

8-2-2012

Winter Drawdown Effects on Swim-up Date and Growth Rate of Age-0 Fishes in Connecticut

Christopher P. McDowell

University of Connecticut - Storrs, cpmcdowell@hotmail.com

Recommended Citation

McDowell, Christopher P., "Winter Drawdown Effects on Swim-up Date and Growth Rate of Age-0 Fishes in Connecticut" (2012). *Master's Theses*. 324.
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Winter Drawdown Effects on Swim-up Date and Growth Rate
of Age-0 Fishes in Connecticut

Christopher Patrick McDowell

B.S, Unity College, 2000

A Thesis

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

At the

University of Connecticut

2012

APPROVAL PAGE

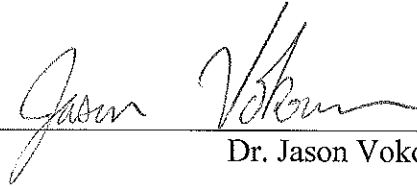
Master of Science Thesis

Winter Drawdown Effects on Swim-up Date and Growth Rate
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Presented by

Christopher Patrick McDowell, B.S.

Major Advisor



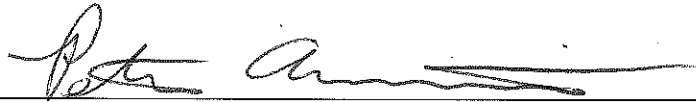
Dr. Jason Vokoun

Associate Advisor



Dr. Patricia Bresnahan

Associate Advisor



Peter Aarrestad

University of Connecticut

2012

ACKNOWLEDGEMENTS

The only place to begin these acknowledgements is with my wife Jessica and my parents Joanne and Rodney. It was only with their unending love, patience, support, guidance and understanding that this educational milestone was achievable. I thank you so much for the roles you have played in helping make me the person I am today.

Secondly, I owe an immense debt of gratitude and thanks to Justin Davis whose knowledge and professional guidance with statistics, SAS and fisheries science enabled me to complete this adventure. You are a true friend who has stuck by me through the most challenging and grueling times this endeavor has thrown at me over the past six and a half years.

I would like to thank those in the Department of Energy and Environmental Protection Inland Fisheries Division (CT DEEP IFD): William Hyatt, Peter Aarrestad, Robert Jacobs, Eileen O'Donnell, Brian Murphy, Neal Hagstrom, Jim Bender and Mindy Barnett who gave me the latitude, funding, equipment, personnel and advice to be able to pursue this project for them.

A very special thanks and much appreciation goes out to Anson Smigel, Brian Eltz, Kevin Job, George Maynard, Brad Trumbo, Matt Golcowski, Joe Cassone, Alexi Kimiatek and Mike Rege whose tireless efforts and dedication helped in the collection and processing of the samples for this project. I would also like to thank (in alphabetical order) the following seasonal staff (from both the University of Connecticut, Storrs and the CT DEEP IFD) that participated during the life of this project in the many facets of the field and laboratory work: Ethan Andrews, Chelsea Apito, Lane Belanger, Peter Booker, Joshua Brown, Trevor Brown, Mark Clifton, Jeffrey Divino, Dustin Edwards,

Chris Hayward, Kyle Klesa, Tyler Mack, James McGuire, Nicholas McMahon, Jason McWade, Amy Narducci, (Sarah) Whitney Pryce, Timothy Sadler, Jennifer Stone, Greg Ulkis, and Alyse Zebrosky. Without their efforts this project would not have been completed.

Lastly, I would like to thank the members of my committee (Dr. Jason Vokoun, Dr. Patricia Bresnahan and Peter Aarrestad) for taking the time out of their busy schedules to review this document.

ABSTRACT

Winter drawdown is a lake management tool which may alter lake ecosystems, at times having desired and undesired outcomes. Drawdowns lower water levels, reduce water volume and surface area, and impact animal and plant communities, particularly in the shoreline areas exposed during water level reductions. This study was undertaken in conjunction with Connecticut Department of Energy and Environmental Protection (CT DEEP) Inland Fisheries Division to add to quantitative scientific information specific to the effects of winter drawdowns on age-0 freshwater fish in small southern New England impoundments. The overall goal was to determine if winter drawdown history and varying drawdown intensities influenced swim-up dates and mean daily growth rates (MDGR) of age-0 yellow perch (*Perca flavescens*), largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*) in five eastern Connecticut lakes. Three objectives were outlined for this project: 1) determine age-0 swim-up dates and MDGR over three consecutive years following varying winter drawdowns; 2) document the water temperatures and date ranges of spawning activities, assess how this timing relates to the current CT DEEP drawdown policy refill deadline date (April 15th) and use the documented seasonality to look for supporting evidence of ecological bet-hedging in the form of protracted spawning behavior by contrasting those temperatures and date ranges among impoundments with varying drawdown histories, as well as look for differential MDGR in fishes swimming up during different times of the growing season; and 3) determine if changes in swim-up dates and MDGR result from changes in four

environmental covariates (i.e. winter drawdown intensity, water temperature, food availability and habitat).

Three types of winter drawdowns were applied to the suite of project lakes: two lakes had a 0.91 meter (m) drawdown; two lakes had a >0.91 m, but ≤ 1.82 m drawdown; and one lake had no drawdown. Subsamples of age-0 fish were retained for otolith extraction each summer following each drawdown to determine relative swim-up dates and MDGR. Covariates of drawdown intensity, water temperature, zooplankton density and percent moveable sediment were collected annually from each lake.

Strong support for varying winter drawdown intensities causing significant changes in swim-up date or MDGR were not found from the results of this study. The drawdowns did not occur as expected due to precipitation type and amount as well as individual lake refill characteristics. This led to variable annual disturbance intensities making the elucidation of drawdown effects on the three fish species statistically challenging.

Otolith data revealed three important pieces of information: first, yellow perch do not exhibit a protracted spawning strategy, whereas largemouth bass and bluegill do in these lakes. Significant differences in mean swim-up date were found with each species within each lake across years and amongst lakes within each year in most instances. Bluegill swim-up co-varied with drawdown history with earlier swim-up dates being found in the drawn down lakes compared to the non-drawn down lake, whereas differences in swim-up for yellow perch and largemouth bass did not co-vary with drawdown history.

Second, MDGR varied inconsistently for yellow perch in regards to drawdown history with no one drawdown history showing consistent trends in growth. With largemouth bass, when swim-up occurred did not affect MDGR, nor were any consistent MDGR patterns found amongst the varying drawdown histories. For bluegill, MDGR differences were observed between early and late swim-up in the two lakes with extensive drawdown histories and one with a brief drawdown history, but no differences in MDGR were found between early or late in the non-drawdown lake. Overall MDGR was faster with the bluegill in the non-drawn down lake compared to the other lakes.

Third, back calculated spawning periods for adult yellow perch, largemouth bass and bluegill compared against the current CT DEEP drawdown policy refill deadline date showed an almost complete overlap in the spawning period with when lakes were refilling for yellow perch; some overlap for early spawning largemouth bass; and no overlap in the bluegill spawning period. Additionally, there is almost a complete overlap with chain pickerel from literature inferred spawning timing. CT DEEP should discuss and potentially modify its timing of lake refill to protect early spawning lentic species. Years with winter and spring droughts could negatively impact spawning of these species through delayed refill limiting access to suitable spawning habitat.

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CHAPTER 1

Introduction, Background and Field Methods

Introduction

Winter drawdown is the manipulation of water levels on impounded waters during winter months. Outside Connecticut, drawdowns are used to aerate lake substrates (Crawford 1957), manage nuisance aquatic plants (Hestand and Carter 1974; Gorman 1979; Goldshalk and Barko 1988) manage and remove nuisance, rough and commercial fishes (Hulsey 1956; Crawford 1957), and to concentrate forage fish species allowing better use by predators (Crawford 1957; Heman et al. 1969). Within Connecticut, drawdowns are used to manage aquatic vegetation, prevent ice damage to docks/boat moorings, and to facilitate shoreline property maintenance (R. Jacobs, Connecticut Department of Energy and Environmental Protection [CT DEEP], personal communication). Within the northeastern United States, this type of management technique is primarily carried out on small impoundments that were once-natural lakes now fitted with water control structures (most often a dam with a single outflow); once-natural lakes that have had their surface area increased by impoundment; and/or impounded swamps and rivers. These waters are often eutrophic and support extensive macrophyte growth. This type of management is relatively inexpensive and free of public-at-large conflicts (i.e. there is rarely lost hydropower or large scale water supply issues in commonly drawn-down small impoundments). This process has occurred in many impounded waters throughout Connecticut upon the requests of lakefront property owners, town officials, and lake associations for many decades.

The CT DEEP regulates winter drawdowns, in accordance with Rocque (1998) on lakes where CT DEEP has property rights. Winter drawdowns are the only seasonal water-level manipulations being permitted within the State at present; excepting water-company controlled areas, flood-control reservoirs operated by the US Army Corps of Engineers and occasionally lakes with state-owned boat launches or water control structures requiring repair. Requests for a winter drawdown are coordinated through the CT DEEP Office of Environmental Review and typically come from State officials, town officials, lake front property owners or lake associations. Current policy states drawdowns cannot begin prior to September 10th (i.e. after Labor Day); duration must be minimal and cannot extend past completion of the stated purpose. If maintained all winter, termination must occur so the lake refills by April 15th (i.e. prior to Opening Day of trout fishing season). A depth of 0.91 meters (m) has been chosen (somewhat arbitrarily) to be the maximum level that an impoundment can be drawn down past the conservation pool height maintained throughout summer by the control structure. However, if a deeper drawdown is requested it is evaluated on a case-by-case basis (P. Aarrestad CT DEEP, personal communication). At times, though, CT DEEP denies drawdowns if the reasoning is not considered justifiable. This makes the issue contentious as drawdown requestors will then involve their local politicians and in one instance (Beseck Lake, Middlefield, CT) politicians have enacted legislation mandating drawdowns that supersede current CT DEEP policy. This, however, is not the norm, nor is it what all parties want to see. Because the mandate of CT DEEP is largely to protect and sustainably manage the environment, they are interested in the ecological impacts winter drawdowns can have on lake ecosystems so as to have a firmer scientific platform

from which to structure policy. The current policy's start and end dates for drawdowns are not based on any ecological reasoning, but instead were instituted to maximize human recreational use of the water body.

Though the main topic of this project centers around fish and the impacts winter drawdowns may impart upon them, the relevant potential aquatic effects of drawdowns, regardless of when they are instituted, run across the entire aquatic science gamete. As aquatic ecosystems are considered webs and not linear chains (Polis and Strong 1996) alterations in one part of the system will inevitably ripple across to other areas. Going forward I will try to paint the picture of the complex nature of aquatic ecosystems and the impacts winter drawdowns can have and how these impacts are intertwined with fish. The littoral zone, which is the portion of the lake that is home to most of the aquatic plant life found in a lake, is an important nutrient exchange area between terrestrial and aquatic habitats (Estes 1972). In a small impoundment ecosystem, the plants found in the littoral zone provide support and protection to a number of organisms that are crucial to the in-lake food web (Estes 1972). Because of this, the littoral zone is considered the most important area of a lake due to the linkage it provides between fish, invertebrates and vegetation (Estes 1972). This zone is where most fish spawn; it is a nursery area for young fish and subsequently a feeding area for larger predators. Additionally, it is a winter refuge area for hibernating amphibians and turtles, as well as a feeding location for waterfowl (Estes 1972; Hestand 1977). It is also the area most likely to be impacted by a winter drawdown, as a substantial portion of it will be dewatered and exposed to desiccation and freezing.

Drawdowns may change water quality through the input of additional nutrients back into the water column released from organic matter found in aquatic plants and bottom substrate (Estes 1972). This may lead to the increased occurrence of noxious and undesirable [to humans] algal blooms (Gorman 1979; EPA 1990), as well as low dissolved oxygen levels from the increased decomposition of organic material, consequently resulting in large lake wide fish kills (Coon 1998; EPA 1990; McGowan et al. 2005).

Modifications to the fine and organic portions of the littoral substrate occurs through erosion, ice scouring, re-deposition, drying, compaction and oxidation (Estes 1972; Hale and Bayne 1982, McGowan et al. 2005). Fine organic sediment particles may be transported out of the littoral zone to deeper water or completely removed from the lake, leaving a ring of large coarse substrates around the shoreline (Estes 1972; Beard 1973; Hestand 1977; Cooke et al. 1993; McGowan et al. 2005). Biota (aquatic macrophytes, benthic invertebrates and nest forming fishes) that are adapted to finer sized substrates will realize shifts in their distribution, composition and density (Hale and Bayne 1982; Mitzner 1991; Clark et al. 1998).

The vascular aquatic plant community that makes up the littoral zone is foundational to the food web, providing vertical support and protection to algae, other epiphytic plants and various aquatic organisms that are the forage base for fishes (Estes 1972). Though drawdowns are an effective management tool for keeping many aquatic vegetation species in check, temporary or complete shifts in species composition, relative abundance and diversity will result from desiccation and exposure to climactic fluctuations on the vegetative parts, which will in turn change the character of the littoral

zone (Beard 1973; Hestand and Carter 1974; Nichols 1975; Gorman 1979; Tazik et al. 1982; Siver et al. 1986; Godshalk and Barko 1988; Cooke et al. 1993). Because drawdowns do not discriminate between which aquatic vegetation it exposes (i.e. native, invasive, drawdown tolerant or intolerant) some lakes will realize expansion of the area occupied by desirable and/or undesirable plants; in others it may reduce it (Hestand 1977; Godshalk and Barko 1988; McGowan et al. 2005). Expansion of certain submerged plant species during a drawdown may occur from increased seed production or through the transportation of vegetative parts (Hestand 1977; McGowan et al. 2005). Floating plants will most likely perish if stranded and allowed to dry out, but they may also move toward the lake center with the changing water levels.

Water level fluctuations that are extreme enough to alter lake substrates and prevent (re)growth of aquatic plants, will inevitably alter in-lake habitat and food web structure for those organisms that are dependent on the littoral zone for their life cycle (Estes 1972; Hestand 1977; iEP inc. 1990). Shifts in abundance, distribution and species composition of periphyton, plankton and zooplankton upon which higher organisms, such as fish, feed will inevitably occur. Alterations of the entire predator-prey dynamic of the in-lake ecosystem occur not only from the afore mentioned shifts, but because withdrawing water from a lake results in everything mobile within the water column moving closer together and everything immobile along the bank becoming exposed to the elements (Hestand 1977). The importance of these food sources to the fish community and resulting fish catches has been discussed by Doan (1942). Because most young fish feed on plankton, and some species continue to do so as adults, factors affecting the abundance of the appropriate types of plankton and zooplankton may ultimately affect

fish abundance later on (Doan 1942). In some small artificial ponds fertilized for plankton production there was almost a direct correlation in fish produced to the standing plankton crop (Doan 1942). There have also been negative correlations found between herring catches and the quantity of phytoplankton present and positive correlations between herring catches and the copepod *Calanus* (Doan 1942). In apparent contrast, however, Wegner et al. (1974) found that the simplest and most economical method for increasing the abundance and production of foundational food sources was through extreme water fluctuations during the plant-growing season. This, however, will not work during northeastern United States winter drawdowns because it is outside the growing season.

A pressing concern to fisheries biologists has been the potential effects drawdowns have on the phenology of lake-residing fishes (Estes 1972). Fall/winter drawdowns have been shown to negatively impact fall spawning lake trout nests in Canadian reservoirs; sauger and northern pike spawning failure and egg loss in some Missouri mainstream reservoirs; walleye in some northern lakes; and gizzard shad, which ultimately affected largemouth bass growth due to lack of forage the following year (Estes 1972). Gadboury and Patalas (1984) showed that overwinter drawdown reduced whitefish and Cisco hatching success by dewatering their spawning areas and desiccating the eggs; whereas in years with little to no drawdown strong year-classes of these fish occurred. Studies conducted on reservoir fisheries have found that the timing of the drawdown and its subsequent refill can cause loss of Centrarchidae eggs affecting year-class formation, but typically not causing a complete year-class failure (Estes 1972; Mitzner 1991). Water levels not raised soon enough in the spring have been shown to

prevent pike and walleye from accessing their spawning areas (Gadbury and Patalas 1984). In Connecticut, chain pickerel, a native apex predator, is one of the first in-lake species to spawn just after ice-out (Webster 1942). It requires access to shallow coves and bays that have abundant aquatic vegetation to deposit their eggs (Carlander 1969). If lakes are not refilled by the time water temperature and photoperiod triggers this species to commence spawning, access to suitable habitat will be an issue, ultimately effecting year-class formation. Jacobs and O'Donnell (2009) documented declines in adult chain pickerel numbers in lakes that receive repeated winter drawdowns compared to those lakes that do not have drawdowns because of loss of near shore aquatic vegetation. This points towards Connecticut's current winter drawdown regime negatively impacting the ability of this species to spawn and subsequently suppressing their populations.

Though winter drawdowns have the capability to exert many negative effects upon a fishery, it has the potential to be used as a tool to control the number of small fish in a lake by concentrating them into a reduced area without the benefit of littoral vegetation cover so their numbers can be thinned through predation (Lantz et al. 1967; Estes 1972; Nichols 1975; Hestand 1977). This type of management would, however, have to occur when water temperatures were still warm enough that predatory fish digestion was still active. Management in this manner has sometimes lead to increased growth of predatory fishes with an accompanied increase in sport fishing harvest (Pierce et al. 1963; Lantz et al. 1967; Wegener and Williams 1974) other times it has not (Estes 1972).

This project has been structured to attempt to determine whether varying winter drawdown regimes affect swim-up dates and mean daily growth rates (MDGR) of age-0

yellow perch (*Perca flavescens*), largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*), which are both important aquatic ecosystem and recreational species. Age-0 fish were chosen as the focus of this study because accurately predicting year-class strength of fish populations is an integral part in successfully managing fisheries (Sammons and Bettoli 1998). Past methods of stock assessment have focused on sampling adult members of the fish population. Literature has now shown that fish year-class strength is often fixed before the end of a cohort's first growing season (Sammons and Bettoli 1998). Earlier hatched fish of certain species have a competitive advantage over later hatched individuals, in that they have a longer and usually more environmentally favorable growing period relative to individuals hatching later. This, therefore, allows them to attain greater lengths and weights, which removes them from some predation pressures sooner and consequently increases survival during the harsh energetically taxing environmental conditions that winter brings (Post and Prankevicus 1987; Phillips et al. 1995; Cargenelli and Gross 1996; Ludson and DeVires 1997; Pine et al. 2000; Shoup and Wahl 2008). Because it appears that faster growth during a fishes first months of life is critical to survival (Radtko 1989; Jackson and Noble 1995; Shoup and Wahl 2008) anything that may interrupt the spring phenology of these fishes resulting in later hatching, is crucial information for managers.

Focus

This project centers around comparisons in population-level demographics among five lakes in eastern Connecticut, with a focus on the critical first year of life of the three fish species mentioned earlier. Among lakes, different drawdown levels (used as a measure of disturbance severity) were applied through three successive winters. Data

collection took place during subsequent summers. Though target drawdown levels were sought for each lake each year, rarely were those levels reached or maintained throughout the drawdown process. This led to unique drawdown intensities applied to each waterbody.

The study design and lake selection was dictated by political and physical realities. As with most watershed-based environmental science, the lakes themselves are not classic replicates; differences in size, control structure, and surrounding land use exist. However, the impoundments are restricted to a small geographic area encompassed within a single ecosystem type (central hardwoods, eastern deciduous forest) and have had similar geologic histories.

CT DEEP Bureau of Natural Resources (BNR) Inland Fisheries Division (IFD) funded this cooperative research project through the Sport Fish Restoration Act with the University of Connecticut (UConn) between Fall 2006 through Winter 2009 due to the lack of scientific investigation conducted into the potential ecological effects of winter drawdowns in small southern New England impoundments. It was hypothesized that this project would provide quantitative information for states on the impacts of varying winter drawdown levels on age-0 fishes, which would allow for more informed management schemes relative to winter drawdown regulation implementation.

Objectives

Three objectives were developed for this project: 1) determine swim-up dates (which served as a surrogate for hatch date) and MDGR over three consecutive years for age-0 yellow perch, largemouth bass and bluegill in five study lakes located in eastern Connecticut following each year of drawdown; 2) document water temperatures and date

ranges of spawning activities, assess how this timing relates to the current CT DEEP drawdown policy refill deadline date (April 15th) and use the documented seasonality to look for supporting evidence of ecological bet-hedging in the form of protracted spawning behavior, as well as look for differential MDGR in fishes swimming up during different times of the growing season; and 3) determine if changes in swim-up dates and MDGR result from changes in four environmental covariates (i.e. winter drawdown intensity, water temperature, food availability and habitat).

Background

Setting

Five lakes in eastern Connecticut were chosen for this study (Figure 1.1). The experimental drawdowns were carried out over three consecutive winters (2006/2007, 2007/2008, and 2008/2009). The lakes were recommended based on the capability of maintaining the target water surface elevations and expected community support. The depths to which the lakes were drawn down were dictated by policy, public sentiment, physical ability of the water control structures, and cooperation by nature. Of the lakes selected, two, Bigelow Pond, in Union (having only been drawn down once prior to the commencement of this project 0.91 m for the installation of the current water control structure), and Powers Lake, in East Lyme (having not been drawn down in 20+ years) received a 0.91 m drawdown for three consecutive winters. Two lakes, Gardner Lake, in Bozrah-Montville-Salem, and Middle Bolton Lake, in Vernon, having received annual 0.91 m winter drawdowns for many years, received an experimental deep winter drawdown (not exceeding 1.82 m) for the same three consecutive winters as the two 0.91 m lakes. The final lake, Uncas Lake, in Lyme served as the study's control as it cannot be

drawn down (as it has no water control structure) and therefore has never been drawn down.

Study Sites

Shallow Drawdown Lakes (not to exceed 0.91 m)

Bigelow Pond, Union (Table 1.1) is a natural, state owned, lake found in a mostly undeveloped wooded/wetland watershed within Bigelow Hollow State Park (Jacobs and O'Donnell 2002). The pond is fed by Bigelow Brook at the northern end, which flows out of Mashapaug Lake. The dam at Bigelow Pond is manmade and earthen. The water control structure has raised the water level 2.4 m above its natural height. Lake substrate is sand, gravel and mud. Submergent vegetation is dense to depths of 2.7 m throughout the pond, with the dominant species being tapegrass, pondweeds, and bladderworts; floating mats of white water lily and water-shield are also present (Jacobs and O'Donnell 2002).

Powers Lake, East Lyme (Table 1.1) is an artificial impoundment located in a mostly wooded/wetland watershed with small amounts of agricultural and residential development. The shoreline is undeveloped and wooded. Yale University School of Engineering owns most of the shoreline with a lab located on the southwestern shore. The lake has a state owned boat launch and a partial manmade earthen dam. The lake is fed by four small streams and drains to the southeast into the Pattagansett River. Lake substrate is composed of sand, gravel, ledge, boulders and mud. Submergent vegetation is sparse and includes variable water-milfoil, bladderwort and pondweed; white water lily, water-shield and yellow pond lily are limited to the shallow coves around the lake (Jacobs and O'Donnell 2002).

Deep Drawdown Lakes (not to exceed 1.82 m)

Middle Bolton Lake, Vernon (Table 1.1) is an artificial impoundment located in a mostly wooded/wetland watershed with a moderate amount of agricultural and residential development. The shoreline is partially wooded and heavily developed, with residences lining most of the shoreline area. There is a state owned boat launch and manmade earthen dam. The lake is fed by surface runoff and from the overflow of Upper Bolton Lake. Middle Bolton drains into Lower Bolton Lake through a spillway over the concrete portion of the earthen dam. Lake substrate is sand, gravel, rubble and boulders covered by organic mud. Submerged vegetation is considered sparse to moderate in the shallow water with water-milfoil the dominant species; also present are a few floating mats of water-shield (Jacobs and O'Donnell 2002).

Gardner Lake, Bozrah-Montville-Salem (Table 1.1) is a natural lake located in a mostly wooded/wetland watershed with moderate amounts of agricultural and residential development. The shoreline is mostly developed with residential homes. It has a state owned boat launch and dam. The dam is manmade and earthen. The lake is fed by five brooks: one on the western shore, three on the southern shore, and one on the northern shore. The lake substrate is composed of sand, gravel, rubble and boulders, with scattered areas of organic mud. Aquatic plant growth is moderate, with the majority of the vegetation found in the northern and southern areas of the lake (Jacobs and O'Donnell 2002). The dominant submergent species include pondweed, tapegrass and bladderwort; floating mats of white water-lily, yellow pond-lily and water-shield are present; and fanwort, (an invasive non-native species) was discovered in the north cove in 2000 (Jacobs and O'Donnell 2002). Gardner Lake is only able to be drawn down 1.4 m due to

a morphological characteristic of the lake (i.e. a raised sandbar that separates the dam area from the rest of the lake); this is the level that was targeted for each winter drawdown.

Non-drawn Down Lake

Uncas Lake, a.k.a. Hog Pond, Lyme (Table 1.1) is a natural lake located in a mostly undeveloped woodland watershed. The northern shoreline is wooded, undeveloped state forest, whereas the southern shore has a few residences. There is a small state owned car-top boat launch. The lake is fed by several small brooks, one of which flows from Norwich Pond, and an unnamed marsh. Uncas Lake naturally drains west into Falls Brook. Lake substrate is composed of sand, mud, gravel and boulders. Aquatic vegetation is considered common in the northern and southeastern portions of the pond. The dominant submergent species found include: fern pondweed, floating-leaved pondweed, common bladderwort and water-nymph. Also present are scattered floating mats of white water-lily, water-shield, pondweeds and some yellow pond lily. Emergent vegetation includes: pickerelweed, water lobelia and pipewort (Jacobs and O'Donnell 2002).

Field Methods

Lake Selection

As in most watershed-based environmental science, the lakes themselves are not classic replicates; differences in size, control structure, and surrounding land use exist. The lakes were chosen based on policy, public sentiment, and physical ability of the water control structures.

Each of the five lakes had sampling zones chosen through visual inspection of the lake prior to the drawdowns commencing in Fall 2006. Every lake had five sampling zones, (except Gardner Lake which had six due to its larger size), that were spread around the lake and representative of the major features of the lake such as coves, points, steep slopes, shallow areas, and varying substrate types.

Drawdown Procedure

Winter drawdowns for the four drawn down study lakes (Bigelow Pond, Powers Lake, Middle Bolton Lake, and Gardner Lake) were carried out in accordance with the current CT DEEP drawdown policy. Drawdowns began between October 1st and 20th each year (2006/2007, 2007/2008, and 2008/2009). Water levels were recorded bi-weekly. These values were plotted and simple linear interpolation was used to create a drawdown progression chart for each lake (Figure 1.2 and 1.3). At the end of February or beginning of March the water control structures were shut and/or weir boards replaced and the water level allowed to rise as fast as incoming streams and runoff supplied. Each lake refilled to its conservation pool height by April 15th. The targeted drawdown depth, duration and stability of water elevation at the drawdown depth and what was actually documented during the three years of this study fluctuated greatly from year to year (Figures 1.2 and 1.3). This resulted in unique drawdown intensities based on lake morphology, weather patterns, and drawdown characteristics. Of specific note, Powers Lake did not meet its drawdown objective of 0.91 m at all during the study; however its maximum depth of drawdown was very close (0.85 m). This was primarily due to the design of the weir structure. Had an additional weir board been removed the lake level would have been lowered greater than the target level. Gardner Lake did not reach its

drawdown goal of 1.4 m during 2006 or 2008 because of heavy rains within the watershed. During the 2008/2009 drawdown no lake achieved its target level, again because of heavy rains across the eastern part of Connecticut.

Age-0 Fish Collection

Because the focus of this study is on the critical first year of life of age-0 fish, which are new organisms each year of this project, each year of data collection is independent from the last. Age-0 fish were collected using two methods: seining and nighttime boat electrofishing. Both methods targeted only the area within the standard zones that had been exposed by the drawdown. Beach seining was conducted one to three times each month on each lake beginning in May and going through September each year during 2007 through 2009. A 9.1 m long, 0.3 centimeter (cm) mesh seine with a 1.2 m by 1.2 m by 1.5 m tall bag was used. Sampling occurred between the hours of 0700 and 1500. Nighttime boat electrofishing used a 5.8 m aluminum hull Jon boat with a model VVP-15 control unit, powered by a Honda 6500 Watt (W) generator built by Coffelt Electronics Inc. The electrode array consisted of six, 1.8 m anodes (0.6 cm braided stainless cables) mounted from two booms approximately 1.8 m ahead of the boat's bow. The boat hull served as the cathode. Electrofishing was done in a pulsed DC mode (80 pulses per second, 60% pulse width) at 200-400 volts and three to nine amps, depending on water conductivity. The shocking crew consisted of four to five people. Electrofishing was conducted during June, July and August 2007, 2008 and 2009 either the week after both seining events occurred for that month on that lake or between the first and second seining events. The technique consisted of starting one-half hour after sunset and continuing until all zones were sampled (which took approximately 4-5 hours). The boat

slowly moved along the shoreline in water generally less than 1.5 m deep with the electric current controlled via a foot pedal on the boat's bow. A 'pulsed' technique was used where an area was shocked for approximately five to ten seconds as the boat slowly crept forward, then the foot pedal was released for a similar amount of time in order to move forward into a new area as all captured fish were placed in a live well. Dip nets with 0.3 cm mesh attached to 3.0 m long poles were used to capture age-0 fish. Each fish was identified and measured to the nearest millimeter (mm) and recorded on length-frequency (LF) sheets. Those fish that could not be positively identified in the field were brought back to the laboratory and identified using a dissecting scope and larval identification keys published by Auer (1982) and Lipson and Moran (1974).

Attempts to collect 20 fish per five mm length group were made at the onset of the project so as to ensure enough fish were being collected. Required sampling effort per five mm length group was later determined by selecting one month of the 2007 sample year that contained close to 20 individuals per five mm length group for all length groups. All fish were aged for this month. From the ages obtained the required sampling effort for each species for each five mm length group was determined using the following formula:

$$\text{Required Sampling Effort} = [(100 \times \text{standard deviation} / \text{mean age}) / 10]^2 \quad \text{Equation 1.1}$$

From the above calculation it was determined that three fish per five mm length group were sufficient to achieve a 10% coefficient of variation for the mean. Individuals retained for otolith removal were euthanized in an ice water bath in accordance with Nickum et al. (2004). Fish were stored in individual bottles of 97% ethyl alcohol (Murphy and Willis 1996).

Temperature Profiles

Hourly water temperatures in degrees Celsius (°C) were collected from each study lake using 3-4 Onset HOBO^R Water Temp Pros (V1 and V3). Loggers were placed in three areas of each lake (four in Gardner Lake due to its large size) prior to refill between February and March. One temperature logger was placed in the deepest area of each lake and suspended approximately one m below the surface from an anchored tether. The others were placed on the shallow side of the littoral zone in approximately one m of water. Temperature loggers were removed in early October prior to commencement of the next drawdown. Hourly readings for all loggers within a lake were averaged to create one reading for each hour; this single mean value was plotted for each hour using Sigma Plot (SigmaPlot Exact Graphs and Data Analysis 2001 for Windows version 7.0; Systat Software Inc. Technology Drive, San Jose, California.) to create a graphical representation of the temperature profile in each lake during the sampling season (Figure 1.4).

Zooplankton Collection

Zooplankton densities within each lake were assessed by conducting two vertical plankton tows within each zone (one on the shallow side of the littoral area, and one on the deep side of the littoral area) on the same day using a standard plankton net (150 micrometer (µm) mesh, 29.21 cm diameter and 96.52 cm long) each month from May through September. Plankton samples were preserved in a 5% Formalin solution containing Rose Bengal. All zooplanktors were counted from three randomly selected one milliliter (ml) aliquots. Mean density was calculated by dividing the expanded number of zooplanktors in each 100 ml sample by the total water strained through the

plankton net. Mean zone densities were created for a lake-level estimate of density for each lake for each month from May through September.

Sediment Composition

Substrate samples were collected annually during late September to early October using a method similar to Zweig and Rabeni (2001). Using a spade, two shovelfuls of bottom substrate, chosen at random locations, from each zone of each lake were taken in approximately 0.5 m of water or where that level would be if water levels were low. Samples were separated into particle size categories based on the Wentworth Scale (Table 1.2) by Giller and Malmqvist (2004). Three weight measurements (in grams) were taken for each sample in each size category and a mean weight calculated. A subsample of the smallest size category, silt, was dried in an oven before weighing. This value was then expanded to determine the weight of all the silt in the sample. Sediment size categories were then lumped into two overarching categories: 'non-moveable' (i.e. 2 μ m, 16 mm, 64 mm, 90 mm, 128 mm and 180 mm) and 'moveable' (63 μ m, sand, silt and organics). The percentage of each category out of the entire sample was then calculated.

Table 1.1 Drawdown project lake descriptions. Information compiled from Jacobs and O'Donnell (2002).

Lake	Drawdown History	Drawdown To Be Implemented (m)	Lake Size (ha [⋆])	Depth (m)		Trophic State	Drainage Basin	Watershed Size (ha)	Stratification Yes/Partial/No Depth (m)	Hypolimnion Present	# Of Fish Species Present
				Max	Mean						
Bigelow Pond	Brief	0.91	9.9	4.7	2.3	early meso. [‡] - eutrophic	Thames	1,543.9	Partial (3.0)	No	10 [*]
Powers Lake	Brief	0.91	58.3	4.3	2.1	early meso.	Southeast Coastal	257.8	No	No	9 [^]
Middle Bolton Lake	Extensive	>0.91 but ≤1.82	50	6.1	3.7	meso. – late meso.	Thames	787.5	Partial (4.0)	No	11 [†]
Gardner Lake	Extensive	>0.91 but ≤1.82	211.2	11.9	4.3	meso.	Thames	1,431.4	Yes (7.0-9.1)	Yes	20 [§]
Uncas Lake	None	None	27.9	11.9	7.3	meso.	Connecticut	395.4	Yes (4.9-7.9)	Yes	13 ^Δ

[⋆]ha = hectares

[‡]Meso. = mesotrophic.

^{*} Bigelow Pond - largemouth bass, stocked brown and rainbow trout, chain pickerel, black crappie, yellow perch, bluegill, pumpkinseed, brown bullhead, and white sucker.

[^] Powers Lake - largemouth bass, chain pickerel, black crappie, yellow perch, brown bullhead, bluegill, pumpkinseed, golden shiner and American eel.

[†] Middle Bolton Lake - largemouth and smallmouth bass, chain pickerel, black crappie, yellow perch, brown bullhead, bluegill, pumpkinseed, green sunfish, golden shiner, and banded killifish.

[§] Gardner Lake - largemouth and smallmouth bass, stocked brown and rainbow trout, chain pickerel, stocked walleye, channel and white catfish, black crappie, yellow perch, brown bullhead, bluegill, pumpkinseed, redbreast sunfish, tessellated darter, common and golden shiner, banded killifish, white sucker, and American eel.

^Δ Uncas Lake - largemouth bass, stocked brown and rainbow trout, chain pickerel, yellow perch, bluegill, pumpkinseed, golden shiner, banded killifish, landlocked alewife, creek chubsucker, white sucker, and American eel.

Table 1.2 Major Wentworth particle size classifications in millimeters (mm) for substrate from Giller and Malmqvist (2004).

Size Category	Particle Diameter <i>(range in mm)</i>
Boulder	>256
Cobble	64-256
Pebble	16-64
Gravel	2-16
Sand	0.063-2
Silt	0.0039-0.063

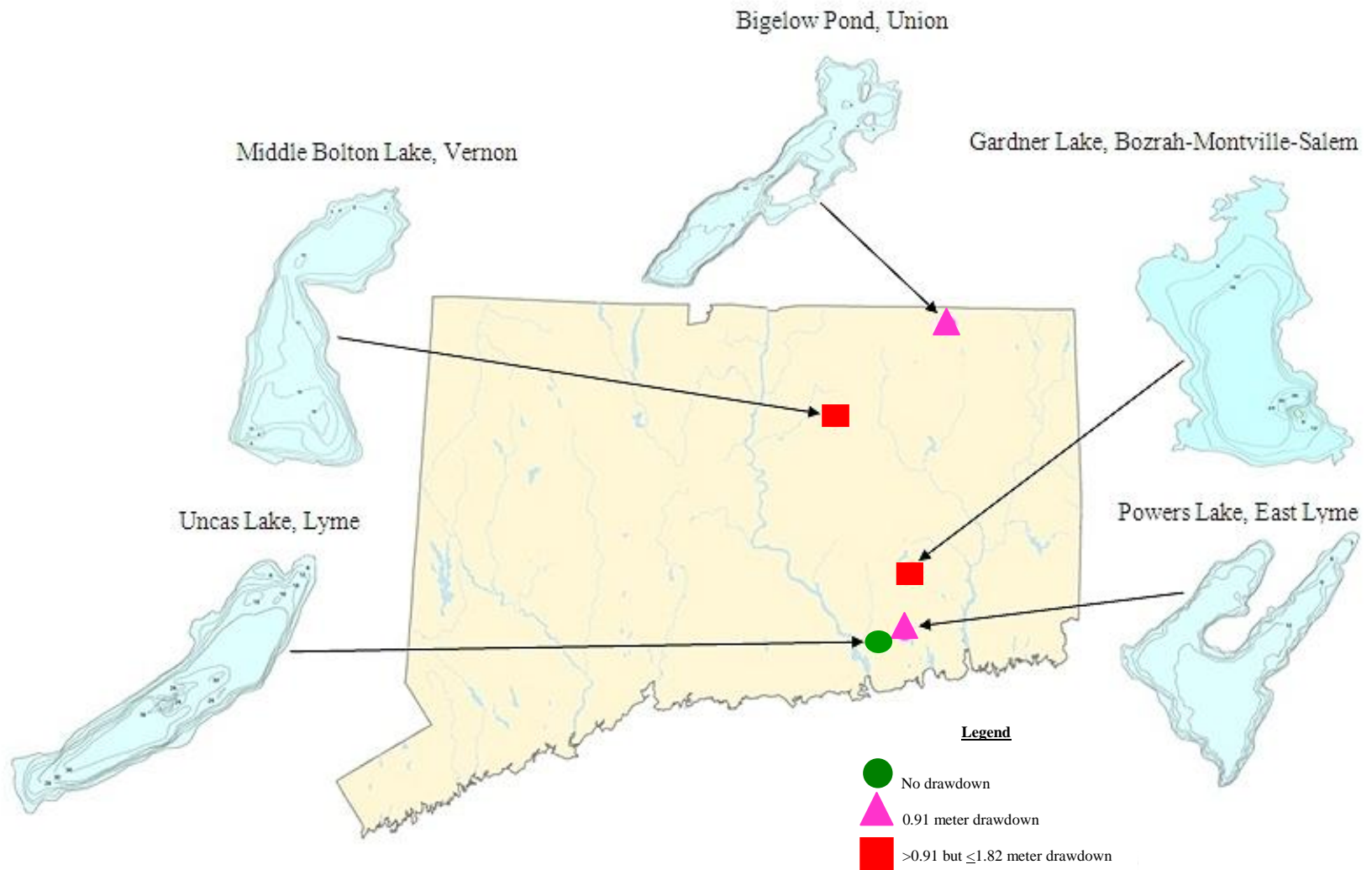


Figure 1.1 Drawdown project lakes.

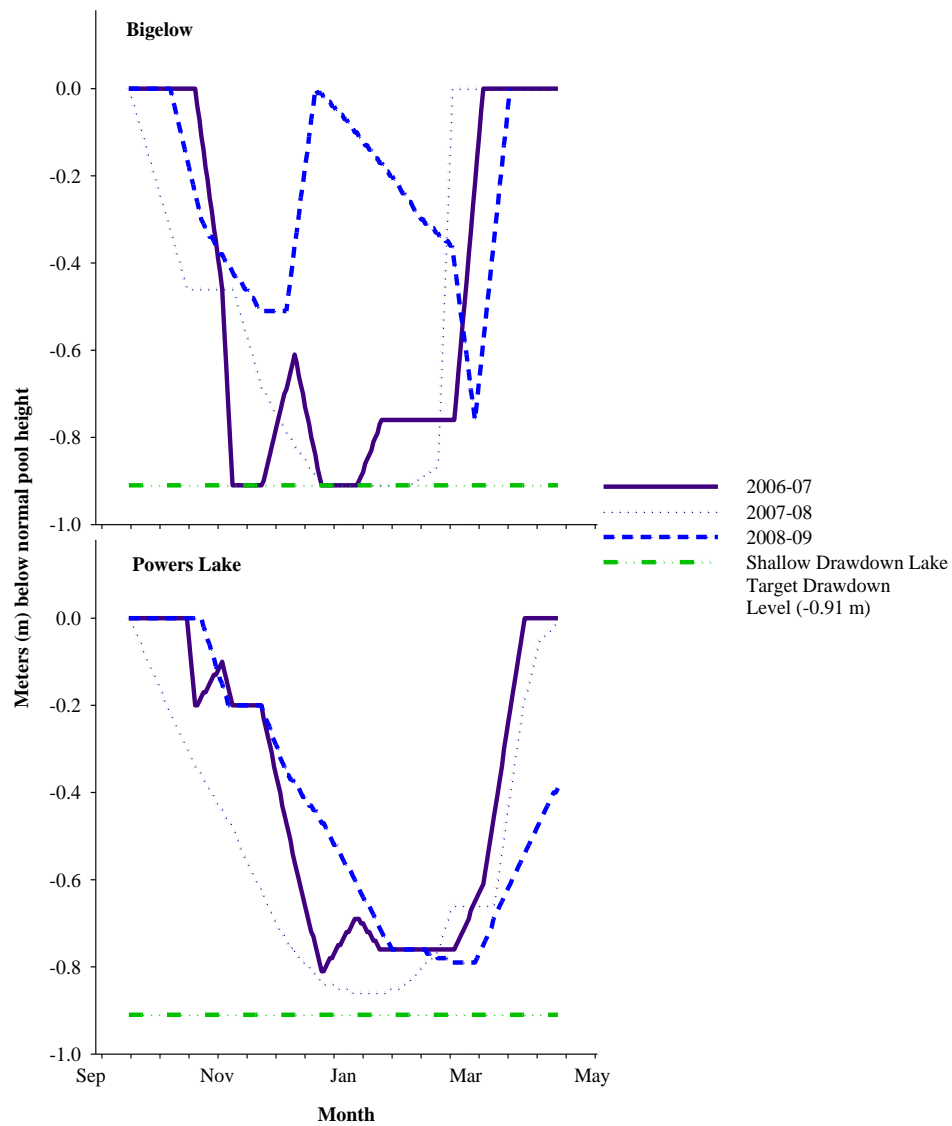


Figure 1.2 Drawdown progression for Bigelow Pond and Powers Lake, the shallow drawdown project lakes. Drawdowns not to exceed 0.91 meters (m) for all years of the study (2006/2007, 2007/2008, and 2008/2009).

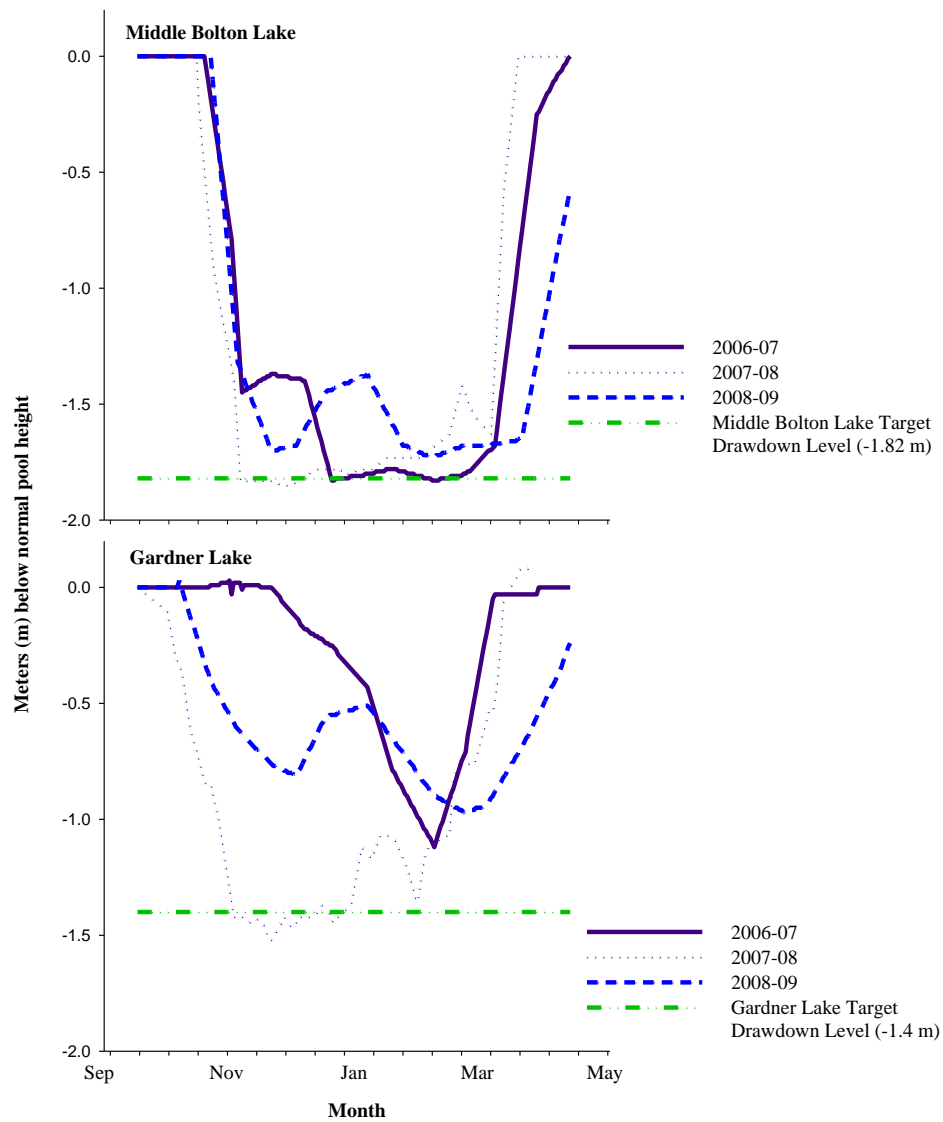


Figure 1.3 Drawdown progression for Middle Bolton Lake and Gardner Lake, the deep drawdown project lakes. Drawdowns to be greater than 0.91 meters (m), but not exceed 1.82 m for all years of the study (2006/2007, 2007/2008, and 2008/2009).

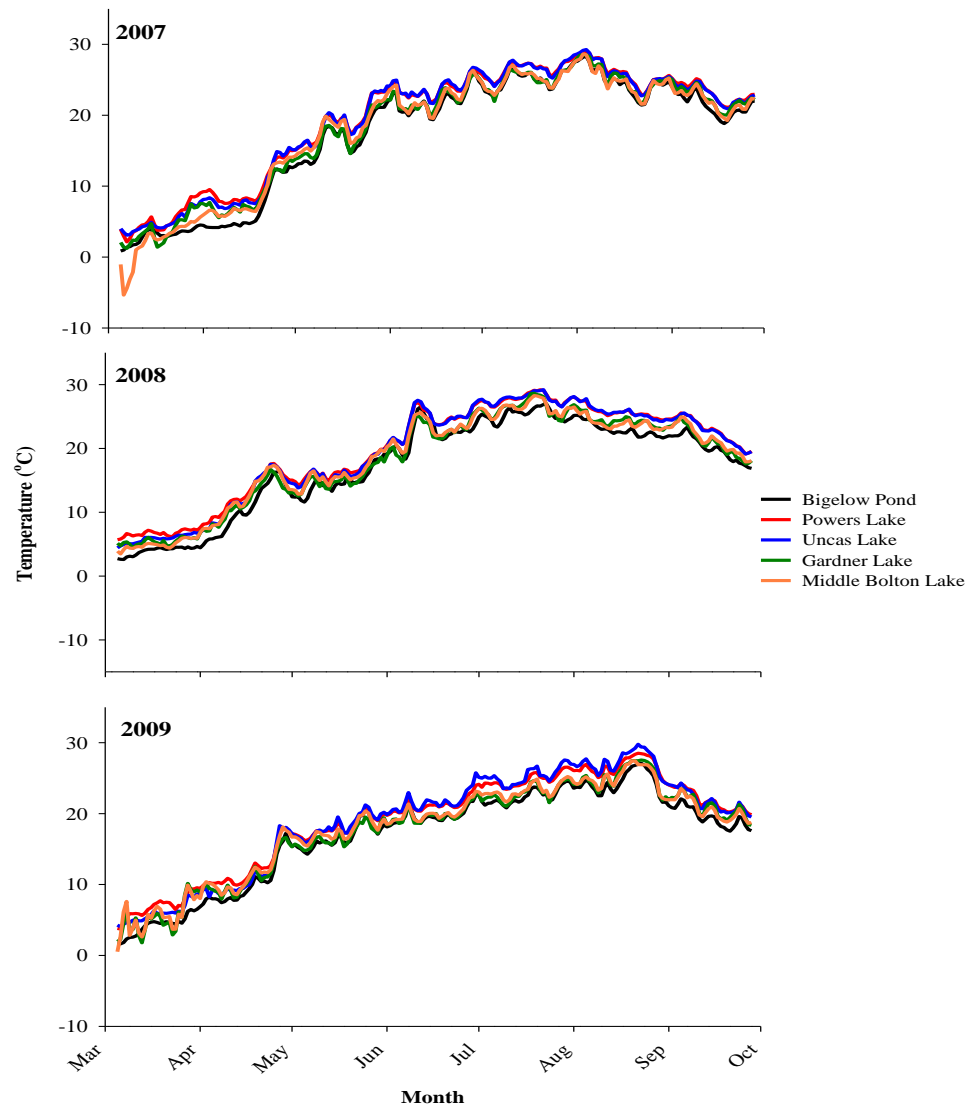


Figure 1.4 Temperature profiles, in degrees Celsius ($^{\circ}\text{C}$), by year for each project lake. Temperature profiles for each lake are a mean of three to four temperature loggers that were all within one meter (m) of the surface scattered around each lake. One logger in each lake was submerged one m below the surface in the deepest portion of the lake, whereas the other loggers were scattered around each lake and submerged one m below the surface in the littoral zone.

CHAPTER 2

Swim-up Dates and Growth Rates of Age-0 Fishes in Small Southern New England Impoundments Determined from Otoliths

Introduction

On impoundments where winter drawdowns are performed it is useful to understand the reproductive timing and growth patterns of age-0 fishes to minimize potential disruption or postponement of spawning activity. Temporal variability in hatching dates has consequences for both growth and recruitment of fish year classes (Jolley et al. 2009). Most warmwater lentic fish species breed in the spring, and use the littoral zone for nesting and aquatic vegetation for a nursery and refuge area (Estes 1972; Hestand 1977), thus the potential exists that the drawdown process may impact fish breeding if it offsets or delays aspects of the spring phenology of the impoundment.

One of the earliest members of the common lentic fish community to spawn is yellow perch. They initiate at water temperatures between 7-11 degrees Celsius (°C) (Essex Marine Laboratory 1972), which typically corresponds to 'ice-out' on small impoundments in southern New England. Yellow perch are night time broadcast spawners; eggs are fertilized by males as the female releases them (Carlander 1997; Werner 2004). Eggs will take from 2-30 days to hatch in water temperatures ranging from 3.3-25.4 °C, with colder temperatures leading to longer developmental times (Carlander 1997). Larvae hatch at a length of 4.5-7.0 millimeters (mm) (Carlander 1997; Werner 2004) and the fry remain close to the bottom and inactive while absorbing the

yolk sac (Werner 2004), after which fry become pelagic for a short period before moving back into the littoral area (Carlander 1997; Werner 2004).

Largemouth bass spawning occurs when water temperatures are between 11.5-24 °C (Carlander 1977). Solitary males construct a single nest in soft, non-silty, substrate in depths between 0.15-2 meters (m) and fertilize eggs from a single gravid female that selects and enters the nest (Carlander 1977; Werner 2004). Females may only release half their eggs during the first spawn, then release the rest during a second and occasionally third fractional spawn (Davis and Lock 1997). Eggs hatch in three to five days at water temperatures between 21-25 °C, with colder temperatures leading to longer developmental times (Carlander 1977). Fry swim-up at an approximate length of five mm. One week after swim-up they switch to exogenous feeding (Carlander 1977; Miller and Storck 1982; Werner 2004). Fry remain together in tight groups for another month, with the male parent guarding them (Werner 2004; Jacobs and O'Donnell 2009). They will then spend the majority of their lifecycle in and around the littoral zone.

Bluegills are colonial synchronous breeding fish with the ability to spawn multiple times throughout the spawning season, often in distinct bouts (Carlander 1977; Carngelli and Gross 1996; Jolley et al. 2009). Males initiate spawning by building nests in littoral zone substrate in approximately 0.15-1.20 m of water when water temperatures range between 17-26 °C, which typically occurs during or after largemouth bass spawning (Carlander 1977; Carngelli and Gross 1996; Werner 2004). Eggs hatch at water temperatures between 18.5-28.5 °C and become free swimming approximately four days after hatching or when they reach a mean length of five mm (Carlander 1977; Werner 2004; Spotte 2007). Upon swim-up, and after absorption of the yolk-sac, bluegill larvae

begin exogenous feeding and leave the nesting area and move into the littoral zone until they reach 10-12 mm (Spotte 2007). At this point they leave the littoral zone and move out into the three m depth area of the limnetic zone until they reach between 22-25 mm (which takes around six to seven weeks). Upon reaching this size, they then move back into the littoral zone and remain there for the majority of their life (Werner 2004; Spotte 2007).

Earlier hatching in fish can allow faster relative growth rates during the first months of life and has been found to be correlated with increased survival (Goodgame and Miranda 1993; Cargnelli and Gross 1996; Ludson and DeVires 1997; Pine et al. 2000). If early hatching offers a competitive advantage, one might expect evolution to drive fish reproduction towards a single, synchronous early spawning event (Cargnelli and Gross 1996), however some lentic fish species display multiple spawning bouts and protracted spawning seasons. These protracted spawning seasons can be considered a form of ecological 'bet hedging' (Phillips et al. 1995; Jolley et al. 2009). This likely occurs because survival of age-0 fish is still highly variable and partly dependent on environmental conditions (Jolley et al. 2009). Though earlier hatching may bestow benefits, survival of eggs and fragile larvae is still uncertain and if circumstances cause earlier hatched individuals to be lost, other hatching events at different times will hedge against a complete year class failure. Protracted spawning has been documented in largemouth bass in Connecticut (Webster 1942) and elsewhere in the country (Jackson 1979; Philips et al. 1995; Davis and Lock 1997; Waters and Noble 2004). It has also been documented in bluegill (Carlander 1977; Carnelli and Gross 1996; Santucci and Wahl

2003; Jolley et al. 2009), and to a lesser extent with yellow perch (Collingsworth and Marschall 2011).

Using the daily rings found in otoliths of age-0 yellow perch, largemouth bass and bluegill, the swim-up dates were reconstructed for five small impoundments typical of the southern New England landscape (and typical of those subject to winter drawdowns) over the course of three consecutive summers. The aging of age-0 fish from otoliths assumes that increments are formed on a daily basis, which requires proper validation of the relationship between increment deposition and age (Jones 1986). Daily rings have been validated as a technique for determining both age and growth for yellow perch (Post and Prankevicius 1987), largemouth bass (Schmidt 1980; Miller and Storck 1982; Taubert and Tranquilli 1982; Jones 1986), and bluegill (Taubert and Coble 1977; Jones 1986).

My objectives were to document the water temperatures and date ranges of spawning activities, assess how this timing relates to the current CT DEEP drawdown policy refill deadline date (April 15th) and use the documented seasonality to look for supporting evidence of ecological bet-hedging in the form of protracted spawning behavior by contrasting those temperatures and date ranges among impoundments with varying drawdown histories. Additionally, I looked for differential mean daily growth rates (MDGR) in fishes swimming up during different times of the growing season. A structuring hypothesis of this research is to expect differential early life MDGR at those impoundments with longer drawdown histories. There might be more asynchronous spawning behavior (i.e. greater bet-hedging in the form of more protracted spawning seasons) occurring at these water bodies because of the increased disturbance resulting

from the drawdown and therefore greater variation because fish hatched later in the season should grow slower as they would enter an ecosystem in the presence of more competitors than early hatched individuals.

Methods

Age-0 Fish Otolith Preparation

Daily rings on otoliths extracted from age-0 fish were used to calculate swim-up dates (which were used as a surrogate for actual hatch dates), and MDGR. Direct counts back to the hatch date are not possible because daily growth rings from the yolk sac larval stage (i.e. pre-swim-up) are not distinguishable from one another (Pine et al. 2000).

Three fish per five mm length group were retained for otolith extraction as per Chapter 1, Methods. Age-0 otolith preparation involved a combination of methods put forth by Miller and Storck (1982) and Taubert and Coble (1977). Both sagittal otoliths were removed from specimens when possible. One otolith from each fish was mounted on a glass microscope slide using Crystal Bond™ thermoplastic cement then ground and polished using 400, 600 & 1200 grit sandpaper to expose the focus or ‘kernel’ for aging. The microscope slide was labeled with ID number, lake, and species. Lengths and dates collected were not recorded on the glass slides so as not to induce reader bias when estimating ages. Daily ring increments were counted along the longest radius. Otoliths were viewed using two different microscopes: an Olympus CX41 Compound Scope with a 10X eyepiece and objectives from 10x to 40X with a 50X oil immersion objective, in conjunction with a Fiber-lite Dolan-Jenner Industries Inc. light source and a Fisher Scientific Micromaster Model E with a 10x eyepiece and objectives from 4x to 40x with a 100x oil immersion objective with a 30 Watt (W) internal light source. Daily rings were

counted by two separate readers and used to back-calculate swim-up dates (Miller and Stork 1984; Schmidt and Fabrizio 1980). If ring counts differed by less than 10% or by +/- three rings they were averaged (Miller and Storck 1982). If counts differed by greater amounts, they were rejected and redone (Miller and Storck 1982). If disagreement remained the otolith was discussed and recounted. If agreement could not be reached after three separate recountings the otolith was discarded and another otolith from a similar sized fish was prepped, and age-estimated as described above.

Determination and Comparison of Age-0 Swim-up Dates and Their Relation to Water Temperature

The swim-up date for each aged fish was calculated by subtracting the day-of-year that the individual fish was sampled from the number of daily rings counted on the sagittal otolith. An age-length key approach (Iseley and Grabowski 2007) was used to estimate the age structure of age-0 fish collected at each lake during each study year. Age-length keys were created for each species in each lake for each year using the age-estimated subsample of fish. Age-length keys were then applied to length-frequency data (all gears pooled) from specific months that represented the earliest sampling period during which all cohorts were present in the population, i.e. all spawning had been completed (yellow perch: May; largemouth bass: August; bluegill: September). Length-frequencies were constructed for each species for each lake each year using five mm bins. Individuals were then grouped into 10-day hatch classes similar to Partridge and DeVries (1999) and Pine and Allen (2001) for swim-up date calculations. Analysis of variance (ANOVA) was then used to test for differences in mean swim-up date for each species

within each lake across years and amongst lakes within each year (PROC ANOVA; Statistical Analysis System [SAS] version 9.2; SAS Institute, Carry, North Carolina).

A two-way ANOVA was used to test if mean water temperature had an influence on swim-up date within each lake across years and if the different mean water temperatures within each lake resulted in different swim-up dates across lakes within a year for each of the three fish species (PROC ANOVA; Statistical Analysis System [SAS] version 9.2; SAS Institute, Carry, North Carolina). Two separate full models were used in this ANOVA process. The first model included year, mean water temperature and the mean water temperature*year interaction. The second full model included lake, mean water temperature and the mean water temperature*lake interaction. The variable ‘mean water temperature’ was the water temperature on the day each fish swam-up. This value was derived from the temperature logger data collected from each lake (see Chapter 1, Methods, Temperature Profiles for how temperature data was collected). To perform the ANOVA calculations a new variable called ‘midhatch’ was created, which is the median value of each 10-day hatch class. This was created because each 10-day hatch class is a categorical value and ANOVA requires continuous variables to run. Data for the ANOVA was taken from the age-length key, which provided counts of fish in each hatch class category.

Mean Daily Growth Rate Determination and Analysis for Age-0 Fishes

For yellow perch simple linear regression equations of length (mm) versus (vs.) age (number of daily rings counted from otoliths) were created to provide a characterization of growth for each lake and year using the age estimated subsample of fish. A slightly different approach was taken to determine MDGR for largemouth bass

and bluegill. Calculations were performed on 10-day hatch classes similar to Partridge and DeVries (1999) and Pine and Allen (2001) using the entire age estimated subsample of fish, as opposed to the month specific length frequency data, so as to have a more complete representation of the sample season's growth rates as well as to have a larger sample size. The formula for largemouth bass from Miller and Storck (1984) was used to calculate MDGR for both largemouth bass and bluegill:

$$\text{Daily Growth Rate} = \frac{(\text{Total length at capture} - 5 \text{ mm})}{\text{Fish age in days}} \quad \text{Equation 2.1}$$

Daily Growth Rate = total number of mm the fish grew in a 24 hour period
 Total length at capture = the length of the fish in mm at time of capture
 5 mm = estimated length at swim-up from Miller and Storck (1982)
 Fish age in days = mean number of daily rings counted on the sagittal otolith from the two readers

The same formula was used for bluegill because Partridge and DeVries (1999) estimated the time at which bluegill began exogenous feeding and swim-up to also be five mm. Similar formulas put forth by Phelps et al. (2008) for smallmouth bass; Pine et al. (2000) for largemouth bass and Travnichek et al. (1996) for black crappie lent credence to using the largemouth bass formula to calculate both largemouth bass and bluegill MDGR.

To address whether those impoundments with longer drawdown histories might have more asynchronous spawning and therefore might have distinctly different MDGR than the other impoundments the following procedures were carried out for each species: for yellow perch the length vs. age data was analyzed using an ANOVA model to test for a year effect and lake effect on age-0 yellow perch growth (PROC ANOVA; Statistical Analysis System [SAS] version 9.2; SAS Institute, Carry, North Carolina). For largemouth bass and bluegill, which were mentioned in this chapter's Introduction as

having protracted spawning seasons, MDGR were grouped into “early” swim-up (and therefore “early” spawning) and “late” swim-up (and therefore “late” spawning). The median of the swim-up date range (all years and lakes pooled) for a species was used to divide “early” and “late” spawning classes”. Tests on the effect of year, lake, and swim-up class (i.e. “early” vs. “late”) on MDGR were carried out using ANOVA (PROC ANOVA; Statistical Analysis System [SAS] version 9.2; SAS Institute, Carry, North Carolina). Full models were run including all possible interactions. Mean separation tests (Least Squares Mean and Tukey Honestly Significant Difference (HSD) tests) were used to test for differences between MDGRs in various swim-up date classes within each lake across years, as well as amongst lakes within years.

Spawning Initiation for Adult Fishes

Using the scientific literature (see Chapter 2, Introduction) and the age-0 swim-up data obtained for this project (see Chapter 2, Methods, Determination and Comparison of Age-0 Swim-up Dates and Their Relation to Water Temperature) the spawning period for adult yellow perch, largemouth bass and bluegill was framed for each lake each year. The number of days post-fertilization was calculated from age-0 swim-up dates and was used to back-calculate the range of days when active spawning theoretically occurred. From these spawning date ranges the mean and range of water temperatures during these periods were calculated using the water temperature data collected from each lake’s temperature loggers (see Chapter 1, Methods, Temperature Profiles). This data was then graphed to see how the spawning season for these species fell in relation to the current CT DEEP drawdown refill deadline date. Because data were not directly gathered on chain pickerel in the project lakes, but this species is one of Connecticut’s earliest in-lake

spawners and one of the most likely to be impacted by the current drawdown policy (see Chapter 1, Introduction) the spawning temperature for this species (8 °C) was gathered from Carlander (1969), then the date range that spawning could occur in the project lakes was determined and graphed along with the inferred spawning dates for the other species involved in the project.

Results

Determination and Comparison of Age-0 Swim-up Dates and Their Relation to Water Temperature

Yellow Perch

Yellow perch swam-up over a short, approximately, one month period (early-April to early-May), with peak swim-up occurring during mid-April (Figure 2.1). No multi-modality in swim-up frequency was noted in any of the project lakes, such that protracted spawning was limited and no evidence of multiple bouts was found. Yellow perch mean swim-up dates differed within each lake across years (Uncas Lake, only one year of data; Bigelow Pond, no data; Powers Lake, $F = 323.95$; $df = 5, 1844$; $P = <.0001$; Middle Bolton Lake, $F = 427.92$; $df = 5, 1792$; $P = <.0001$; Gardner Lake, $F = 84.12$; $df = 5, 3945$; $P = <.0001$). Differences were also found amongst lakes within each year (2007, $F = 82.56$; $df = 5, 3187$; $P = <.0001$; 2008, $F = 70253.7$; $df = 7, 1704$; $P = <.0001$; 2009, $F = 779.43$; $df = 5, 2930$; $P = <.0001$). These differences though were not attributable to varying drawdown history, as no consistent, directional shifts in swim-up timing were produced when compared against the non-drawn down water body (Uncas Lake) or when compared amongst just the drawn down lakes.

The water temperatures that occurred during swim-up for age-0 yellow perch in all project lakes in all years (Table 2.1) were within the water temperature range described by Essex Marine Laboratory (1972) with project lake water temperatures ranging from 4.6-18.5 °C and Essex Marine Laboratory's summary water temperatures ranging from 3.3-25.4 °C. Water temperature explained some of the variation in swim-up date in the study lakes both within each lake across years (mean water temperature*year interaction: Uncas Lake, only one year of data; Bigelow Pond, no data; Powers Lake, $F = 322.03$; $df = 5, 1844$; $P = <.0001$; Middle Bolton Lake, $F = 96.92$; $df = 5, 1792$; $P = <.0001$; Gardner Lake, $F = 74.64$; $df = 5, 3945$; $P = <.0001$), as well as amongst lakes within each year (mean water temperature*lake interaction: 2007, $F = 90.04$; $df = 5, 3187$; $P = <.0001$; 2008, $F = 70199.3$; $df = 7, 1704$; $P = <.0001$; 2009, $F = 480.45$; $df = 5, 2930$; $P = <.0001$). Yellow perch in the two extensive drawdown history lakes (i.e. Middle Bolton Lake and Gardner Lake) appear to initiate swim-up at cooler water temperatures compared to the other project lakes, but swim-up in these two lakes still completed in line with the other lakes. Because no yellow perch were collected in Bigelow Pond during the course of this study, and too few yellow perch were collected from Uncas Lake during 2007 or 2009 comparisons amongst drawdown histories were difficult and limit interpretation.

Largemouth Bass

Largemouth bass swam-up over a protracted period lasting over three months (mid-April to late-July), with peak swim-up occurring during mid-May to mid-June (Figure 2.2). Four multi-modal swim-up events were documented in two lakes (Powers Lake and Gardner Lake in 2008 and 2009), which may lend more evidence to a

protracted spawning season with multiple peak bouts occurring as a form of bet hedging for this species. However, low sample sizes in these lakes during these years may be resulting in this multi-modality. Caution is recommended in interpreting these modal results. Largemouth bass mean swim-up dates differed within each lake across years (Uncas Lake, $F = 105.29$; $df = 5, 303$; $P = <.0001$; Bigelow Pond, $F = 52.24$; $df = 5, 231$; $P = <.0001$; Powers Lake, $F = 3.37$; $df = 5, 96$; $P = 0.0385$; Middle Bolton Lake, $F = 44.80$; $df = 5, 241$; $P = <.0001$; Gardner Lake, $F = 64.07$; $df = 5, 43$; $P = <.0001$). Differences were also found amongst lakes within 2007 ($F = 2.75$; $df = 9, 219$; $P = 0.0292$) and 2009 ($F = 8.22$; $df = 8, 12$; $P = 0.0031$), but not 2008 ($F = 0.88$; $df = 8, 153$; $P = 0.4509$). These differences, though, were not attributable to varying drawdown history as no consistent, directional shifts in swim-up timing were produced when compared against the non-drawn down water body or when compared amongst just the drawn down lakes.

The range of water temperatures that age-0 largemouth bass were swimming-up during in all project lakes in all years (Table 2.2.) was wider than the range described by Carlander (1977), with project lake water temperatures ranging from 7.7-28.6 °C and Carlander's summary water temperatures ranging from 21-25 °C. Largemouth bass in the project lakes were able to swim-up at cooler water temperatures and continue into warmer water temperatures then described by Carlander (1977). Water temperature explained some of the variation in swim-up date in the study lakes both within each lake across years (mean water temperature*year interaction: Uncas Lake, $F = 93.58$; $df = 5, 303$; $P = <.0001$; Bigelow Pond, $F = 57.10$; $df = 5, 231$; $P = <.0001$; Powers Lake, $F = 3.35$; $df = 5, 96$; $P = 0.0391$; Middle Bolton Lake, $F = 36.37$; $df = 5, 241$; $P = <.0001$;

Gardner Lake, $F = 54.56$; $df = 5, 43$; $P = <.0001$), as well as amongst lakes only within 2009 (mean water temperature*lake interaction: $F = 10.02$; $df = 8, 12$; $P = 0.0014$), but not 2007 (mean water temperature*lake interaction: $F = 2.08$; $df = 9, 219$; $P = 0.0849$) or 2008 (mean water temperature*lake interaction: $F = 0.41$; $df = 8, 153$; $P = 0.7452$). No clear trends regarding drawdown history and swim-up time related to water temperature were found.

Bluegill

Bluegill swam-up over a protracted period lasting approximately three months (late-May to mid-August), with peak swim-up occurring during June through July (Figure 2.3). Only one instance of multi-modality in swim-up frequency was noted at Gardner Lake in 2008. Bluegill mean swim-up differed within each lake across years (Powers Lake, $F = 73.90$; $df = 5, 248$; $P = <.0001$; Middle Bolton Lake, $F = 25.05$; $df = 3, 152$; $P = <.0001$; Gardner Lake, $F = 56.15$; $df = 5, 541$; $P = <.0001$), except for Uncas Lake ($F = 0.70$; $df = 5, 58$; $P = 0.5025$) and Bigelow Pond ($F = 0.56$; $df = 5, 76$; $P = 0.5731$). Differences were also found amongst lakes within each year (2007, $F = 9.15$; $df = 9, 583$; $P = <.0001$; 2008, $F = 106.05$; $df = 6, 224$; $P = <.0001$; 2009, $F = 10.41$; $df = 9, 206$; $P = <.0001$). These differences in swim-up appeared to co-vary with winter drawdown history with earlier swim-up dates in the drawn down lakes compared to the non-drawn down lake, but there were some inconsistencies regarding all drawn down lakes continuing to have earlier swim-up throughout the length of this study.

The range of water temperatures that occurred during swim-up (Table 2.3) within the project lakes fell mostly within the range described by Spotte (2007): project lake water temperature range 14.3-29.8 °C and Spotte's summary water temperature range

18.5-28.5 °C. Some lakes (Table 2.3) though, had swim-up occurring in cooler water temperatures and continuing into warmer water temperatures than Spotte described. Water temperature explained some of the variation in swim-up date in the study lakes within each lake across years for Powers Lake (mean water temperature*year interaction: $F = 81.78$; $df = 5, 248$; $P = <.0001$), Middle Bolton Lake (mean water temperature*year interaction: $F = 38.54$; $df = 3, 152$; $P = <.0001$) and Gardner Lake (mean water temperature*year interaction: $F = 74.03$; $df = 5, 541$; $P = <.0001$), but not within Uncas Lake (mean water temperature*year interaction: $F = 0.97$; $df = 5, 58$; $P = 0.3860$) or Bigelow Pond (mean water temperature*year interaction: $F = 0.51$; $df = 5, 76$; $P = 0.6038$). Differences amongst lakes within each year were also found (2007, mean water temperature*lake interaction: $F = 7.41$; $df = 9, 583$; $P = <.0001$; 2008, mean water temperature*lake interaction: $F = 4.06$; $df = 6, 224$; $P = 0.0186$; 2009, mean water temperature*lake interaction: $F = 11.91$; $df = 9, 206$; $P = <.0001$). Bluegill in the two extensive drawdown history lakes (i.e. Middle Bolton Lake and Gardner Lake) inconsistently appear to swim-up at cooler water temperatures compared to the other project lakes, but swim-up in these two lakes still completed in line with the other project lakes (except Middle Bolton Lake in 2008). Uncas Lake, on the other hand, during 2007 and 2008 had swim-up continue into warmer water temperatures than the majority of project lakes, as well as what was described by Spotte (2007).

Mean Daily Growth Rate Determination and Analysis for Age-0 Fishes

Yellow Perch

It was previously established in the Results section of this chapter that yellow perch did not exhibit protracted spawning behavior and that drawdown history did not

appear to shift swim-up dates in these study lakes. Therefore, it might be expected that the growth rates of these age-0 individuals would be fairly similar within lakes and perhaps between lakes. Simple linear regression of length vs. age was used to characterize the growth rates for this species in each lake and year where they were captured (Figure 2.4). Using this growth data, tests of year effect and lake effect were carried out and showed no consistent, directional shifts in growth compared within lakes across years or amongst lakes within a year (i.e. the drawdown history of the lake does not appear to co-vary with growth). However, because no yellow perch were captured at Bigelow Pond during the three years of this project and no yellow perch were captured at Uncas Lake during 2007 and 2009 comparisons made with the remaining lakes should be viewed with caution.

Growth for yellow perch varied inconsistently in regards to drawdown history from year to year within each lake, with significant differences in growth found at Middle Bolton Lake (age*year interaction: $F = 5.40$; $df = 5, 235$; $P = 0.0051$) and Gardner Lake (age*year interaction: $F = 6.53$; $df = 5, 300$; $P = 0.0017$), but not Powers Lake (age*year interaction: $F = 0.01$; $df = 5, 176$; $P = 0.9937$). Rate of growth increased at Gardner Lake, decreased slightly at Middle Bolton Lake and remained constant at Powers Lake during the course of the study (Figure 2.4). Growth rate differences amongst lakes within each year (i.e. a lake effect) were inconsistent between the lakes, with no one drawdown history showing a consistent trend in growth (Figure 2.4). Differences in growth rates were found during 2007 (age*lake interaction: $F = 9.77$; $df = 5, 381$; $P = <.0001$) and 2009 (age*lake interaction: $F = 3.58$; $df = 5, 184$; $P = 0.0297$), but not 2008 (age*lake interaction: $F = 0.93$; $df = 7, 170$; $P = 0.4272$).

Largemouth Bass

The separation of largemouth bass swim-up timing resulted in “early” swim-up being classified as less than or equal to day-of-year 159, which was up to and including June 7 or 8 depending on the year; “late” was greater than day-of-year 159). When largemouth bass swam-up (i.e. early versus late) did not explain a significant amount of the variance in their MDGR (early vs. late: $F = 1.27$; $df = 29, 1192$; $P = 0.2594$). However, differences in MDGR existed amongst lakes within 2007 ($F = 37.68$; $df = 4, 607$; $P = <.0001$) and 2009 ($F = 21.88$; $df = 4, 248$; $P = <.0001$), but not 2008 ($F = 0.83$; $df = 4, 352$; $P = 0.5048$). MDGR differences revealed no consistent patterns compared to the other lakes (i.e. no one drawdown history) when using the Tukey HSD test (Figure 2.5).

Bluegill

The separation of bluegill swim-up timing resulted in “early” swim-up being classified as less than or equal to day-of-year 169, which was up to and including June 17 or 18 depending on the year; “late” was greater than day-of-year 169. When bluegill swam-up (i.e. early versus late) did play a part in explaining a significant amount of the variance in their MDGR (early vs. late interaction: $F = 12.89$; $df = 28, 938$; $P = 0.0003$). Additionally, the differences that were observed between when bluegill swam-up were partially attributable to the lake they were from with both lake ($F = 20.72$; $df = 28, 938$; $P = <.0001$) and the lake*early vs. late interaction ($F = 8.86$; $df = 28, 938$; $P = <.0001$) being significant. Year ($F = 0.35$; $df = 28, 938$; $P = 0.7016$) did not play a significant part in explaining the variance in MDGR, (i.e. the year in which bluegill swam-up did not

significantly affect their MDGR). This fact allowed for lumping of the data for further analysis.

Early spawned age-0 bluegills tended to grow faster than later spawned ones in three of the five project lakes (Powers Lake, Middle Bolton Lake and Gardner Lake). One short drawdown history lake (Bigelow Pond) and the non-drawn down lake (Uncas Lake) showed no differences in MDGR between early and late hatched individuals (Figure 2.6). Two of the lakes that showed significant differences in early versus late MDGR were lakes with extensive drawdown histories (Middle Bolton Lake and Gardner Lake) and the other (Powers Lake), had a brief drawdown history. Additionally, whether or not the lake had a drawdown history (i.e. no history versus any type of history) does appear to affect the MDGR of age-0 bluegill because the MDGR of individuals in the non-drawn down lake are significantly different from those lakes that have drawdown histories (Figure 2.6). Caution is advised however, in the extent of interpretation here, because only one lake was used in this project with no drawdown history, so there is the distinct possibility that this lake could be an anomaly.

Spawning Initiation for Adult Fishes

Back calculated spawning periods for adult yellow perch, largemouth bass and bluegill involved in this study can be found in Table 2.4. For adult yellow perch (Table 2.4) in all the project lakes, except in Powers Lake during 2008, spawning initiated at cooler water temperatures compared to those described by Essex Marine Laboratory (1972) for this area (range for project lakes: -1.1-6.9 °C vs. Essex Marine Laboratory range: 7-11°C). For Powers Lake in 2008 spawning initiated within Essex Marine Laboratory's described range. Within all the project lakes spawning continued into

warmer water temperatures (range: 13.1-18.5 °C), however, the mean water temperature values all fell within Essex Marine Laboratory's range for this area, except again for Powers Lake in 2008, which was just above the upper level (12.7 °C).

For adult largemouth bass (Table 2.4) in all the project lakes, except Powers Lake during 2007, spawning initiated within the range of water temperatures provided in Carlander (1977) for this area (range for project lakes: 11.9-18.8 °C vs. Carlander's range: 11.5-24 °C). In Powers Lake during 2007 spawning initiated at a cooler water temperature (7.2 °C). For 73% of the project lakes across all years, spawning continued into warmer water temperatures (range: 25.1-28.5 °C) then described by Carlander (1977). The other 27% fell within his described range. Mean water temperature values however, all fell within Carlander's water temperature range for this species for this area.

For adult bluegill (Table 2.4) in the project lakes, spawning initiated within the range provided by Carlander (1977) for this area (range for project lakes: 17.8-23.8 °C vs. Carlander's range: 17-26 °C), except for Powers Lake 2008, Middle Bolton Lake 2007 and 2008, and Gardner Lake 2008 and 2009 where spawning initiated at slightly cooler water temperatures (range: 14.6-16.6 °C). Spawning continued within the range specified by Carlander (1977) except for Middle Bolton 2008 where it extended into slightly warmer water temperatures (29.1 °C). Mean water temperature values however, all fell within Carlander's water temperature range for this species for this area.

Graphing of the inferred spawning timing of adult chain pickerel, yellow perch largemouth bass and bluegill in relation to the current CT DEEP drawdown policy refill deadline date revealed a substantial overlap with chain pickerel and yellow perch

spawning and to a lesser extent early spawning largemouth bass as the lakes are refilling (Figure 2.7).

Discussion

My results did not document a strong protracted spawning behavior in the yellow perch populations in this suite of study lakes, which falls in line with the lack of scientific literature regarding this species having such a strategy. In the majority of lakes, spawning is occurring over only a one month period. Swim-up mostly reflected this with a swim-up range of 11-31 days.

With largemouth bass in the project lakes I did document a protracted spawning strategy lasting from mid-April to late-July, with the majority occurring between mid-May through mid-June with slight variations between water bodies. This is similar to the spawning period (mid-May through mid-June) documented by Webster (1942). Other areas throughout North America have also documented a protracted spawning strategy with this species similar to what I have documented in my project lakes. In Lake George, Minnesota, Kramer and Smith (1962) recorded a spawning period lasting from April through May. In experimental ponds in Illinois, Isely et al. (1987) documented spawning of northern strain largemouth bass for 40 days. Protracted swim-up, which infers protracted spawning, was documented in a flood control reservoir in North Carolina (Philips et al. 1995). Within southern lakes, Davis and Lock (1997) documented female largemouth bass releasing only half of their eggs during the first spawn, the other half during a second spawn and sometimes a third spawn up to one month after completion of the second event. In four Florida lakes, Rogers et al. (2006) found Florida strain largemouth bass spawning for a three month period and Waters and Noble (2004) also

documented low levels of multiple spawning bouts occurring in a Puerto Rican reservoir over a four month period.

With bluegill in the project lakes I also documented a protracted spawning strategy lasting from late-May to mid-August. Bluegill, which have a widespread range throughout North America, have been recorded as spawning as long as temperatures allow throughout their growing season. Carlander (1977) lists a number of waters located in numerous states from Florida, Texas, Illinois and Wisconsin where bluegill spawning lasted from three to seven months. Carnielli and Gross (1996) documented a two month synchronous spawning period for the bluegill population in Lake Opinicon, Ontario; Jolley et al. (2009) found protracted spawning in five separate bluegill populations in five separate lakes located in Nebraska and South Dakota and Santucci and Wahl (2003) documented the bluegill population in Ridge Lake, Illinois spawning for 2.5-4 months.

Significant differences in mean swim-up date were found within each lake across years and amongst lakes within each year for the three age-0 species studied. For yellow perch and largemouth bass, drawdown history does not appear to be a regulating mechanism affecting their swim-up dates. For bluegill, earlier swim-up dates were found in those lakes that had drawdown histories, as opposed to the one lake without a drawdown history, this is tied to the fact that spawning was found to initiate earlier in these drawn down lakes compared to the non-drawn down lake. However, with only one non-drawn down lake included in this study these results should be interpreted with caution. Additionally, without the benefit of pre-disturbance swim-up date data on these lakes, treatment conclusions are difficult to render. Though many studies have listed water level fluctuations as a mechanism affecting year class-strength and recruitment of

fishes (Hulsey 1956; Lantz et al. 1967; Aggus 1979; Gadboury and Patalas 1984; Kohler et al. 1993; Roger and Bergersen 1995; Pine et al. 2000) our results suggest, at least in terms of swim-up, two of our studied species are not affected by winter water level fluctuations.

I would also present that because swim-up dates for yellow perch did not appear affected by drawdown history (e.g., yellow perch are the earliest spawning fish in this project and the species most likely to experience and be affected by fluctuating water levels and temperatures due to a winter drawdown, as the lake could still be refilling when spawning is initiating for this species) the early swim-up dates recorded for the bluegills in the drawn down lakes compared to the non-drawn down lake might be due to some other environmental mechanism outside our drawdown regimes. By the time bluegill were swimming up in the drawn down lakes water levels had already reached full pool height a few months prior, and water temperatures had stabilized, so water level fluctuations related to the winter drawdown regimes could not be a contributing factor.

Water temperature significantly explained some of the variance surrounding swim-up date within the study lakes for most years for all three species as would be expected. Numerous studies have already documented that water temperature affects both adult and age-0 fish life cycles including spawning (Summerfelt 1975; Shuter et al. 1980), hatching (Johansen and Krogh 1914; Badenhuizen 1969), and growth (Strawn 1961; Eipper 1975; Isely 1981). Ranges of swim-up temperatures for the project lakes fell mostly within the ranges described in the literature for each species, though for some lakes and years, swim-up initiated at cooler water temperatures than described in the literature. Yellow perch were one of the species where swim-up initiation began at cooler

water temperatures then described in the literature. Though it was already established that the date at which swim-up is occurring for yellow perch does not appear to co-vary with drawdown history, it does appear that in those lakes with extensive drawdown histories swim-up is occurring at cooler water temperatures compared to the other project lakes. Yellow perch are a unique species in that they have been repeatedly documented as having highly variable year class success (Forney 1971; Kallemeyn 1987; Isermann and Willis 2008). Factors that are regulating spawning and swim-up in this species are currently unclear, though it is known that water temperature does play a role in growth (Power and Van Den Heuvel 1999). Isermann and Willis (2008) suggest that some sort of internal “thermal heterogeneity” among lakes may explain spawning and swim-up for this species. Had I been able to document protracted spawning or swim-up in these lakes I might have been able to frame an explanation in regards to it could be a response to variable environmental conditions (Isermann and Willis 2008) brought about by the winter drawdowns. However, because this was not documented, the reason why yellow perch began swimming up (and spawning) in cooler water temperatures in the two lakes with extensive drawdown histories, but yet had swim-up dates that did not show consistent directional shifts compared to the other lakes, remains elusive.

For largemouth bass, though water temperature significantly explained some of the variance in swim-up date within each lake across years, as well as amongst lakes within only one year and this species also initiated swim-up at cooler water temperatures then described in the literature, no clear trends regarding swim-up date, water temperature, spawning and drawdown history were documented.

With bluegill, water temperature significantly explained some of the variance in swim-up date within three of the lakes with drawdown histories across years and across all lakes within each year. Water temperatures at which swim-up initiated were variable compared to the literature. In the two extensive drawdown history lakes swim-up initiated at cooler water temperatures compared to the other project lakes and there was evidence that differences in swim-up were present that appeared to co-vary with winter drawdown history, with earlier swim-up dates occurring in the lakes with drawdown histories compared to the non-drawn down lake. There was some inconsistency though, regarding all drawn down lakes continuing to have earlier swim-up throughout the length of this study. Interestingly, the early spawned individuals in the extensive drawdown history lakes had significantly different, and faster growth rates, then their later spawned brethren in the same lake. MDGR in these extensive drawdown history lakes was still not as fast as MDGR found in the non-drawn down lake. The earlier swim-up and faster MDGR in cooler water temperatures in those two lakes compared to the later spawned individuals in the same lakes counters the argument found in certain peer reviewed literature (i.e. Crecco and Savoy 1985; Rice et al. 1987; Pine et al. 2000; Santucci and Wahl 2003) regarding early swim-up being associated with slower MDGR in cooler water temperatures. Some internal mechanism within these project lakes with extensive drawdown histories is resulting in earlier swim-up at cooler water temperatures with faster MDGR then the later individuals in the same lake, but yet still not as fast as rates found in the non-drawn down lake. Perhaps some genetic selection has evolved in these two lakes that has chosen for earlier hatching individuals so as to take advantage of some in-lake variable not measured here, but conditions are still not as good as they could be in

those two lakes compared to the non-drawn down lake that has some level of year long water level stability. If the literature mentioned in this Chapter's Introduction is correct then the early hatched fish should still have higher recruitment success than their later brethren.

Mating systems and spawning strategies have evolved over time to be somewhat plastic to handle both gradual and the occasional extreme fluctuations in various local environmental variables and conditions (Winemiller 2005; Rogers et al. 2006). Protracted spawning in fishes is an evolutionary form of 'bet-hedging' designed to address their environment's dynamic nature so as to ensure species resiliency (Phillips et al. 1995; Paller 1997; Isermann and Willis 2008; Jolley et al. 2009). This 'bet-hedging' mechanism, though, does come with a drawback; within the scientific literature cases of differential growth between fish hatching at different times of the year, i.e. early vs. late have been documented (Phillips et al. 1995; Pine et al. 2000; Pine and Allen 2001; Santucci and Wahl 2003). Differential rates of growth directly relates to a fish's ability to consume high energy prey and therefore create enough energy reserves to survive their first winter (Phillips et al. 1995; Ludsin and DeVires 2000; Jolley et al 2009;), as well as be removed from certain size-dependent predation pressures (Goodgame and Miranda 1993; Phillips et al. 1995). The structuring hypotheses of this research was that those impoundments with longer drawdown histories might have more asynchronous spawning (i.e. greater bet-hedging in the form of more protracted spawning seasons) and would therefore have greater variation in MDGR (i.e. differential growth) because fish hatched later in the season should grow slower as they would enter an ecosystem in the presence of more competitors than early born individuals. With age-0 yellow perch, in these study

lakes, this hypothesis does not appear to be true. MDGR for age-0 yellow perch showed no consistent, directional changes regardless of drawdown history when compared within lakes across years and amongst lakes within each year. Add to this the already stated evidence from the work done with this project of this species having a short duration spawning period and it can therefore be said that the drawdown regimes enacted in this study are not affecting this species in terms of swim-up date or MDGR. However, without a full time series of data from the non-drawn down lake it is difficult to formulate an effective discussion on the effects drawdowns have on age-0 yellow perch growth. Drawdowns that result in winter adult fish kills, or result in the lake not refilling by spawning initiation for this species because of harsh winter weather or spring drought conditions may result in noticeable shifts in spawning and swim-up date.

For largemouth bass, a similar rejection of the differential growth hypothesis would be warranted. It was found that MDGR was not affected by when they swam up and differences found in MDGR were inconsistent between lakes, with no one drawdown history showing a consistent pattern of growth compared to any other. One possible reason for this is because lake levels and water temperatures had equalized by the time this species was swimming up and it is possible that their food sources were not greatly impacted by the drawdown regimes implemented. The diet structure of age-0 Centrarchidae is complex (Applegate and Mullan 1967; Applegate et al. 1967). Largemouth bass are to some extent generalist feeders, as they go through the fry to fingerling stages (Applegate et al. 1967) so switching to another food source may mute any measurable negative impacts at this early life stage that could be detected by our metrics. As long as this species can attain a size where it has less gape limitations,

because piscivorous fish are considered gape-limited as they consume only prey they can swallow whole (Hambright 1991), survival due to limited food supplies should not be an issue in these Connecticut lakes.

With bluegills in this study I cannot reject the differential growth hypothesis I put forth because in three of the four lakes receiving a drawdown, when an individual swam up (i.e. early in the season or late in the season) did affect their rate of growth and in the majority of those lakes studied that have winter drawdowns, hatching early bestows faster growth. Whether or not this earlier swim-up, faster growth results in better recruitment to the following year then later hatched slow growing individuals in these lakes is something for another study to investigate. Studies elsewhere throughout the country have already documented that earlier hatched fish are able to attain appropriate energy reserves and therefore reduce their likelihood of overwinter mortality (Ludsin and DeVries 1997) as well as be removed from some predation pressures (Post and Prankevicus 1987). Because MDGR in the non-drawn down lake were not different between early and late swim-up and were faster than the drawn down lakes in general, it could be theorized that the inherent year long stability of the non-drawdown lake might be playing some part in keeping the food source for bluegills stable in this lake. However, the bluegills in this non-drawn down lake were previously documented as swimming up later than those found in the drawn down lakes, so this may run counter to the theory that swimming up earlier leads to faster growth, as has already been presented. It is quite possible that some other environmental factor not reviewed in this project is driving these systems. Perhaps because bluegills are less of a generalist feeder than largemouth bass, relying mostly on plankton and invertebrates as their primary food source, as they are

gape limited predators (Beard 1982), it is possible that some aspect of their first exogenous food source is remaining more stable in the non-drawn down lake than in the drawn down lakes.

The graphing of inferred adult spawning of chain pickerel, yellow perch, largemouth bass and bluegill revealed that the current CT DEEP drawdown policy refill deadline date overlaps chain pickerel and yellow perch spawning and to a lesser extent early spawning largemouth bass. Spawning of chain pickerel and yellow perch is occurring during the refill process and though no significant changes were, as previously mentioned, noted in the age-0 yellow perch in this project, CT DEEP IFD has begun to document declines in adult chain pickerel in lakes that receive repeated drawdowns (see Chapter 1, Introduction). With a changing climate leading to more micro-droughts like what was seen during the winter and spring of 2012, where many lakes that were drawn down in Connecticut were not yet refilled by mid- to late May, there may be future year-class issues because of limited access to suitable spawning substrate and interruption of spawning activity from fluctuating water levels for a number of spring spawning species.

Conclusions

In this chapter I characterized, over three consecutive summers: 1) the swim-up dates and associated water temperatures of three age-0 fish species (i.e. yellow perch, largemouth bass and bluegill); 2) their MDGR; and 3) the water temperatures and date ranges of spawning activity for the adult counterparts of these species within a suite of lakes typical of southern New England impoundments that are usually subject to winter drawdowns. Together, these results provide some insights into whether the early-hatch advantage and bet-hedging theories apply in these impoundments and whether or not

varying drawdown histories may affect swim-up date and daily growth rates. It has also shed light on how the current CT DEEP drawdown policy interplays with spawning timing of four important Connecticut fish species and how discussion and future research may be warranted regarding how the policy's refill date must now adapt to our changing climate.

The first summer of life is considered in many peer reviewed articles to be a 'critical period' for determining future fish species abundances in small lakes and ponds (Kohler et al. 1993; Pine et al. 2000; Santucci and Wahl 2003). By altering when a particular fish species spawns, and consequently when their progeny swim-up, a potential cascading effect (sometimes negative, sometimes positive) can occur to that population. Results from this chapter suggest that the manner in which the drawdowns occurred and the history of the drawdowns on this suite of lakes did not produce strong directional shifts in swim-up date. The question of how water temperature, swim-up initiation and drawdown history tie together with regards to yellow perch and bluegill has opened the door for future research. Additionally, what mechanisms are driving variable growth rates for bluegill in regards to drawdown history, but not yellow perch and largemouth bass warrants further investigation.

Table 2.1 Yellow perch swim-up dates and ancillary summary statistics.

Lake (Drawdown Regime)	Year	n	Mean DOY† (Month/Day)	Median DOY (Month/Day)	Mode DOY (Month/Day)	Standard Deviation	Range DOY (Month/Day) [Water Temp Range °C]	95% C.I.	Total Days of Swim-up
‡Uncas Lake	2007	0	-	-	-	-	-	-	-
*(No drawdown or drawdown history)	2008	242	111 (4/20)	115 (4/25)	115	76.71	105-115 (4/15-4/25) [10.6-18.4°C]	+/-62.66	11
	2009	0	-	-	-	-	-	-	-
^Bigelow Pond	2007	0	-	-	-	-	-	-	-
** (Brief drawdown history)	2008	0	-	-	-	-	-	-	-
	2009	0	-	-	-	-	-	-	-
Powers Lake (Brief drawdown history)	2007	138	118 (4/28)	115 (4/25)	115	52.47	115-125 (4/25-5/5) [13.5-17.0°C]	+/-56.76	11
	2008	94	119 (4/28)	115 (4/24)	115	46.59	115-125 (4/24-5/4) [13.8-18.3°C]	+/-61.05	11
	2009	1617	106 (4/16)	105 (4/15)	105	213.30	95-125 (4/5-5/5) [9.2-18.5°C]	+/-16.88	31
Middle Bolton Lake	2007	351	114 (4/24)	115 (4/25)	115	94.50	95-125 (4/5-5/5) [5.2-16.0°C]	+/-16.05	31
*** (Extensive drawdown history)	2008	505	107 (4/16)	105 (4/14)	105	82.88	105-115 (4/14-4/24) [10.2-18.3°C]	+/-46.86	11
	2009	942	108 (4/18)	105 (4/15)	105	137.04	105-115 (4/15-4/25) [8.8-14.7°C]	+/-56.73	11
Gardner Lake	2007	2706	111 (4/21)	115 (4/25)	115	252.81	95-125 (4/5-5/5) [4.6-16.2°C]	+/-15.47	31
(Extensive drawdown history)	2008	871	106 (4/15)	105 (4/14)	105	80.68	95-115 (4/4-4/24) [6.8-18.4°C]	+/-11.76	21
	2009	376	109 (4/19)	105 (4/15)	105	81.93	95-115 (4/5-4/25) [6.3-14.7°C]	+/-18.18	21

†DOY = day-of-year.

‡Too few age-0 yellow perch were captured in this lake on the month specified in the methodology to perform analysis with.

^Only two age-0 yellow perch were captured at Bigelow Pond during the three years this study was performed.

*Control lake = no drawdowns ever carried out.

**Brief drawdown history lake = no appreciable drawdown history present on these lakes within the past 20 years. During the three year period of this project a maximum of a 0.91 meter (m) drawdown was implemented.

***Extensive drawdown history lake = there is an extensive winter drawdown history at these lakes where a 0.91 m drawdown has been carried out for a number of years prior to this study. During the three year period of this study a >0.91 but ≤1.82 m was implemented.

Table 2.2 Largemouth bass swim-up dates and ancillary summary statistics.

Lake (Drawdown Regime)	Year	n	Mean DOY† (Month/Day)	Median DOY (Month/Day)	Mode DOY (Month/Day)	Standard Deviation	Range DOY (Month/Day) [Water Temp Range °C]	95% C.I.	Total Days of Swim-up
Uncas Lake *(No drawdown or drawdown history)	2007	183	156 (6/5)	155 (6/4)	165	70.00	135-185 (5/15-7/4) [16.9-27.3 °C]	+/-13.30	51
	2008	109	153 (6/1)	155 (6/3)	155	49.52	135-165 (5/14-6/13) [13.9-28.6 °C]	+/-15.09	31
	2009	17	143 (5/23)	145 (5/25)	145	31.14	125-185 (5/5-7/4) [15.1-27.6 °C]	+/-19.41	61
Bigelow Pond **(Brief drawdown history)	2007	196	156 (6/5)	155 (6/4)	155	43.65	125-195 (5/25-7/14) [18.2-27.9 °C]	+/-7.63	51
	2008	33	156 (6/4)	155 (6/3)	155	20.60	145-175 (5/24-6/23) [13.8-27.5 °C]	+/-11.41	31
	2009	8	168 (6/17)	155 (6/4)	145	40.62	145-205 (5/25-7/24) [16.8-24.3 °C]	+/-45.70	61
Powers Lake (Brief drawdown history)	2007	93	146 (5/26)	145 (5/25)	145	50.33	105-175 (4/15-6/24) [7.7-25.3 °C]	+/-12.34	71
	2008	4	150 (5/29)	150 (5/29)	145,155	10.00	145-155 (5/24-6/3) [16.4-22.2 °C]	+/-63.53	11
	2009	5	163 (6/12)	165 (6/14)	155,165	11.83	155-175 (6/4-6/24) [19.4-22.6 °C]	+/-22.77	21
Middle Bolton Lake ***(<i>Extensive</i> drawdown history)	2007	163	150 (5/30)	145 (5/25)	145	65.93	135-165 (5/15-6/14) [15.6-25.7 °C]	+/-16.43	31
	2008	58	152 (5/31)	155 (6/3)	155	30.01	125-165 (5/4-6/13) [12.2-26.8 °C]	+/-10.94	41
	2009	26	137 (5/17)	135 (5/15)	135	27.40	125-175 (5/5-6/24) [14.7-22.4 °C]	+/-14.92	51
Gardner Lake (<i>Extensive</i> drawdown history)	2007	30	148 (5/28)	145 (5/25)	155	29.89	135-155 (5/15-6/4) [14.0-25.1 °C]	+/-23.48	21
	2008	17	153 (6/1)	155 (6/3)	145,155,165	23.85	135-165 (5/14-6/13) [13.2-26.3 °C]	+/-18.41	31
	2009	2	160 (6/9)	160 (6/9)	145,175	21.21	145-175 (5/25-6/24) [16.6-22.8 °C]	+/-190.59	31

†DOY = day-of-year.

*Control lake = no drawdowns ever carried out.

**Brief drawdown history lake = no appreciable drawdown history present on these lakes within the past 20 years. During the three year period of this project a maximum of a 0.91 meter (m) drawdown was implemented.

***Extensive drawdown history lake = there is an extensive winter drawdown history at these lakes where a 0.91 m drawdown has been carried out for a number of years prior to this study. During the three year period of this study a >0.91 but ≤1.82 m was implemented.

Table 2.3 Bluegill swim-up dates and ancillary summary statistics.

Lake (Drawdown Regime)	Year	n	Mean DOY† (Month/Day)	Median DOY (Month/Day)	Mode DOY (Month/Day)	Standard Deviation	Range DOY (Month/Day) [Water Temp Range °C]	95% C.I.	Total Days of Swim-up
Uncas Lake *(No drawdown or drawdown history)	2007	7	206 (7/25)	205 (7/24)	205	11.95	195-215 (7/14-8/3) [24.6-29.8 °C]	+/- 19.44	21
	2008	44	187 (7/5)	185 (7/3)	185	29.91	175-195 (6/23-7/13) [24.3-29.2 °C]	+/- 19.4	21
	2009	13	193 (7/12)	195 (7/14)	195	17.1	175-215 (6/24-8/3) [20.7-28.5 °C]	+/- 13.17	41
Bigelow Pond **(Brief drawdown history)	2007	13	172 (6/21)	175 (6/24)	175	20.48	155-195 (6/4-7/14) [19.0-24.5 °C]	+/- 15.77	41
	2008	65	184 (7/2)	185 (7/3)	185	36.41	165-215 (6/13-8/2) [20.6-27.5 °C]	+/- 12.54	51
	2009	4	213 (8/1)	215 (8/15)	215	8.66	205-215 (7/24-8/3) [21.3-25.4 °C]	+/- 55.02	11
Powers Lake (Brief drawdown history)	2007	193	169 (6/18)	165 (6/14)	165	81.77	155-195 (6/4-7/14) [21.1-28.2 °C]	+/- 16.34	41
	2008	43	162 (6/10)	165 (6/13)	165	29.21	155-175 (6/3-6/23) [20.2-28.1 °C]	+/- 19.17	21
	2009	18	167 (6/16)	165 (6/14)	165	20.68	155-195 (6/4-7/14) [19.4-24.9 °C]	+/- 13.54	41
Middle Bolton Lake *** (Extensive drawdown history)	2007	142	160 (6/9)	155 (6/4)	165	52.82	145-205 (5/25-7/24) [14.3-28.1 °C]	+/- 11.39	61
	2008	0	-	-	-	-	-	-	-
	2009	14	193 (7/11)	195 (7/13)	225	48.68	155-225 (6/3-8/12) [18.7-29.1 °C]	+/- 33.43	71
Gardner Lake (Extensive drawdown history)	2007	238	171 (6/20)	175 (6/24)	175	72.67	155-185 (6/4-7/4) [19.0-26.9 °C]	+/- 14.99	31
	2008	142	170 (6/18)	165 (6/13)	165,175	65.48	155-165 (6/3-6/13) [17.3-26.3 °C]	+/- 15.26	11
	2009	167	172 (6/21)	175 (6/24)	165	68.65	155-205 (6/4-7/24) [17.2-25.6 °C]	+/- 14.75	51

†DOY = day-of-year.

*Control lake = no drawdowns ever carried out.

**Brief drawdown history lake = no appreciable drawdown history present on these lakes within the past 20 years. During the three year period of this project a maximum of a 0.91 meter (m) drawdown was implemented.

***Extensive drawdown history lake = there is an extensive winter drawdown history at these lakes where a 0.91 m drawdown has been carried out for a number of years prior to this study. During the three year period of this study a >0.91 but ≤1.82 m was implemented.

Table 2.4 Back calculated spawning season, temperature ranges and means in degrees Celsius (°C) for adult yellow perch, largemouth bass and bluegill determined from data derived from scientific literature and age-0 progeny swim-up date analysis.

Species	Lake	Year	Spawning Day-of-Year (Month/Day)	Spawning Season Temperature Range (°C)	Spawning Season Mean Temperature (°C)
<i>Yellow perch</i>	Uncas	2007	-	-	-
		2008	83-108 (3/23-4/17)	5.5-13.9	8.5
		2009	-	-	-
	Bigelow	2007	-	-	-
		2008	-	-	-
		2009	-	-	-
	Powers	2007	93-118 (4/3-4/28)	6.9-14.9	9.7
		2008	93-118 (4/2-4/27)	7.4-18.3	12.7
		2009	73-118 (3/14-4/28)	5.0-18.5	10.1
	M. Bolton	2007	73-118 (3/14-4/28)	2.1-14.6	6.6
		2008	83-108 (3/23-4/17)	4.1-13.9	8.2
		2009	83-108 (3/24-4/18)	0.9-13.1	8.9
	Gardner	2007	73-118 (3/14-4/28)	1-14.3	6.8
		2008	73-108 (3/13-4/17)	3.8-13.6	7.3
		2009	73-108 (3/14-4/18)	-1.1-14.2	7.7
<i>Largemouth bass</i>	Uncas	2007	130-182 (5/10-7/1)	16.9-27.3	22.5
		2008	130-162 (5/9-6/10)	15.3-28.5	18.4
		2009	120-182 (4/30-7/1)	15.1-27.6	19.9
	Bigelow	2007	120-192 (4/30-7/11)	12.1-27.9	20
		2008	140-172 (5/19-6/20)	13.6-27.5	19.8
		2009	140-202 (5/20-7/21)	15.1-24.3	20.2
	Powers	2007	100-172 (4/10-6/21)	7.2-25.3	17.9
		2008	140-152 (5/19-5/31)	15.6-20.6	17.8
		2009	150-172 (5/30-6/21)	18.8-22.6	20.7
	M. Bolton	2007	130-162 (5/10-6/11)	15.6-25.7	20.2
		2008	120-162 (4/29-6/10)	12.2-26.7	17
		2009	120-172 (4/30-6/21)	14.7-22.3	18.3
	Gardner	2007	130-152 (5/10-6/4)	14.0-25.1	19.1
		2008	130-162 (5/9-6/10)	11.9-26.3	17
		2009	140-172 (5/20-6/21)	15.0-22.8	19
<i>Bluegill</i>	Uncas	2007	185-205 (7/4-7/24)	23.8-28.3	26.3
		2008	165-185 (6/13-7/3)	23.1-28.4	25.4
		2009	165-205 (6/14-7/24)	20.5-28.5	23.8
	Bigelow	2007	145-185 (5/25-7/4)	18.2-26.9	22
		2008	155-205 (6/3-7/23)	17.8-27.5	23.8
		2009	195-205 (7/14-7/24)	20.9-24.3	22.7
	Powers	2007	145-185 (5/25-7/4)	20.6-27.3	23.8
		2008	145-165 (5/24-6/13)	16.4-28.1	21.6
		2009	145-185 (5/25-7/4)	18.8-24.9	21.2
	M. Bolton	2007	135-195 (5/15-7/14)	15.6-28.1	22.2
		2008	-	-	-
		2009	145-215 (5/24-8/2)	15.7-29.1	23.9
	Gardner	2007	145-175 (5/25-6/24)	18.4-25.1	21.7
		2008	145-155 (5/24-6/3)	14.6-21.3	17.9
		2009	145-195 (5/25-7/14)	16.6-24.1	20.2

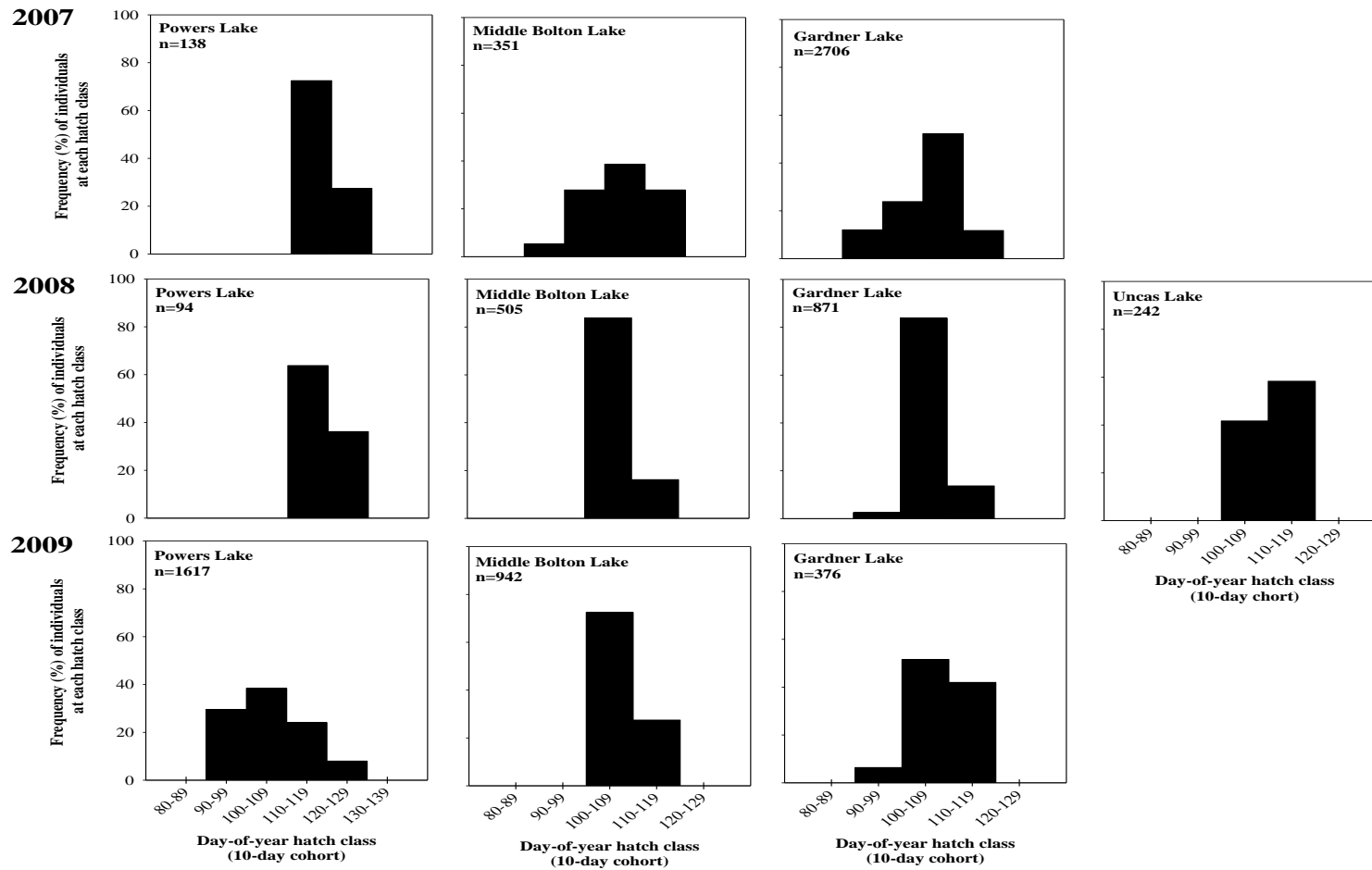


Figure 2.1 Yellow perch swim-up frequency depiction for each of the project lakes each year. No yellow perch were sampled during the chosen month for swim-up frequency analysis in Bigelow Pond (2007, 2008 and 2009) or Uncas Lake (2007 and 2009).

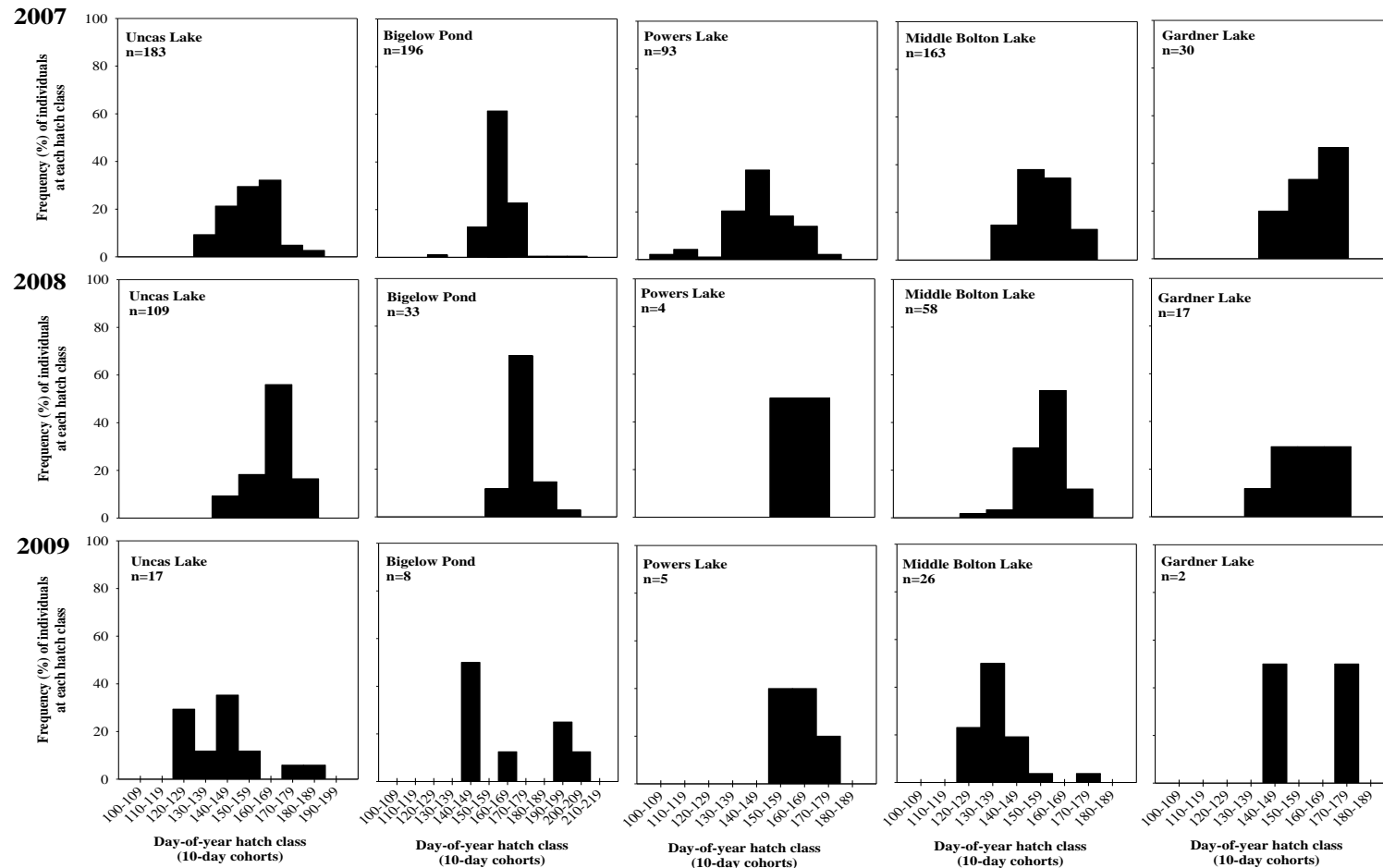


Figure 2.2 Largemouth bass swim-up frequency depiction for each of the project lakes each year.

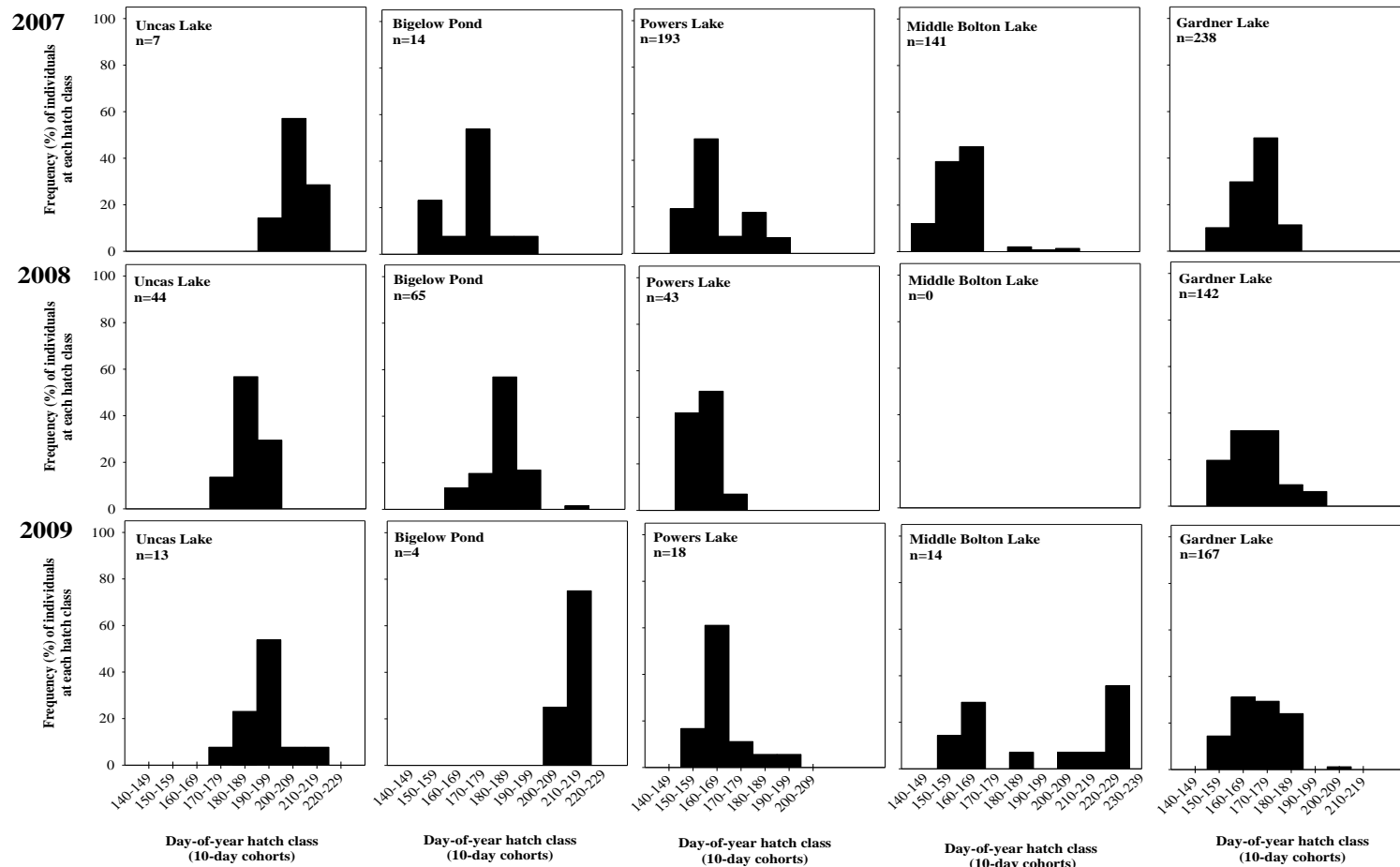


Figure 2.3 Bluegill swim-up frequency depiction for each of the project lakes each year. No bluegills were sampled during the chosen month for swim-up frequency analysis in Middle Bolton Lake in 2008.

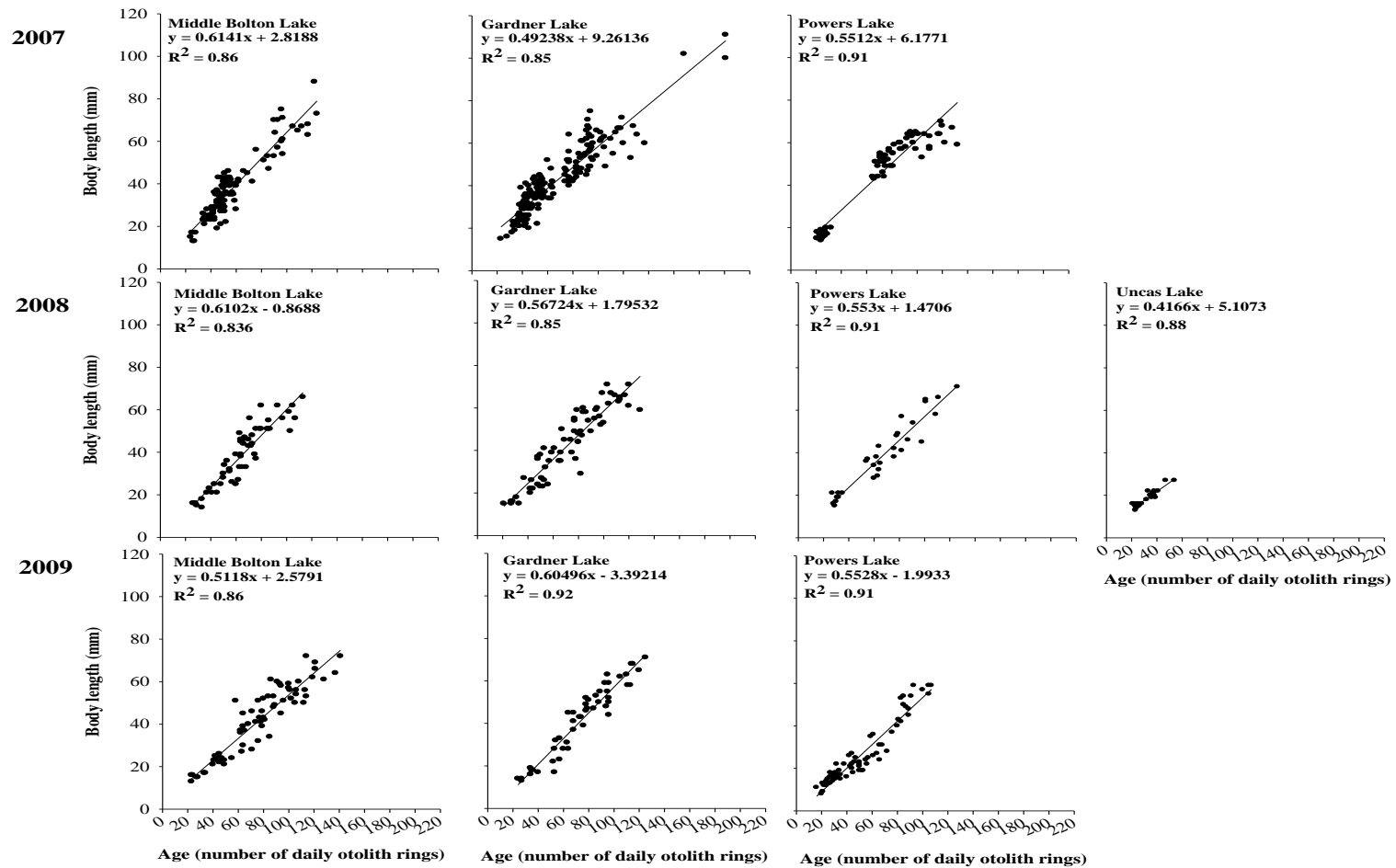


Figure 2.4 Linear regression of length in millimeters (mm) versus age (number of daily rings counted from otoliths) as a representation of growth for the drawdown project lakes where yellow perch were captured and aged. Too few yellow perch were sampled in Bigelow Pond (all years) and Uncas Lake (2007 and 2009) for analysis.

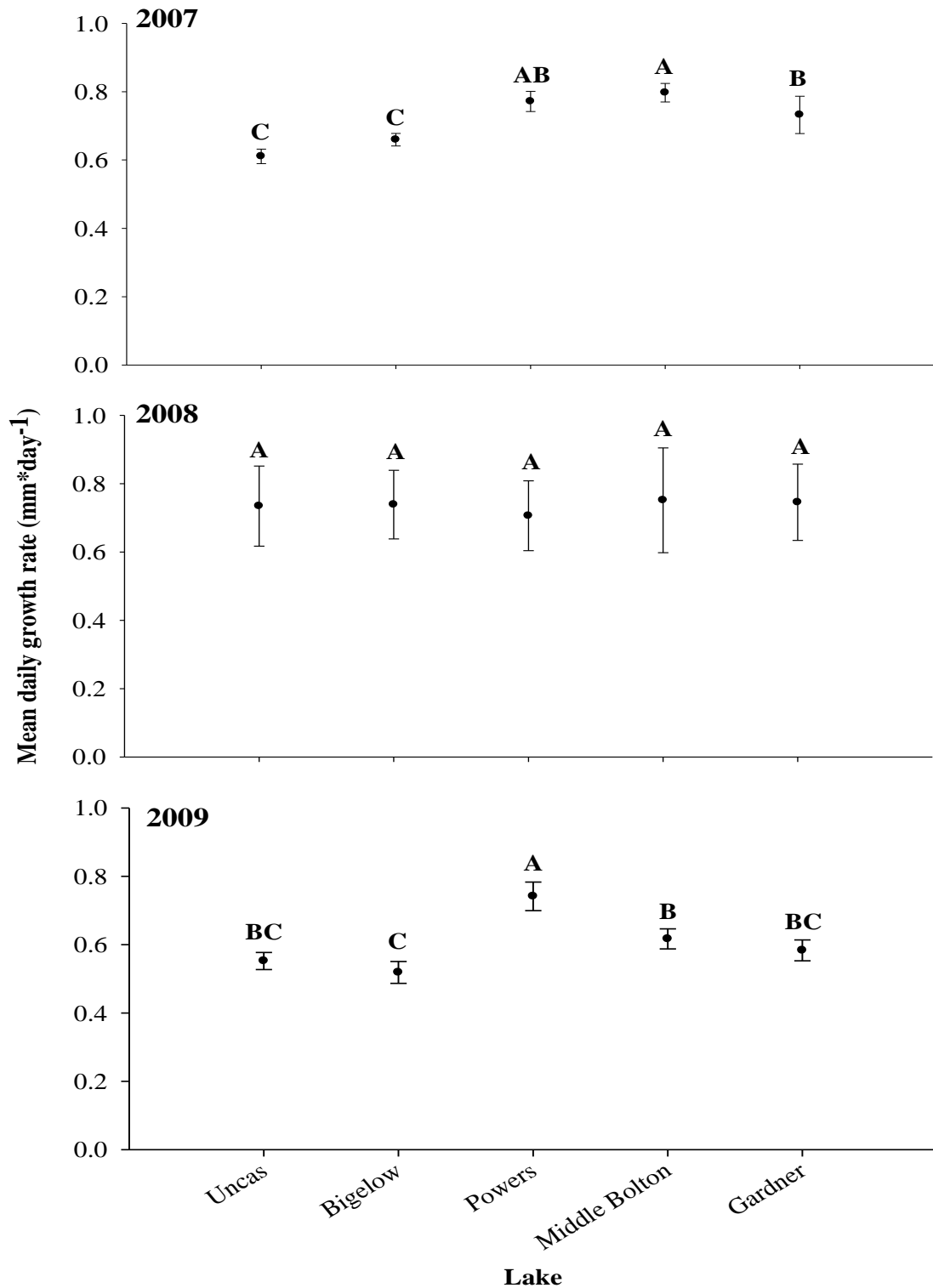


Figure 2.5 Mean daily growth rates in millimeters per day (mm*day⁻¹) for largemouth bass in the study lakes. Error bars are 95% confidence intervals. Different letters indicate means significantly different at $\alpha = 0.05$ within that year using the Tukey Honestly Significant Difference test.

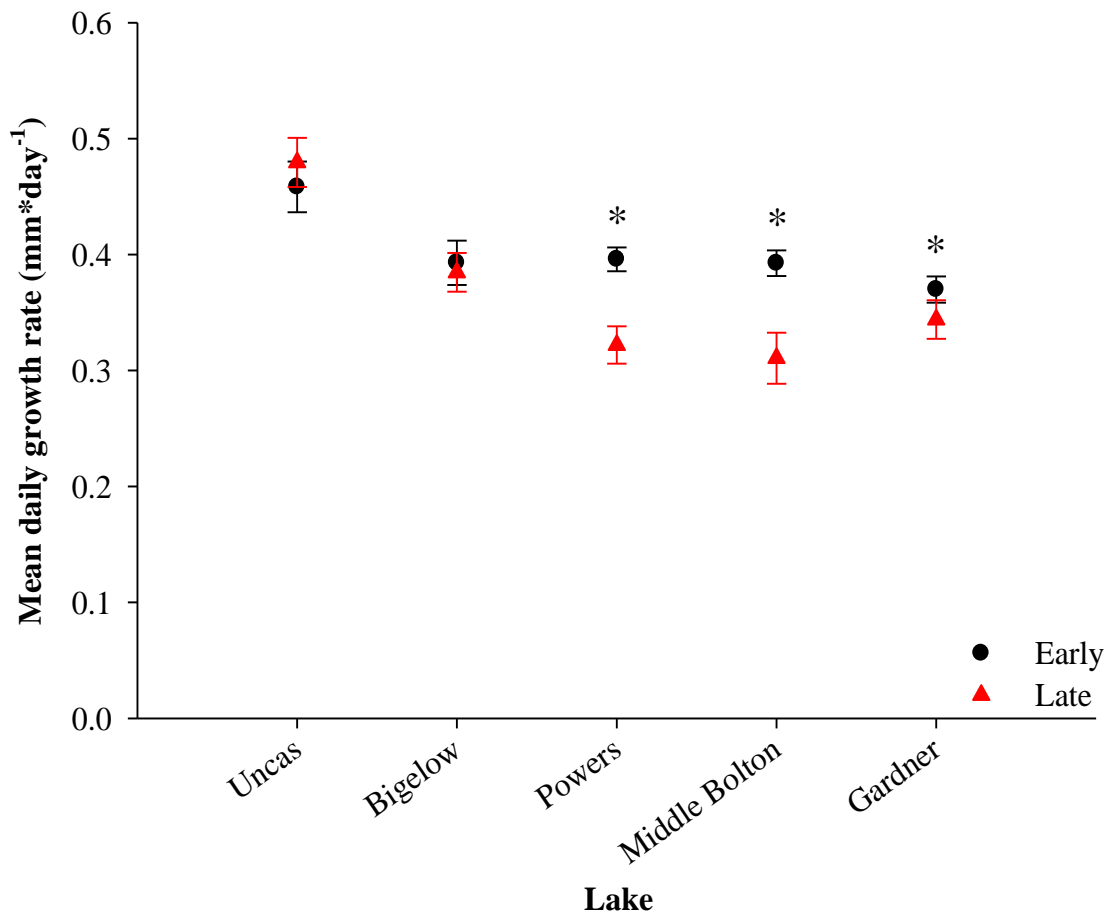


Figure 2.6 Mean daily growth rates in millimeters per day (mm*day⁻¹) for early and late spawned bluegill in the study lakes during 2007-2009 (all years combined). Error bars are 95% confidence intervals. Asterisks indicate means significantly different from $\alpha = 0.05$ using the Least Squares Mean test.

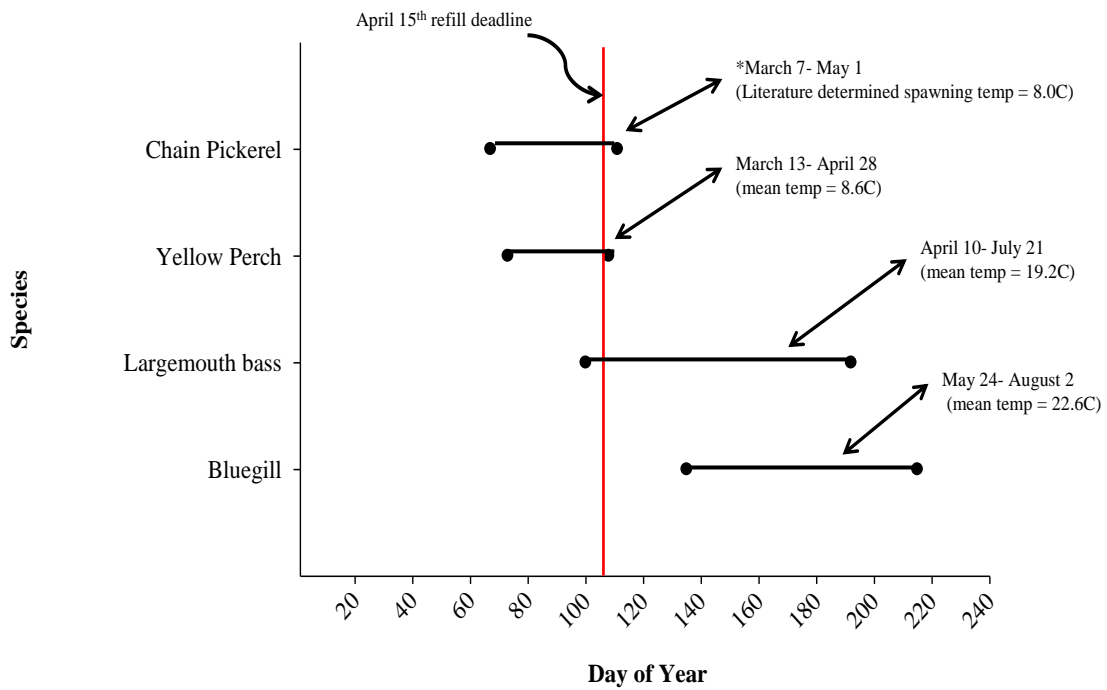


Figure 2.7 Inferred spawning timing of adult fishes. *Because data were not directly gathered on chain pickerel for this project the spawning temperature for this species was obtained from the literature then the date range that spawning could occur in the project lakes was determined. ‘Mean temp’ is the mean water temperature at which spawning occurred in the project lakes. The age-0 data, water temperature data and incubation length from the scientific literature were used to conservatively infer back to when spawning of the adults of each species was occurring.

CHAPTER 3

Do Winter Drawdowns Affect the Swim-up Dates and Daily Growth Rates of Age-0 Fishes in Small Southern New England Impoundments?

Introduction

The first year of life is a critical period for many fishes (Pine et al. 2000), with growth and survival (especially during the first winter in temperate regions) setting patterns of recruitment to the adult population (Partridge and DeVries 1999, Pine and Allen 2001, Phelps et al. 2008, Jolley et al. 2009). Survival is directly affected by suitable quantities and types of forage (Pine and Allen 2001; Pine et al. 2000) and size selective predation rates (Pine et al. 2000), which in turn are tied to the amount of available refuge habitat (Bennett et al. 1973, Savino and Stein 1982, Swales 1982). Indirectly, survival is affected through changes in hatch date and growth rate resulting from alterations to water level and water temperature (Aggus 1979; Pine et al. 2000, Pine and Allen 2001).

Hatch timing (i.e. swim-up date) and growth rate are considered important determinants regulating recruitment to the adult population for those species that experience size-selective over-winter mortality (Jolley et al. 2009). In gape-limited fishes, differences in hatch timing may affect growth (and therefore gape) and ultimately how quickly individuals can consume larger, high energy content, prey items. The consumption of larger prey allows fish to take in more energy while at the same time expending less energy. By consuming more energy a fish should be able to grow to a survivable size prior to the onset of the first winter (Jolley et al. 2009), as well as be removed from size-selective predation of gape-limited predators (Partridge and DeVries 1999). If altered hatch timing shifts growth off of a preferable timetable, smaller gapes

may leave fish with smaller, low energy, prey items and therefore limit the body size achieved prior to winter.

To explore the possibility that swim-up date and mean daily growth rates (MDGR) might be effected following a winter drawdown, otoliths were removed from age-0 yellow perch, largemouth bass and bluegill and the daily rings counted. As was explained in Chapter 2, otoliths are a useful tool for determining swim-up times and growth rates of these three species. From the ring counts I sought to determine if varying winter drawdown intensities might influence the swim-up date and MDGR of these three species within five impoundments in eastern Connecticut. Other characteristics of a waterbody known to affect early life history, were also measured, which included: water temperature, food availability and habitat.

Methods

Variables based on field data (see Chapter 1 and 2, Methods for collection and processing details) used in the analysis for this chapter were: *drawdown intensity*, day-of-year each species reported *minimum spawning temperature* was reached (Table 3.1), *mean zooplankton density* for the month prior to when individual fish were sampled, and *percent moveable sediment* (grams) for each lake each year fish were sampled. These variables were then used to determine the magnitude and direction of varying winter drawdown intensities on two dependent covariates: swim-up date and MDGR for age-0 yellow perch, largemouth bass and bluegill. Up to 50 individual fish from each lake each year were randomly chosen from the length frequency data for use in the analysis. Ages of these fish were assigned using the methods applied in Chapter 2. Since age-0 fish are

being studied, the data from each lake in successive years were considered independent from each other for modeling purposes.

The new variable *drawdown intensity* was an index value created to represent the intensity of the winter drawdowns at each impoundment. It was created by taking the total volume of water removed (cubic meters), multiplied by the area of lake bottom exposed (hectares) at a two-week time step and then summed over the duration of the drawdown. Readings of water height from the control structures at each impoundment were used to indicate water surface elevations relative to conservation pool heights. The total volume removed and bottom area exposed were then derived by reducing the water height within a Geographic Information System layered over bathymetry of the lake bottom.

Variables were tested for normality using the Shapiro-Wilk test (Statistical Analysis System [SAS] version 9.2; SAS Institute, Carry, North Carolina). After failing the initial test for normality all covariates were log transformed to attempt to normalize data, except for *percent movable sediment*, which was arcsine square root transformed because it was a percentage. Each discrete transformed variable was then individually mean centered against its entire covariate data set by subtracting the mean of each covariate, then dividing it by that covariate set's overall standard deviation (McCune & Grace 2002). Mean centering allows for data coming from multiple different sources to be given equal weighting for multivariate analysis.

To reduce the complexity of the data set, the transformed, mean centered variables were used to perform a principal components analysis (PCA; McCune and Mefford 2006, PC-ORD5, MjM Software, Gleneden Beach, Oregon). PCA is an

eigenvector method of ordination that seeks to maximize the information contained in the original variables in a smaller number of composite variables known as principal components or axes (McCune and Grace 2002). In this case, PCA was not used for statistical inference so the requirement of multivariate normality was relaxed (McCune & Grace 2002). The composite principal components (PC) were then used to develop mixed, nested models with unequal random effects covariates (Littell et al. 2006) designed to test the ideas regarding what might affect the swim-up date and MDGR of these three species based on the literature and expected outcomes in a lake ecosystem exposed to winter drawdowns. The information-theoretic approach (Burnham and Anderson 2002) was used for model selection to better understand the relative importance (relative to other variables represented in the PC), magnitude, and direction of varying winter drawdown intensities on the two dependent variables for the three age-0 fish species.

Using Akaike's Information Criterion (AIC) and related measures of model weight to represent support for models, the given approach simultaneously tested multiple hypotheses formally expressed as mathematical models against each other to determine which models are best-supported by the data. An information criterion is calculated for each of a set of candidate models; the AIC score for a model is based on both the statistical likelihood estimate for the model, as well as the number of parameters in the model (models with higher numbers of parameters are typically penalized). AIC scores are then used to compare the various candidate models and select those that offer the best relative explanation of the data. This modeling approach confers several advantages over traditional frequentist approaches (e.g. stepwise linear regression),

including: 1) it allows models to “compete” simultaneously for support (i.e. simultaneous multiple hypothesis testing); 2) it does not rely on arbitrary “p” value thresholds to determine statistical “significance”; and 3) it provides a formalized means of evaluating the tradeoff between model complexity and explanatory power (Burnham and Anderson 2002).

The smaller the AIC score for a particular model relative to the other models in the competition, the greater relative explanatory power of that model; therefore, the model with the lowest AIC score within each round of competition is considered the “best” model.

The AIC difference (Δ_i) for a given model i represents the reduction in AIC score for that model relative to the best model; the larger Δ_i is, the less plausible that model i is the best model. In general, models for which Δ_i ranges between zero and two have substantial support from the data. Models with Δ_i values of four to seven have considerably less support, while those with Δ_i greater than 10 have essentially no support (Burnham and Anderson 2002).

The Akaike weight (w_i) for a given model i represents the weight of evidence that model i is the actual best model relative to all other models in the competition (i.e. w_i values for all candidate models sum to one). Evidence ratios (ER) provide a way to evaluate the relative weight of evidence for various models; ER for model i represents the ratio of that model’s Akaike weight to that of the best model in the set. ER values greater than three indicate that there is relatively little evidence in favor of model i (Burnham and Anderson 2002).

The modeling approach for swim-up date and MDGR consisted of proposing a candidate set of ecologically plausible linear models using combinations of PC covariate groups. The candidate set was fitted with ‘lake’ and ‘year’ present in each model.

Results

Strong relationships were not present for the covariates chosen for this study after PCA was performed. Results for the PCA were ambiguous and explained little variation relative to drawdown intensity, i.e. lake years with higher drawdown intensities did not group together in multivariate space, nor did lake years with low drawdown intensities group together for any of the three species (Figure 3.1).

Disregarding sign (e.g. positive or negative), each species ended up having different loading values for each resultant PC variable (Table 3.2). For example, yellow perch on the PC1 axis had *minimum spawning temperature* receiving the highest loading, -0.8688; *percent moveable sediment* received the second highest loading on the PC1 axis with -0.7124; *drawdown intensity* received the third highest loading on the PC1 axis with -0.6238; and *mean zooplankton density* received the fourth highest loading on the PC1 axis with -0.2994. Drawdown intensity did not dominant the loadings for any PC axis, except perhaps for largemouth bass, but rather shared loadings with the other variables in the PC axis (Table 3.2). No single variable measured had a singly dominant loading on either PC1 or PC2 for any species.

Newly created PC covariates for each species were incorporated into a candidate set of mixed models (Tables 3.3a, 3.3b and 3.4). All models converged and were considered better than a naïve model (i.e. a model with no parameters), but did not explain much of the variation found around swim-up date or MDGR. This was more

prevalent in the models used to test for effects on swim-up date as all the candidate sets selected the ‘global model’ as the single most supported model (Tables 3.3a and 3.3b). In the models used to test for effects on MDGR, simpler models were chosen over the ‘global model’ (Table 3.4).

A sum of weights was calculated for the PC variables for each modeling exercise for each species (Tables 3.5 and 3.6). PC1 for yellow perch and PC2 for largemouth bass (Table 3.5) received the greatest weight for the swim-up date models. For both species the covariate *minimum spawning temperature* composed the highest loading on each of these axes (Table 3.2). With bluegill, PC1 and PC2 received the greatest weight for the swim-up date models (Table 3.5). The covariate *mean zooplankton density* had the highest loading on the PC1 axis; however *percent moveable sediment* ranked a close second on the PC1 axis as well (Table 3.2). The covariate *minimum spawning temperature* received the highest loading on the PC2 axis (Table 3.2). Neither ‘lake’ nor ‘year’ as an interaction term explained much, if any, of the variation surrounding the swim-up date models for any of these three species, because the PC1 or PC2 variables provided the entirety of the weight.

With the MDGR models for largemouth bass PC3 received the greatest weight (Table 3.6). The covariate *mean zooplankton density* received the highest loading on this axis (Table 3.2). However PC1 and PC2 tied in their weights (Table 3.6). PC1 (*drawdown intensity*) and for PC2 (*minimum spawning temperature*) received the highest loading on these axes respectively (Table 3.2).

With the MDGR models for bluegill PC1 received the greatest weight for this set of models (Table 3.6). The covariate *mean zooplankton density* received the highest

loading on this axis; however *percent moveable sediment* ranked a close second on the PC1 axis as well (Table 3.2). Neither ‘lake’ nor ‘year’ as an interaction term explained much if any of the variation surrounding the MDGR models for either of the species because the individual PC variables provided the entirety of the weight.

Discussion

Strong support for varying winter drawdown intensities causing significant changes in swim-up date or MDGR for any of the three species studied was not found from the results of this study. The hypothesized responses and effects of the winter drawdowns were not obvious within the dataset, as the PCA results did not group lakes with higher drawdown intensities (or conversely lower intensities) and no graphical separation in multivariate space along a gradient of drawdown intensity was found. The candidate set of mixed models did not explain much of the variation for either swim-up date or MDGR, but did explain more variation than parameterless models. Possible explanations for why these models did not perform as expected can be traced back to the covariates chosen for this study and how they did not show strong changes related to the drawdown regimes.

The weighting procedure applied to the PC variables within the swim-up mixed models revealed that the covariate *minimum spawning temperature* loaded heavily on the various PC axes for the three species. (However, caution is required in the interpretation here because other covariates loaded heavily on the same axes that temperature was highly ranked on and so direct interpretation is difficult because the other covariates are somehow interacting on these axes as well). Because it is widely known that water temperature affects many aspects of a fish’s life cycle, especially spawning (Summerfelt

1975; Shuter et al. 1980), hatching (Johansen and Krogh 1914; Badenhuizen 1969), and growth (Strawn 1961; Eipper 1975; Isely 1981) it makes sense that within the swim-up models this covariate would be playing a part in swim-up date. Issues that arise in the early stages of life can effect the required growth needed for age-0 fish to attain the required size for the critical life stage switch from endogenous to exogenous feeding (Toetz 1966). The results of Chapter 2 shed light upon how water temperature explains some part of the variation surrounding swim-up date for these three species in these lakes and how the interaction of the drawdown regimes, swim-up date and water temperature are difficult to interpret. The results from this chapter add more support that the drawdown intensities enacted during this study do not produce strong directional shifts in water temperature that effect swim-up as neither ‘lake’ nor ‘year’ as an interaction term explained much if any of the variation within these models when combined with the temperature covariate. The water temperatures in all lakes equalized and warmed basically in sync regardless of drawdown intensity (including the lake that had no drawdown enacted upon it) as was seen in Figure 1.4 from Chapter 1. This was likely due to the rapid refilling of the lakes (even during the drawdown process); with full pool height often reached after a single rain event. Lack of lasting temperature regime shifts during this study suggests that for later spawning centrachids (i.e. largemouth bass and bluegill) timing of the spawn will rarely be affected by drawdowns in the range of those observed. Should lakes not be brought back to full pool height prior to the onset of spawning season, perhaps during a year where an extensive winter or spring drought is occurring, complications in year-class strength and ultimately recruitment to the adult

population may arise from inopportune water level and water temperature fluctuations (Lantz et al. 1967; Aggus 1979; Pine et al. 2000, Pine and Allen 2001).

From the weighting procedure applied to the PC variables within the MDGR mixed models for largemouth bass and bluegill the covariate *mean zooplankton density* received high weightings. (However, caution is again required in the interpretation here because other covariates loaded heavily on the same axes that zooplankton density was highly ranked on and so direct interpretation is difficult because the other covariates are somehow interacting as well on these axes.) As zooplankton are the primary food source for age-0 fish (Applegate et al. 1967; Carlander 1977; Carlander 1997) it makes sense that within the MDGR models this covariate would be playing a part in growth. However, this is where the limitations of this modeling exercise appear. Our results in this chapter showed that the drawdown regimes applied to this set of candidate lakes did not appear to significantly impact the food source for these age-0 fishes in a way that would affect their growth as neither ‘lake’ nor ‘year’ as an interaction term explained much if any of the variation within these models when combined with the zooplankton density covariate. This runs counter to the results in Chapter 2 that showed growth rates for bluegills were different between lakes with different drawdown regimes and were different for when an individual swam-up. The modeling approach used in Chapter 3 used a specific set of variables that appeared to all be interacting with each other, as was mentioned earlier. This fact may have muted this test’s ability to show differences regarding drawdown intensity, as opposed to the specific test applied in Chapter 2.

McGowan et al. (2005) found that zooplankton abundance was not significantly impacted by winter drawdowns on small prairie lakes that had water reductions of up to

50% of the lake level carried out with resultant freezing and desiccation of the lake sediments. It is quite possible that with this modeling exercise the abundance of a specific zooplankton species required for adequate growth of age-0 largemouth bass and bluegill did not fall below some trigger level where growth would be noticeably impaired. Another possibility is that if a specific food species did decrease, a similar nutrient rich food source was still present. These two species are, to one extent or another, generalist feeders when they are feeding on zooplankton, though they do have specific zooplanktors they favor over others (Applegate and Mullan 1967; Siefert 1972; Carlander 1977; Carlander 1997).

It has been well established in the peer reviewed literature that frequent exposure of bottom sediments through drawdowns to air through time will result in shoreline coarsening (Hale and Bayne 1982; Wagner and Falter 2002), changes to the chemical composition of the bottom sediments (Estes 1972; Plotkin 1979; Wagner and Falter 2002; McGowan et al. 2005) and changes in the rooted aquatic vegetation community (Cooke et al. 1993; Wagner and Falter 2002). With this study, shoreline coarsening did not happen as quickly and to the extent necessary to adversely impact age-0 fish habitat the way we measured it. A potential reason why no change was observed may be due to the 'new' drawdown lakes (i.e. Bigelow Pond and Powers Lake) not having had a long enough time series of data taken with continual drawdowns being enacted for there to be noticeable effects. Whereas the lakes historically subjected to deep drawdown (i.e. Gardner Lake and Middle Bolton Lake) have already had their littoral zone sediments effected through years of repeated drawdowns. Further, the drawdowns (with perhaps the exception of the 'deep' drawdown at Middle Bolton Lake) either did not expose enough of the littoral zone

or coarsen the sediments in this zone extensively enough to express a change. Another possibility is the release upon reinundation of phosphorous, nitrogen and other nutrients (Plotkin 1979; Geiger 1983; Cooke et al. 1993; McGowan et al. 2005) into the already nutrient rich lakes of this study allowed for the maintenance of required nutrient levels so that littoral vegetation was not impacted by changes in bottom substrate. (This same idea could be applied to the plankton community previously discussed.) It was observed that many undisturbed areas of littoral habitat existed in all the drawn down lakes, and in some instances were quite expansive, covering more area than that exposed during the drawdown. These areas may act as recolonizing zones for the rest of the lakes from which seeds, root shoots and broken vegetative parts for established, invasive and drawdown resistant macrophyte species originate and then spread out to other areas of the lake upon reinundation (Nichols 1975; Hestand 1977; McGowan et al. 2005). A fine line exists between too high and too low nutrient levels for aquatic macrophyte success. If the levels are too high then macrophyte establishment will be suppressed from shading by dense populations of phytoplankton; if too low then establishment will be suppressed from lack of appropriate nutrients (Davis and Brinson 1980). It would appear that our drawdown regimes did not push these systems far enough past their tipping point. It can therefore be expected that for lakes with high water clarity, shallow depth, moderate nutrient loading and expansive littoral areas, that shallow drawdowns may be a relatively minor disturbance to rooted aquatic macrophytes and plankton communities during the short term because the bottom sediments are not changed as drastically and as rapidly as expected.

Conclusions

With this work I attempted to characterize whether or not variations in swim-up date and MDGR of three age-0 fish species commonly found in Connecticut lakes could be explained by varying winter drawdown intensity and fluctuations in environmental variables that potentially could be affected by these drawdowns. The results shed light not only on the complex nature of environmental data, but on the resiliency of lake ecosystems to absorb short term environmental perturbations.

Though significant variations in swim-up date or MDGR were not found with this modeling exercise, it is quite plausible that I did not observe the correct sequence or intensity of events that would produce noticeable changes on these two dependent variables or on any one or combination of the covariates used. One must be careful not to misinterpret these results to mean that the drawdown regimes enacted in this study are benign, only that we did not expose detectable effects over the conditions and duration we observed. Ecosystems and the organisms therein, can be highly resilient to external perturbations (Paller 1997). The timing, extent and intensity of such perturbations, such as winter drawdowns, will inevitably determine how a fish community is able to return to a pre-perturbation condition (Paller 1997).

Though the topic of first winter survival of age-0 fishes has been explored by numerous scientists (Oliver et al. 1979; Toneys and Coble 1979; Shuter et al. 1980; Danylchuk and Fox 1994a; Santucci and Wahl 2003.), future research in Connecticut on this topic should investigate how winter drawdowns affect the overwintering ability of Connecticut's lake residing age-0 and age-1 fish species and if artificial population suppression is occurring because of the current drawdown regime.

Table 3.1 Day-of-year the minimum spawning temperature, in degrees Celsius (°C), was reached in each lake for each species for each year. A literature review was used to determine the temperature each species typically spawned at in the region studied. Mean water temperature data from temperature loggers for all zones combined were then reviewed for each lake and year to determine the day-of-year the cited minimum spawning temperature was reached.

Species (Spawning temperature in °C from literature)	Lake	Year	Day-of-Year Spawning Temperature Reached
Yellow perch (7*)	Bigelow Pond	2007	110
		2008	100
		2009	87
	Powers Lake	2007	84
		2008	66
		2009	69
	Middle Bolton Lake	2007	101
		2008	92
		2009	74
	Gardner Lake	2007	86
		2008	86
		2009	69
	Uncas Lake	2007	86
		2008	85
		2009	76
Largemouth bass (11.5 [§])	Bigelow Pond	2007	113
		2008	109
		2009	109
	Powers Lake	2007	111
		2008	101
		2009	100
	Middle Bolton Lake	2007	112
		2008	101
		2009	107
	Gardner Lake	2007	113
		2008	101
		2009	99
	Uncas Lake	2007	112
		2008	102
		2009	109
Bluegill (17 [§])	Bigelow Pond	2007	130
		2008	117
		2009	118
	Powers Lake	2007	125
		2008	114
		2009	117
	Middle Bolton Lake	2007	129
		2008	113
		2009	117
	Gardner Lake	2007	129
		2008	114
		2009	117
	Uncas Lake	2007	124
		2008	113
		2009	116

*Carlander, 1997.

[§]Carlander, 1977.

Table 3.2 Principal component analysis (PCA) loadings for each species.

Species	Covariate [†]	Principal Component Loadings		
		PC1	PC2	PC3
Yellow perch	drawdown intensity [§]	-0.6238	-0.2251	0.7476
	minimum spawning temperature ^Δ	-0.8688	-0.0342	-0.369
	mean zooplankton density [‡]	-0.2994	-0.8881	-0.2453
	percent moveable sediment [*]	-0.7124	0.612	-0.1016
Largemouth bass	drawdown intensity	-0.8651	0.0937	0.3102
	minimum spawning temperature	0.4665	-0.8051	-0.1122
	mean zooplankton density	0.6135	0.1621	0.7723
	percent moveable sediment	-0.473	-0.7554	0.3238
Bluegill	drawdown intensity	0.6449	0.6418	-0.188
	minimum spawning temperature	0.5169	-0.7644	0.2097
	mean zooplankton density	-0.7661	-0.2571	-0.5287
	percent moveable sediment	0.7636	-0.2825	-0.5136

[†]All covariates were transformed and mean centered.

[§]Drawdown intensity is the volume (cubic meters) of water removed during the drawdown*the lake bottom exposed (hectares) over time.

^ΔMinimum spawning temperature is the day-of-year each species minimum spawning temperature was reached in each lake. Water temperature data was gathered from temperature loggers placed within each lake; see Chapter 1, Methods. Minimum spawning temperature values were taken from the scientific literature; see Chapter 2, Introduction.

[‡]Mean zooplankton density is for the month prior to when individual fish were sampled.

^{*}Moveable sediment constituted the combination of the 63 micrometer, sand, silt and organics portion of the sediment sample.

Table 3.3a Akaike's Information Criterion (AIC) modeling results for assessing the effects of the principal component (PC) variables on swim-up date for yellow perch and largemouth bass.

Species	Variables in the model	AIC	Δ_i	wi	Evidence Ratio
Yellow perch	PC3 PC1 PC3*LakeName PC1*LakeName PC3*Year PC1*Year	3487.767	0.000	1.000	1.000
	PC1 PC2 PC1*LakeName PC2*LakeName PC1*Year PC2*Year	3507.601	19.834	0.000	20269.106
	PC3 PC1 PC3*Year PC1*LakeName	3582.546	94.779	0.000	381113205661752000000.000
	PC1 PC2 PC1*LakeName	3596.929	109.162	0.000	506119532960657000000000.000
	PC1 PC1*LakeName	3604.505	116.738	0.000	2235446436847640000000000.000
	PC3 PC1	3673.122	185.355	0.000	17752302430625800000000000000000000000.000
	PC2	3680.988	193.221	0.000	90647122793830400000000000000000000000.000
	PC1	3685.739	197.972	0.000	97499730236705600000000000000000000000.000
	PC3*PC1	3694.482	206.715	0.000	77214773844022000000000000000000000000.000
Largemouth bass	PC1 PC2 PC1*LakeName PC2*LakeName PC1*Year PC2*Year	5811.829	0.000	0.996	1.000
	PC2 PC3 PC2*LakeName PC3*LakeName PC2*Year PC3*Year	5822.877	11.047	0.004	250.567
	PC1 PC2 PC1*Year PC2*LakeName	5880.086	68.257	0.000	663530721303610.000
	PC2 PC3 PC2*LakeName	5889.306	77.477	0.000	66670909702037300.000
	PC2 PC2*LakeName	5898.121	86.292	0.000	5471575818934580000.000
	PC1 PC3	5927.527	115.698	0.000	13290243981424300000000000.000
	PC1 PC2	5928.066	116.237	0.000	17396470432511400000000000.000
	PC2	5950.461	138.632	0.000	126898141317910000000000000000.000
	PC1*PC2	5998.002	186.173	0.000	26728372879858500000000000000000000000.000

Table 3.3b Akaike's Information Criterion (AIC) modeling results for assessing the effects of the principal component (PC) variables on swim-up date for bluegill.

Species	Variables in the model	AIC	Δ_i	wi	Evidence Ratio
Bluegill	PC1 PC2 PC1*LakeName PC2*LakeName PC1*Year PC2*Year	5482.006	0.000	1.000	1.000
	PC1 PC2 PC1*Year PC2*LakeName	5535.153	53.147	0.000	347279889741.648
	PC1 PC1*LakeName PC1*Year	5535.859	53.853	0.000	494342444685.115
	PC2 PC1 PC2*LakeName	5545.995	63.988	0.000	78508995133591.300
	PC2 PC2*LakeName	5552.399	70.392	0.000	1929873034353830.000
	PC1 PC2	5588.828	106.822	0.000	157039068585930000000000.000
	PC1 PC3	5590.209	108.202	0.000	313212696522786000000000.000
	PC1	5594.606	112.599	0.000	282268223263253000000000.000
	PC1*PC2	5598.166	116.160	0.000	167388084546465000000000.000

Table 3.4 Akaike's Information Criterion (AIC) modeling results for assessing the effects of the principal component (PC) variables on mean daily growth rate (MDGR) for largemouth bass and bluegill.

Species	Variables in the Model	AIC	Δ_i	wi	Evidence_ratio
Largemouth bass	PC2 PC2*LakeName	-1458.772	0.000	0.689	1.000
	PC2 PC3 PC2*LakeName	-1457.004	1.767	0.285	2.420
	PC1 PC2 PC1*Year PC2*LakeName	-1452.099	6.672	0.025	28.108
	PC1 PC2 PC1*LakeName PC2*LakeName PC1*Year PC2*Year	-1446.596	12.176	0.002	440.429
	PC2 PC3 PC2*LakeName PC3*LakeName PC2*Year PC3*Year	-1440.526	18.246	0.000	9162.149
	PC1 PC3	-1436.796	21.976	0.000	59156.484
	PC1 PC2	-1436.286	22.485	0.000	76316.401
	PC2	-1432.573	26.199	0.000	488589.915
	PC1*PC2	-1360.542	98.229	0.000	2138956039531750000000.000
Bluegill	PC1	-2403.439	0.000	0.422	1.000
	PC1*PC2	-2403.270	0.170	0.387	1.089
	PC2 PC2*LakeName	-2400.855	2.584	0.116	3.640
	PC1 PC2	-2399.025	4.415	0.046	9.092
	PC1 PC3	-2397.401	6.039	0.021	20.479
	PC2 PC1 PC2*LakeName	-2395.234	8.205	0.007	60.498
	PC1 PC1*LakeName PC1*Year	-2391.866	11.574	0.001	326.011
	PC1 PC2 PC1*Year PC2*LakeName	-2387.009	16.431	0.000	3697.383
	PC2 PC1 PC2*LakeName PC1*LakeName PC2*Year PC1*Year	-2367.002	36.438	0.000	81716424.648

Table 3.5 Sum of weights for the principal component (PC) variables included in the swim-up date Akaike's Information Criterion (AIC) model candidate sets for yellow perch, largemouth bass and bluegill.

Model	Species	PC Variable	Sum of Weights
Swim-up date	Yellow perch	PC 1	1.000
		PC2	0.000
		PC3	1.000
		PC1*PC2	0.000
		PC2*PC3	0.000
		PC1*PC3	0.000
		PC1*LakeName	1.000
		PC2*LakeName	0.000
		PC3*LakeName	0.000
		PC1*Year	1.000
		PC2*Year	0.000
		PC3*Year	1.000
	Largemouth bass	PC 1	0.996
		PC2	1.000
		PC3	0.004
		PC1*PC2	0.000
		PC2*PC3	0.000
		PC1*PC3	0.000
		PC1*LakeName	0.996
		PC2*LakeName	0.996
		PC3*LakeName	0.004
		PC1*Year	0.996
		PC2*Year	1.000
		PC3*Year	0.004
	Bluegill	PC 1	1.000
		PC2	1.000
		PC3	0.000
		PC1*PC2	0.000
		PC2*PC3	0.000
		PC1*PC3	0.000
		PC1*LakeName	1.000
		PC2*LakeName	1.000
		PC3*LakeName	0.000
		PC1*Year	1.000
		PC2*Year	1.000
		PC3*Year	0.000

Table 3.6 Sum of weights for the principal component (PC) variables included in the mean daily growth rate (MDGR) Akaike's Information Criterion (AIC) model candidate sets for largemouth bass and bluegill.

Model	Species	PC Variable	Sum of Weights
MDGR	Largemouth bass	PC 1	0.026
		PC2	0.026
		PC3	0.285
		PC1*PC2	0.000
		PC2*PC3	0.000
		PC1*PC3	0.000
		PC1*LakeName	0.002
		PC2*LakeName	1.000
		PC3*LakeName	0.000
		PC1*Year	0.026
		PC2*Year	0.002
		PC3*Year	0.000
	Bluegill	PC 1	0.884
		PC2	0.557
		PC3	0.021
		PC1*PC2	0.387
		PC2*PC3	0.000
		PC1*PC3	0.000
		PC1*LakeName	0.001
		PC2*LakeName	0.123
		PC3*LakeName	0.000
		PC1*Year	0.001
		PC2*Year	0.000
		PC3*Year	0.000

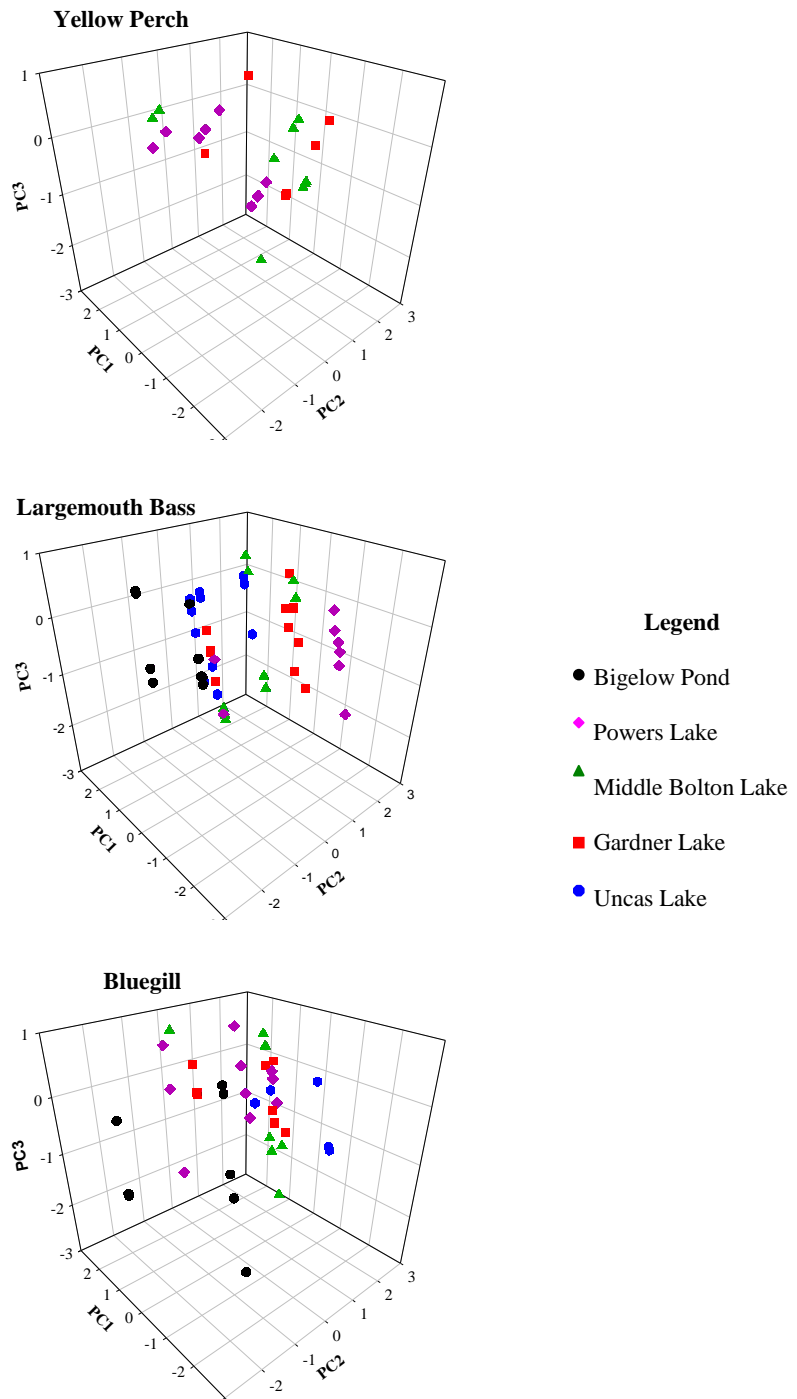


Figure 3.1 Graphical representation of principal component (PC) loadings in multivariate space for yellow perch, largemouth bass and bluegill. Up to 50 fish per lake per year were used for principal component analysis (PCA). Symbols are groups of fish with the same PC values. All years for each individual lake were given the same symbol.

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