four early life stages. Note differences in y-axes.

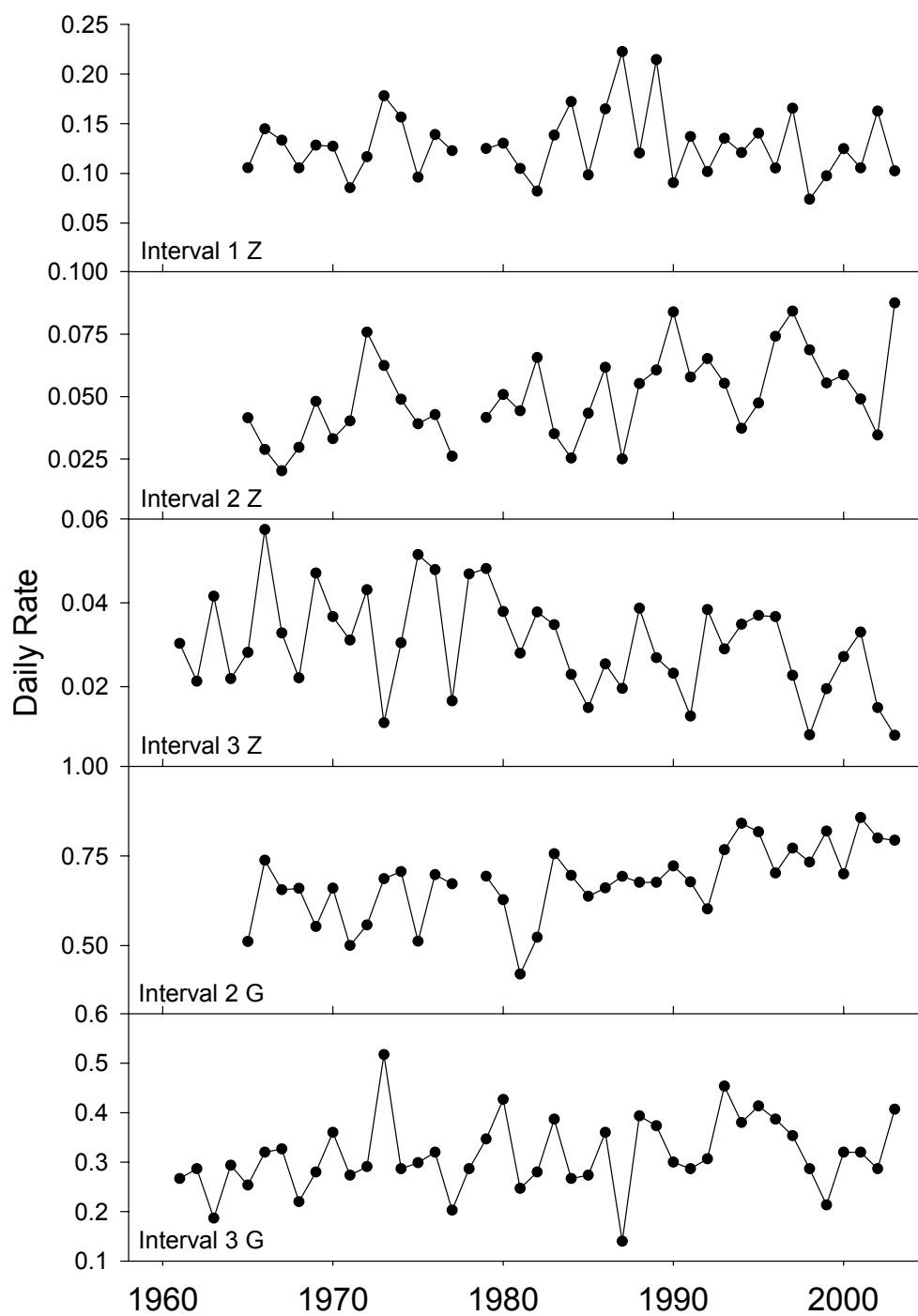


Figure 1-2. Estimated daily mortality (Z) and growth rates (G) for multiple early-life-stage intervals of age-0 yellow perch. Note differences in y-axes.

significantly during interval 2 ($N = 38$, $R^2 = 0.378$, $P < 0.001$; Figure 1-2) and marginally during interval 3 ($N = 43$, $R^2 = 0.069$, $P = 0.089$; Figure 1-2). Limited data for growth rates between the 8 and 18mm larvae survey indicated that no temporal trend was present ($N = 11$, $R^2 = 0.044$, $P = 0.538$). Unlike intervals 2 and 3, the most recent estimate of growth rate (2001) during this larval interval was the lowest observed growth rate during the 11 years for which data were available (Appendix 1-1). Combined, the increased age-0 growth rates during both intervals 2 and 3 have led to noticeably larger age-0 yellow perch on both 1 August and 15 October during recent years (Table 1-1).

Contrary to *a priori* expectations, daily mortality rates were not related to density during any interval (interval 1: $N = 38$, $R^2 = 0.023$, $P = 0.359$; interval 2: $N = 38$, $R^2 < 0.001$, $P = 0.913$; interval 3: $N = 43$, $R^2 = 0.021$, $P = 0.353$; Figure 1-3). Likewise, growth from the 8mm to 18mm survey was not related to the density of larval yellow perch ($N = 11$, $R^2 = 0.129$, $P = 0.278$). However, subsequent growth rates of age-0 yellow perch were highly density dependent, especially during the period from 18mm to 1 August (interval 2: $N = 38$, $R^2 = 0.506$, $P < 0.001$; interval 3: $N = 43$, $R^2 = 0.137$, $P = 0.015$; Figure 1-3). Although these increased growth rates produced larger age-0 yellow perch, decreased mortality rates for years with larger average individual body lengths were not evident in interval 2 ($N = 38$, $R^2 = 0.016$, $P = 0.452$; Appendix 1-2). During interval 3, instantaneous mortality rates were lower during years with larger fish, but unexplained variability was high ($N = 43$, $R^2 = 0.099$, $P = 0.040$; Appendix 1-2).

Significant temporal trends occurred for some explanatory variables. Secchi depth measurements have generally been high during recent years, but a significant time trend was only present during interval 2, when average Secchi depth measurements increased over time (interval 1: $N = 33$, $R^2 = 0.012$, $P = 0.542$; interval

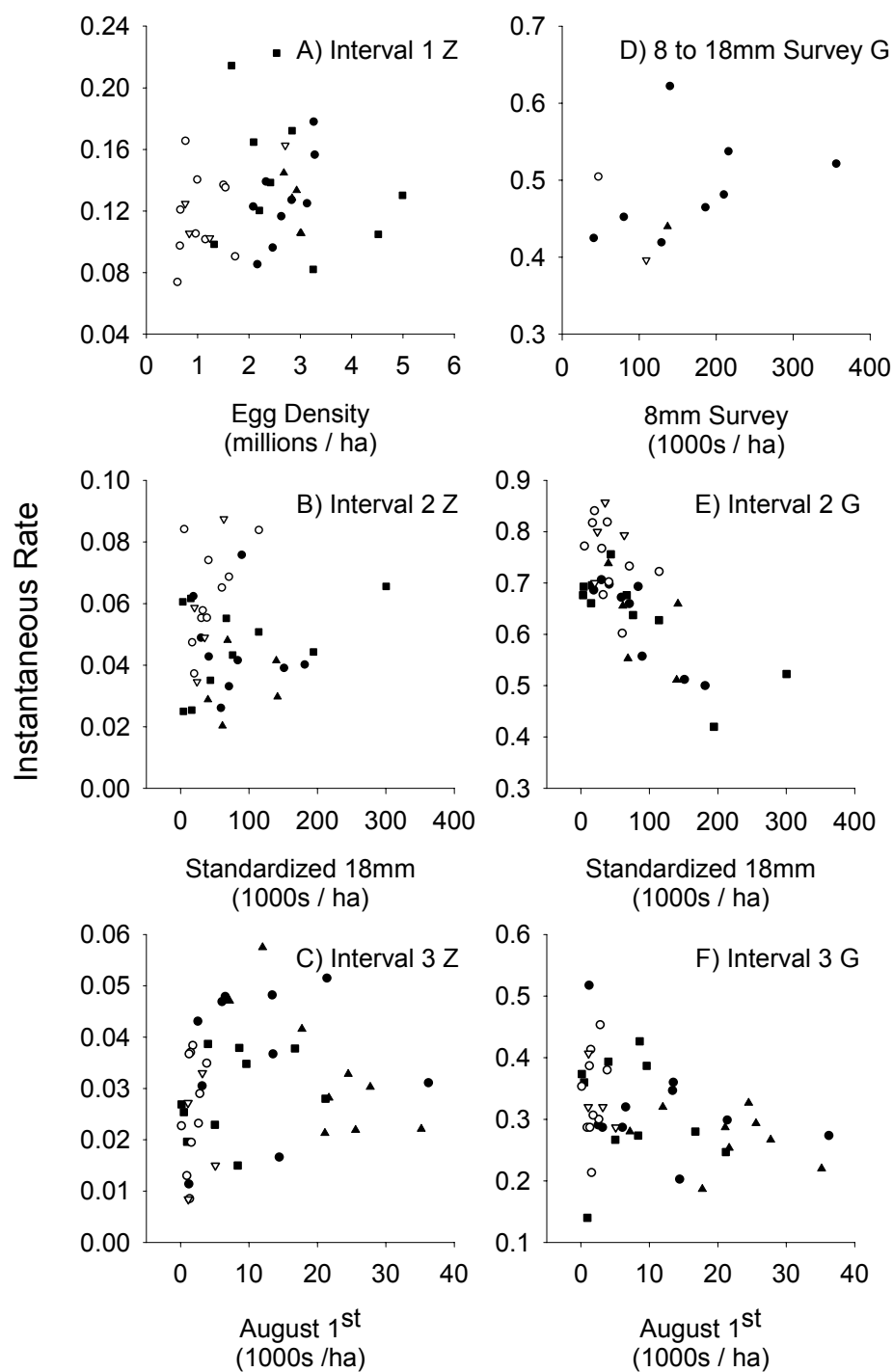


Figure 1-3. Instantaneous daily mortality (A-C) and growth (D-F) rates relative to the density of age-0 yellow perch and several early life stages. Symbols represent different decades (▲ = 1960s; ● = 1970s; ■ = 1980s; ○ = 1990s; ▽ = 2000s).

2: $N = 33$, $R^2 = 0.276$, $P = 0.002$; interval 3: $N = 34$, $R^2 = 0.004$, $P = 0.709$; Tables 1-2 – 1-4). Average water temperature at 2m did not show a continuous temporal trend within any of the early-life-stage intervals considered here (all $P > 0.1$; Tables 1-2 – 1-4). However when all temperature data were considered for the entire growing period (1 May to 15 Oct. for each year), a moderate increase in temperature is present over time ($N = 36$, $R^2 = 0.128$, $P = 0.032$, $Y = -30.38 + 0.025X$; Appendix 1-3). Our index of high-wind events during interval 1 ranged from 2 to 18 days, suggesting that considerable annual variability was present, but there was not a significant trend with time ($N = 33$, $R^2 = 0.060$, $P = 0.168$; Table 1-2).

The index of total *Daphnia* spp. biomass did not exhibit conspicuous time trends during any interval (all $P > 0.1$; Tables 1-2 – 1-3). All metrics of traditional predator biomass were generally lower during recent years compared with earlier periods of high biomass, and individual measures of different predator groups were often highly correlated (multiple pairwise $\rho > 0.6$; data shown in Appendix 1-4). Therefore, we summed across predator groups and calculated a single ratio of total predator biomass to age-0 yellow perch density for each interval. Indices of age-0 gizzard shad abundance were highest during the late 1980s and early 1990s; whereas, age-0 white perch have remained at relatively low densities since the production of the last strong cohort in 1987 (Tables 1-3 – 1-4).

Multiple Regression Analyses

We performed multiple regression analyses to predict variability in mortality and growth rates of age-0 yellow perch over time (1970-2003). The predictor variables included in the multiple regression models and directional hypotheses are shown in Tables 1-5 – 1-7. The regression model for mortality during interval 1 was highly significant (Table 1-5), and water temperature was significantly related to the

Table 1-2. Summary of physical and biological observations for interval 1 in Oneida Lake. Z_1 = instantaneous mortality rate of age-0 yellow perch, DayDiff = the difference in number of days between when Oneida Lake reached 10 °C and the day age-0 yellow perch achieved 18mm (growth rates were unavailable), Secchi = measure of water clarity (m), °C = average water temperature at 2m, Wind = index of high-wind events, Daph = *Daphnia* spp. biomass, and P:P = ratio of predator biomass to initial age-0 yellow perch density.

Year	Z ₁	DayDiff	Secchi	°C	Daph	Wind	P:P
1961
1962
1963
1964
1965	0.106
1966	0.145
1967	0.133
1968	0.106
1969	0.128	42
1970	0.127	43	6.48	17.3	307.7	14	0.024
1971	0.085	36	6.15	17.2	220.4	6	0.026
1972	0.117	33	3.10	16.5	163.9	7	0.021
1973	0.178	54	5.40	16.0	262.4	11	0.017
1974	0.157	47	5.37	15.6	181.3	18	0.017
1975	0.096	34	5.21	17.1	481.7	8	0.024
1976	0.139	36	3.59	15.3	214.2	14	0.026
1977	0.123	39	4.99	15.9	150.4	10	0.026
1978	0.025
1979	0.125	39	5.60	16.7	131.0	5	0.019
1980	0.130	32	3.65	13.6	162.0	11	0.017
1981	0.105	40	3.73	15.8	165.3	10	0.022
1982	0.082	43	3.61	15.8	173.5	4	0.022
1983	0.139	36	4.32	15.0	361.0	9	0.029
1984	0.172	36	3.04	14.4	449.3	16	0.023
1985	0.098	45	3.12	15.7	183.2	12	0.043
1986	0.165	45	3.20	14.6	179.5	10	0.029
1987	0.223	44	4.38	14.5	499.3	2	0.023
1988	0.120	34	2.02	15.1	85.2	2	0.030
1989	0.215	26	4.68	14.7	353.2	11	0.036
1990	0.091	58	3.54	14.9	264.8	8	0.031
1991	0.137	34	4.51	15.6	304.5	9	0.031
1992	0.102	30	3.37	15.6	193.2	6	0.038
1993	0.135	43	4.07	15.3	119.8	11	0.022
1994	0.121	38	5.61	15.8	39.8	11	0.036
1995	0.140	39	7.32	15.7	475.2	10	0.024
1996	0.105	35	5.12	16.0	325.4	6	0.026
1997	0.166	36	6.74	14.5	349.5	14	0.030
1998	0.074	43	3.66	17.1	49.6	6	0.036
1999	0.098	35	5.30	16.3	117.9	8	0.045
2000	0.125	42	3.91	15.4	104.4	4	0.038
2001	0.106	44	5.00	15.9	239.6	6	0.045
2002	0.163	60	5.78	15.4	209.7	11	0.018
2003	0.103	43	6.41	15.7	139.9	8	0.031

Table 1-3. Summary of physical and biological observations for interval 2 in Oneida Lake. Z_2 = instantaneous mortality rate of age-0 yellow perch, G_2 = daily growth rate during interval 2, $\bar{x}TL_2$ = average total length during interval 2, Secchi = measure of water clarity (m), $^{\circ}C$ = average water temperature at 2m, Daph = *Daphnia* spp. biomass, P:P = ratio of predator biomass to initial age-0 yellow perch density, and LfGzd = density of larval gizzard shad. Density estimates for age-0 white perch are shown in Table 1-4.

Year	Z ₂	G ₂	xTL ₂	Secchi	°C	Daph	P:P	LfGzd
1961
1962
1963
1964
1965	0.042	0.511	29.5
1966	0.029	0.738	33.5
1967	0.020	0.656	32.8
1968	0.030	0.660	33.5
1969	0.048	0.553	31.0
1970	0.033	0.660	34.5	4.62	21.8	296.0	0.94	0
1971	0.040	0.500	28.0	3.45	22.9	24.6	0.31	0
1972	0.076	0.557	31.1	2.35	21.3	78.3	0.61	0
1973	0.062	0.686	33.1	3.93	23.0	152.2	2.88	0
1974	0.049	0.707	34.3	3.10	21.1	141.2	1.86	0
1975	0.039	0.512	30.8	2.81	22.6	73.9	0.39	0
1976	0.043	0.698	33.0	3.00	21.4	202.0	1.48	0
1977	0.026	0.672	36.2	2.72	20.9	115.8	0.91	0
1978	0
1979	0.042	0.693	33.3	3.71	21.7	220.4	0.72	0
1980	0.051	0.628	34.0	2.82	20.3	206.9	0.76	0
1981	0.044	0.420	28.5	2.03	21.9	67.6	0.52	0
1982	0.066	0.523	29.5	2.13	21.5	109.3	0.24	0
1983	0.035	0.756	34.3	3.01	23.4	241.9	1.63	0
1984	0.025	0.696	34.0	3.09	21.6	238.7	4.07	355
1985	0.043	0.637	34.3	2.40	19.9	196.8	0.75	170
1986	0.062	0.661	36.5	2.10	19.8	234.2	4.11	146
1987	0.025	0.693	37.8	3.40	21.5	199.7	14.86	941
1988	0.055	0.677	35.3	3.45	22.3	339.6	0.98	350
1989	0.061	0.677	35.3	4.38	22.1	182.7	18.16	880
1990	0.084	0.722	34.3	2.99	22.1	154.4	0.46	479
1991	0.058	0.677	39.0	2.51	22.8	112.6	1.43	768
1992	0.065	0.602	34.3	3.42	20.2	186.3	0.72	673
1993	0.055	0.767	34.5	4.05	22.1	116.0	1.12	208
1994	0.037	0.841	36.5	4.45	23.1	165.2	1.21	9
1995	0.047	0.817	39.3	5.44	23.0	282.2	1.43	23
1996	0.074	0.702	34.5	4.52	21.7	178.3	0.61	1
1997	0.084	0.772	35.8	4.03	22.1	149.0	4.32	3
1998	0.069	0.733	39.3	3.80	21.8	120.7	0.31	1
1999	0.055	0.819	41.8	4.33	23.5	143.4	0.77	19
2000	0.059	0.700	35.5	3.54	21.2	243.7	1.41	75
2001	0.049	0.857	39.0	5.04	22.1	300.2	1.05	211
2002	0.035	0.800	36.0	4.50	23.6	224.6	2.05	58
2003	0.088	0.794	36.3	4.90	22.5	185.6	0.61	8

Table 1-4. Summary of physical and biological observations for interval 3 in Oneida Lake. Z_3 = instantaneous mortality rate of age-0 yellow perch, G_3 = daily growth rate during interval 3, $\bar{x}TL_3$ = average total length during interval 3, Secchi = measure of water clarity (m), °C = average water temperature at 2m, Daph = *Daphnia* spp. biomass, P:P = ratio of predator biomass to initial age-0 yellow perch density, GzdinWe = index of age-0 gizzard shad based on walleye diets, and Age0Wp = density of age-0 white perch.

Year	Z ₃	G ₃	xTL ₃	Secchi	°C	Daph	P:P	GzdinWe	Age0Wp
1961	0.030	0.267	50.0	1114
1962	0.021	0.287	62.3	310
1963	0.042	0.187	54.0	54
1964	0.022	0.293	60.0	61
1965	0.028	0.253	50.5	963
1966	0.058	0.320	61.0	1320
1967	0.033	0.327	59.8	132
1968	0.022	0.220	57.3	12
1969	0.047	0.280	54.5	81
1970	0.037	0.360	64.5	2.8	21.6	194.3	4.9	0.00	178
1971	0.031	0.273	48.3	2.3	21.1	10.2	1.6	0.00	91
1972	0.043	0.291	55.1	3.5	20.1	107.5	21.6	0.00	30
1973	0.011	0.517	67.6	3.3	21.7	100.4	44.8	0.00	2155
1974	0.031	0.287	61.3	2.2	19.7	83.9	17.6	0.01	355
1975	0.052	0.299	54.8	1.7	18.9	1.6	2.7	0.00	207
1976	0.048	0.320	60.0	2.2	18.7	193.0	9.3	0.00	385
1977	0.017	0.203	61.9	1.7	19.0	4.8	3.7	0.00	957
1978	0.047	0.287	62.3	2.5	21.4	171.9	9.4	0.00	37
1979	0.048	0.347	61.5	2.2	19.8	101.8	4.5	0.00	1594
1980	0.038	0.427	66.0	2.0	20.9	146.3	10.1	0.00	7539
1981	0.028	0.247	48.3	1.8	18.7	9.6	4.8	0.00	278
1982	0.038	0.280	51.5	1.7	19.5	69.5	4.3	0.00	4820
1983	0.035	0.387	65.0	2.1	21.4	129.4	7.4	0.00	7698
1984	0.023	0.267	60.0	1.4	20.3	56.1	13.1	0.97	364
1985	0.015	0.273	60.8	1.7	20.2	28.7	6.8	0.36	102
1986	0.025	0.360	68.5	2.0	18.6	154.8	130.3	0.05	17
1987	0.020	0.140	62.8	1.9	18.8	1.9	61.9	1.96	4570
1988	0.039	0.393	67.3	2.6	20.3	99.0	16.4	0.30	4
1989	0.027	0.373	66.5	2.2	19.9	18.5	399.6	5.42	886
1990	0.023	0.300	61.8	1.7	20.3	9.4	20.2	4.91	74
1991	0.013	0.287	70.8	1.6	20.5	10.6	51.5	3.81	86
1992	0.038	0.307	62.0	2.3	18.9	162.1	24.5	0.22	48
1993	0.029	0.453	68.0	3.6	20.1	25.9	12.0	0.01	797
1994	0.035	0.380	69.3	2.6	19.7	84.9	6.2	0.71	61
1995	0.037	0.413	76.0	3.3	21.1	114.8	16.8	0.06	476
1996	0.037	0.387	65.5	2.9	21.0	95.6	19.7	0.10	454
1997	0.023	0.353	66.8	2.2	19.9	47.7	208.2	0.00	956
1998	0.009	0.287	71.3	2.0	21.5	33.4	16.4	0.00	125
1999	0.020	0.213	73.5	1.7	20.8	46.8	19.1	0.25	8
2000	0.027	0.320	65.0	1.9	20.4	89.6	26.6	2.32	590
2001	0.033	0.320	72.0	2.1	21.8	89.4	11.6	0.88	59
2002	0.015	0.287	64.8	2.4	22.3	66.2	9.7	1.03	1145
2003	0.008	0.407	69.8	2.3	21.2	176.5	34.1	0.36	51

Table 1-5. Multiple regression results for instantaneous mortality (Z) during three early-life-stage intervals for years 1970-2003 (no larval data in 1978). Symbols presented below explanatory variable represent *a priori* hypotheses for the direction of coefficients. Blank cells indicate that an explanatory variable was not included in the multiple regression analysis. Potential explanatory variables include average individual total length during the interval (TL; for interval 1, the difference in the day of 18mm achievement and day of 10°C water temperature was used to account for the constant duration of the calculated interval), water clarity (Secchi), water temperature (°C), an index of high-wind events (Wind), predator biomass relative to yellow perch egg density (P:P), an interval-specific estimate of age-0 gizzard shad (Age-0 Gzd), and an index of age-0 white perch (Age-0 Wp). See text for additional descriptions. Values are standardized regression coefficients with associated P values.

Response Variable	N	P	R ²	Potential Explanatory Variables						
				TL -	Secchi +	°C -	Wind +	P:P +	Age-0 Gzd -	Age-0 Wp -
Z ₁	33	0.003	0.47	-0.04 (0.772)	0.27 (0.094)	-0.63 (<0.001)	0.09 (0.561)	-0.22 (0.151)		
Z ₂	33	0.914	0.07	-0.02 (0.926)	0.16 (0.560)	-0.14 (0.522)		-0.20 (0.477)	0.12 (0.663)	-0.13 (0.520)
Z ₃	34	0.129	0.29	-0.26 (0.181)	0.36 (0.066)	-0.28 (0.156)		-0.12 (0.563)	-0.07 (0.740)	0.12 (0.464)

Table 1-6. Multiple regression results for growth (G) during three early-life-stage intervals for years 1970-2003 (G_{8to18} = growth from the 8mm larval survey to the 18mm larval survey; no larval data in 1978 for interval 2). Symbols presented below explanatory variable represent *a priori* hypotheses for the direction of coefficients. Potential explanatory variables include interval-specific age-0 yellow perch density (Age-0 Yp), water clarity (Secchi), water temperature ($^{\circ}$ C), Zp = cyclopoid copepod density for G_{8to18} or *Daphnia* spp. biomass for interval 2 and interval 3, an interval-specific estimate of age-0 gizzard shad (Age-0 Gzd), and an index of age-0 white perch (Age-0 Wp). See text for additional descriptions. Values are standardized regression coefficients with associated P values.

Response Variable	N	P	R ²	Potential Explanatory Variables					
				Age-0 Yp -	Secchi - \rightarrow +	$^{\circ}$ C +	Zp +	Age-0 Gzd -	Age-0 Wp -
G_{8to18}	10	0.030	0.84	0.08 (0.749)	-0.27 (0.296)	0.65 (0.036)	0.43 (0.130)		
G_2	33	<0.001	0.74	-0.54 (<0.001)	0.34 (0.036)	0.14 (0.265)	0.14 (0.284)	-0.12 (0.263)	0.09 (0.392)
G_3	34	0.002	0.51	-0.03 (0.853)	0.55 (0.002)	0.12 (0.430)	0.27 (0.115)	0.15 (0.385)	0.18 (0.207)

Table 1-7. Multiple regression results for growth (G) during three early-life-stage intervals for years 1970-2003 (G_{8to18} = growth from the 8mm larval survey to the 18mm larval survey; no larval data in 1978 for interval 2). Symbols presented below explanatory variable represent *a priori* hypotheses for the direction of coefficients. Potential explanatory variables include interval-specific age-0 yellow perch density (Age-0 Yp), water clarity (Secchi), water temperature ($^{\circ}$ C), *Daphnia pulicaria* density (Daph. pul.), an interval-specific estimate of age-0 gizzard shad (Age-0 Gzd), and an index of age-0 white perch (Age-0 Wp). See text for additional descriptions. Values are standardized regression coefficients with associated P values.

Response Variable	N	P	R^2	Potential Explanatory Variables					
				Age-0 Yp -	Secchi - \rightarrow +	$^{\circ}$ C +	Daph. pul. +	Age-0 Gzd -	Age-0 Wp -
G_{8to18}	10	0.08	0.76	0.11 (0.756)	-0.51 (0.078)	0.68 (0.064)	-0.18 (0.543)		
G_2	33	<0.001	0.74	-0.62 (<0.001)	0.47 (0.004)	0.06 (0.615)	-0.15 (0.223)	-0.12 (0.255)	0.18 (0.118)
G_3	34	0.003	0.50	-0.06 (0.696)	0.52 (0.005)	0.16 (0.293)	0.24 (0.149)	0.108 (0.514)	0.18 (0.198)

instantaneous mortality rate. No other variable was significant, including the high-wind index. Although we identified an increase in yellow perch mortality during interval 2 over time (Figure 1-2), none of the included explanatory variables were close to significant (Table 1-5). For both interval 2 and interval 3, the regression model for mortality was non-significant (Table 1-5). But, Secchi depth was most strongly related to mortality in the presence of the other variables included in the model for interval 3. The multiple regression models for growth rates during intervals 2 and 3 were highly significant (Table 1-6). Average Secchi depth readings were significantly related to growth rates during both early-life-stage intervals (Table 1-6). In addition to Secchi, the initial larval density of age-0 yellow perch was significantly related to yellow perch growth rate during interval 2 (Table 1-6). Replacing the index of total *Daphnia* spp. biomass with *Daphnia pulicaria* density had only a minor effect on these results (Table 1-7). In a multiple regression analysis using 10 years of data (1969 not included) for the growth rate from 8mm to 18mm, temperature was the most significant explanatory variable, followed by Secchi depth (Table 1-6). Secchi depth and density of cyclopoid copepods were correlated ($r = -0.65$) during this early interval, and Secchi became a significant predictor of yellow perch growth (standardized coefficient = -0.55 ; $P = 0.040$) when cyclopoid density was removed from the regression model ($N = 10$, $R^2 = 0.74$, $P = 0.033$).

DISCUSSION

The Decline of Age-0 Yellow Perch & the Role of Density

Our measures of age-0 yellow perch at multiple early life stages revealed a sustained period of low densities in Oneida Lake. Egg production has declined over time, but mortality during interval 1 was variable across years with no distinct

temporal trend. Through frequent sampling of individual cohorts across four decades, we saw increased mortality of age-0 yellow perch during interval 2 as they transition from the larval stage to late summer, followed by a moderate decline in mortality rates during interval 3 when age-0 yellow perch are primarily demersal. The increased mortality during interval 2 compounds the problem of reduced egg production, and the combination of these two factors has led to low densities of age-0 yellow perch throughout their first year of life.

Beyond the more traditional assumptions of predator satiation and food limitation, density-dependent mechanisms can affect mortality and growth rates by influencing activity levels and risk-sensitive foraging behaviors. For young fishes, a high population density likely increases the amount of time or space needed to acquire food. Walters (2000) proposed that mortality should increase with population density for juvenile marine fishes. In this case, a high population density could necessitate individuals to increase foraging activities to obtain food (i.e., mortality occurs through increased number of encounters with predators) or minimize foraging risks at the cost of a lower growth rate (i.e., mortality occurs through increased vulnerability within an encounter with a predator). Initially, we saw the opposite trend in Oneida Lake – depensatory mortality was strongly evident when predation from walleye was the primary regulator of the age-0 yellow perch population (Forney 1971, 1977, 1980). However, this negative relationship between age-0 yellow perch density and mortality did not hold when all available data were considered. The disruption of the depensatory-mortality relationship, particularly for interval 3, was due to several observed years with low mortality and low yellow perch density. Lower-than-expected mortality rates for low-density cohorts suggest that yellow perch could be avoiding predation, but neither the predator biomass index nor average individual size of age-0 yellow perch was identified as important in the multiple regression analysis,

given the suite of variables included (see below). Because we have not typically measured high mortality for dense cohorts of age-0 yellow perch during any early-life-stage interval, it is unlikely that previous high densities of age-0 yellow perch affected activity levels to the point of increasing mortality as suggested by Walters (2000). However, the shift from increasing pelagic mortality (interval 2) to decreasing demersal mortality (interval 3) may indicate a change in the localized environments experienced by these separate early life stages in Oneida Lake. Such a change could reduce the vulnerability of age-0 yellow perch to predation, potentially through direct habitat separation from potential predators in interval 3 or indirectly through reduced activity levels resulting from access to increased or new sources of benthic food items.

Growth rates were density dependent in both interval 2 and interval 3, but density-dependent growth was not present in the more limited data available from the 8mm to 18mm larval surveys. That growth was not density dependent during the first interval is not surprising given that newly-hatched larvae are initially endogenous feeders. Mayer et al. (2000) also found density dependent growth (grams per day) of juvenile yellow perch, with additional growth occurring during years after zebra mussel establishment that was not explained by juvenile yellow perch density alone. Density-dependent growth during intervals 2 and 3 suggests competition for food resources, but evidence from multiple regression analyses does not directly support this explanation (see below). However, growth of age-0 yellow perch at high densities may have been suppressed based on a combination of behavioral factors and localized food limitation. Because age-0 yellow perch tend to form large schools, young yellow perch may experience a localized depletion of food resources. If the energetic costs of schooling are particularly high relative to the amount of food available to dense aggregations of yellow perch, then growth rates should improve at reduced densities (e.g., Boisclair and Leggett 1989).

A Changing Ecosystem & Conclusions from Regression Analyses

Changing ecological conditions in Oneida Lake have altered the environment experienced by age-0 yellow perch. One of the major changes is a decrease in chlorophyll-*a* and an increase in water clarity associated with the invasion of zebra mussels in 1992 (Mayer et al. 2001; Idrisi et al. 2001; Table 1-3). In Oneida Lake, increased water clarity has also contributed to increased diversity and extent of submerged aquatic vegetation in the littoral zone (Zhu et al. *in press*), which could affect both mortality and growth of young yellow perch when they occupy these inshore areas (during intervals 2 and 3). Increased macrophytes may alter the availability of littoral prey items for young yellow perch while also promoting a new suite of potential predators (e.g., black basses *Micropterus* spp.; see Chapter 3), especially if young fish select structurally complex habitats in clear waters (Snickars et al. 2004). Our multiple regression analyses suggested that Secchi depth was strongly related to growth but only marginally significant to mortality during interval 3.

Interestingly, Secchi depth was negatively associated with yellow perch growth from 8mm to 18mm but was positively associated with growth during later early-life-stage intervals. This may be associated with differences in foraging behavior and vulnerability relative to age-0 yellow perch size and changes in water clarity. Utne-Palm (2002) summarized potential size-dependent effects of turbidity on predator-prey interactions and suggested that small predators, which forage upon prey in close proximity, benefit from both the increased contrast between a nearby potential prey and its background as well as the protective cover of turbid water (see also Johnson and Hines 1999). On the other hand, larger predators, with a greater reactive volume, experience a limited visual field under the same conditions (Utne-Palm 2002).

Changing ecological conditions (e.g., Secchi, water temperature) can indirectly influence mortality and growth of young fish or interact with other important variables, but our multiple regression approach assumed direct, linear relations between the response and explanatory variables. Even so, that Secchi depth was identified as important in all growth models as well as interval 3 mortality indicates the potential for changing ecological conditions to become dominant factors for determining successful recruitment. However, the exact role of water clarity in relation to mortality and growth rates remains unclear. Increased water clarity may indirectly influence mortality by altering activity rates of young perch. As an example, the vertical distribution of zooplankton may change under conditions of increased light penetration in natural settings, so that while zooplankton density may decline in shallow water overall zooplankton abundance does not. If this occurs, zooplanktivorous yellow perch may respond by increasing their foraging area, which would likely increase their exposure to predators. In contrast, yellow perch are more developed by the end of the first year of life and can be flexible in their diet choices. Increased water clarity may increase the amount of good foraging habitats for these young yellow perch. This could be the result of either increased light penetration promoting a larger visual-foraging realm or through more direct association with benthic production related to zebra mussels. Ecological changes may modify spatial overlap between predators and prey, and these potential shifts warrant future consideration.

Temperature is an important influence on fishes and can even contribute to correlation of year class strength at the regional scale (Koonce et al 1977; Casselman 2002). The average water temperature in Oneida Lake during the growing season of age-0 yellow perch has increased over time (Appendix 1-3). Over the past several decades, duration of winter ice cover on Oneida Lake has decreased (CBFS,

unpublished data), and complete ice cover did not occur on Oneida Lake during the winter of 2001-2002. Changing springtime warming patterns would likely affect the timing of yellow perch spawning, hatching period, and duration of the larval period. In Oneida Lake, larval yellow perch are generally reaching 18mm earlier in the spring (Figure 1-4A), and the extent of this shift in timing is correlated with warmer May water temperatures ($N = 35$, $R^2 = 0.605$, $P < 0.001$; Figure 1-4B). Because we do not have annual estimates of hatch date, we have not determined if the earlier achievement of 18mm is due to earlier hatch dates, increased growth rates after hatching, or both. However, a positive relation between temperature and larval growth from the 8mm to 18mm survey was consistent with our *a priori* hypotheses that these young fish would grow more quickly when water temperatures were warmer. Clady (1976) also found increased survival of prolarval yellow perch during years with higher mean temperatures and that survival was more strongly correlated to mean temperature than the observed daily warming rates. Also, temperature was identified as the most significant explanatory variable for mortality during interval 1, indicating that warmer water temperatures are associated with lower mortality during the early life stages of yellow perch in Oneida Lake. A likely reason is that warmer temperatures allow for a more rapid transition through the interval with the highest daily mortality rates. Interestingly, temperature was not significantly related to growth or mortality rates, with the other variables included, for either interval 2 or 3.

Previous work has identified high winds as a source of egg mortality (Clady and Hutchinson 1975; Roseman et al. 2001). However, Clady (1976) found low year-to-year variability in survival of yellow perch prolarvae (egg to 8mm) and that their survival was more highly correlated with air temperature than either average daily or average maximum daily wind speed. Our multiple regression analysis for mortality during interval 1 suggests that high-wind events, in the presence of the other included

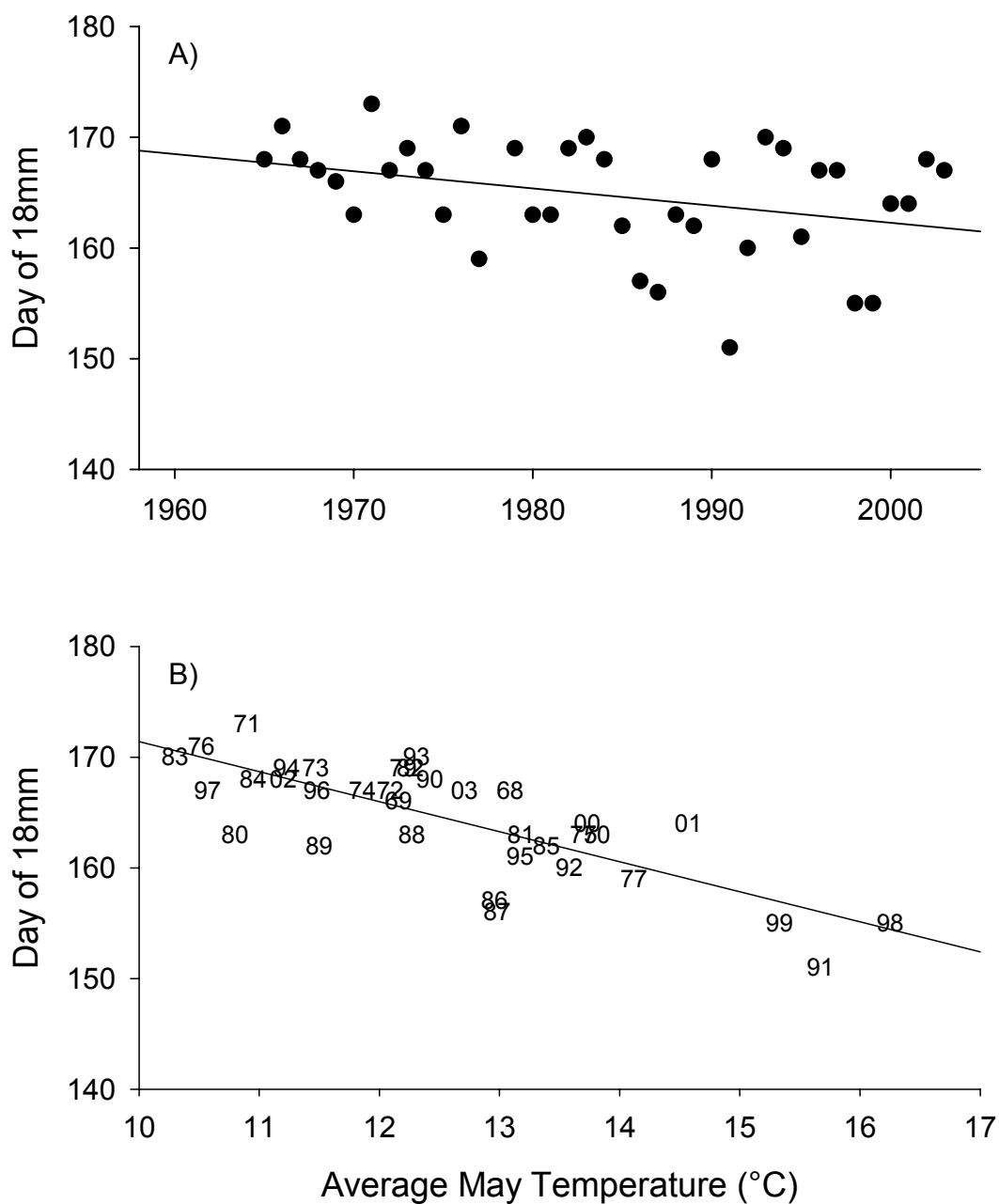


Figure 1-4. A) Shifts in temporal occurrences of the day of 18mm achievement by larval yellow perch, and B) the day of 18mm achievement against average May water temperature at 2m from 1968-2003 (no larval data for 1978).

variables, were not significantly correlated to early mortality across all years. If yellow perch spawn at deeper depths as a result of increased water clarity then egg masses may be less sensitive to winds. Because wind-driven water currents can also determine the spatial distribution of larval fishes in Oneida Lake (Houde 1969; Houde and Forney 1970), wind may still be an important intermediary influence of mortality if larvae become concentrated in unfavorable habitats. The current analysis used averages as descriptors of conditions experienced during early-life-stage intervals of age-0 yellow perch, and this approach may not be best suited to detect the effects of rapid changes in short-term events such as severe storms. Extreme high wind events may be detrimental to the survival of young fishes on the scale of hours or days, but have not persisted throughout a sequence of years to be identified as strongly and directly related to the early yellow perch mortality.

Age-0 yellow perch traditionally have been the principle prey for walleye in Oneida Lake (Forney 1974; Nielsen 1980). In addition to walleye, white perch and yellow perch comprise a large portion of Oneida Lake's fish biomass, and we considered them to be potential age-0 fish predators. However, our assessment of these three species indicates that their overall biomass has also declined noticeably during the period of reduced age-0 yellow perch densities. For the multiple regression analyses of early-life-stage mortality, we adjusted this estimate of potential predator biomass to be relative to the density of age-0 yellow perch at the beginning of each life stage interval. Although this index of predator biomass was scaled to be relative to the amount of age-0 yellow perch present, predatory variables were not selected with a positive coefficient in the mortality regression models. Gopalan et al. (1998) also reported significant declines in young-of-year yellow perch during a period when they were rarely found in walleye diets. Of course, it is also possible (or even likely)

that predation has increased from other species, namely those in changing inshore habitats, for which long-term data were not available.

Fluctuations in biotic interactions, such as competition and buffering of predation through alternative forage, also were expected to coincide with the changes in mortality rates. The role of competition for food resources within the age-0 fish community may vary with the degree of diet overlap, relative hatch dates, and the relative abundance of larval fishes (DeVries and Stein 1992; Garvey and Stein 1998; Irwin et al. 2003). In Oneida Lake, both age-0 white perch and age-0 gizzard shad feed on zooplankton (Prout et al. 1990; Roseman et al. 1996). Gizzard shad can also act as a forage buffer, reducing the effects of predation on juveniles of other species (Aday et al. 2003). However, neither mortality nor growth of age-0 yellow perch was strongly related to the indices of age-0 gizzard shad or age-0 white perch during either interval 2 or 3.

In Oneida Lake, gizzard shad and white perch typically hatch after yellow perch, and both species are capable of rapid growth and can achieve a large end-of-year size. Because of the later appearance of young, these species likely do not provide a buffer to larval yellow perch. The later hatch dates of gizzards shad and white perch have also been suggested to diminish the competitive interactions between these species and yellow perch (Prout et al. 1990; Roseman et al. 1996). When gizzard shad and white perch biomass is high during late summer and potentially able to influence zooplankton density, age-0 yellow perch are large enough to switch consumption to benthic invertebrates (Roseman et al. 1996).

Alternative forage species may ultimately produce negative effects, if predator biomass is increased and buffering is inconsistent. Our indices of age-0 white perch and age-0 gizzard shad in Oneida Lake were high just prior to the decline in yellow perch but then quickly diminished. If alternative forage temporarily supported the

adult walleye population beyond the level that would have occurred if the traditional predator-prey linkage between walleye and yellow perch had remained unaltered, then age-0 yellow perch could experience a sharp increase in predation once alternative forage species are no longer available (e.g., apparent competition; Holt 1977). Roseman et al. (1996) also implied that the benefits of buffering could be temporary if predator populations are maintained at an increased level and the buffering species is not. In particular, larval yellow perch would have an initial high vulnerability because larval yellow perch hatch before many other species in Oneida Lake. Even though we considered multiple early life stages, such a mechanism would be difficult to detect because intense predation on larval stages during a short window of time could severely reduce age-0 density without conveying a proportional benefit to ichthyoplanktivores that would be detectable as increased predator biomass.

We expected *Daphnia* spp. biomass to be related to yellow perch growth and possibly to mortality. In earlier studies, zooplanktivory by abundant yellow perch was shown to depress the *Daphnia* spp. population in Oneida Lake (Mills and Forney 1983), and thus influence the composition of the zooplankton community (Mills et al. 1987; Mills and Forney 1988). Using data from 1968-1983, Mills et al. (1987) describe a threshold regulation of *Daphnia pulicaria* (previously *D. pulex*) by age-0 yellow perch, such that *Daphnia pulicaria* densities were low during years when age-0 yellow perch density exceeded 14,400/ha or biomass exceeded 20 kg/ha. However, we have not seen a major change in total *Daphnia* spp. biomass in Oneida Lake in recent years, even though phosphorus levels have been reduced (Zhu et al. *in press*) and chlorophyll levels declined after the filter-feeding zebra mussel became established (Idrisi et al. 2001). In the multiple regression analyses, the index of *Daphnia* spp. biomass was not highly related to age-0 yellow perch growth rates in any time interval. This was true for both total *Daphnia* spp. biomass index and an

analysis using only *Daphnia pulicaria* density. Although a negative correlation between yellow perch biomass and *Daphnia* spp. biomass was still seen in Oneida Lake for years up to 1996 (Hall and Rudstam 1999), the converse – that *Daphnia* spp. biomass is correlated with age-0 yellow perch growth and mortality – was not supported by our analyses. Similarly, Whiteside et al. (1985) did not find a correlation between zooplankton abundance and growth of larval yellow perch.

Responses to major shifts in ecosystem structure can be complex, and even if altered conditions are reset, the return to the original ecosystem state may not occur (Carpenter 2003). In this sense, it is unrealistic to expect an increase in the yellow perch population via the same pathways that preceded ecological changes. Continued spread of nonindigenous species and climatic change (accompanied by the potential increased frequency of severe climatic events) may induce future regime shifts, further complicating efforts to understand complex food-web interactions. If the Oneida Lake fish community continues to become less dominated by walleye and yellow perch, identifying the factors related to the population dynamics of these two species is likely to be more difficult. In recent years, age-0 yellow perch are reaching a substantially larger size by 1 August, but increased body size has not compensated for increased mortality for determining the success of age-0 yellow perch to their first fall. If larger larvae take greater risks, they may have a higher probability of being selected as prey, resulting in increased mortality associated with increased larval growth rates (Pepin 1991). Therefore, fast growth may be both beneficial (from increased availability of food resources) and detrimental (if larvae experience increased exposure to predators) to some larval fish. However, we suggest that the benefits of increased growth rates are delayed beyond the period when the additional growth is achieved so that the overall success of a cohort is not firmly set at a single early life stage. Growth and mortality of age-0 yellow perch in Oneida Lake interact through a process of delayed

compensation so that while early increased mortality further reduces density, increased growth results in a larger end-of-year size, which benefits over-winter survival (e.g., Fitzgerald et al. *in press*).

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CHAPTER TWO

Confronting Multiple Long-term Data Sets to Evaluate Walleye Density, Gear Catchability, and Changes in Mortality in Oneida Lake, New York

ABSTRACT

Since the late 1950s, standardized sampling in Oneida Lake has produced three long-term data sets (trawl catch per unit effort, gillnet catch at age, and adult mark-recapture population estimates) for walleye *Sander vitreus*. The mark-recapture estimates provide a measure of absolute abundance over a number of non-consecutive years for adult walleye (age-4+) only. However, walleye collected in trawls and gillnets have been aged, providing independent, age-specific estimates of their relative abundance over time. Due to the lack of direct estimates of population abundance for sub-adult fish, the age-specific catchabilities of the sampling gears are largely unknown. We combined the three long-term data sets for walleye to simultaneously estimate mortality, gear catchabilities, and density using a non-linear minimization routine and investigated effects of assigning different weights to the input data on parameter estimation. Although age-specific catchabilities differed between the trawl and gillnet, ranks of cohort abundance were highly correlated, indicating that both gears measured year class strength. With constraints of constant fishing mortality for adult walleye, fixed natural mortality, and age- and gear-specific but time invariant catchabilities, the baseline model produced realistic estimates. We also compare the estimated gillnet catchability values with a selectivity curve based on catches in different mesh sizes. Allowing fishing mortality and an additional mortality term, reflecting double-crested cormorant *Phalacrocorax auritus* predation, to vary between

two time periods as a function of imposed vulnerabilities increased estimated sub-adult mortality and slightly decreased the fishing mortality estimate during the second period when cormorants were abundant and more restrictive size limits were in place.

INTRODUCTION

A common objective of traditional fisheries catch-at-age models is to use observed catch statistics to estimate both population abundance and exploitation rates through time (Hilborn and Walters 1992). Virtual population analysis (or cohort analysis) uses backwards projections to estimate previous abundance levels; whereas, integrated analysis (or statistical catch-at-age analysis) estimates abundances for all ages at the initial start time and for the earliest included age (usually considered an index of recruitment) for all years and then projects forward through time (Haddon 2001). A key component of these models is catch-at-age data from the fishery, which has limitations associated with potential non-linearity between catchability and population size. Fishers usually have high incentive to maximize catch per effort, which often occurs through advancements in technology, allowing for increased catchability of the target organism. Therefore, it is preferable to combine data from several sources (e.g., from a fishery and a standardized, fishery-independent survey) to improve stock assessments (Maunder 2001).

Fisheries managers often have several independent indices of abundance, but multiple measures can be difficult to reconcile into a best estimate of the development of the population over time. For example, data collected from gillnet surveys are generally viewed as an index of relative abundance; whereas, data collected from trawl surveys could be considered a measure of absolute abundance if certain extrapolative assumptions about the sampled areas are made and size-specific avoidance or trawl

“herding” are taken into account. In the case of these and other sampling approaches, gear biases and sampling variability can cause catch data to misrepresent the abundance of different age groups or size classes. As such, it is necessary to know the catchability associated with each gear in order to compare density estimates across sampling techniques.

Multiple gear types are often used to sample fish communities because gears typically vary in their ability to capture organisms of interest. As a consequence, the resulting catches provide different information, often producing a more complete picture of the fish community (Olin and Malinen 2003). But, comparisons of catches across gear types are not straightforward, especially in cases where gear types were originally selected more for their differences than their similarities. Differences in gear selectivity would therefore produce different levels of bias, even within a sub-set of ages of a single population (e.g., juvenile largemouth bass *Micropterus salmoides*; Jackson and Noble 1995). In addition, gear efficacy can vary between day and night. Comparison of day and night sampling is used in conjunction with multiple gear types in fish community assessment and can aid in the identification of gear bias (Pierce et al. 2001; Olin and Malinen 2003). Beyond day-night differences, the catchability of various gear types may also be related to population density, violating common assumptions of catch-per-effort indices (Rogers et al. 2003). For example, gear saturation can occur at high population levels, leading to reduced catchability, and saturation points relative to population density likely vary among gear types.

Catchability can also vary across ages or sizes within a single gear type. Therefore, it is often necessary to make adjustments using age-specific (or size-specific) selectivity curves to more accurately represent numbers-at-age in the population. For gillnets, Anderson (1998) further decomposes total selectivity into encounter, contact, and retention components. These components are influenced by

the size of the fish relative to that of the mesh, the visibility of the net, swimming speed, and activity (Hamley and Regier 1973; Hamley 1975; Rudstam et al. 1984; Willis et al. 1985; Grant et al. 2004). Because mesh visibility is lower for larger mesh sizes, swimming speed increases with fish size, and larger fish can also be entangled in small mesh sizes, gillnet catchability may increase with fish size even if retention probabilities are the same (Hamley and Regier 1973; Hamley 1975). In contrast, trawl catchability likely decreases with fish size because increased swimming speed at larger sizes likely improves the ability to avoid this gear (Wardle 1983). In addition, trawl catchability can be affected by water clarity (Nielsen 1983; Buijse et al. 1992), towing speed, and trawl material and construction (Wardle 1983). Variation in behavior, activity periods, and habitat preference among life stages of fish can further bias catches in most gears (Willis et al. 1985; Rudstam and Johnson 1992).

In Oneida Lake, New York, only periodic estimates of angler harvest exist (VanDeValk et al. 2005a), but standardized sampling has produced three long-term data sets, each of which provides a measure of walleye *Sander vitreus* abundance at multiple ages. For nearly half a century, walleye in Oneida Lake have been routinely collected in trawls and gillnets, with known effort. Walleye collected in both gear types have been aged, providing the opportunity for independent, age-specific estimates of their relative abundance. The presence of two long-term data series with contrasting selectivity should aid our estimation of the effects of age structure on the catchability of both the trawl and gillnets. In addition, the population of age-4 and older walleye has been estimated by mark-recapture for 21 years since 1958. Previously, correlation between mark-recapture estimates and gillnet catches have been examined (Jackson et al. *in review*). For Oneida Lake, we do not expect any of our sampling approaches to influence the size structure or abundance of walleye or the subsequent catch rates of other gear types (Jackson et al. *in review*). We have not to

date combined the three long-term data series to obtain a maximum likelihood estimate of the population for multiple age groups of walleye.

We expect a change in walleye mortality based on changing conditions in Oneida Lake. During the early 1990s, the establishment of zebra mussels *Dreissena polymorpha* (possibly combined with decreased nutrient loading) led to increased water clarity and photic zone depth in Oneida Lake (Idrisi et al. 2001). By contributing to these and other changes, zebra mussels likely act as “ecosystem engineers” (sensu Jones et al. 1994) in Oneida Lake, causing shifts in lower level trophic dynamics and enhanced littoral macrophyte growth (Mayer et al. 2002; Zhu et al. *in press*). At the same time, the abundance of double-crested cormorants *Phalacrocorax auritus* on Oneida Lake has increased, introducing a new source of predation on sub-adult walleye and yellow perch (Coleman 2003; Rudstam et al. 2004). Previously, VanDeValk et al. (2002) and Rudstam et al. (2004) used cormorant diet data to document the negative impact of cormorants on Oneida Lake’s percid community. However, Rudstam et al. (2004) based their estimates of sub-adult mortality on a subset of the available data (CPE of age-1 walleye in trawls and subsequent mark-recapture estimates at age 4). Here, we wish to simultaneously use the three long-term data sources for Oneida Lake walleye to evaluate possible changes in walleye mortality associated with the recent period of changing conditions.

We used AD Model Builder[®] (Otter Research Ltd. 2000) software to estimate age-specific gear catchabilities, mortality, and the density of sub-adult walleye using input data from all three long-term data sets for walleye in Oneida Lake. First, we constructed a baseline model where an instantaneous natural mortality rate was calculated from independent data (see methods) and set equivalent for all ages and an instantaneous fishing mortality rate was estimated for age-3 and older walleye but held constant over time. To test for temporal changes in mortality associated with the

changing conditions in Oneida Lake, we also estimated mortality separately for two time periods (1958-1989 and 1990-2003) using assumptions of age-specific vulnerability to both cormorants and anglers. Rudstam et al. (2004) used a similar separation of time periods to assess cormorant-driven walleye mortality. Our hypothesis was that mortality of sub-adult walleye has increased during recent years due to increased vulnerability to visually feeding top-predators (the result of clearer water after the introduction of zebra mussels) and the increased presence of piscivorous cormorants. Further, we hypothesized that mortality of adult walleye has decreased due to more restrictive harvest regulations and an assumed lower angling effort during recent years. Our objectives were to: 1) estimate annual sub-adult walleye density along with age-specific catchabilities of two collection gears by simultaneously using the three available long-term data sources, and 2) use two models of different complexity to evaluate potential changes in walleye mortality over time in Oneida Lake.

METHODS

Description of study site

Oneida Lake has the largest (207 km²) surface area of any lake entirely in New York State and is one of the most studied freshwater ecosystems in North America (Adams and Hankinson 1928; Harman and Forney 1970; Greeson 1971; Mills et al. 1978; Forney 1980; Mills and Forney 1988; Hall and Rudstam 1999; Rudstam et al. 2004). In addition to offering long-term data series on multiple trophic levels ranging from algae to top predators, Oneida Lake provides important recreational and economic resources to much of central New York and the northeastern USA. Walleye and yellow perch are the most sought after sport fishes, and both species are important

components of the Oneida Lake food web (Forney 1980; Mills and Forney 1988). Recently, multiple angling tournaments have targeted black bass *Micropterus* spp., and lake sturgeon *Acipenser fulvescens* (a threatened species in NY state) has successfully been reintroduced into Oneida Lake (Jackson et al. 2002).

Indices of walleye abundance

Gillnet catch data for walleye are available for all years from 1958-2003 except for 1974. During each of these years, multifilament gillnets were used to sample 15 fixed sites in a standardized sequence from June through September. At each site, two nets (300ft x 6ft depth) were set on bottom and allowed to fish overnight for approximately 12 hours. Each net consisted of two gangs of six 25ft panels so that mesh size (stretch mesh) ranged from 1.5in to 4in at 0.5in increments. During 1963 through 1967, gillnet sampling was conducted using one white net and one colored (red, green, or black) net. During other years, two white nets were used at each site. Scales were removed from individuals for age determination, and the age data were combined across sites to determine annual age distributions of the total catch. To compare the relative strength of walleye cohorts with that from the trawl, we summed the gillnet catch-at-age estimates for each walleye cohort (catch at age-1 to age-7) over time and used this as an indicator of year-class strength. The standardized gillnet survey was not completed in Oneida Lake during 1974; therefore, catch-at-age estimates for cohorts present during this year were calculated from the catches of adjacent years using the average of age-specific ratios of the catch-at-age and catch-at-age+1 during 1958-1972. Estimation of missing values for both the gillnet and trawl was necessary to better evaluate year-class strength, as measured by the two gears; however, these estimated values were not influential for parameter estimation in the model (see below). Comparisons of year-class strength were made using a Spearman

rank correlation on all cohorts from 1960 to 1996 for which the cumulative catch data were available for ages 1 through 7.

Walleye abundance in Oneida Lake has been assessed with a summer-fall bottom trawl survey at ten standardized locations since 1961. Each site was sampled weekly for about 15 consecutive weeks. The bottom trawl has a 5.5m footrope, and each haul samples approximately 0.1ha of bottom surface area with a transect length of approximately 280m. To facilitate comparisons with population estimates, we converted total trawl catches to catch per hectare swept (CPUE). During seven years, age-7 walleye were not specifically identified in the ageing process for trawl-caught fish. Instead, they were included as part of an age-7 and older group. For the cohort-level comparison between trawls and gillnets, we estimated the density of age-7 walleye for these few years from the number of age-6 walleye the previous year using a calculated ratio of catches of age-6 and age-7 walleye during the following year. For a comparison with gillnet catches, walleye densities were totaled within cohorts, which was then used as an indicator of year-class strength.

Since 1958, the population size of adult walleye has been periodically estimated using mark-recapture methods (N = 21 years; Forney 1967; Forney 1980; Rudstam et al 2004; Jackson et al. *in review*). Unlike the long-term data sets from trawl and gillnet sampling, the mark-recapture population estimates are for adult fish only (Table 2-1). During early spring (usually April), adult walleye were collected in trap nets near Scriba Creek by the Oneida Fish Cultural Station staff, Constantia, New York and near Shackelton Point by personnel from the Cornell Biological Field Station (CBFS). Individual walleye were marked (12,000-26,000 per year) using a year-specific fin clip (Eipper and Forney 1965). Occasionally, additional walleye were captured and marked at other locations using trap nets and electrofishing surveys; however, these collections usually contributed less than 20% of the total

Table 2-1. Summary of input data used in walleye estimation model. From each year's gillnet collection, a sub-sample of walleye were aged. This age distribution was adjusted upward to the total catch, when necessary (see text for additional description), and used for the observed catch at age. Mark-recapture estimates were conducted for age-4 to age-7 walleye for 21 nonconsecutive years ranging from 1958 to 2003.

Source	Years	N	Description
Gillnet	1958-1973, 1975-2003	315	Observed gillnet catch at age (1-7) and time
Trawl	1961-2003 ¹	294	Observed density based on trawl catch at age (1-7) and time
Adults	Nonconsecutive	84	Observed density at age (4-7) and time estimated from using mark-recapture techniques

¹ During 7 years from 1961-2003, age-7 walleye were not uniquely identified. Rather, they were included as part of an age-7+ age group; therefore, model estimates were not influenced by these observations.

number of marked fish (Forney 1967). Throughout the summer and fall, recaptures were collected primarily using electrofishing and large trawls (with approximately equal effort in all areas of the lake), but occasionally using gillnets and trap nets (1958-1960; Forney 1967). Population estimates were calculated for each age group of adult walleye using Bailey's (1951) modification of the Petersen formula (additional details for Oneida Lake in Forney 1967, 1980; VanDeValk et al 2002, and Jackson et al. *in review*).

Parameter estimation

We used AD Model Builder[®] (v. 6.3) software with the Visual Studio C++ compiler to construct and perform nonlinear estimation procedures. Based on the relative availability of the three input data sources, the estimation portion of this study targeted age-1 to age-7 walleye during the period of 1958 through 2003. We began by constructing a baseline model to evaluate age-specific catchability values for both sampling gears. We canceled the influence of the few missing trawl values and the missing gillnet catch from 1974 using a matrix of weighting factors (0 or 1; Table 2-1). Age-0 data were not included in the estimation model due to the very low catchability of this age class in gillnets as well as likely high variability in predation due to high vulnerability of this age class to cannibalism (Chevalier 1973). Parameters estimated in the baseline model included: age-specific catchability values for both the trawl and gillnet separately, an instantaneous fishing mortality rate for age-3 and older walleye, and an initialization vector of walleye density (Appendix 2-1). Most parameters were initialized and estimated as \log_e values, but we report back-transformed values. In the baseline model, density (as number per hectare) was assigned an initialization value of 33.1 based on the average catch of age-1 walleye in the trawl and a previous trawl-catchability estimate for adult walleye. An

instantaneous natural mortality rate of -0.101 was applied to all age classes. The calculations used to estimate this instantaneous natural mortality value were based on data for adult walleye, but we felt that it was reasonable to also apply this rate to sub-adults because, throughout most of the sampled period, we expect that late-year age-1 and age-2 walleye would have few predators as they outgrow the size-selective piscivorous fish present (Chevalier 1973) and anglers catch few walleye at these young ages (VanDeValk et al. 2005a). In addition to the fixed instantaneous rate of natural mortality, an instantaneous fishing mortality rate was estimated by the model and affected age-3 and older walleye. This parameter was initialized at -0.242 based on measures of adult walleye survival and angler harvest during 1958, 1959, 1997, and 2002 (Forney 1967; VanDeValk et al. 2005b; Appendix 2-2).

Variability in catch-at-age data occasionally suggests survival rates greater than 100%; therefore, we included the constraint of an exponential decline in abundance over time. This additional model structure was provided by the function:

$$(1) \quad N_{(i+1,j+1)} = N_{(i,j)} e^{-zt},$$

where $N_{(i,j)}$ is the density of a cohort during year i at age j , $N_{(i+1,j+1)}$ is the density of the same cohort during the following year, z is an instantaneous annual mortality rate (all sources) and t equals one year. The values used to initialize the density matrix were constructed as an overall mean coupled with a series of bounded deviations.

For both the gillnet and trawl, we assumed that age-specific gear catchabilities remained constant across years. The age-specific total catch for gillnets was estimated from the predicted population size of walleye and an age-specific gillnet catchability:

$$(2) \quad C_{G(i,j)} = N_{(i,j)} q_{G(j)},$$

where $C_{G(i,j)}$ is the predicted total catch-at-age- j of walleye in the standard gillnets during year i , $N_{(i,j)}$ is the estimated density of age- j walleye in the lake during year i , and $q_{G(j)}$ is the estimated age-specific catchability of the standard gillnets. Likewise, trawl CPUE was estimated using the predicted annual age-specific abundance of walleye and the parameters for trawl catchability:

$$(3) \quad C_{T(i,j)} = N_{(i,j)} q_{T(j)},$$

where $C_{T(i,j)}$ is the predicted catch-per-unit-effort of age- j walleye captured in trawls during year i , $N_{(i,j)}$ is the estimated density of age- j walleye in the lake during year i , and $q_{T(j)}$ is the estimated age-specific catchability of the bottom trawl.

The estimation of parameters was driven by a nonlinear estimation procedure, which varies parameter values to minimize differences between the observed and predicted values for gillnet catches, the trawl CPUE, and the adult mark-recapture population estimates (the objective function). The objective function was built as the sum of three separate concentrated negative log-likelihood functions that were specific to each of the input data sets. When error residuals are normally distributed and have constant variance, the minimization of residual sum of squares is adequate for determining parameter values. In fact, the minimization of residual sum of squares and the minimization of the negative log-likelihood would produce the same parameter estimates in this case (e.g., simple linear regression; Hilborn and Mangel 1997; Haddon 2001). In our case, using a likelihood approach rather than minimizing the sum of squares allowed us to better quantify the error associated with each estimated parameter. The likelihood function for the commonly used normal distribution is determined by taking the product of the individual observation likelihoods, assuming they are independent and identically distributed:

$$(4) \quad L(x | \mu, \sigma^2) = \prod_{i=1}^n \left[\frac{1}{\sqrt{2\pi\sigma^2}} \exp \left\{ -\frac{1}{2\sigma^2} (x_i - \mu)^2 \right\} \right],$$

where the observations (x) have mean μ and variance σ^2 . For each input data source, the number of observations, n , may be different. The objective function in AD Model Builder[®] is a minimization procedure, so the minimization of the negative log-likelihood was used, which is equivalent to maximizing the likelihood function shown above. The negative log-likelihood form of the normal distribution is:

$$(5) \quad -\ln L = -l(x | \mu, \sigma^2) = \frac{n}{2} \ln(2\pi\sigma^2) + \frac{1}{2\sigma^2} \sum_{i=1}^n (x_i - \mu)^2.$$

We used a concentrated form of the negative log-likelihood function to minimize the difference between the supplied input data and the estimated values for catch-at-age in gillnets, trawl CPUE, and adult population density. The traditional form of the negative log-likelihood was reduced to a concentrated form by replacing σ^2 with its maximum likelihood estimate and simplifying:

$$(6) \quad \text{Concentrated}[-\ln L] = \frac{n}{2} \ln \left(2\pi \frac{\sum_{i=1}^n (x_i - \mu)^2}{n} \right) + \frac{n}{2}.$$

The objective function was the sum of the three concentrated negative log-likelihood functions after weighting coefficients were applied.

Weighting coefficients are usually applied to various functions to affect the contributions of separate sets of information to overall parameter estimation. In our case, the data for adult walleye density and trawl CPUE were both input into AD Model Builder[®] as number per hectare; however, the sampling area of the passive

gillnet was unknown. Differences in the unknown age-specific catchabilities of the passive and active gears also add to the complexity. Likewise, it is more difficult to assess the effects of the variance of each independent data set when performing nonlinear estimation of multiple parameters. For the baseline model with constant mortality, we applied weighting coefficients to the concentrated log-likelihood functions so that the importance of fitting predicted values to the observed data was approximately equal for each of the three input data sets. To further assess the effects of our assumption to weight each input data set equally, we reran a modified baseline model three times, in each case adjusting the weighting coefficient of a single input data set by a factor of ten, which allowed that data set to dominate the influence of the parameter estimation over the other two.

While the baseline model achieved simultaneous use of all three long-term data sets for estimating parameters, we also wished to include additional information to better represent the changing conditions of Oneida Lake. In order to detect temporal changes in mortality, the baseline model was modified to include two periods (1958-1989 and 1990-2003) of mortality for both sub-adult and adult walleye. Henceforth, we refer to this model as the multi-mortality model. For the multi-mortality model, the fixed instantaneous natural mortality rate and the initialization of the instantaneous fishing mortality rate were the same as in the baseline approach, and all mortality parameters were instantaneous rates. To simplify interpretations, the weighting coefficients used with the concentrated negative log likelihood functions were retained from the baseline model. An additional instantaneous mortality rate was implemented to reflect cormorant predation. This parameter was initialized using the same value as used to initialize the instantaneous fishing mortality rate. The multi-mortality model also differed from the baseline model in that both the instantaneous fishing mortality

rate and the instantaneous cormorant mortality rate were each applied to age groups based on assumptions of vulnerability during two time periods.

For each time period in the multi-mortality model, we calculated the proportion of each walleye age group that was vulnerable to cormorants and anglers using average total length-at-age values, which were based on back-calculations from walleye scales. First, the back-calculated length-at-age values were averaged between sexes, based on an equal sex ratio in gillnet catch of the Oneida Lake walleye population (Cornell Biological Field Station unpublished data). These back-calculated total length-at-age values coincide with springtime annulus formation, which precedes the timing of peak angler harvest and cormorant presence; therefore, we calculated age-specific growth rates for each year and used these to project length-at-age estimates forward three months into the growing season. Using these annual projected size-at-age estimates, we then determined if each age class was vulnerable to that year's minimum length limit in effect for angler harvest from Oneida Lake. Prior to 1975, no minimum size limit was in place, so we assumed that anglers would not have harvested walleye that were less than 12in (305mm). In 1979 and 1980, the minimum length limit was 12in, and it was 18in (457mm) from 2001-2003. For all other years, the minimum length limit was 15in (381mm). We did not attempt to account for changes in the creel limit. Likewise, we used the projected total length-at-age values to estimate vulnerability of the age groups to cormorants during time period two. We assumed that cormorants were capable of consuming walleye less than 14.2in (360mm; J. Coleman unpublished data), and then we determined if an age group was vulnerable based on each projected total length-at-age. Beyond this maximum size threshold, we did not attempt to incorporate prey selectivity of cormorants. Based on this knife-edge assignment of vulnerability to angler harvest and cormorant predation

for each age, we averaged across years to establish the average proportion of each age class vulnerable to each potential source of mortality for the two time periods.

For both additional sources of mortality, the estimated proportion vulnerable during each time period was used to weight the influence of the two estimated instantaneous mortality rates. Using fishing mortality as an example, an age group (N_j) can be separated into vulnerable (V_j) and invulnerable (refuge, R_j) components as:

$$(7) \quad N_j = (V_j + R_j).$$

Then, the transition of a partially vulnerable age group to the following year (N_{j+1}) can be represented as:

$$(8) \quad N_{j+1} = N_j e^{-(f')} e^{-(m)} = \left(\left(\frac{V_j}{N_j} \right) e^{-(f)} + \left(1 - \frac{V_j}{N_j} \right) \right) e^{-(m)}$$

where f' represents the instantaneous mortality rate due to angler harvest that applies to the partially vulnerable population that is present, m represents the instantaneous natural mortality rate, V_j is the number of individuals in the age group that is vulnerable to the instantaneous harvest mortality rate and R_j is the number of individuals in the age group that experiences a refuge from this harvest mortality. Applying f' to the entire age group should produce an equivalent harvest estimate as applying f to the vulnerable portion of the age group. Then, f' can be calculated for each age class from f and the proportion vulnerable (V/N) by rearranging equation 8 as:

$$(9) \quad f' = - \left[\ln \left(\left(\frac{V_j}{N_j} \right) e^{-(f)} + \left(1 - \frac{V_j}{N_j} \right) \right) \right].$$

Within each of the two time periods, the calculated proportion of each age class

vulnerable $\left(\frac{V_j}{N_j} \right)$ to both estimated mortality rates was held constant. Using this

approach, only one additional instantaneous mortality parameter (representing cormorant predation) was estimated in the multi-mortality model, but the influence of both estimated instantaneous mortality parameters on each age class could change between time periods.

RESULTS

Indices of walleye abundance

Gillnet effort was constant for all 45 available years, and the annual total catch of walleye in gillnets ranged from 75 to 836. The average proportion of the total gillnet catch of walleye that was aged annually was 96% (range = 66-100%). Given the mesh sizes used, catchability of walleye in the Oneida gillnets should peak at some intermediate age (i.e., a size range of 400-470mm; Forney et al. 1994), and catch-at-age values for gillnets were typically low for younger ages (Appendix 2-3). Although the catch of age-1 walleye in gillnets was typically lower than for older ages of a cohort, strong year classes of walleye typically produced large catches at age-1. Trawl effort ranged from 113 to 272 hauls per year (mean = 153) from 1961 to 2003. As expected, trawl CPUE typically declined as the cohort aged for both strong (Appendix 2-4A) and recent, weak (Appendix 2-4B) year-classes, and catches were highest for age-1 walleye for 29 of 37 complete cohorts (data for age-1 to age-7). Although the size-dependent catchability of the gillnet and trawl were expected to be different, both gears produced similar rankings of the strength of walleye cohorts across years (Spearman rank correlation, $N = 37$, $r_s = 0.912$, $P < 0.001$; Figure 2-1).

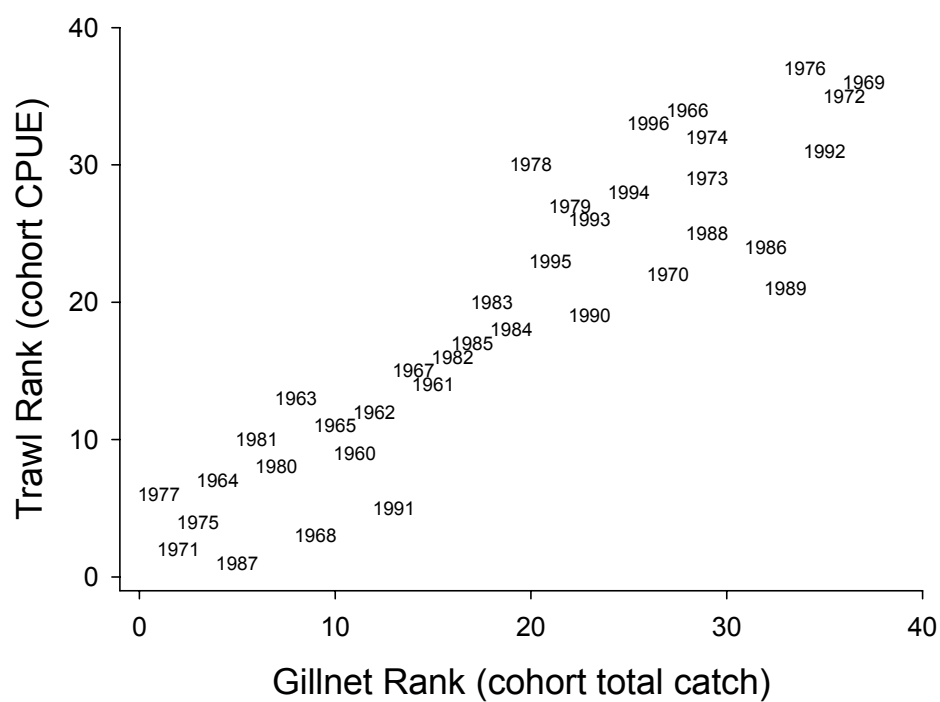


Figure 2-1. Spearman rank correlation of walleye year-class strength in gillnets (cohort total catch from age-1 to age-7) versus rank of year-class strength in 18' bottom trawls (cohort total CPUE age-1 to age-7) for 1960 to 1996.

To serve as reference points for comparison with model estimates, catchabilities of adult walleye in gillnets and trawls were also calculated using adult mark-recapture estimates as measures of population size. This suggested a decreasing trend in catchability of adult walleye in gillnets from age 4 to age 7 (Figure 2-2). This calculation was based on the total annual catch-at-age of adult walleye collected at the 15 standard sites and should not be expected to range between 0 and 1 because the annual gillnet survey samples an unknown area of the lake. This trend in catchability was expected because older fish are reaching sizes larger than the peak size selectivity of the largest mesh sizes used in our survey nets (Forney et al. 1994). The catchability of adult walleye in bottom trawls also was low and displayed a decreasing trend with increased age (Figure 2-2). Mark-recapture estimates for adult walleye suggested that walleye density was low during recent years (Appendix 2-5).

Parameter estimation – baseline model

The baseline model estimated an initialization value for walleye density (6.2 walleye / ha) and an annual instantaneous fishing mortality rate of -0.242, which was additive to the fixed instantaneous natural mortality rate (-0.101; yielding a total instantaneous mortality rate = -0.344 or a total annual survival = 70.9%) for adult walleye. Age-specific estimates of trawl catchability decreased from age-1 to age-7 (Figure 2-3A), when age-specific mortality was held constant over time. In the baseline model, the estimated values for gillnet catchability were lowest for age-1 and peaked for age-6 (Figure 2-3B).

To assess the effects of the weighting coefficients applied to the input data sources, the baseline model was rerun with each input data (gillnet catch-at-age, trawl CPUE, and adult density) set allowed to dominate the objective function. The annual adult survival estimated for these three additional model runs, with alternating highest

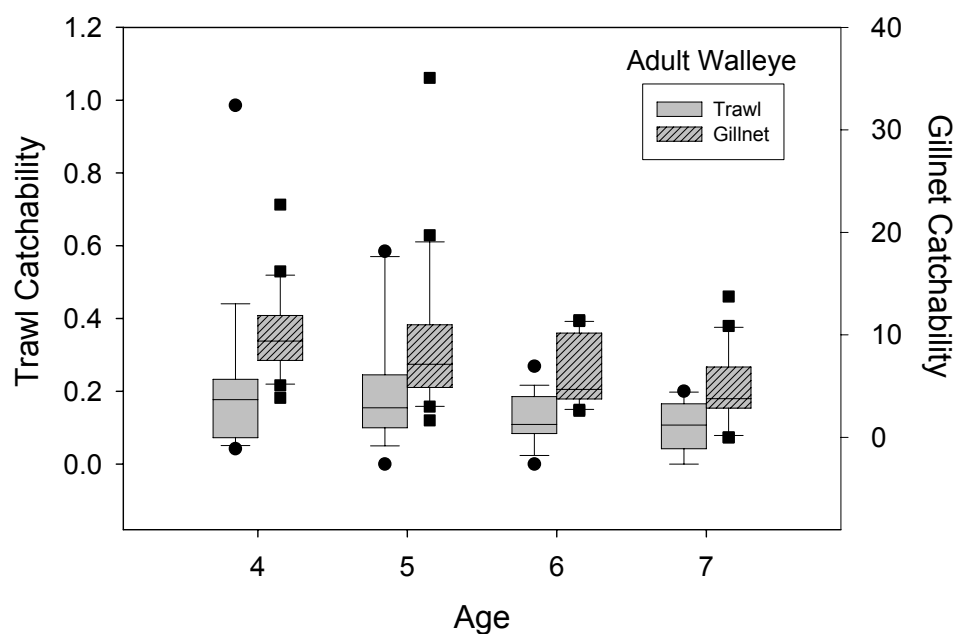


Figure 2-2. Age-specific catchability values for adult walleye, based on mark-recapture population estimates for adult walleye and both the CPUE (# / ha) of annual bottom trawls (extreme values are circles) and the annual total catch of gillnets (extreme values are squares) set at 15 standard sites. Boxes span 25th to 75th percentile, whiskers represent the 10th and 90th percentile, and a horizontal line in each box represents the median.

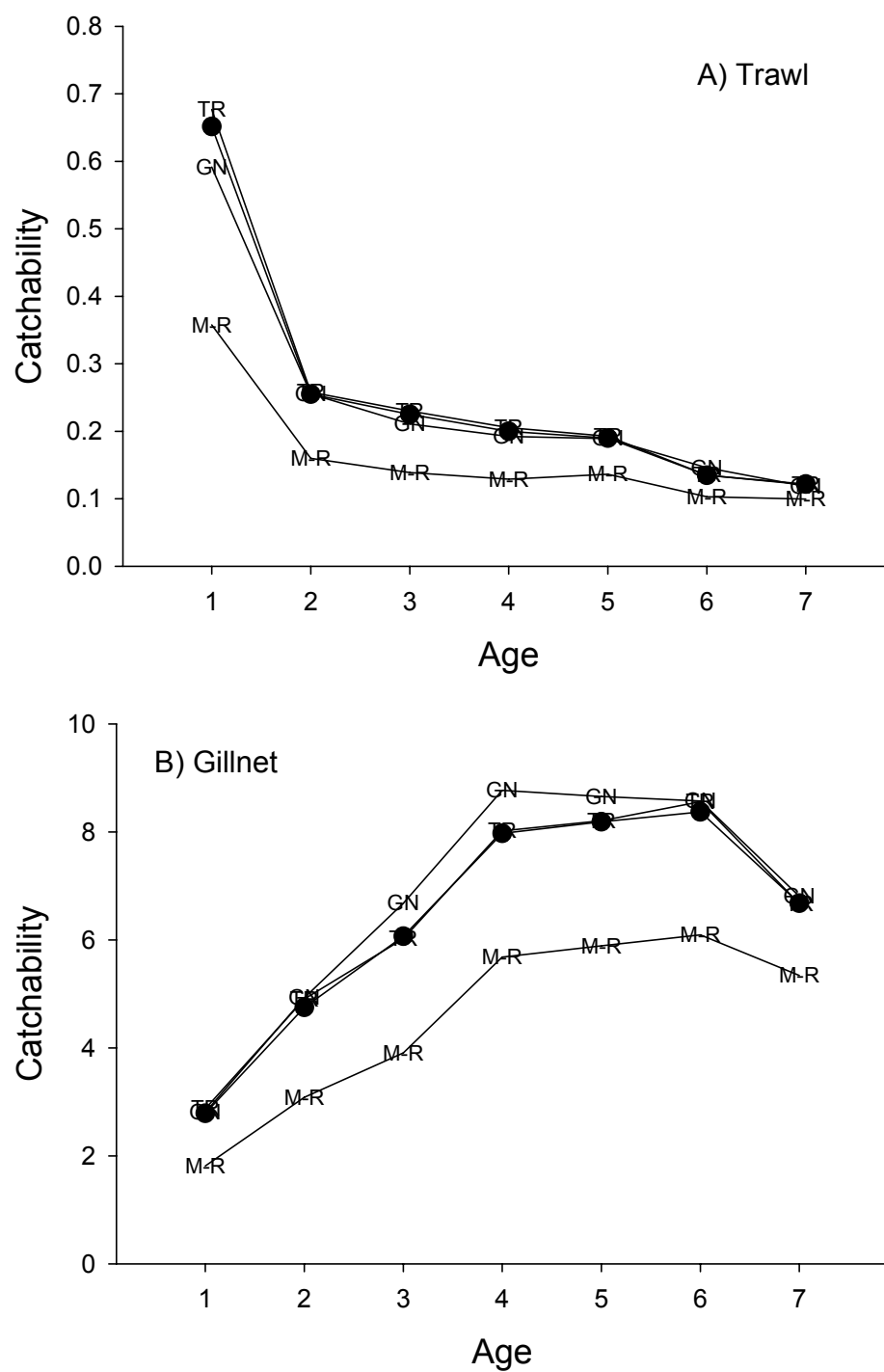


Figure 2-3. Age-specific catchability estimates for the A) trawl and B) gillnet. Gillnet estimates are based on annual sampling at 15 locations. Circles indicate estimates from the baseline model. M-R, TR, and GN represent modified baseline conditions where the influence of each indicated data set was increased by a factor of 10.

influence on input data, were 71.4% (gillnet), 71.0% (trawl), and 68.5% (adult mark-recapture estimates). The estimated age-specific catchability values for both the gillnet and trawl were approximately the same when more weight was given to either the gillnet or trawl input data sets (Figure 2-3). However, when the mark-recapture estimates were closely fit by the model, the gear catchability estimates shifted downward for all age classes (Figure 2-3).

Parameter estimation – multi-mortality model

In both time periods of the multiple-mortality model, all ages were affected by the same fixed natural mortality rate. We allowed fishing mortality to be a function of size and size limits. For the first time period (1958-1989), we assumed annual mortality of age-2 and older walleye was also influenced by fishing mortality in proportion to their vulnerability to angling size limits. As such, the annual survival of age-1 walleye during the initial time period (90.4%) was unchanged from the baseline model. The survival of age-2 walleye (89.7%) was slightly lower in the multi-mortality scenario than the baseline because length-at-age values suggested a small proportion of age-2 walleye would have been vulnerable to angler harvest during the first time period, when some years had no length-based harvest restrictions (we assumed a 12in minimum harvest size for these years). The overall survival of age-3 and 4 walleye (77.0 and 72.1%) were higher than the estimate for adults in the more general baseline model. However, the survival values for age-5 and age-6 walleye in the first time period were lower than the baseline model (68.6 and 67.9%) due to fishing mortality having the greatest influence on these two ages.

Survival estimates for walleye were quite different for the two time periods (Figure 2-4). Due to more restrictive length limits during the second time period (1990-2002) and therefore lower calculated vulnerability values, the influence of the

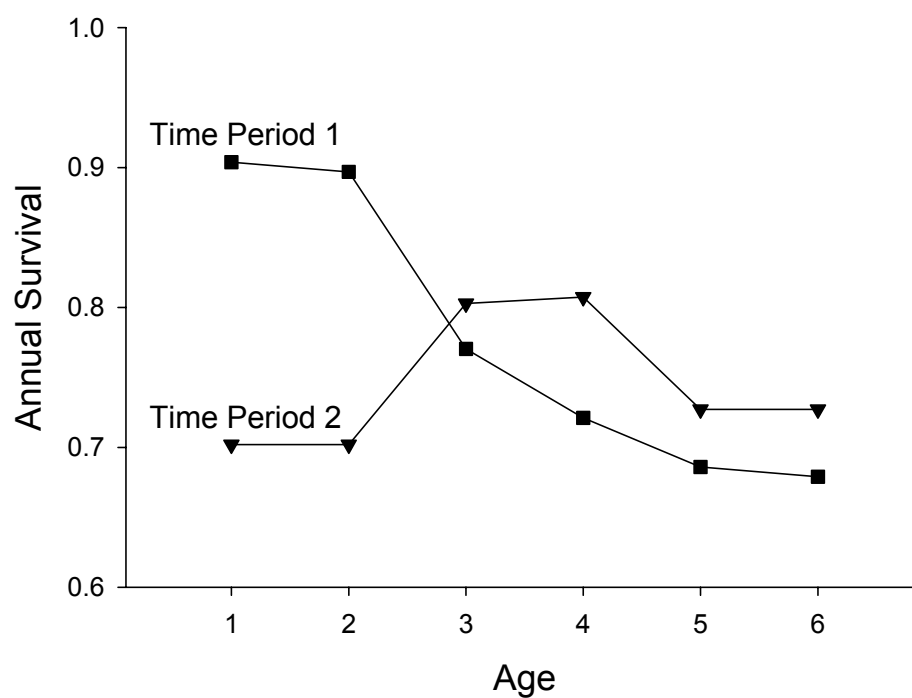


Figure 2-4. Estimated annual survival of walleye by age for two time periods as determined in the multi-mortality model. Time period 1 (1958-1989) is represented with squares and time period 2 (1990-2003) is represented with triangles.

fishing mortality on each age class was less than for the first time period. As such, the survival estimates for age-3 and older walleye in the second time period (80.3, 80.7, 72.7, and 72.7% respectively) were all greater than the baseline and also higher than those estimated for time period one. Because age-1 and age-2 walleye were both fully influenced by the additional mortality term reflecting cormorant predation (which was unbounded), the survival estimate for these two ages (70.2%) was substantially lower than the annual survival reflecting only natural mortality. As we expected, the multiple-mortality model suggested a strong decline in the survival of sub-adult walleye in Oneida Lake after 1990. The high survival estimate for age-4 walleye represents our expectation that these fish had outgrown vulnerability to cormorants but remained protected from angler harvest via recent length restrictions. Overall, the two mortality parameters included in the multiple-mortality model suggested mortality beyond the fixed natural mortality level, although the direction of influence of these two mortality parameters was not predetermined in the model's structure. The additional mortality term applied to adult ages in proportion to their potential vulnerability to angling ($Z = -0.286$) was estimated to be only a slightly larger source of mortality than was estimated for sub-adults during the second time period ($Z = -0.253$), although the actual influence of these two additional parameters varied among ages.

As a result of the initial recruitment vector and mortality parameters estimated in the multi-mortality model, density of sub-adult walleye was low during the second time period (Figure 2-5). A lower number of age-1 walleye (associated with higher mortality between age 0 and age 1) likely contributed to the overall decline in our catches. The catchability estimates in the multi-mortality scenario for both the gillnet and trawl had similar shapes as those estimated from the baseline model (Figure 2-6). The peak catchability estimate for the gillnets remained associated with age-6 walleye,

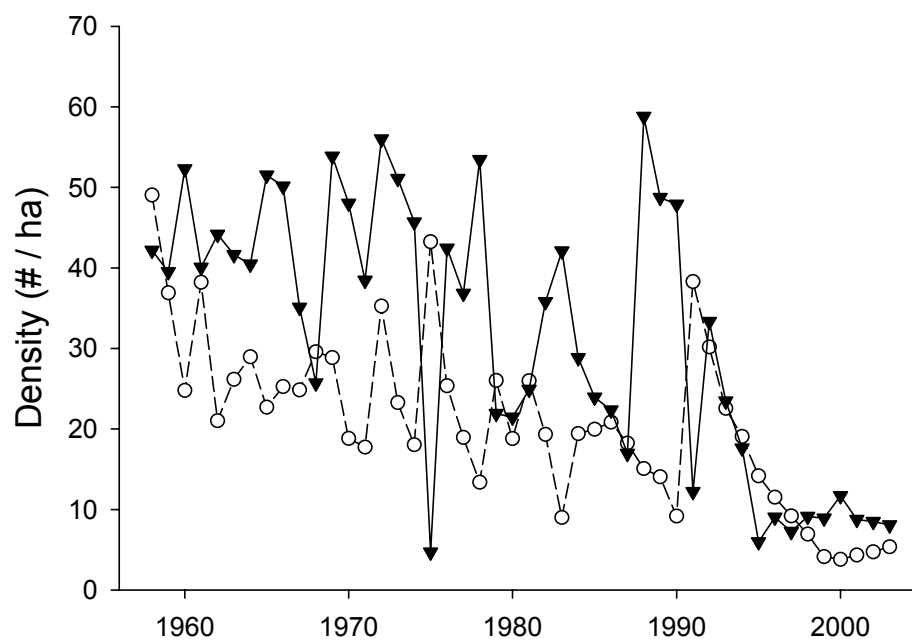


Figure 2-5. Estimated density of sub-adult (age-1 through age-3; triangles) and adult (age-4 through age-7; open circles) walleye in Oneida Lake from 1958 through 2003 based on the multi-mortality scenario.

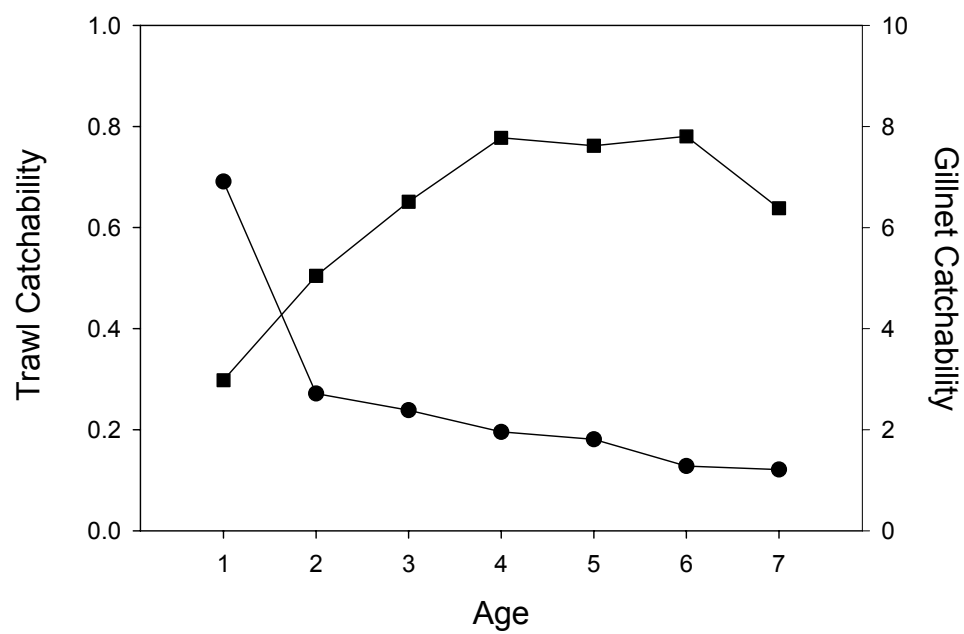


Figure 2-6. Estimated age-specific trawl (circles) and gillnet (squares) catchability for walleye in Oneida Lake based on the multi-mortality scenario.

although the catchability estimates for age-4, -5, and -6 walleye were slightly lower in the multi-mortality scenario. A visual inspection of residuals for all three input data series revealed that strong time trends were not present (Appendix 2-6).

DISCUSSION

Fish populations are often sampled using both passive and active gears, but catch rates of these gear types are not directly comparable unless the relative catchabilities are known. The problems associated with comparing or combining data from the two sampling approaches generally arises from the difficulty in quantifying the sampling area of the passive gear. However, both gear types provide information on the size of the population. In Oneida Lake, the catch-at-age data from trawls and gillnets differed, but the relative strengths of walleye cohorts identified by the gears were highly correlated. Using a minimal number of limiting assumptions, we estimated age-specific density of age-1 to age-7 walleye in Oneida Lake as well as age-specific catchability values for both the standard gillnet and trawl. This approach simultaneously used weighted contributions from three data sets (gillnet, trawls, and adult mark-recapture), which were collected over a 46 year period.

The choice of weighting coefficients used to regulate the influence of each input data set on the estimates had relatively little influence on the parameter estimates themselves, except when the mark-recapture data set was given a much higher weight than given to the data sets from the two sampling gears. The mark-recapture population estimates were available for the adult age classes covering 21 non-consecutive years from 1958 to 2003. Although we have confidence in these estimates as indicators of adult walleye abundance, this input data set contained no direct estimates for sub-adults and had no estimates for many of the years that the

population was sampled with both the trawl and gillnet. Therefore, we felt that giving the adult mark-recapture data set even higher weighting might produce biased estimates of young walleye. We also considered that the different age-biases associated with the two walleye collection gears could counter-balance each other: trawl data are likely better than gillnets to serve as an indicator of sub-adult abundance while gillnets are likely better than the trawls as an indicator of adult abundance.

Our model estimates did include the assumption that age-specific gear catchability has not changed in Oneida Lake over the study period. This assumption is reasonable because the sampling protocols and gears have been standardized on Oneida Lake for nearly a half-century. This is in contrast to many organized commercial fisheries where technological advancements can lead to increased catchability over time. However, caution is necessary when applying the assumption of constant catchability over time, even for standardized sampling (Gordoa and Hightower 1991). Catchability may also respond to fluctuations in abundance (Peterman and Steer 1981) and to changes in environmental conditions, such as temperature, oxygen levels, or water clarity (Nielsen 1983). Additionally, ecological changes may indirectly affect catchability by influencing encounter probabilities of various gears if the foraging behaviors or preferred habitats of the target species are altered (Henderson and Wong 1991). However, we have shown elsewhere that neither abundance nor environmental conditions have had strong effects on the gillnet catchability of adult walleye in Oneida Lake (Jackson et al. *in review*).

The relative size selectivity of gillnets can be estimated from the length distributions of fish captured in different mesh sizes (Hamley 1975). For Oneida Lake, Forney et al. (1994) used the length distribution of Oneida Lake walleye captured in different mesh sizes to construct mesh selectivity curves where the modal length and standard deviation of the selectivity curves were linear functions of the

mesh size and the relative selectivities at the modal length of each mesh size were assumed to be equal (Figure 2-7). However, the catchability of larger fish may actually be higher than predicted from these curves because large mesh may be less visible than small mesh (Hamley 1975) or because larger fish may have a higher encounter rate (Rudstam et al. 1984) or become more easily entangled (Grant et al. 2004). Hamley and Regier (1973) found substantially higher catchability for larger walleye in a study where a known population was fished with experimental gillnets. Our results generally support the shape of the Forney et al. (1994) curve (Figure 2-7), although our estimated catchability appeared to increase slightly faster with fish length. Our observations suggest an additional increase in the previous selectivity curve with fish length to the 0.3 power (Cornell Biological Field Station, unpublished data). This increase is not as large as predicted by the Hamley and Regier (1973) curves, but their selectivity curves were highest for fish lengths that were much larger than included here.

Compared to studies using gillnets, less attention has been given to assessing freshwater trawl selectivity. Olin and Malinen (2003) found that large (>19.9 cm) perch *Perca fluviatilis* and pikeperch *Sander lucioperca* were under-represented in trawl catches relative to gillnets. Our estimated values for trawl catchability also suggest walleye are captured with reduced efficiency at larger sizes. Larger individuals may avoid an approaching towed gear through a greater physical ability to escape the path of the gear, although vision might also play an important role in gear avoidance (Glass and Wardle 1989). Because we were also interested in temporal changes in mortality, we did not assess the concurrent changes in water clarity or light penetration on trawl catchability.

We hypothesized that mortality of sub-adult walleye in Oneida Lake had increased as a result of increased predation by cormorants (Rudstam et al. 2004). To

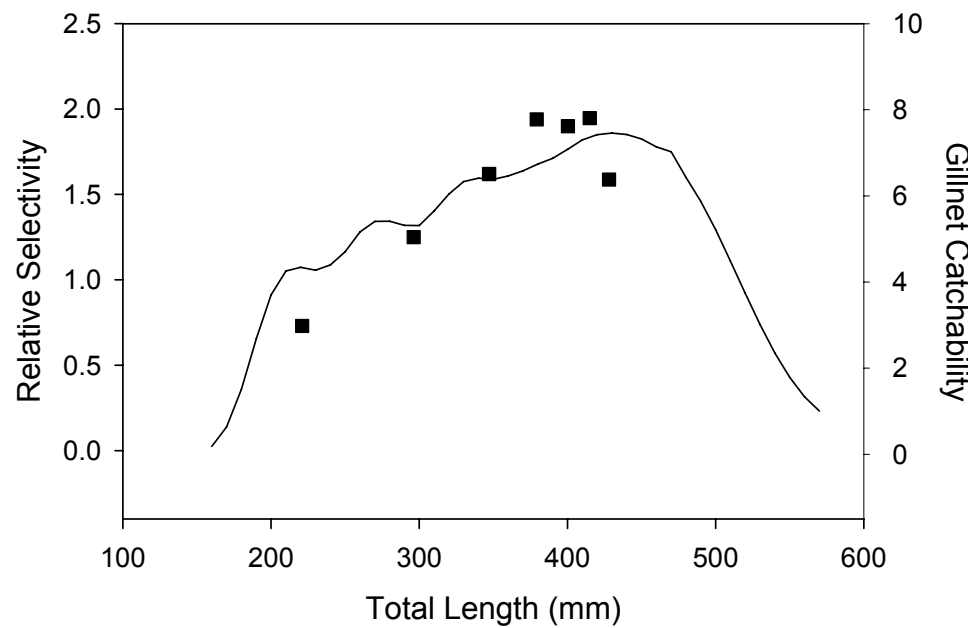


Figure 2-7. Estimated age-specific gillnet catchability (squares) for walleye in Oneida Lake based on the multi-mortality scenario and a selectivity curve (line) based on the catch of walleye in different mesh sizes (Forney et al 1994). The age-specific catchability values were assigned length-at-age values based on estimated growth rates and back-calculated length-at-age estimates using all available data (1958-2002).

test this hypothesis, we added a mortality term to represent predation from cormorants for years after 1990, the year Rudstam et al. (2004) argued as reasonable for dividing the data series into pre- and post-cormorant years. It was not possible to allow mortality to vary across years simultaneously with age-specific catchability parameters, as this appeared to over-parameterize the model. Using the three long-term data series, the model estimated increased mortality of sub-adult walleye during the second time period supporting the findings of Rudstam et al. (2004), although this does not directly identify the causative source of this additional mortality. Also, a cormorant hazing program was initiated on Oneida Lake in 1998 shortly after the dramatic increase in cormorant abundance, such that consumption by cormorants was likely variable across years. Rudstam et al. (2004) provide a more thorough discussion of cormorant-walleye and cormorant-yellow perch interactions in Oneida Lake.

Variability in angler effort further complicates assessments of mortality. Historically, adult walleye in Oneida Lake experienced heavy fishing pressure (Forney 1967), but angler harvest can be highly variable, as evidenced by a comment by the Editor of *The Conservationist* in 1961: “Oneida Lake fishermen—and they are legion—have long tried to guess why walleyed pike fishing, for which the lake is famous, could be so good one year, almost a waste of time the next” (cited by Forney and Eipper 1961). In Oneida Lake, angler catch rates are primarily determined by the availability of forage fish to walleye and largely unrelated to walleye abundance (Forney and Eipper 1961; Forney 1965; VanDeValk et al. 2005a). During recent years, adult walleye survival should have benefited from more restrictive harvest regulations, which were in place during years when cormorant mortality was affecting sub-adults. For Oneida Lake, exploitation by anglers has been measured for only a few years, and due to this lack of long-term information, we did not attempt to directly

include variable angler harvest in this estimation exercise. However, if harvest is known, then this information could be included in the estimation model. When angler harvest quickly reduces adult walleye density, growth rates may increase in the following year if the remaining individuals benefit from increased access to food resources. On the other hand, recruitment may suffer if an abundant adult population heavily cannibalizes sub-adult walleye. However, the included data for sub-adult walleye were collected at time periods beyond when these individuals were most vulnerable to fish predation, including cannibalism (Chevalier 1973). Mortality of age-1 walleye in Oneida Lake is expected to be primarily due to predation and most of this mortality likely occurred prior to our sampling. During our sampling period, age-1 walleye would have outgrown some gape-limited predators, and age-0 fishes, namely age-0 yellow perch, typically dominate the diets of adult walleye (Chevalier 1973; Forney 1974).

Our estimation model simultaneously used multiple long-term data sets to estimate walleye density, mortality, and catchability associated with the standard trawl and gillnet surveys. Even under highly restrictive constraints on mortality, the model produced age-specific catchability estimates of the anticipated form for both gillnet and trawl. The estimated catchability for gillnets increased sharply with age as did previously calculated relative selectivity values. The estimated catchability in trawls declined sharply over the first two age classes. Results from a multi-mortality scenario, where an additional parameter was estimated and allowed to influence annual survival rates, suggested that sub-adult walleye survival in recent years (1990-2003) is substantially lower than previous years (1958-1989), a decrease that has been attributed to cormorant predation (Rudstam et al. 2004). Estimated mortality rates for sub-adults are currently similar to those for adult walleye. In a previous, detailed study comparing angler harvest and cormorant predation in Oneida Lake during the

1997-1998 angling season, VanDeValk et al. (2002) found that cormorants can remove young percids at levels comparable to angler harvest of adults. The findings of VanDeValk et al. (2002) were based, in large part, on a creel survey and measures of cormorant diets. Our results, which relied on data from direct sampling of the walleye population, further support this comparison of multiple mortality sources that differentially affect age-classes of walleye.

Our final estimate of walleye population structure is generally congruent with earlier estimates for adult walleye, which were based mostly on mark-recapture and a trap-net index (Mills and Forney 1988, Rudstam et al. 2004). The current model uses all three available long-term data series and, in contrast to earlier calculations, consistently produces realistic declines in walleye abundance with age. However, the imposed constraints on mortality do not allow this model to track year-to-year changes in mortality caused by variable harvest rates.

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CHAPTER THREE

Long-term Trends in the Oneida Lake Fish Community Across Periods of Ecological Change

ABSTRACT

We evaluated the long-term gillnet and bottom trawl catches from Oneida Lake from 1962 through 2003 to identify changes in fish abundance for several species after the introduction of zebra mussels. Gillnets were used to sample 15 fixed locations in the same order each year, and bottom trawls were used to sample ten additional fixed locations. Species-specific catches were standardized and combined within three general habitat affiliations for gillnets (“Pelagic”: walleye *Sander vitreus*, yellow perch *Perca flavescens*, white perch *Morone americana*, gizzard shad *Dorosoma cepedianum*; “Littoral”: smallmouth bass *Micropterus dolomieu*, pumpkinseed *Lepomis gibbosus*, and “Benthic”: channel catfish *Ictalurus punctatus*, brown bullhead *Ameiurus nebulosus*, freshwater drum *Aplodinotus grunniens*, common carp *Cyprinus carpio*, white sucker *Catostomus commersonii*, and redhorse sucker *Moxostoma* spp.) and trawls (“Pelagic”: age-0 walleye, age-0 yellow perch, age-0 white perch, age-0 gizzard shad; “Littoral”: age-0 smallmouth bass, age-0 pumpkinseed, and “Benthic”: age-0 trout-perch *Percopsis omiscomaycus*, age-0 tessellated darters *Etheostoma olmstedii*, age-0 logperch *Percina caprodes*, and age-0 freshwater drum.). Changes in gillnet catches of these three groups between pre- and post-zebra mussel time periods followed our *a priori* expectations of responses to zebra mussels: Pelagic fishes declined while catches of Littoral and Benthic fish increased. Trawl CPUE for the Pelagic grouping also declined, but the Littoral and Benthic fishes did not change between periods.

We also evaluated changes in species-specific catches using two approaches. First, we compared catches between pre- and post-zebra mussel periods. Further, we established 30-year population trajectories based on catches during years before zebra mussels (1962-1991) and compared post-zebra mussel catches to these expected values. These 30-year population trajectories indicated declining catches of percid fishes (walleye, yellow perch, logperch, and tessellated darters). However, the decline in percids was also influenced by a concomitant increase in the abundance of double-crested cormorants *Phalacrocorax auritus*. Due to recent low abundance of yellow perch, walleye, and white perch, total annual catches in both gears have been reduced. Gillnet catches of smallmouth bass and pumpkinseed sunfish remained high throughout much of the zebra mussel period. Although gillnet catches of Benthic fishes was higher during the post-zebra mussel period, few of the benthic-affiliated species showed increased catches above their 30-year trajectories. Nevertheless, most benthic species produced fairly stable catches at relatively high levels during the post-zebra mussel period. The ability to directly consume zebra mussels is likely an important influence on fish community structure in systems that have recently experienced the establishment of zebra mussels.

INTRODUCTION

Ecosystem-level study and ecosystem-based fishery management are being increasingly emphasized as important frameworks for understanding and maintaining the use of aquatic resources (Carpenter et al. 1995; Link 2002; Pikitch et al. 2004). The recent acceleration of this movement is due, in part, to a recognition that a more holistic approach to assessment is required because many fish species are being heavily overexploited (Pauly et al. 2000), targeted fishing still affects multiple species

(through by-catch, habitat alterations, or restructuring a community), regime shifts are resulting from human-induced ecological change and spread of invasive species (Carpenter 2003; Scheffer and Carpenter 2003), and the effects of a perturbation can be mediated through food-web interactions. In aquatic ecosystems, the drivers of change can arise either rapidly (e.g., invasive species) or through a more incremental change over a longer term (e.g., global warming). In addition to differences in their operative time scales, stressors can induce differential and indirect shifts through multiple components of an ecosystem, thus complicating estimation of their effects. This capacity for cascading effects combined with the limited recovery potential of some low-density populations often prevents a return to prior conditions, even if a stressor is successfully removed (Botsford et al. 1997; Carpenter 2003). Ultimately, understanding how relationships in complex food webs have changed due to previous perturbations can improve assessments by reducing areas of uncertainty, promoting precautionary management, and enhancing the ability to predict and respond to future stressors (e.g., ecosystem forecasting; Botsford et al. 1997; Link 2002).

Aquatic ecosystems are often unavailable for controlled manipulation given the broad and diverse resources that they provide. Even so, these resources are both subject to large-scale management actions and sensitive to uncontrolled biological invasions. For example, multimillion-dollar nutrient abatement programs, advanced by the 1972 Great Lakes Water Quality Agreement between Canada and the US, have been implemented to achieve increased water clarity and associated aesthetic benefits (Ludsin et al. 2001; Mills et al. 2003). Changes in system productivity can be influential on the composition of a fish community, as measures of species richness respond to changes in system productivity (Ludsin et al. 2001). Moreover, the establishment of exotic organisms in aquatic ecosystems can impact overall energy transfer within the system, negatively affect indigenous organisms, and produce

unexpected changes in fish population dynamics even to the point of jeopardizing traditionally strong fisheries (Mills et al. 1994). When planned management actions and unplanned invasions occur over the same time period, debate over the relative importance of different factors is likely to occur (Dobiesz et al. 2005). Therefore, the ability to identify sometimes-subtle interrelationships that can have disproportional influence on system function is important for measuring responses to large-scale changes. While the function of fishes in aquatic food webs has received much attention, community responses to redirection of nutrient pathways (e.g., “benthification”, Mills et al. 2003) and unplanned introductions remain poorly understood.

In many freshwater systems, zebra mussels *Dreissena polymorpha* have disrupted trophic interactions (Nalepa and Schloesser 1993; MacIsaac 1996; Strayer et al. 1999; Mayer et al. 2000). Zebra mussels can redirect energy pathways towards benthic habitats by removing suspended particulate matter by grazing, accumulating their own body tissue, and producing biodeposits (Strayer et al. 1999; Mayer et al. 2002). If macroinvertebrates respond positively to increased benthic food resources and structural habitats promoted by zebra mussel colonies (Stewart and Haynes 1994), then benthic feeding fish populations should also experience increased food resources. Direct alteration of the physical structure of benthic habitats by vast mats of zebra mussels may also affect fish spawning grounds. In addition to these direct effects, zebra mussel grazing leads to increased water clarity and photic-zone depth (Idrisi et al. 2001). In terms of fish community dynamics, substantial changes in water clarity and light penetration can alter which species hold a competitive foraging advantage. Likewise, increased light penetration may affect predator-prey interactions in aquatic communities if prey suffer increased exposure to predators through an increase in either predator foraging efficiency or prey recognition by predators (Hinshaw 1985).

For young fishes, the loss of suspended sediment or algae may reduce refuge areas so that they become more susceptible to predation (Johnson and Hines 1999). In addition to altering the visual foraging arenas shared by pelagic predators and their prey, increased light penetration also allows for the extension of submersed plant growth to greater depths, therefore altering littoral habitats (Zhu et al. *in press*). Increased growth of aquatic macrophytes should increase suitable habitats for littoral fishes such as centrarchids, especially if other climatic changes, such as increased water temperature (Casselman 2002), also contribute to conditions that are favorable to a centrarchid community. Combined, zebra mussels can have substantial influence on aquatic food webs either through inducing shifts in nutrient pathways or modifying the physical environment. For fishes, the effects can be numerous, even for fishes that do not directly interact with zebra mussels.

Because of the rapid expansion of zebra mussels in North America and expectations of their ability to alter system properties to the point of influencing fish populations, measures of fish-zebra mussel connections are becoming more readily available (Mayer et al. 2000; Cobb and Watzin 2002; Magoulick and Lewis 2002; Beekey et al 2004; Andraso 2005); however, measures of fish community responses to zebra mussels remain rare (but see Trometer and Busch 1999; Strayer et al. 2004), probably due to a lack of long-term data. Long-term studies on individual systems provide unique opportunities for evaluating system responses to both unplanned ecological changes and large-scale management by providing data on both pre- and post-perturbation conditions. Nearly a half-century of continued research on Oneida Lake provides one of the most complete long-term data series available for a North American fish community (Forney 1980; Mills and Forney 1988; Hall and Rudstam 1999). Standardized sampling has produced catch data for multiple species of the Oneida Lake fish community and allows for an evaluation of long-term patterns in

abundance relative to a major ecological perturbation such as the introduction of zebra mussels.

We evaluated temporal shifts in Oneida Lake fish community data, collected over a >40 year time period, when the lake experienced an introduction and rapid establishment of zebra mussels. First, we developed *a priori* expectations for fish community responses to zebra mussels driven changes based on assumptions of general habitat affiliation (Pelagic, Littoral, and Benthic, see Methods for species groupings) and tested for species-specific abundance differences between the pre- (1962-1991) and post-zebra mussel (1992-2002) time periods. We predicted reduced catches of Pelagic fishes, but increased catches of both Littoral and Benthic fishes due to shifts in energy pathways produced by zebra mussels. Second, we examined temporal trends for individual species in order to evaluate abundance during the post-zebra mussel period against 30-year population trajectories rather than a single measure of the pre-introduction period. This is similar to an approach used by Strayer et al. (2004) to evaluate changes in abundance for some age-0 fishes before and after zebra mussel invasion. In this way, consideration of the temporal dynamics in motion before the introduction of the exotic bivalve was also possible.

METHODS

Study Site and Timeline of Food Web Changes

Oneida Lake has the largest surface-area of any lake entirely inside the borders of New York State, although it is relatively shallow (mean depth = 6.1m). Walleye *Sander vitreus* and yellow perch *Perca flavescens* are important components of the food web, and recreational anglers target both species throughout much of the year. During the period of 1962-2002, Oneida Lake has experienced notable ecological

changes. In the 1980s, there was periodic high-production of young by invasive white perch *Morone americana* and gizzard shad *Dorosoma cepedianum*. By 1992, zebra mussels were found in high abundance and are believed to have the potential to act as “ecosystem engineers” (sensu Jones et al. 1994) in Oneida Lake (Mayer et al. 2002). During the zebra mussel period, Oneida Lake has also experienced a rapid increase in the abundance of piscivorous double-crested cormorants *Phalacrocorax auritus* followed by management aimed to reduce their numbers.

Gillnet Catches

We examined temporal trends in annual total catch in gillnets for 12 species for 1962 through 2002. Each year, 15 fixed locations were sampled, with one gillnet site sampled per week in the same order from June through September. At each site, two nets (91.44 m length x 1.83 m depth) were set on bottom and allowed to fish overnight for approximately 12 hours. Each net consisted of two gangs of six 7.6m panels so that mesh size ranged from 38mm to 102mm at 12.7mm increments (stretch mesh). Gillnet were not used to survey the standard sites in 1974. During 1963 through 1967, gillnet sampling was conducted using one white net and one colored (red, green, or black) net. During all other years, two white nets were used at each site.

We considered changes in catches of three general categories based on habitat affiliation (“Pelagic”: walleye, yellow perch, white perch, gizzard shad; “Littoral”: smallmouth bass *Micropterus dolomieu*, pumpkinseed *Lepomis gibbosus*, and “Benthic”: channel catfish *Ictalurus punctatus*, brown bullhead *Ameiurus nebulosus*, freshwater drum *Aplodinotus grunniens*, common carp *Cyprinus carpio*, white sucker *Catostomus commersonii*, and redhorse sucker *Moxostoma* spp.).

Bottom Trawl Catches

Annual abundances of age-0 fishes were based on catch-per-unit effort from Oneida Lake bottom trawl collections. During each year, ten standard sites were sampled using a bottom trawl with a 5.5m foot-rope from July to October. At these ten sites, trawl effort ranged from 90 to 160 hauls per year from 1962 to 2002. Each trawl haul covered approximately 0.1 ha of bottom surface area (Forney 1976; VanDeValk et al. 2002) with a transect length of approximately 280m. Fish collected in trawls were identified as either age-0 or adult. We only used trawl data for age-0 fishes. As for gillnets, we assigned species into three general categories based on habitat affiliation to evaluate shifts in the relative composition of bottom trawl catches over time (“Pelagic”: age-0 walleye, age-0 yellow perch, age-0 white perch, age-0 gizzard shad; “Littoral”: age-0 smallmouth bass, age-0 pumpkinseed, and “Benthic”: age-0 trout-perch *Percopsis omiscomaycus*, age-0 darters *Etheostoma* spp., age-0 logperch *Percina caprodes*, and age-0 freshwater drum. In Oneida Lake, catches of *Etheostoma* spp. were usually tessellated darters *Etheostoma olmstedii*. The species included in the Benthic habitat grouping differed between the summaries of gillnet catch and trawl CPUE because the gears were used to target different age groups due to their different catchabilities (e.g., Chapter 2).

Analyses

To evaluate trends within general habitat affiliations, species-specific catches were standardized (scaled and centered) and then summed across species within the three habitat categories (Pelagic, Littoral, and Benthic):

$$(1) \quad \text{Standardized Catch} = \sum_{i=1}^n \frac{Obs_{i,j} - \bar{x}_i}{SD_i}$$

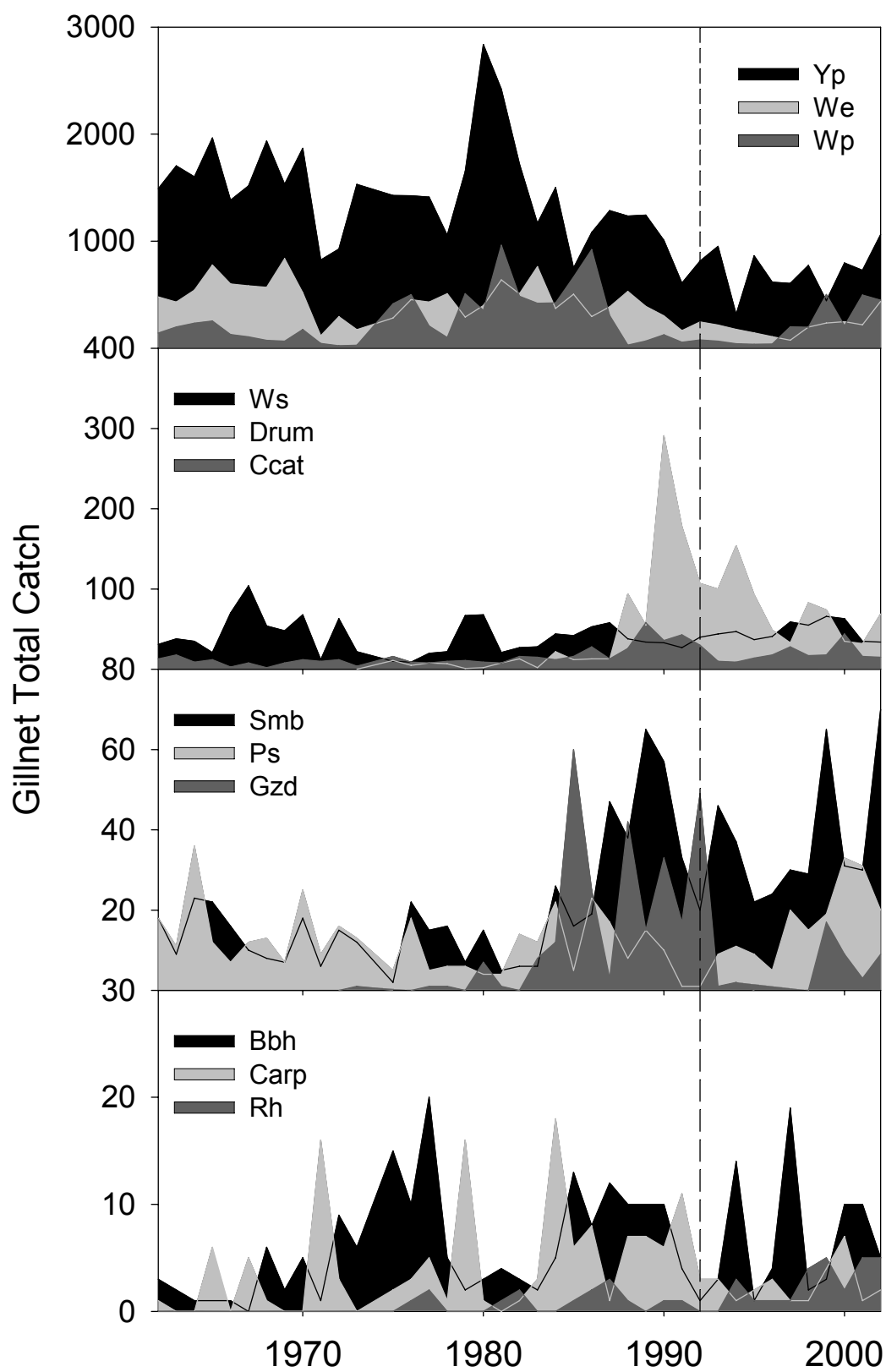
where $Obs_{i,j}$ is the observed annual catch of species i during year j , \bar{x}_i is the average catch of species i over all years, and SD_i is the Standard Deviation of the i^{th} species over all years. For these groups and all included species, we used a Wilcoxon rank-sum test to compare pre- and post-zebra mussel periods for both gillnet catches and trawl CPUE. We then followed an approach of Strayer et al. (2004) to identify species-specific shifts in temporal patterns after the introduction of zebra mussels. Because certain species were not captured in all years, we transformed catches (catch + c , where c = the species-specific minimum catch over all observations) prior to plotting data on a \log_{10} scale. For both gillnet catches and trawl CPUE, we used simple linear regression to establish species-specific trajectories, using $\log_{10}(\text{catch} + c)$ transformed data, through the 30-year period prior to the introduction of zebra mussels. We then used paired t-test to compare observed catches, transformed using $\log_{10}(\text{catch} + c)$, during the post-zebra mussel period with projections from the 30-year population trajectories to further evaluate our *a priori* directional hypotheses of species-specific responses (an increase or a decrease) to zebra mussel establishment in Oneida Lake.

RESULTS

Gillnet Catches

During a 40-year sampling period, over 80,000 individual fish of the twelve species considered here were captured in multi-filament gillnets (Appendix 3-1). Of these, yellow perch were the most frequently caught and comprised over 60% of the total catch (Figure 3-1). Walleye and white perch were the next most abundant species in gillnets and, combined with yellow perch, comprised over 90% of the total catch. Declines in these three species over time contributed to noticeable differences in gillnet catches between the pre- and post-zebra mussel periods. For instance, the

Figure 3-1. Annual total catch for several fish species collected in Oneida Lake gillnets. Note that y-axis scales differ among species. The dashed vertical line indicates 1992, the year when zebra mussels became abundant in Oneida Lake. Species codes are presented in Table 3-1.



median of annual total catches before 1992 was nearly twice that of more recent years. During the 29 years with gillnet sampling before zebra mussel introduction (no data for 1974), total annual gillnet catch of the included 12 species exceeded 1500 individuals in 26 years. During the 11 post-zebra mussel years, total annual catch exceeded 1500 individuals only twice. Between periods, the contribution of yellow perch, walleye, and white perch to total annual gillnet catch decreased by ten percentage points.

Abundance of Pelagic, Littoral and Benthic species groups changed in accordance with *a priori* directional expectations (Table 3-1). During the zebra mussel period, gillnet catches of Pelagic fishes were also lower than predicted from the previous 30-year population trajectory (Table 3-1; Figure 3-2). In contrast, gillnet catches of littoral fishes continued to increase throughout the post-zebra mussel period but were not significantly higher than the 30-year population trajectory (Table 3-1; Figure 3-2). Catches of Benthic fishes remained at a relatively high level throughout the zebra mussel period but did not continue at the high rate of increase established in the previous 30-year period (Table 3-1; Figure 3-2). Catches of Benthic fishes during the post-zebra mussel period were actually significantly lower than predicted from this trajectory.

Of the 12 species included for gillnets, catches of six were significantly different between zebra mussel periods in the direction of the *a priori* expectation (Table 3-1). The observed percent changes in average catch between time periods were inconsistent with *a priori* directional expectations in only two cases (gizzard shad and common carp; Table 3-1). Catches of walleye were consistently low throughout most the post-zebra mussel period, and these catches suggested an even greater decline than expected from the 30-year declining trajectory (Table 3-1; Figure 3-3). The average annual total catch of walleye during the zebra mussel period ($N =$

Table 3-1. Percent change in the average annual total catch in gillnets and in average CPUE of age-0 fishes in bottom trawls from the pre- to post-zebra mussel period for several species collected from Oneida Lake, New York. We = walleye, Yp = yellow perch, Wp = white perch, Gzd = gizzard shad, Smb = smallmouth bass, Ps = pumpkinseed sunfish, Ccat= channel catfish, Bbh = brown bullhead, Drum = freshwater drum, Carp = common carp, Ws = white sucker, Rh = redhorse, Dart = *Etheostoma* spp., Lp = logperch, and Tp = trout-perch. Tests for general habitat groupings (Pelagic, Littoral, and Benthic) are based on standardized data summed across species. H_a = directional hypothesis for expected change in catch, P_P = one-way tests for differences in the Wilcoxon rank-sum scores between the pre- and post-zebra mussel periods, P_T = one-way paired t-test of differences between observed values and predicted values from 30-year population trajectories. For comparisons of observed and species-specific 30-year population trajectories, data were $\log_{10}(\text{catch} + c)$ transformed. See text for additional details.

Gillnet					Trawl				
Species	H_a	% Change	P_P	P_T	Species	H_a	% Change	P_P	P_T
Pelagic	-		<0.001	<0.001	Pelagic	-		<0.001	<0.001
We	-	-53.8	<0.001	0.002	We	-	-78.4	0.004	0.970
Yp	-	-50.1	<0.001	0.001	Yp	-	-72.1	0.003	0.968
Wp	-	-23.9	0.284	0.014	Wp	-	-68.9	0.220	0.023
Gzd	-	5.0	0.758	<0.001	Gzd	-	-78.0	0.062	<0.001
Littoral	+		0.013	0.058	Littoral	+		0.265	0.215
Smb	+	90.5	0.001	0.163	Smb	+	306.1	0.017	0.057
Ps	+	28.8	0.162	0.024	Ps	+	-93.4	0.994	0.996
Benthic	+		0.006	0.999	Benthic	+		0.315	0.001
Ccat	+	29.7	0.021	0.999	Dart	+	-78.6	0.988	<0.001
Bbh	+	9.7	0.458	0.999	Lp	+	-61.2	0.913	0.003
Drum	+	197.4	<0.001	0.994	Drum	+	96.9	0.046	0.995
Carp	+	-42.3	0.567	>0.999	Tp	+	137.2	0.001	<0.001
Ws	+	17.7	0.081	<0.001					
Rh	+	374.5	0.002	0.237					

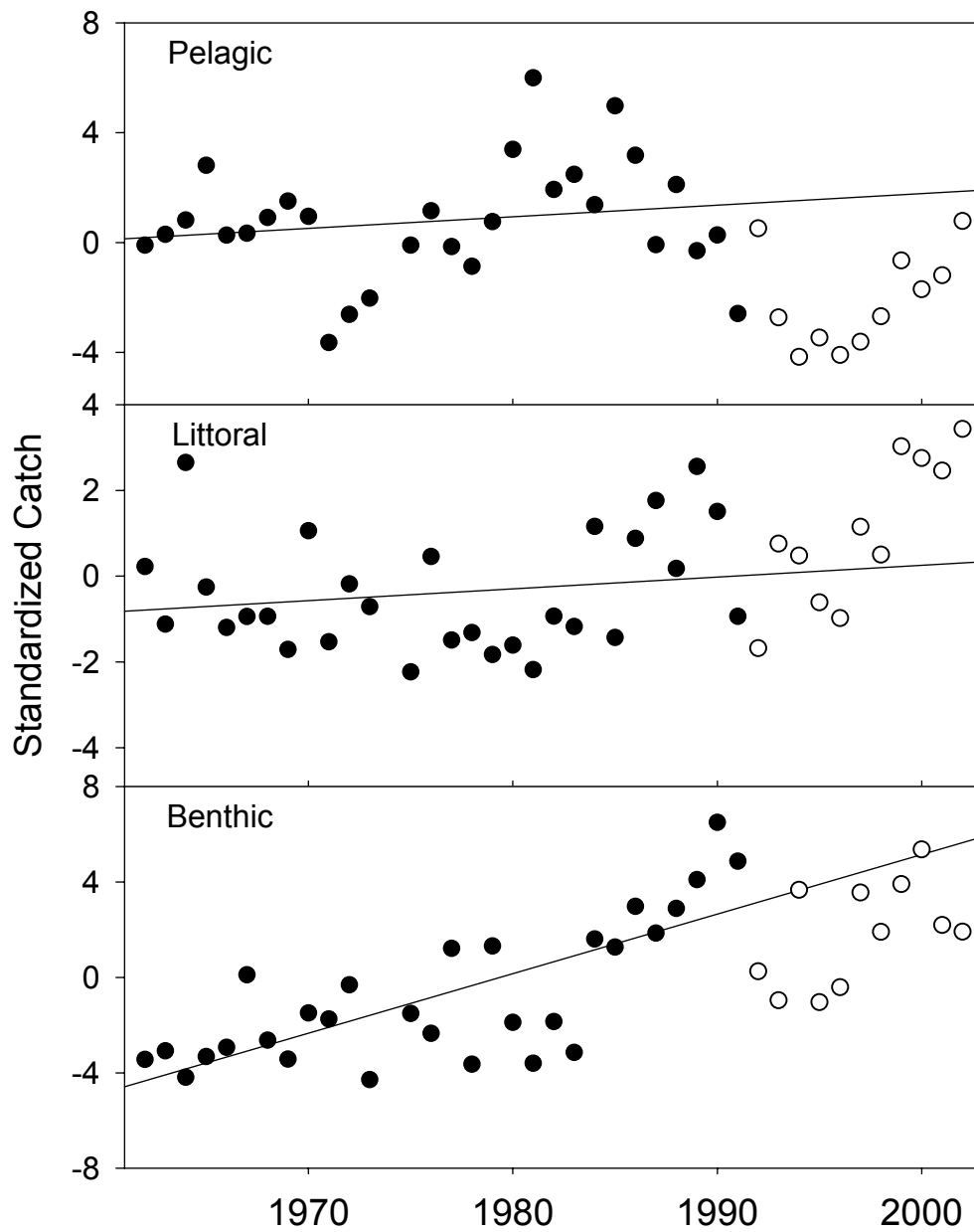
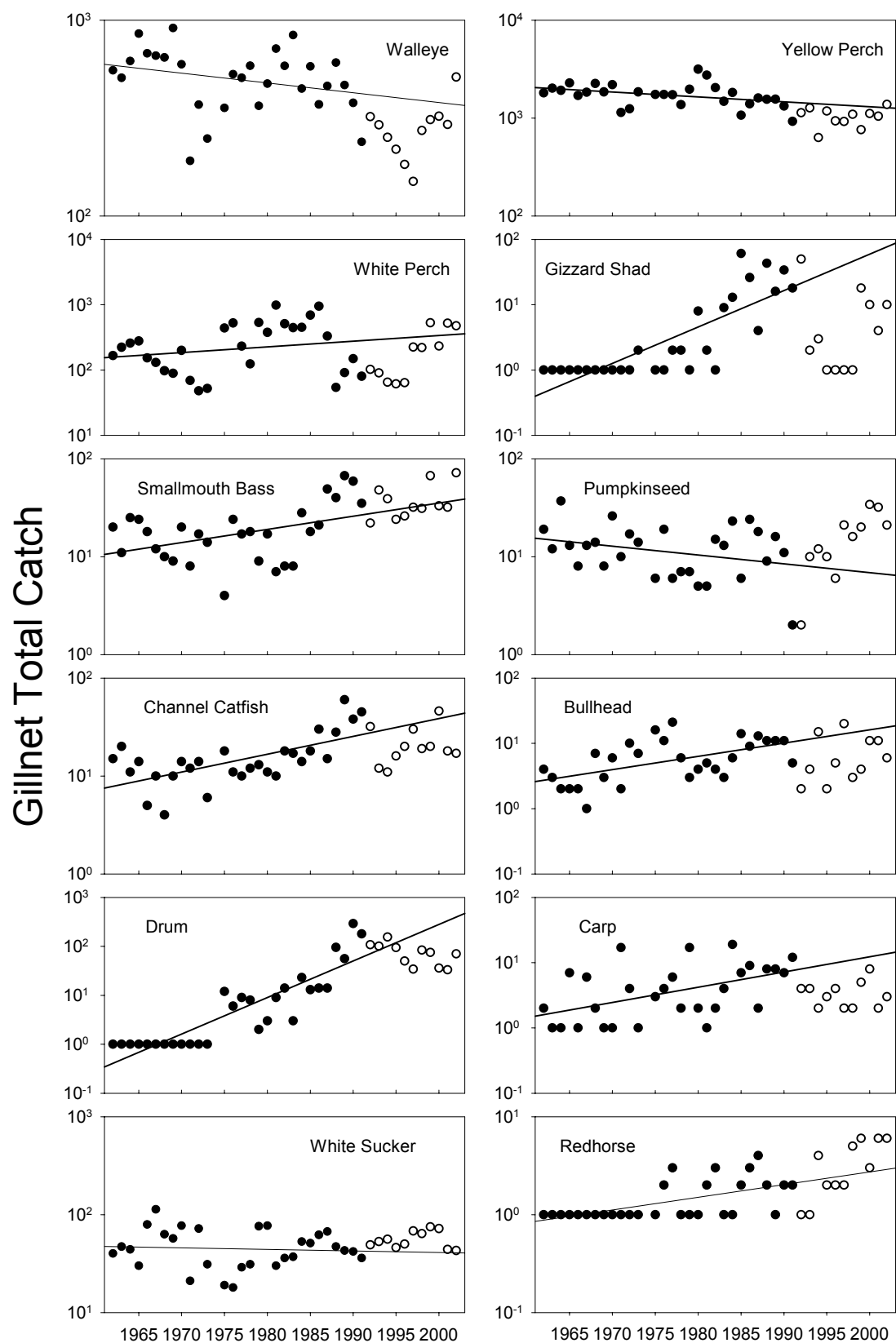


Figure 3-2. Standardized annual total catch of fish collected in Oneida Lake gillnets before (1962-1991) and after (1992-2002) the introduction of zebra mussels based on habitat affiliation. Regression lines are fit to pre-zebra mussel years (solid circles) to represent a 30-year trajectory. Post-zebra mussels catches (open circles) above the regression line indicate an increase and open circles below the regression line indicate reduced catches. Note that y-axis scales differ among plots.

Figure 3-3. Annual total catch of fish collected in Oneida Lake gillnets before (1962-1991) and after (1992-2002) the introduction of zebra mussels. Regression lines are fit to pre-zebra mussel years (solid circles) to represent a 30-year population trajectory. Post-zebra mussels catches (open circles) above the regression line indicate an increase and open circles below the regression line indicate reduced catches. Note that y-axis scales differ among species and are logarithmic.



11, $\bar{x} = 209$) was less than half of average annual total catch before zebra mussels ($N = 29$, $\bar{x} = 453$). Gillnet catches of yellow perch also showed a continuous decline over time, and catches during the post-zebra mussel period were lower than predicted from the 30-year declining trajectory during the first 10 years of the zebra mussel period (Figure 3-3). The 30-year trajectory of white perch during the pre-zebra mussel period was influenced by a period of high catches during the mid 1980s. Likewise, the gillnet catches of gizzard shad changed quickly over time, from multiple years with zero catches to relatively high catches during the late 1980s through the early 1990s. For both of these species, gillnet catches reached their highest level prior to zebra mussels, but then catches of both species were low for a several-year period after zebra mussels were established, including four years of zero catches for gizzard shad (Figure 3-3). As such, we did not detect a significant decline in gillnet catches between zebra-mussel periods for either white perch or gizzard shad, but catches of both species were lower than projected values (Table 3-1).

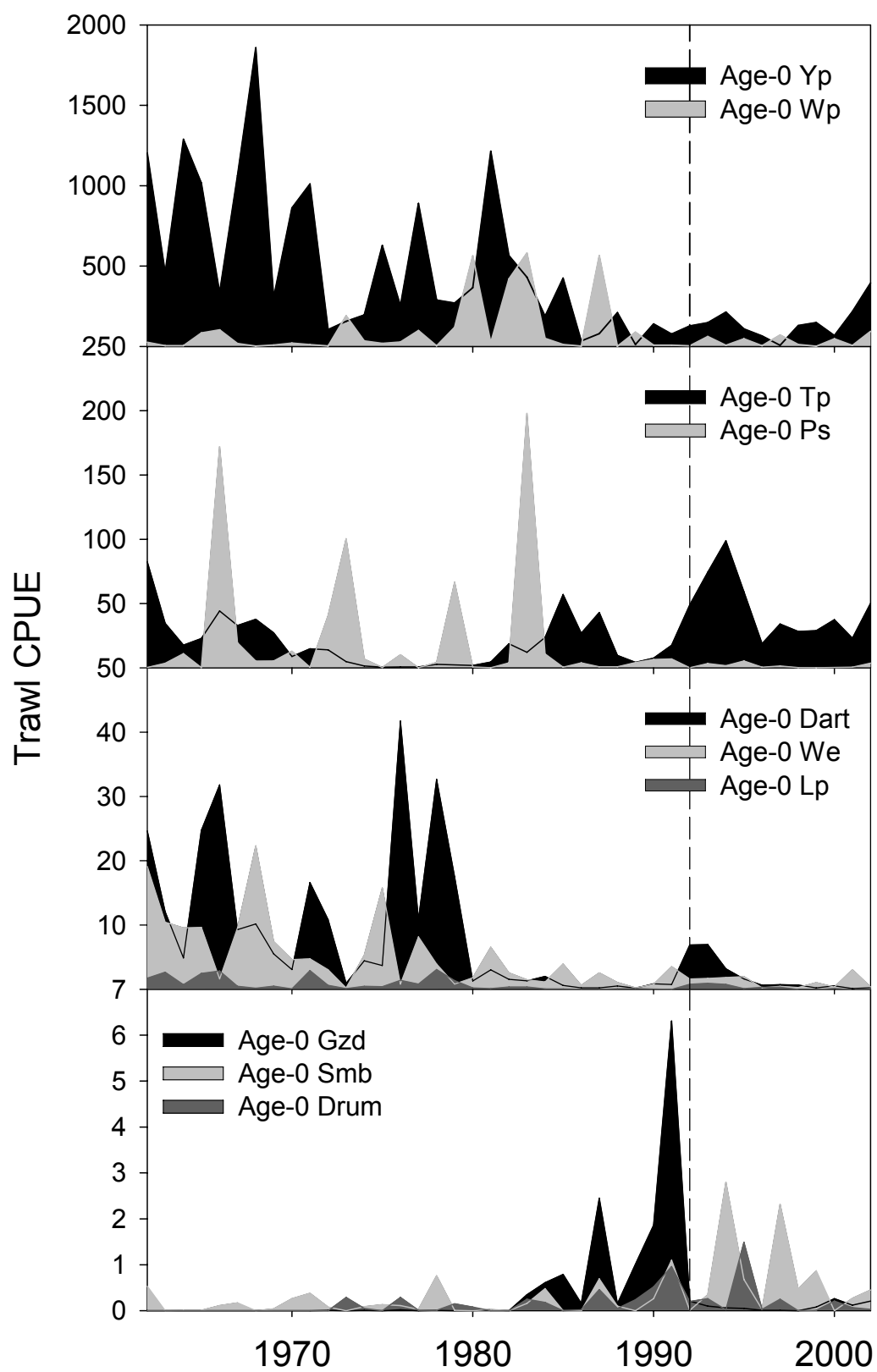
Littoral species were usually captured in gillnets with less frequency than the Pelagic species; however, both smallmouth bass and pumpkinseed sunfish were captured in gillnets during all 40 years of collection (Figure 3-3). The 30-year trajectory of smallmouth bass catches in gillnets increased over time, with high catches occurring just prior to zebra mussel introduction. During the post-zebra mussel years, catches of smallmouth bass either closely followed the pre-zebra mussel trajectory or were even higher, including the highest annual gillnet catch occurring in 2002. Initially, the 30-year trajectory based on gillnet catches of pumpkinseed sunfish was opposite to that of smallmouth bass with a general decline occurring over time. However, the pattern of gillnet catches of pumpkinseed sunfish changed markedly during years when zebra mussels were present, as catches began to increase over time (Table 3-1; Figure 3-3).

Gillnet catches of Benthic fishes were generally higher during the post-zebra mussel period. However, the post-zebra mussel catches of Benthic species were less consistent relative to their respective 30-year trajectories than for other habitat groupings (Figure 3-3). Contrary to expectations, the patterns of gillnet catches for several Benthic fishes were often lower during zebra mussel period than was suggested by their 30-year population trajectories, although catches remained relatively high compared to many previous years (Figure 3-3). Although they did not show an increase beyond previous temporal patterns, gillnet catches of channel catfish, brown bullhead, freshwater drum, and redhorse fluctuated around a fairly stable catch rate throughout the last several years. Of the gillnet-captured Benthic fishes included here, only white sucker and redhorse had a majority of higher-than-expected gillnet catches during zebra mussel years (Figure 3-3). During all years in the zebra mussel period, white suckers were caught at higher levels than suggested by their 30-year trajectory (Table 3-1; Figure 3-3). Although previously found in Oneida Lake, redhorse were not captured in gillnets until 1976 but were caught in each of the last 9 years through 2002.

Bottom Trawl Catches

Forty-one years of standardized bottom trawl surveys collected over 3 million individuals of the ten species included here (Appendix 3-2). Of this staggering total, over 75% were age-0 yellow perch (Figure 3-4). The next most frequently captured were age-0 white perch, age-0 trout-perch, age-0 pumpkinseed sunfish, and age-0 *Etheostoma* spp. Age-0 fishes from the remaining six species considered here each contributed less than 1% of the total bottom-trawl catch. From the pre- to post-zebra mussel period, the decline in median CPUE for bottom trawls was even more

Figure 3-4. Annual CPUE of age-0 fishes for several species collected in Oneida Lake bottom trawls. Note that y-axis scales differ among species. The dashed vertical line indicates 1992, the year when zebra mussels became abundant in Oneida Lake. Species codes are presented in Table 3-1.



substantial than for gillnet total catch. Median trawl CPUE during the pre-zebra mussel years was more than three times higher than the median for the last 11 years.

As for gillnets, trawl CPUE of Pelagic fishes remained consistently low, and all observations were lower during the zebra mussel period than expected based on a 30-year trajectory (Table 3-1; Figure 3-5). The Littoral grouping did not show a prominent temporal trend but was typified by occasional high catches, which occurred during both the pre- and post-period (Figure 3-5). Examination of trawl CPUE of Benthic fishes revealed a strong decline over the 30-year pre-zebra mussel period, with all recent catches above expectations (Figure 3-5).

Of the ten species included for bottom trawl CPUE, five species had significant directional changes that were consistent with *a priori* expectations (Table 3-1). Based on 30 years of observations, age-0 percid fishes (walleye, yellow perch, *Etheostoma* spp., and logperch) were in strong decline in Oneida Lake prior to the introduction of zebra mussels (Figure 3-6). Trawl CPUE for both walleye and yellow perch was lower during the post-zebra mussel period; however, recent catches did not decline below projected catches (Table 3-1; Figure 3-6). Although abundance did not increase during the post zebra mussel period, the catches of *Etheostoma* spp., and logperch were significantly above expected values, partly due to the steepness of the prior observed declines (Table 3-1; Figure 3-6). During the post-zebra mussel period, trawl CPUE of white perch and gizzard shad did not reach their previous maximum potential, but abundance of these age-0 fishes remained relatively consistent through these 11 years. Trawl CPUE for smallmouth bass and pumpkinseed sunfish showed opposite responses – trawl CPUE for smallmouth bass was highest during the post-zebra mussel period while trawl CPUE for pumpkinseed sunfish was lower (Table 3-1). While most of the observed trawl CPUE values for pumpkinseed sunfish were below expectations (Figure 3-6), the absence of a year with high trawl CPUE is

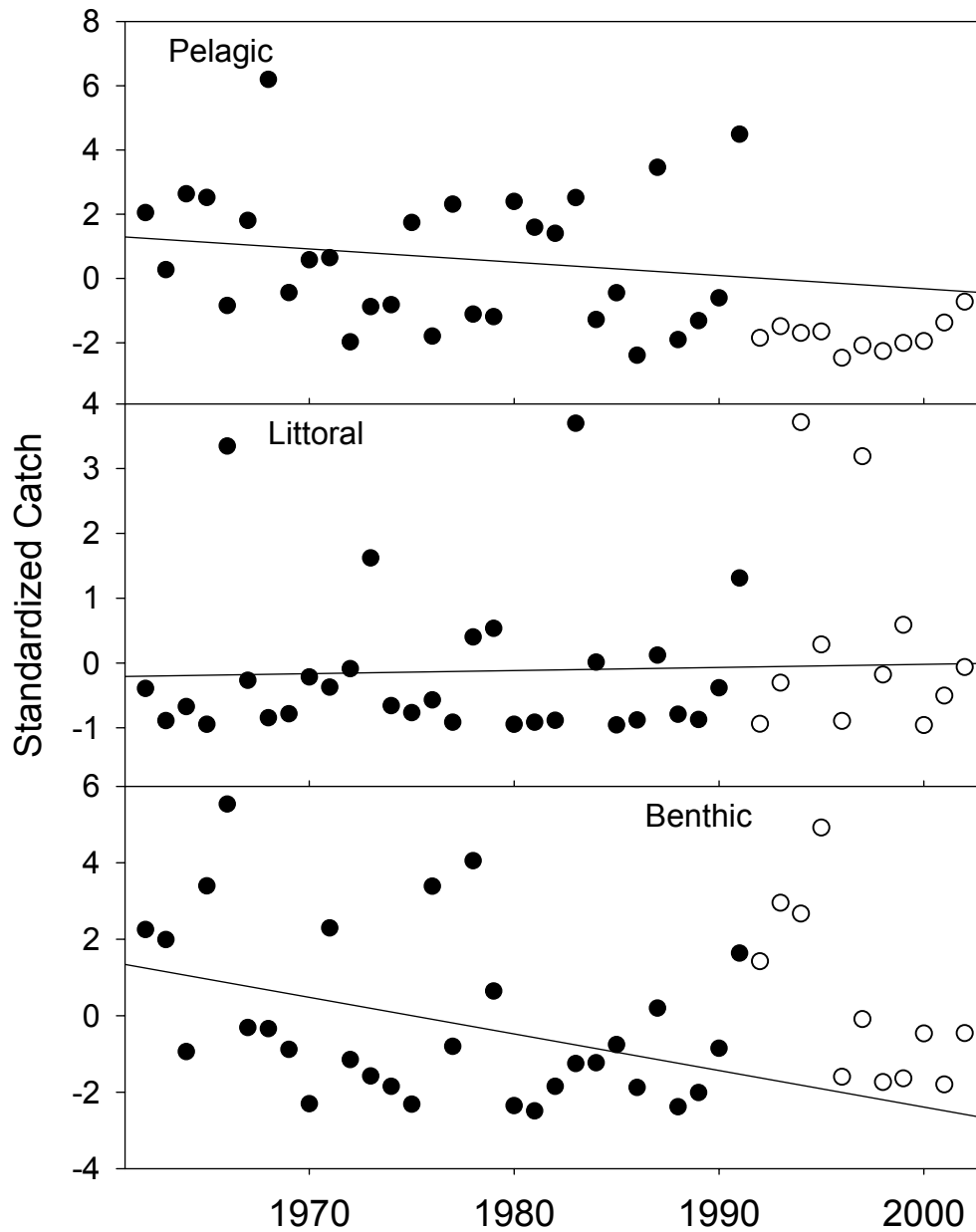
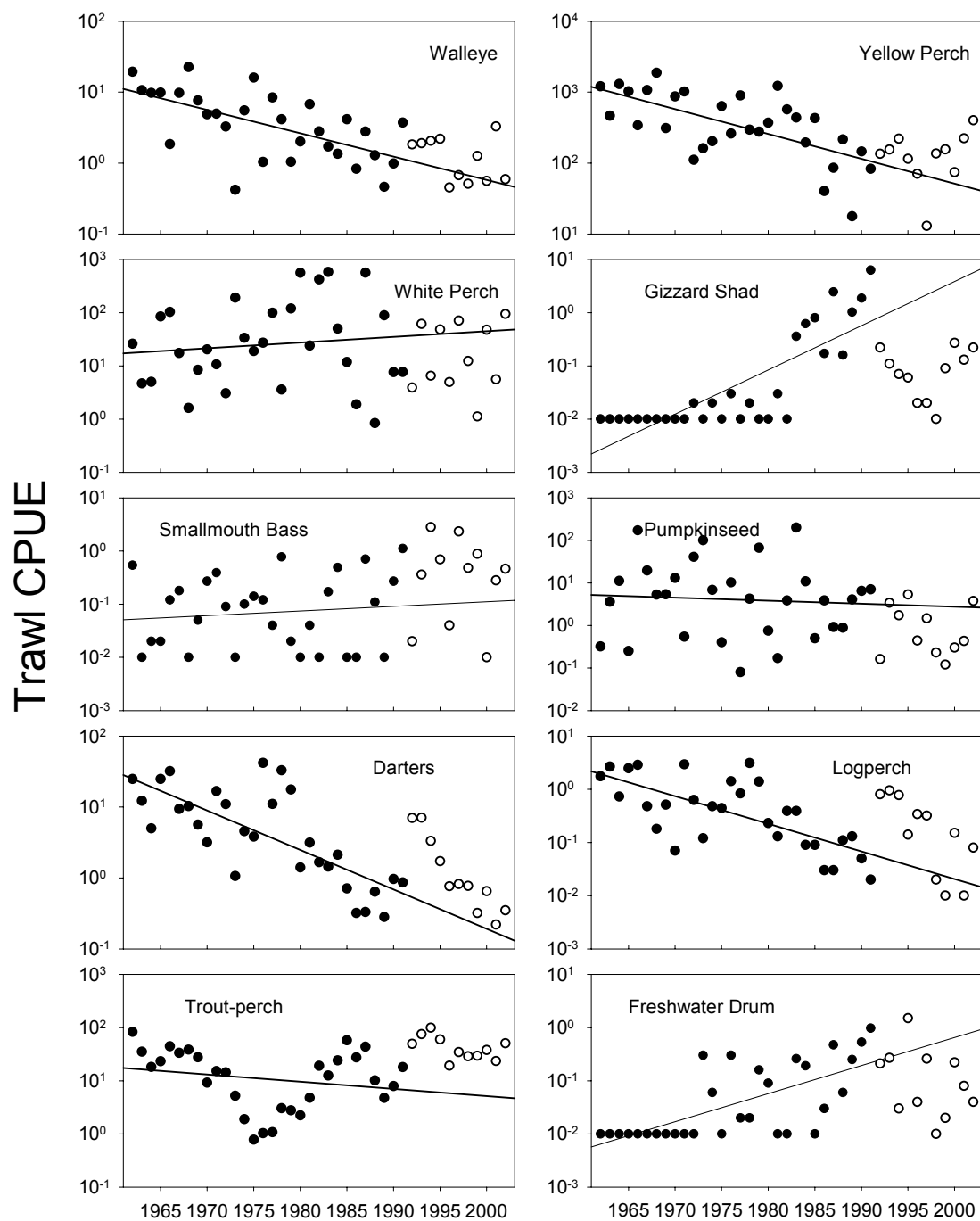


Figure 3-5. Standardized annual CPUE of fish collected in Oneida Lake bottom trawls before (1962-1991) and after (1992-2002) the introduction of zebra mussels based on habitat affiliation. Regression lines are fit to pre-zebra mussel years (solid circles) to represent a 30-year trajectory. Post-zebra mussels catches (open circles) above the regression line indicate an increase and open circles below the regression line indicate reduced catches. Note that y-axis scales differ among plots.

Figure 3-6. Annual CPUE of age-0 fish collected in Oneida Lake bottom trawls before (1962-1991) and after (1992-2002) the introduction of zebra mussels. Regression lines are fit to pre-zebra mussel years (solid circles) to represent a 30-year population trajectory. Post-zebra mussels catches (open circles) above the regression line indicate an increase and open circles below the regression line indicate reduced catches. Note that y-axis scales differ among species and are logarithmic.



perhaps a better description of the change between periods (Figure 3-6). Trawl CPUE of age-0 trout-perch was more cyclical than other included species during the 30-year pre-zebra mussel period, but observed values remained high through the post-zebra mussel period (Figure 3-6). In fact, even the lowest trawl CPUE value for trout-perch during the post-zebra mussel period was relatively high compared to most observations from the earlier period. The 30-year trajectory for age-0 freshwater drum was again influenced by a long period of successive zero-catch years during the initial years of collection (Figure 3-6). Because of this, age-0 freshwater drum often had lower than projected trawl CPUE during the post-zebra mussel period, but this period also produced the highest trawl CPUE and only a single zero-catch year for age-0 freshwater drum.

DISCUSSION

We expected catches of Pelagic fish to decline after the invasion of zebra mussels but that catches of Littoral and Benthic fish would increase. Between the pre- and post-zebra mussel periods, gillnet catches of each of these groups were significantly different and changes were consistent with *a priori* expectations. The Pelagic grouping was the only category to have a significant decline in trawl CPUE between zebra mussel periods. Additionally, both gillnet catches and trawl CPUE for Pelagic fishes declined significantly below their 30-year population trajectory during the post-zebra mussel period. Although trawl CPUE for the Benthic category did not differ between periods, measures during the post-zebra period were significantly higher than projected from the 30-year population trajectory.

Standardized sampling of the Oneida Lake fish community has produced long-term indices of relative abundance for numerous species, and we used two methods to

compare pre- and post-zebra catches. By comparing catches between the pre- and post-zebra mussel periods, we found significant directional changes in gillnet catches for six of the twelve species included here, and all significant changes were consistent with *a priori* directional hypotheses that were based on general habitat affiliations. Annual total catches were lower during the post-zebra mussel period, primarily due to reduced numbers of yellow perch, walleye, and white perch. Five of the ten species represented in trawl collections showed a significant directional change in CPUE that was consistent with expectations. In all cases where the change between pre- and post-zebra mussel periods differed from *a priori* expectations, the observed percent change was negative. Overall, percid fishes (walleye, yellow perch, logperch, and darters) less dominate the current composition of the Oneida Lake fish community than when standardized sampling was initiated. Although catches of several species were strikingly different between the pre- and post-zebra mussel periods, examination of temporal trends across all years revealed that some important community dynamics were likely in motion before the introduction of zebra mussels. As a result, comparing post-zebra mussel catches to values predicted from 30-year population trajectories produced somewhat different conclusions, particularly when populations were increasing or decreasing rapidly prior to the introduction of zebra mussels. For example, the comparisons for freshwater drum, redhorse, and gizzard shad were each influenced by initial sequences of zero-catch years followed by a rapid increase in catches. Because these species were present in Oneida Lake prior to the initiation of the sampling, we felt that these data should be included. Establishing population trajectories that included a plateau would be an alternative to the approach used here and could potentially account for the stabilization of population abundance after a regime shift. Based on general patterns of abundance produced from long-term sampling, the Oneida Lake fish community did not display an immediate, wholesale

shift in response to zebra mussel invasion, but total catches declined and some individual species were dynamic over the 40-year period.

One of our assumptions was that Benthic fishes would benefit from redirected energy pathways that favored production in their associated habitats and that catches of these fishes would increase as a result. We expected that benthic-affiliated fishes might benefit either directly from consuming zebra mussels or indirectly from increased abundance of other benthic prey (Stewart and Haynes 1994). Even though benthic prey abundance may increase in response to zebra mussels, *Dreissena* will likely dominate the benthic invertebrate community (Stewart and Haynes 1994) and the concurrent increase in structural heterogeneity may provide more refuge habitats for other macroinvertebrates. If so, fish species that can consume zebra mussels directly may be most likely to increase in abundance. Yet, zebra mussels have also been associated with declines in important benthic prey, such as *Diporeia*, and the individual condition of certain fishes may suffer as a result, even for species that can consume zebra mussels directly (e.g., lake whitefish; Pothoven et al. 2001). In Oneida Lake, post-zebra mussel gillnet catches of the Benthic group increased, but 30-year population trajectories generally indicated that catches of these fishes were increasing prior to the invasion of zebra mussels. As a result, post-zebra mussel catches for individual Benthic species were sometimes not as high as projected, but strong declines also were not evident. Although not included in the catch data presented here, the success of reintroduction efforts for lake sturgeon *Acipenser fulvescens* may also serve as an indicator of high-yield benthic production in Oneida Lake. Since stocking efforts were initiated in 1995, lake sturgeon have displayed rapid growth rates, and their diets contained primarily benthic prey, including zebra mussels (Jackson et al. 2002).

Even for benthic fishes, diets are variable and only some species consume zebra mussels directly; therefore, assigning species to a benthic grouping based on a general habitat affiliation may have been too broad of an organizational approach. For fishes that do prey directly on zebra mussels, the exotic bivalve typically is more frequently found in the diet of larger individuals (e.g., Jackson et al. 2002), but larger predators may still select for smaller zebra mussels (Morrison et al. 1997). Magoulick and Lewis (2002) found zebra mussels to be an important component of the diet for blue catfish *Ictalurus furcatus*, freshwater drum, and adult redear sunfish *Lepomis microlophus*. Of these, only freshwater drum occurs in Oneida Lake, but French (1993) identified both redear and pumpkinseed sunfish as potential predators of zebra mussels because they possess both upper and lower pharyngeal teeth, which allow for crushing of mollusk shells. The ability to crush zebra mussel shells could provide access to the higher-energy flesh and may allow consumption of zebra mussels to be more energetically profitable. Although we included pumpkinseed sunfish in the Littoral category, Andraso (2005) reported that dreissenid mussels were the most important food item in the diets of pumpkinseed sunfish and that these mussels were usually found crushed. Mercer et al. (1999) also reported zebra mussels in pumpkinseed diets. Further, French (1993) noted finding zebra mussels in the guts of white suckers and greater redhorse *Moxostoma valenciennesi*. In Oneida Lake gillnets, freshwater drum, pumpkinseed sunfish, white sucker, and redhorse all had relatively high catches throughout the zebra mussel period. On the other hand, channel catfish, brown bullhead, and common carp did not have frequent high catches in gillnets relative to pre-zebra mussel years. These species may be tolerant of eutrophic conditions and not experience a shift towards more preferable habitat conditions after zebra mussel establishment. Magoulick and Lewis (2002) examined digestive tract of both channel catfish (n = 798) and common carp (n = 19) but did not

find zebra mussels. Tucker et al. (1996), however, reported zebra mussels in the gut contents of common carp collected from the Mississippi River. Difference in physical tolerances (e.g., foraging in turbid waters, low oxygen concentrations) and diet composition may be more important than general habitat affiliation as organizational traits for future considerations of fish community responses to zebra mussels.

Beyond influencing benthic prey availability, an abundant zebra mussel population can also influence shifts in fish community dynamics through a variety of indirect pathways, including affecting the coverage of aquatic macrophytes, water clarity, and light levels (Idrisi et al. 2001; Zhu et al. *in press*). Robillard and Fox (2006) recently found increased water clarity and increased mean air temperature to be negatively correlated with the relative abundance of walleye and positively correlated with the relative abundance of smallmouth bass for a number of Ontario Lakes. These changes along with increased light penetration could influence the range of suitable habitats and competitive foraging advantages among fishes (e.g., Ryder 1977; Chu et al. 2004; Lester et al. 2004). Lie-in-wait predators such as *Micropterus* spp. would likely benefit from increased light levels; whereas, walleye would likely suffer from a reduced range of dimly-lit habitats in which it could perform superiorly. Once zebra mussels colonized Lake St. Clair, aquatic macrophytes increased, Secchi depth measurements doubled, smallmouth bass abundance tripled, and walleye abundance declined by more than half (Vanderploeg et al. 2002). In Oneida Lake, both gillnet catches and trawl CPUE of walleye were generally much lower in the past decade than during the 30 years before zebra mussels became established. In contrast, both gillnet catches and trawl CPUE of smallmouth bass were higher during the post-zebra mussel period. A continued shift from cool, turbid water towards warm, clear water in Oneida Lake will likely contribute to a further transition from conditions favoring walleye dominance to conditions favoring expansion of smallmouth bass.

Early life stages of fishes may be especially sensitive to the consequences of zebra mussel colonization. For example, zebra mussels may be detrimental to early life stages of fishes if food resources become limited during the fish larval stages (e.g., reduced phytoplankton and small zooplankton; MacIsaac 1996; Caraco et al. 1997) or if larval fish are more vulnerable to predation in clearer waters (Utne-Palm 2002). Artificially increased turbidity levels can enhance overall production of walleye in culture facilities (Bristow et al. 1996) possibly by reducing intra-cohort cannibalism through a more uniform distribution of larvae (Bristow and Summerfeldt 1994). Influencing the rates at which predator-prey encounters occur can have pronounced effects during early life stages, particularly for walleye because their young are also voracious predators and cannibalistic. In laboratory experiments, young age-0 walleye were able to consume identical-sized members of their cohort, and in some cases, the inability to complete ingestion of a large prey item may have resulted in the death of both the predator and its prey (Li and Mathias 1982). If turbid habitats benefit pelagic larvae, then abundant zebra mussel populations likely contribute to unfavorable conditions for some larval fishes. Although we did not have larval estimates for all species included here, we did evaluate shifts in trawl CPUE for several age-0 fishes. For the age-0 fishes considered here, we found an increase in trawl CPUE for only three. Of these, freshwater drum do have pelagic larvae, but smallmouth bass and trout-perch larvae are not routinely collected in open-water larval sampling in Oneida Lake (CBFS, unpublished data). While previous research has documented lower trophic level responses to zebra mussel introductions (such as a decline in phosphorus and an increase in littoral macrophytes; Idrisi et al. 2001; Zhu et al. *in press*), the indirect connection between zebra mussels and fish early life stages has not received the attention it deserves, especially since many freshwater species produce pelagic

larvae and the highest levels of mortality are generally occurring during this time (see Chapter 1).

Oneida Lake is an important aquatic resource experiencing ongoing ecological change, resulting from bottom-up effects of zebra mussel invasion (Mayer et al. 2002), middle-out effects of fluctuating biomass of alternative forage fish species (Fitzgerald et al. *in press*), and top-down effects of the double-crested cormorant (VanDeValk et al. 2002; Rudstam et al. 2004). We chose to focus our current consideration of a 40-year effort to monitor the fish community primarily on the introduction of zebra mussels because this nonindigenous species can affect multiple components of the aquatic food web (Vanderploeg et al. 2002) and evaluations of fish community responses to zebra mussel introductions relative to long-term patterns are rare (e.g., Strayer et al. 2004). The changing conditions occurring in Oneida Lake, including those driven by zebra mussels, are likely affecting survival of age-0 fishes (e.g., Chapter 1), but the additional predation on sub-adult percids by double-crested cormorants would further reduce the number of fishes recruiting to gillnets (VanDeValk et al. 2002; Rudstam et al. 2004; e.g., Chapter 2). In fact, an abundant cormorant population could remove over 1 million fish from Oneida Lake during a single year (VanDeValk et al. 2002). Even so, trawl CPUE of age-0 pumpkinseed sunfish were lower during the post-zebra mussel period, but gillnet catches showed a strong increasing trend in adult catches through this same time period.

Our comparisons of gillnet catches potentially suffered from a lack of independence across annual observations because individual cohorts could be captured during multiple years. If a strong cohort transitioned across the two periods compared here, then it would likely result in more similar catches, which would limit identification of changes over time. However, the ability of a single cohort to dominate the number of fish caught in gillnets for several years in succession would

be limited because of mortality and reduced selectivity of this gear for larger fish (e.g., Chapter 2). To a lesser extent, annual trawl catches of age-0 fishes may also share a certain commonality, if the numbers of age-0 fishes captured during the fall are strongly related to stable parental stocks. Even with these potential deficiencies, both gears produced multiple years of observations for both time periods for several species. Because long-term multi-species data series are not common, we felt these evaluations were warranted, even in light of the potential consecutive influence of a cohort. The current effort represents our first attempt to examine fish community responses to the rapid establishment of zebra mussels in Oneida Lake. This effort is also part of a larger-scale comparative project to evaluate long-term changes in Oneida Lake and the Bay of Quinte, Lake Ontario (Koops et al. 2006), including construction of Ecopath with Ecosim (EwE) models (Christensen and Walters 2004) for both systems (Irwin et al. *in prep.*; Koops et al. *in prep.a*; Koops et al. *in prep.b*).

Understanding the consequences of ecological change is challenged by the complex mechanisms operating in aquatic ecosystems. The effects of a large-scale perturbation can be transmitted through a system via a variety of indirect pathways. Additionally, these effects may attenuate in more distant trophic levels, and compensatory mechanism can further alleviate effects through a sequence of responses. The overall influence of a stressor may further vary depending on the trophic levels with which the stressor most immediately interacts. When management of an ecosystem involves targeted goals at multiple trophic levels (e.g., increased water clarity and stable walleye catches), understanding the effectiveness of each implemented policy becomes more challenging. In some cases, management goals for different components can even be counterproductive so that trade-offs are needed for particular trophic levels. For instance, nutrient reductions can ultimately translate to shifts in the fish community, possibly away from those species that are currently in

favor among anglers (e.g., Ludsin et al. 2001). Exotic species can produce additional, and even unexpected, shifts that are difficult to disentangle from general population stochasticity or responses to planned management actions. We suggest that both direct (e.g., consumption of zebra mussels) and indirect (e.g., unfavorable conditions for pelagic larvae) effects of zebra mussels should be considered when evaluating shifts in fish community dynamics, and that these effects may be particularly pronounced in systems that experience a decline in zooplankton biomass and rely on production of fish species that have low plasticity in their selection of prey items.

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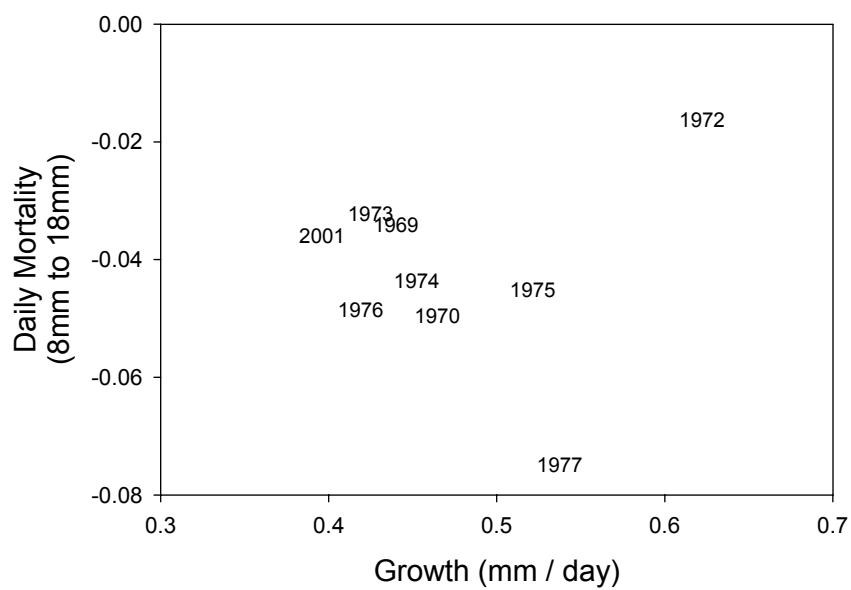
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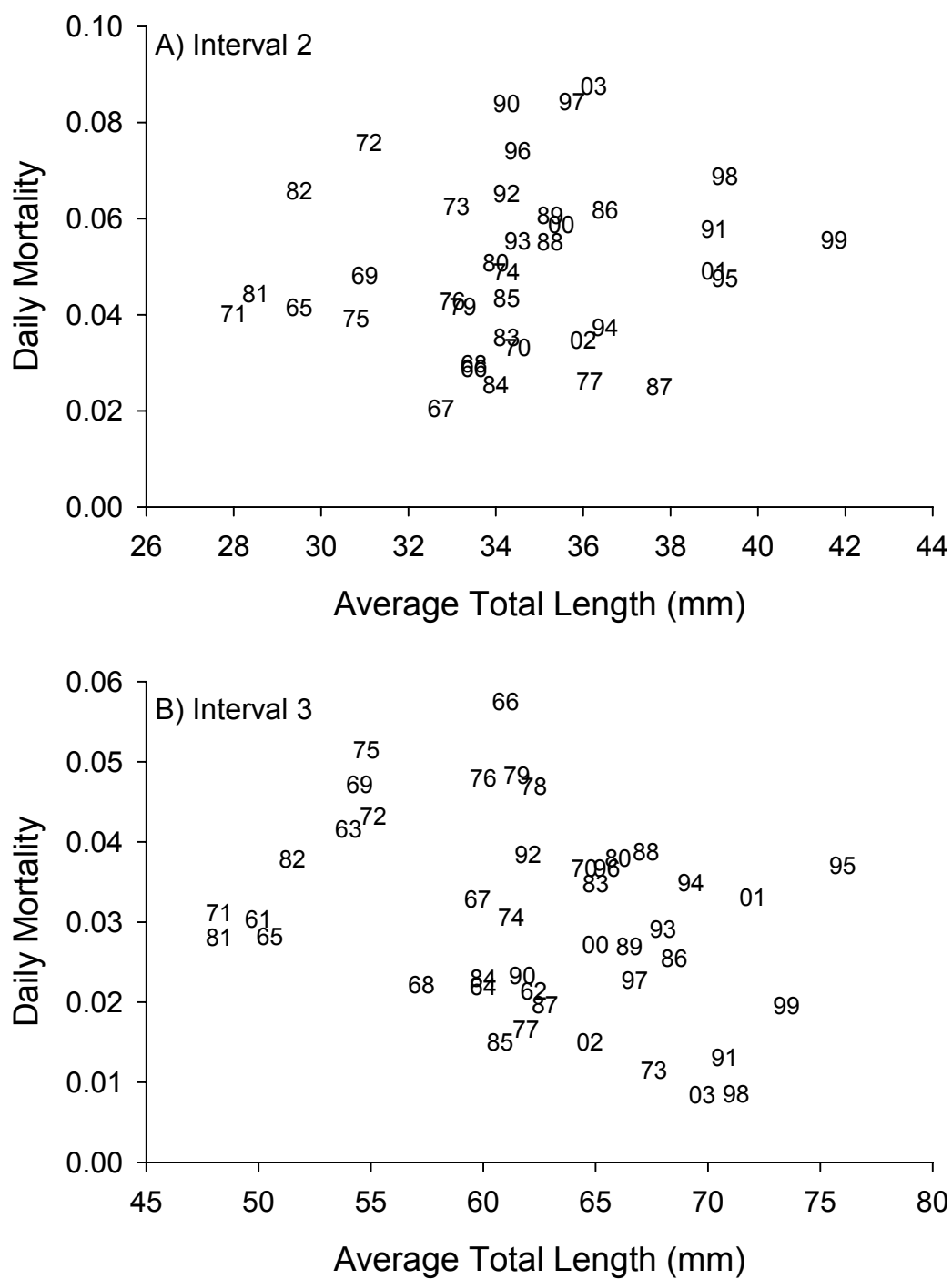
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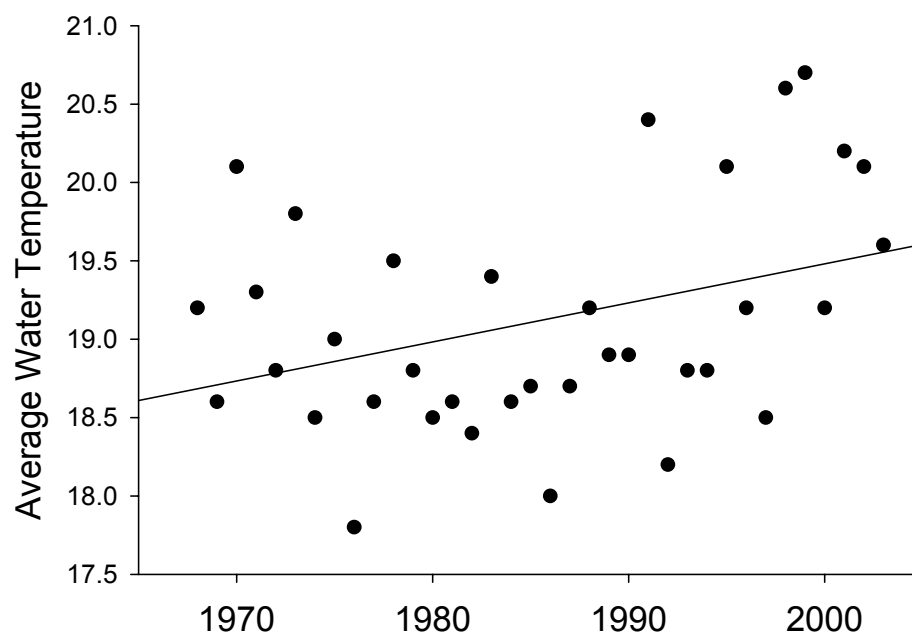
APPENDICES



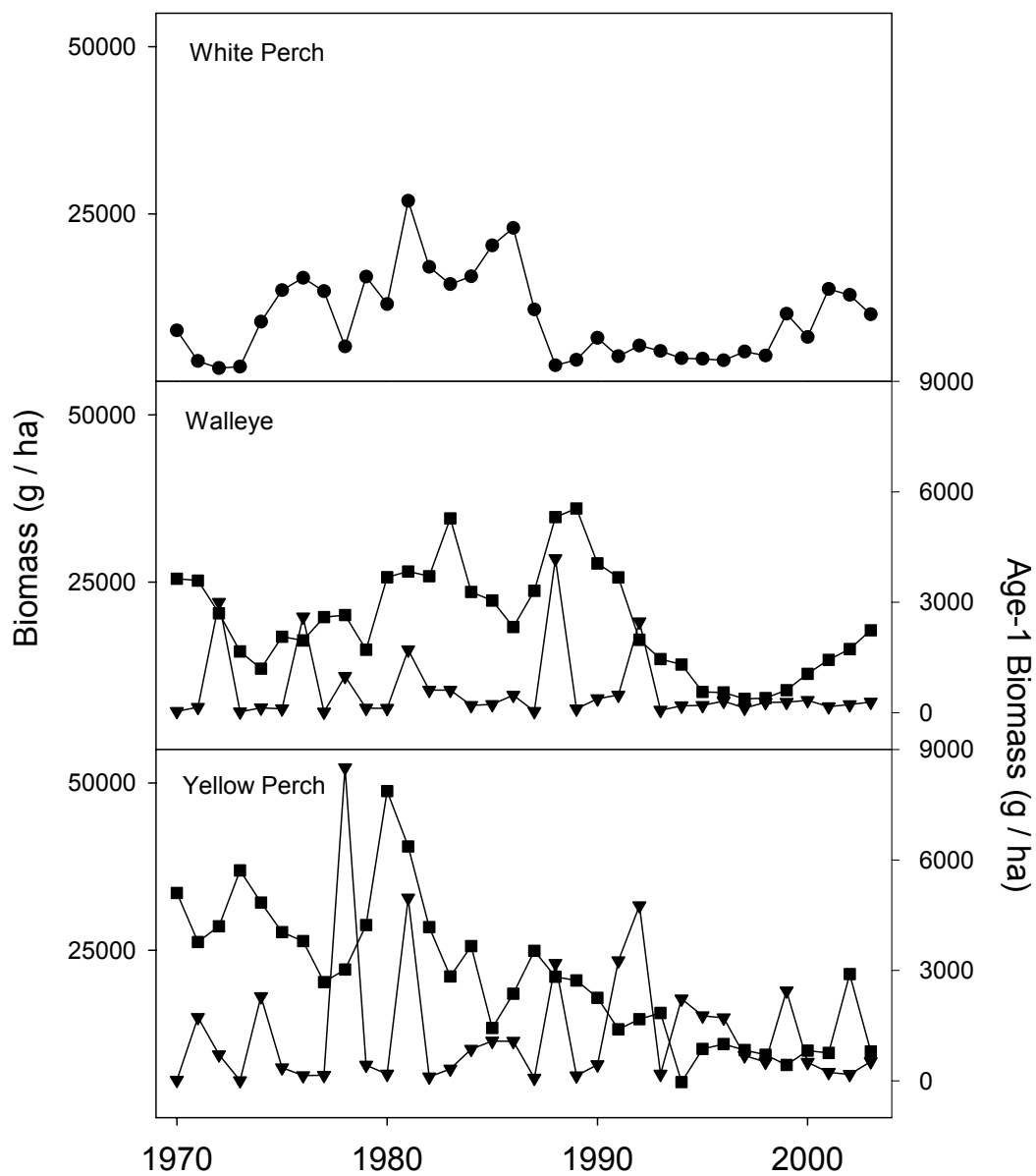
Appendix 1-1. Estimated daily growth and mortality from 8mm to 18mm for yellow perch in Oneida Lake. Data for 1971 and 1998 were not included in the calculation for average daily mortality but were included for average growth.



Appendix 1-2. Instantaneous daily mortality rates of age-0 yellow perch during two early-life-stage intervals relative to average size within the interval.



Appendix 1-3. Average water temperature at 2m from 1 May to 15 October from 1968 through 2003.



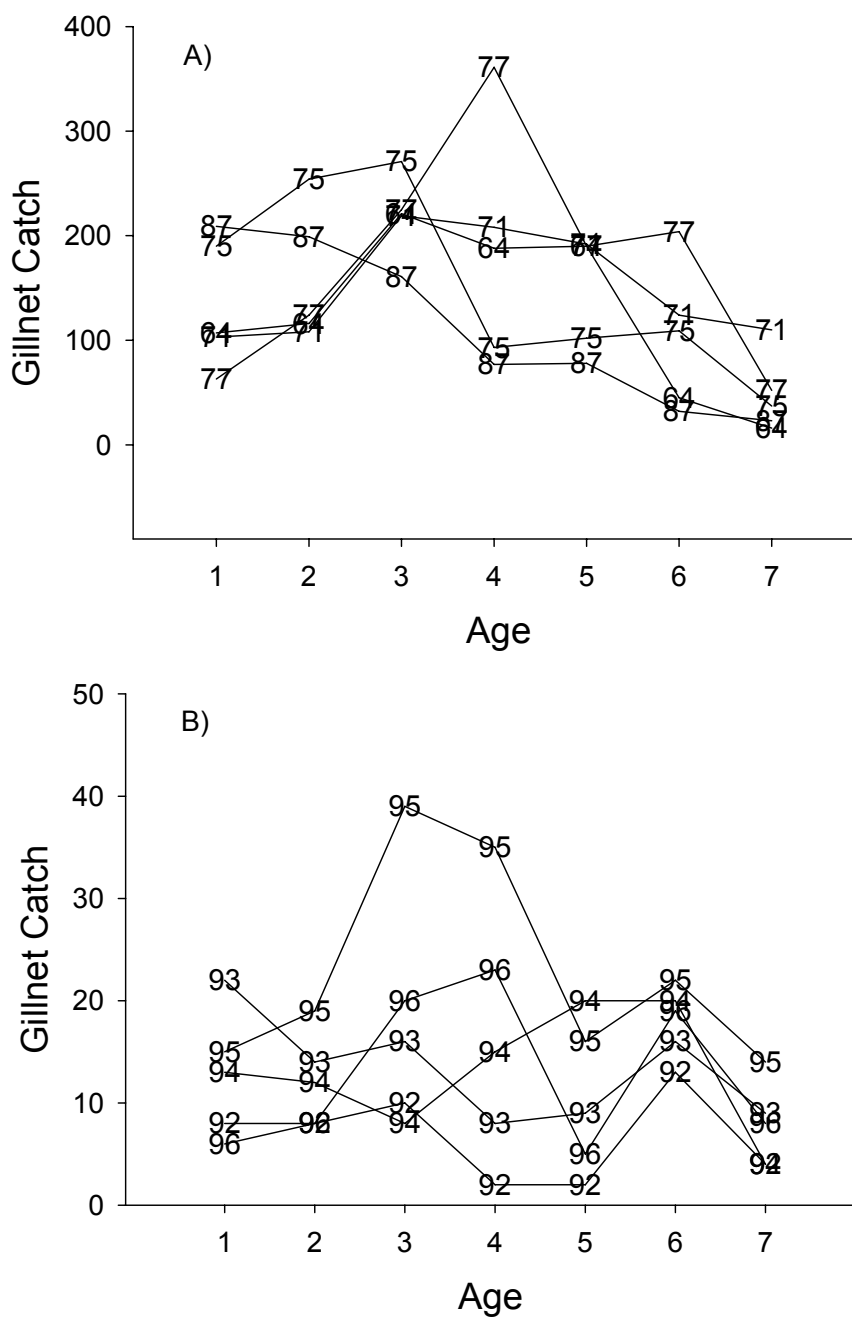
Appendix 1-4. Estimated biomass of potential predators, including white perch, walleye, and yellow perch. For both walleye and yellow perch, age-1 biomass (▼) is presented separate from age-2 and older (■).

Appendix 2-1. Summary of parameters used in walleye estimation model. Selected parameters (shown with a log prefix) were estimated as \log_e values and then exponentiated. Estimated parameters are also shown in bold. Intermediate parameters were used to implement estimated parameters in various model equations. In some cases, weighting factors were applied to eliminate influence of missing data on residuals.

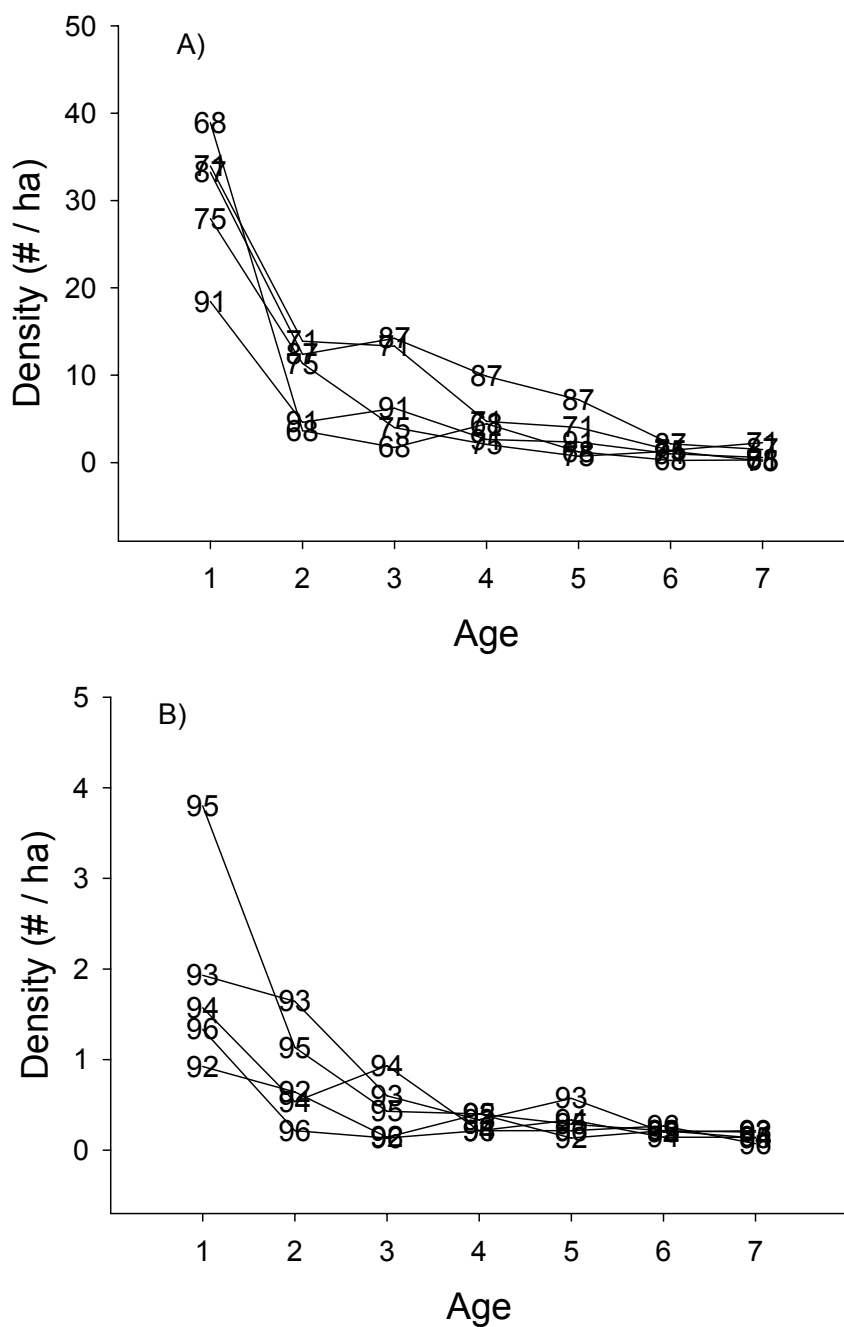
Parameter	N	Type	Description
LogZnat	1	Fixed	Instantaneous mortality rate (natural)
LogC	1	Estimated	Instantaneous mortality rate (cormorant)
LogF	1	Estimated	Instantaneous mortality rate (fishing)
Zm	6	Intermediate	Instantaneous mortality rate (total)
S	6	Intermediate	Annual survival
logNstart	1	Estimated	Initial density value
logNdevsparam	52	Estimated	Bounded deviation values for density
logN0	52	Intermediate	Initial row and column for density matrix
N	322	Intermediate	Matrix of walleye density
Qtrv	7	Estimated	Trawl catchability at age
Qgnv	7	Estimated	Gillnet catchability at age
PTCPUE	322	Intermediate	Predicted trawl catch at age and time
PGNTC	322	Intermediate	Predicted gillnet catch at age and time

Appendix 2-2. Adult (age-4 and older) walleye survival, abundance, and angler exploitation data used to select initialization values for parameters associated with instantaneous natural and instantaneous fishing mortality rates. Annual survival estimates are based on the average of two independent methods (VanDeValk et al. 2005b). Remaining data for 1958 and 1959 are from Forney (1967).

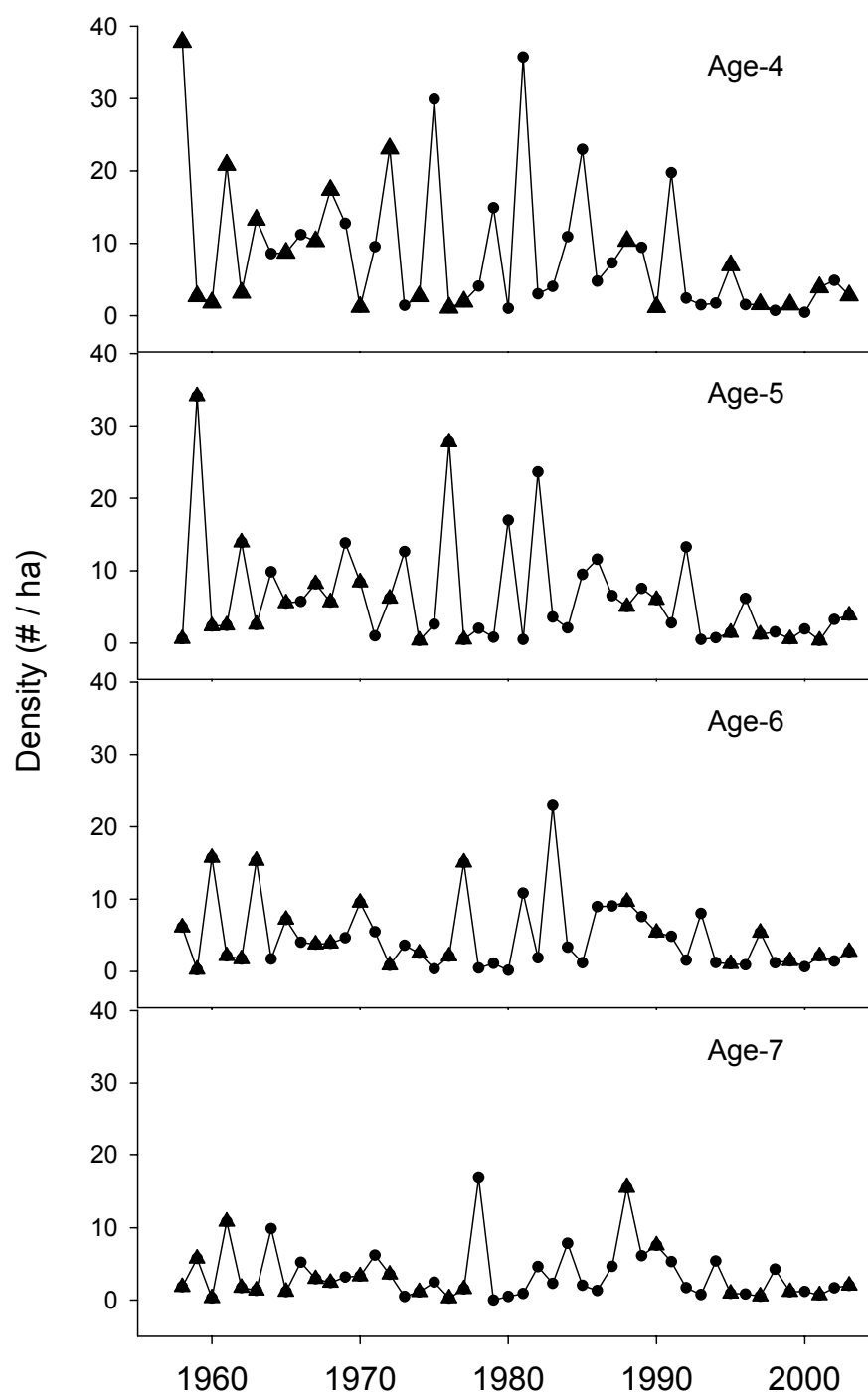
Year	Annual Survival	Adult Abundance	Angler Harvest	Instan. Z	Instan. Fishing	Instan. Natural
1958	0.87	1,035,000	106,000	-0.139	-0.110	-0.030
1959	0.46	960,800	449,000	-0.777	-0.672	-0.104
1997	0.80	251,900	35,400	-0.223	-0.157	-0.066
2002	0.79	345,900	9,587	-0.236	-0.031	-0.205
		Average:		-0.344	-0.242	-0.101



Appendix 2-3. A) Total catch-at-age for the five walleye cohorts most frequently captured in gillnets set at 15 standard sites in Oneida Lake during 1958 to 1996 and B) for five recent cohorts (1992-1996). Note differences in y-axes.

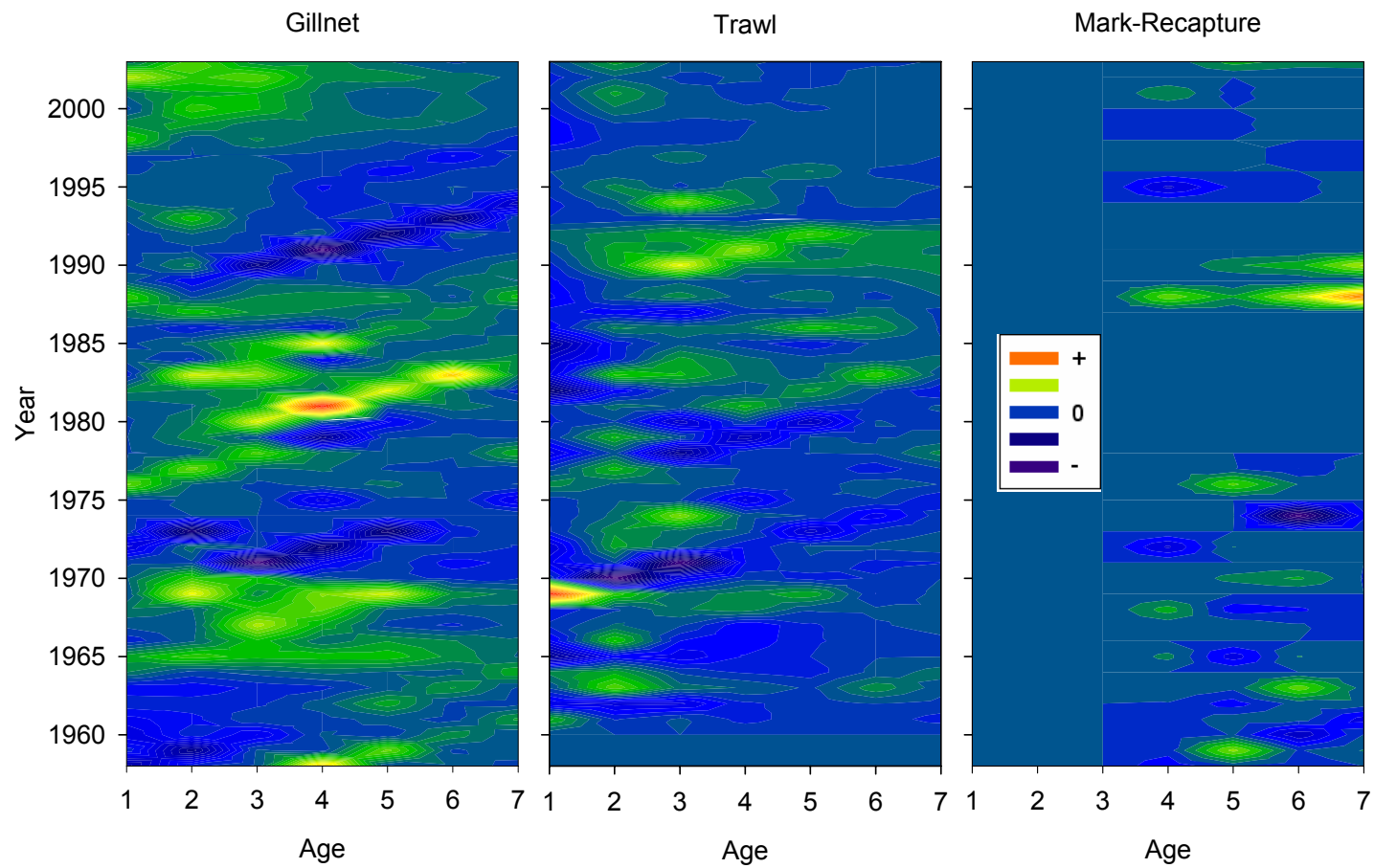


Appendix 2-4. A) CPUE-at-age for the five walleye cohorts most frequently captured in trawls in Oneida Lake during 1961 to 1996 and B) for five recent cohorts (1992-1996). Note differences in y-axes.



Appendix 2-5. Annual age-specific density estimates for adult walleye in Oneida Lake. Values were calculated using three methods, but only standard mark-recapture estimates (triangles) were used as model input data.

Appendix 2-6. Contour plots of residuals (observed – predicted) for three input data series (gillnet catch, trawl CPUE, and mark-recapture estimates). Missing values were assigned a weight of zero; see text for additional details on missing values.



Appendix 3-1. Annual total catch in gillnets at 15 standard locations in Oneida Lake. Species codes are presented in Table 3-1. ND = no data available.

Year	We	Yp	Wp	Gzd	Smb	Ps	Ccat	Bbh	Drum	Carp	Ws	Rh
1962	479	1,491	142	0	18	18	13	3	0	1	31	0
1963	432	1,704	199	0	9	11	18	2	0	0	38	0
1964	543	1,601	233	0	23	36	9	1	0	0	35	0
1965	778	1,965	254	0	22	12	12	1	0	6	21	0
1966	601	1,382	129	0	16	7	3	1	0	0	70	0
1967	583	1,518	106	0	10	12	8	0	0	5	104	0
1968	569	1,936	73	0	8	13	2	6	0	1	54	0
1969	837	1,533	65	0	7	7	8	2	0	0	48	0
1970	519	1,868	175	0	18	25	12	5	0	0	68	0
1971	116	825	45	0	6	9	10	1	0	16	12	0
1972	295	926	24	0	15	16	12	9	0	3	63	0
1973	173	1,531	28	1	12	13	4	6	0	0	22	0
1974	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
1975	281	1,427	415	0	2	5	16	15	11	2	10	0
1976	454	1,424	501	0	22	18	9	10	5	3	9	1
1977	432	1,413	208	1	15	5	8	20	8	5	20	2
1978	510	1,055	100	1	16	6	10	5	7	1	22	0
1979	290	1,651	509	0	7	6	11	2	1	16	67	0
1980	399	2,838	353	7	15	4	9	3	2	1	68	0
1981	639	2,420	963	1	5	4	8	4	8	0	21	1
1982	508	1,722	486	0	6	14	16	3	13	1	27	2
1983	763	1,166	420	8	6	12	15	2	2	3	28	0
1984	372	1,501	424	12	26	22	12	5	22	18	44	0
1985	505	750	666	60	16	5	16	13	12	6	42	1
1986	296	1,081	922	25	19	23	28	8	13	8	53	2
1987	386	1,285	305	3	47	17	13	12	13	1	58	3
1988	531	1,236	30	42	38	8	26	10	94	7	38	1
1989	391	1,245	67	15	65	15	58	10	55	7	34	0
1990	303	1,008	125	33	57	10	36	10	291	6	33	1
1991	164	608	56	17	33	1	43	4	178	11	27	1
1992	246	814	78	49	20	1	30	1	107	3	40	0
1993	217	952	66	1	46	9	10	3	100	3	44	0
1994	177	316	41	2	37	11	9	14	154	1	47	3
1995	144	864	37	0	22	9	14	1	93	2	37	1
1996	108	618	40	0	24	5	18	4	49	3	41	1
1997	75	606	200	0	30	20	28	19	33	1	59	1
1998	198	773	196	0	29	15	17	2	83	1	55	4
1999	235	444	502	17	65	19	18	3	74	4	66	5
2000	248	796	209	9	31	33	44	10	35	7	63	2
2001	218	728	497	3	30	31	16	10	32	1	35	5
2002	437	1,061	450	9	70	20	15	5	69	2	34	5

Appendix 3-2. Annual total catch of age-0 fishes in bottom trawls at 10 standard locations in Oneida Lake. Hauls = number of trawl hauls per year at the 10 standard locations, species codes are presented in Table 3-1.

Year	Hauls	We	Yp	Wp	Gzd	Smb	Ps	Tp	Dart	Lp	Drum
1962	90	1,720	108,255	2,293	0	48	25	7,419	2,218	157	0
1963	120	1,254	54,957	508	0	0	425	4,155	1,450	319	0
1964	140	1,336	180,400	641	0	2	1,555	2,478	683	101	0
1965	140	1,350	142,334	11,738	0	1	29	3,201	3,460	346	0
1966	140	228	46,679	14,379	0	15	24,079	6,185	4,452	399	0
1967	130	1,241	138,011	2,216	0	22	2,533	4,281	1,204	61	0
1968	130	2,900	241,495	156	0	0	680	4,925	1,323	22	0
1969	130	965	39,489	1,041	0	5	693	3,529	719	65	0
1970	140	648	120,557	2,801	0	37	1,816	1,233	429	9	0
1971	130	616	131,350	1,327	0	49	65	1,924	2,160	379	0
1972	110	335	11,515	288	1	9	4,477	1,533	1,193	68	0
1973	150	32	23,268	28,650	0	0	15,061	721	143	17	43
1974	140	744	27,400	4,651	2	12	954	210	621	66	7
1975	120	1,891	75,354	2,219	0	16	43	47	443	52	0
1976	130	106	32,861	3,474	3	14	1,329	83	5,422	182	38
1977	150	1,226	133,333	14,820	0	4	6	104	1,631	123	1
1978	140	549	40,337	442	1	107	585	371	4,573	433	1
1979	130	108	35,023	15,410	0	1	8,655	308	2,274	179	19
1980	140	250	50,991	78,735	0	0	99	258	180	31	11
1981	130	852	157,849	3,059	2	4	17	571	392	15	0
1982	120	310	67,714	50,294	0	0	458	2,241	186	46	0
1983	130	195	56,010	75,488	46	21	25,718	1,572	173	49	33
1984	130	148	24,325	6,449	79	62	1,405	3,085	261	11	24
1985	120	470	50,884	1,366	95	0	55	6,851	72	9	0
1986	130	80	4,366	190	21	0	497	3,510	27	2	2
1987	130	333	10,273	73,420	319	90	114	5,603	29	2	60
1988	130	141	27,198	55	20	13	109	1,265	69	13	6
1989	130	32	1,460	11,520	131	0	526	564	22	16	31
1990	140	108	19,494	999	260	36	899	1,054	119	6	73
1991	160	563	12,218	1,154	1,009	176	1,115	2,810	120	2	154
1992	140	226	17,897	488	30	2	17	6,846	964	110	28
1993	140	237	20,703	8,573	14	49	467	10,410	976	131	36
1994	140	257	29,936	851	9	392	237	13,836	448	107	3
1995	140	277	15,174	6,685	7	95	741	8,292	226	18	208
1996	150	36	9,618	681	1	5	60	2,820	98	50	4
1997	150	69	975	10,534	2	348	213	5,103	107	46	37
1998	140	42	18,160	1,663	0	66	27	3,972	92	1	0
1999	150	157	22,310	105	12	131	12	4,348	31	0	1
2000	140	49	9,452	6,587	36	0	36	5,238	76	19	30
2001	140	428	30,280	721	17	38	55	3,228	16	0	10
2002	150	57	59,123	14,043	31	68	556	7,526	36	10	4