

OVER-WINTER MORTALITY OF GIZZARD SHAD (DOROSOMA
CEPEDIANUM) IN ONEIDA LAKE, NEW YORK

A Thesis

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by

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ABSTRACT

Winter limits resource availability in temperate lakes, exerting a strong influence on the northern distributions of many temperate species by altering the recruitment of age-0 fishes. Recently, there has been growing concern that projected climate change could alter over-winter survival of many fish species and have ecosystem-level effects on all trophic levels of aquatic ecosystems. Oneida Lake has been the focus of a long-term data set across several trophic levels and provides the ideal location to study over-winter mortality in fishes. In Chapter 1, I provide a review of current methods used throughout the literature to address questions involving over-winter mortality in fishes. Specifically, I address methods used, their pros and cons, and what has been learned by the application of each method. Common methods evaluated include experiments, field observations, experiments and field observations, and analysis of long-term data sets. Given that mortality is commonly driven by complex interactions between multiple factors, I suggest researchers use multiple approaches to study fish over-winter mortality. In Chapter 2, I conducted a series of experiments and field sampling to develop a conceptual model of gizzard shad over-winter mortality in Oneida Lake. Gizzard shad exhibited high mortality rates as water temperatures declined prior to ice formation and are highest at temperatures less than 4° C. Habitat sampling demonstrated that shad congregate in high densities in Oneida Lake marinas, which provide a nearshore temperature refuge but may become anoxic during years with consistent ice cover. Within any given year, shad survival is likely a function of length entering winter, rate of temperature decline preceding ice-on, and ice duration.

BIOGRAPHICAL SKETCH

William was born on August 30, 1982 in Brookfield, Wisconsin to Frank and Sandie Fetzer. He grew up in Nashotah, Wisconsin, where he learned to love the outdoors and appreciate the value of nature through his experiences hunting and fishing on the Rupnow Farm with his family, especially his father, brother and god-father Keith Marshall.

William graduated from Arrowhead Union High School in 2001 and enrolled at the University of Wisconsin-Madison to pursue a degree in Wildlife Ecology. During his first two years, he took many different environment-related classes, and decided teaching high school biology would allow him to pass his interest in the natural world to other inquiring minds. In 2003, he applied to and was accepted into the program for secondary education in the School of Education. Prior to enrolling within the program, he received an NSF-REU to work with Dr. Jake Vander Zanden at the Center for Limnology for the summer of 2003. Through his research project, he spent countless hours near or on lakes Mendota and Monona collecting, processing and analyzing samples to establish the pre-zebra mussel food web structure of these lakes. The epiphany that he could have a career studying how lakes work forever change the course of his life. After the summer, he switched majors to Zoology, focused his coursework on aquatic ecology, and continued working for Dr. Vander Zanden. Over the next two years, he became embedded within the social and scientific community at the Center for Limnology, working on a variety of projects, including documenting invasive rusty crayfish distributions in Wisconsin, assisting graduate students with stable isotope processing, and a global meta-analysis of aquatic food-chain-length.

In 2005, William graduated with honors from the University of Wisconsin-Madison with a degree in Zoology and enrolled in a MS/PhD program at Cornell

University in Natural Resources. Cornell University and specifically the Cornell Biological Field Station provided the ideal setting for him to pursue his ever-growing list of questions.

To all the family and friends who have helped me along the way.

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CHAPTER 1:

ASSESSING OVER-WINTER MORTALITY IN FISHES: LESSONS LEARNED FROM METHODS USED

ABSTRACT

Growing concern about the effects of climate change on the structure and function of aquatic ecosystems has stimulated the pace of research on this topic. Over-winter mortality has received considerable attention because of its importance in determining year-class strength and ultimately the distributions of many fishes. Here I provide a review of methods used in over-winter mortality studies. Specifically, I identify commonly used methods, pros and cons of each method, and how each method has contributed to our understanding of what drives over-winter mortality in fish. Across the literature, the four most common methods are experiments, field data, experiments and field data, and analyses of long-term data sets. Experiments are widely used to understand individual responses of fish to winter conditions; however, extrapolation to field conditions is often difficult. Field data is used to identify the response of fish to multiple stressors common during winter month but caution must be used when trying to identify specific mortality drivers. Through the use of experiments and field data, researchers are able to overcome the difficulties associated with each individual method, highlighting the complexity of factors driving over-winter mortality. Analyses of long-term data sets have proven useful in identify density-dependent and density-independent drivers of mortality, but further application is limited by the availability of suitable long-term data sets. As climate change continues to impact aquatic ecosystems, creative applications of multiple

approaches will be necessary to address the complexity of factors driving over-winter mortality in fishes.

INTRODUCTION

Anthropogenic climate change is a concern worldwide, specifically regarding ecosystem structure, function and services. Aquatic ecosystems will undoubtedly be impacted given the driving role of temperature in the structure and function of these ecosystems (Tonn 1990; Schindler 2001). Several review papers have addressed potential impacts of climate change on aquatic ecosystems, proposing mechanisms that will affect these ecosystems and the communities they support (Tonn 1990; Magnuson et al. 1990; Jackson et al. 2001; Schindler et al. 2001; Rahel and Olden 2008). Changes in fish over-winter survival are of particular concern because of its importance in determining year-class strength (Ludsin and DeVries 1997; Hurst and Conover 1998) and ultimately species distributions (Tonn and Magnuson 1982; Shuter and Post 1990). Globally, ice duration in lakes that exhibit winter ice cover has been decreasing at a rate of 6.3 days/ 100 years, and this rate has been increasing in recent decades (Magnuson et al. 2000). As winter severity and duration continue to decline, the application of multiple approaches to understanding over-winter mortality in fish will aid in the prediction of aquatic ecosystem and fish community responses to climate change.

Fisheries scientists have long recognized the importance of over-winter mortality in driving fish populations (Hubbs and Trautman 1935). Initial investigations of fish over-winter mortality focused on documenting and describing mass mortality events in fishes, commonly termed “winterkills” (Storey and Gudger 1936; Hurst 2007). Investigations beyond winterkills, however, were historically ignored, which Hubbs and Trautman (1935) attribute to three reasons. First, university

undergraduates, graduate students, and professors who conduct the majority of fisheries research are not available during winter months due to university obligations. Second, investigations prompted by calls from anglers are limited during winter, since there are generally fewer individuals interacting with the resource. Finally, challenges associated with conducting field work including "...the discomfort of working in and about freezing water," have "...retarded winter investigations." Investigations beyond winterkills aimed to identify and understand fish biological function at cold temperatures, specifically critical temperature thresholds (Fry et al. 1942; Brett 1956; Beitinger et al 2000). Starvation is an additional stress faced by over-wintering fish, as resource scarcity is common and limits feeding in many species (Reimers 1963). Incorporation of both temperature and starvation stress provided the theoretical basis from which further investigation of over-winter mortality in fishes could advance (Hurst 2007).

During the 1980's and 90's, widespread observations of size-selective over-winter mortality stimulated the pace of winter research (Chevalier 1973; Toney and Coble 1979; Miranda and Hubbard 1994; Sogard 1997) as investigators attempted to identify mechanisms driving size-selective mortality or explain conditions in which size-selective mortality would not be expected. Initially, researchers suspected that size-selective mortality was driven by starvation, since smaller fish tend to have fewer energy reserves (Oliver et al. 1979) and metabolize at a higher specific rate (Brett and Groves 1979), limiting their ability to survive through winter. Further studies helped to identify that additional complications unrelated to or in concert with starvation may be the actual cause of mortality, including predation (Chevalier 1973; Fitzgerald et al. 2006). Smaller fish are susceptible to greater predation risks, due to decreased avoidance capabilities, higher risk-taking behavior and a greater suite of potential gape-limited predators (Werner and Gilliam 1984; Sogard 1997). Once the

importance of size-selective over-winter mortality was identified, it could be used to explain the evolution of key life history traits in fish, including growth rates (Conover 1992), age at maturity (Fox and Keast 1991), and spawning times (Conover 1992; Trexler et al. 1992). Several researchers have identified conditions promoting negative size-selective mortality, where smaller fish experience lower mortality rates, particularly in fish that feed during winter months (Lankford and Targett 2001; Connolly and Petersen 2003). In these cases, larger fish have a higher resource demand than smaller fish which they may be unable to meet during times of limited resources common during winter months. Supporting evidence is limited and most research is aimed at understanding conditions which lead to size-selective mortality.

There are other factors in addition to starvation that may be driving over-winter mortality in fishes (Toneys and Coble 1979; Toneys and Coble 1980), and during the late 1990 and 2000's investigators began to re-evaluate these factors in more detail. Osmoregulatory failure, the inability to maintain osmotic pressure of bodily fluids, has been identified as a potential mortality source (Stanley and Colby 1971; Johnson and Evans 1996; McCollum et al. 2003). In smaller fish, a reduced gill surface area to volume ratio decreases their capacity to maintain homeostasis especially at cold temperatures and this can lead to mortality. Membrane fluidity in many fish can also be reduced at cold temperatures if fish are unable to adjust membrane composition to increase/maintain function (Snyder and Hennesey 2003). As membrane fluidity decreases, fish lose their ability to transport materials in/out of cells, leading to increased physiological stress and eventually mortality. Immunosuppression has been observed in cold stressed fish (Lepak and Kraft 2008). As the activity/efficiency of the immune system in fish is reduced, fish become increasingly susceptible to diseases which can lead to mortality. Identifying additional mortality mechanisms related to cold stress is currently an important research topic

(Hurst 2007; Donaldson et al. 2008), and will help to increase our understanding of over-winter mortality.

Fisheries scientists have used a variety of methods to address questions relating to over-winter mortality of fishes. Researchers either use experiments, field observations, or a combination of the two, interpreting experimental results to explain field observations. Experimental studies typically look at fish mortality or physiological responses to cold temperature under controlled conditions providing a powerful tool for identifying mortality drivers on individual fish. Field observation studies typically consist of one year of chronological sampling or two-three years of comparisons, typically comparing survival and physiological responses during a cold and warm year. Increasingly, long-term datasets on climatic conditions and fish recruitment are being used to elucidate the role of over-winter mortality in driving population dynamics of fish populations. Given the rapid increase in research aimed at understanding effects of climate change on fish (Figure 1.1), it seems an appropriate time to evaluate methods used to address over-winter mortality in fishes. Specifically, for each of the different experimental approaches, I discuss how the particular approach is used, the pros and cons of each method, and how they have contributed to our understanding of over-winter survival and recruitment.

METRICS USED

There are several common metrics used to assess over-winter mortality and physiology of fish which vary depending on the specific research questions and objectives of a given study. These metrics include mortality, size/condition, body composition, biochemical signals, and behavior.

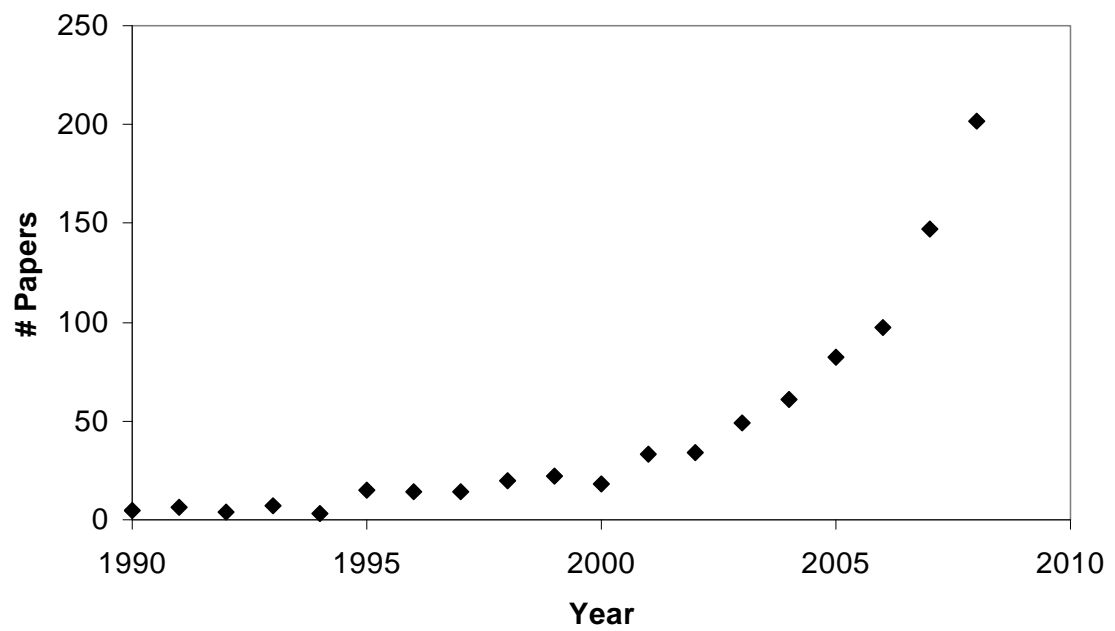


Figure 1.1. Time trend of climate change and fish papers. Number of papers identified using keyword search for “climate change and fish” on Web of Science (conducted March 21, 2009).

Mortality

Measuring or documenting the mortality rates of fish under different winter conditions, either in experimental treatments or field sites, is often the ultimate goal of many over-winter studies. Initially, researchers were interested in mortality to identify lower limits of fish tolerance, by lowering temperatures from different acclimation temperatures until high amounts of mortality were observed (Fry et al. 1942; Brett 1956). Over time, research questions began to explore differences in the rates of mortality across different temperatures, to understand how environmental conditions encountered in the field may influence survival (Johnson and Evans 1991; McCollum et al. 2003). Recently, there has been growing attention into how the rate of temperature decline, or the acclimation rate, affects survival of fish (Beitinger et al. 2000; Lankford and Targett 2001; Reber and Bennett 2007). In addition to mortality, comparisons of fish that die and those that survive can be informative in identifying potential physiological drivers of mortality (Adams et al. 1985). Researchers often measure fish size, body composition, and biochemical signals to try and explain mortality patterns.

Size/Condition

Some measurement of size can be found in nearly all studies of fish over-winter mortality and physiology. Size is an important measure because it can be used to directly test if over-winter mortality is size-selective (Sogard 1997), with the largest fish having the greatest ability to survive. The most basic measurement of size is length. Observed differences in survival of small versus large fish in experiments (Thompson et al. 1991; Bernard and Fox 1997; Pangle et al. 2004) or changes in the length distributions from field collections (Chevalier 1973; Toney and Coble 1979; Miranda and Hubbard 1994; Fitzgerald et al. 2006) suggest over-winter mortality is

often size-selective and may be driven by starvation or predation. In addition to length, fish weight is often measured in experiments and field collections. Weight can be measured as wet weight or dry weight. Wet weight is commonly used because of its ease of measurement; however, dry weight will usually provide the most accurate estimate of changes in the condition and energy content of fish (Hartmann and Brandt 1995; Tucker et al. 2001). This is especially true in studies looking at the physiological responses of fish to winter conditions, as wet weight may not illustrate changes in energy content if water content of fish increases with the use of energy stores (Flath and Diana 1985). Several studies use relationships between length and weight to provide estimates of fish conditions, including condition factor (K) or relative weight (Froese 2006). Despite the usefulness of size in assessing size-selective over-winter mortality, it may not be useful in identifying physiological drivers of mortality.

Body Composition

Body composition is often measured when it is hypothesized that utilization of limited energy resources drives mortality, and can be used to look in greater detail at the specific energy stores utilized by fish. This allows researchers to more accurately identify the actual energy reserves used by fish and potentially track how these are changing over time or across treatments (Pierce et al. 1980; Flath and Diana 1985; Hurst et al. 2000). Energy content measured through bomb calorimetry is one of the most widespread analyses because it is relatively easy to measure and gives accurate measurement of total energy available to the fish (Craig et al. 1978). Changes in energy content are typically thought to reflect changes in lipid content of fish, since this tissue has the highest energy content. Body composition is typically broken into lipid content, protein, and ash-free dry weight, with the percentages reported as

percent of dry weight (Thompson et al. 1991; Pratt and Fox 2002; Pangle et al. 2004). Ash-free dry weight is a measure of the organic material within a sample. Body composition of fish can be broken up into specific tissue types to directly identify tissues utilized by fish (Pastoureaud 1991; van Dijk et al. 2005; Ibarz et al. 2007). Often these studies occur in laboratory settings and compare fed to un-fed fish to identify responses of fish to starvation (Kieffer and Tufts 1998; van Dijk et al. 2005). The ratio of the weight of a specific tissue type to the weight of somatic tissue allows size-independent comparison between fish, including gonadal-somatic index (GSI), hepatic-somatic index (HSI), and visceral-somatic index (VSI). Despite the greater level of detail that these indices provide, they may still limit the ability to identify an exact cause of mortality and are not widely used.

Biochemical signals

Researchers have begun to look in greater detail at physiological indicators of stress in fish exposed to winter conditions in both experiments and field collections. In contrast to indices of size and body composition, these metrics can identify in greater detail specific physiological responses of fish and provide additional certainty into physiological drivers of stress and mortality in over-wintering fish. Initially, indices were limited to measurements of blood serum composition, looking for indicators of stress such as red blood cell counts (Toneys and Coble 1980), osmolarity (Toneys and Coble 1980), glucose (Pastoureaud 1991), and cortisol (Donaldson et al. 2008). These have advanced to look at different reaction byproducts to further our understanding of fish physiology (Larson et al. 2001; Ibarz et al. 2007). These analyses can be especially informative when attempting to identify how fish species respond to periods of starvation by identifying exact energy stores used. Compositional analyses of polyunsaturated fatty acids have demonstrated their

importance over other fatty acids in homeoviscous adaptation of alewife (*Alosa pseudoharengus*) at cold temperatures (Snyder and Hennessy 2003). Increased susceptibility to disease has also been identified as a potential source of over-winter mortality, and analysis of immune responses of fish, specifically white blood cells, have demonstrated immunosuppression in fishes exposed to cold temperatures (Lepak and Kraft 2008). Increasingly, new assays are being developed to further identify direct physiological responses of fish to cold temperatures and to more accurately identify sources of mortality (Donaldson et al. 2008)

Behavior

Behavior of fish exposed to winter conditions can provide valuable insights to identifying drivers of over-winter mortality in fishes. Monitoring behaviors of fish exposed to different experimental treatments can help researchers understand how fish might be acting in the wild, information that is not easily acquired during conditions common during winter months. For instance, activity levels of fish have been shown to increase as their available energy stores decrease, which likely increases susceptibility to predation (Johnson and Evans 1991). Observed differences between species can also be informative in helping to explain differences in energy usage and survival over winter, and can help identify competitive advantages (Johnson and Evans 1991). Feeding regime and temperature have been shown to affect swimming speed (Hurst and Conover 2001) or result in erratic swimming behavior (Fetzer, *pers. obs*), which can be used to infer susceptibility to predation in the wild.

METHODS USED

Studies of fish over-winter mortality and physiology have employed a variety of methods, and the most appropriate method depends on specific research objectives

of a particular study. Here I provide a review of different methods, when they are appropriate and how they have contributed to our current understanding of fish responses to winter conditions.

Experiments

Laboratory experiments are commonly used in studies of over-winter mortality because they allow researchers the opportunity to experimentally test hypotheses. Experiments typically consist of several treatments designed to identify potential causes/drivers of mortality that can be extrapolated to field conditions. However, relating experimental results to the field is usually speculative. Common treatments across the literature include multiple temperatures, fed vs. unfed, varying acclimation rate, or combinations of these factors. Mortality rates, energy use/depletion, and behavior are common metrics used to detect differences between treatments; however, within the laboratory setting, investigators are also able to look in greater detail at the physiology of the fish to identify exact causes of mortality. Researchers may conduct *in situ* field experiments, in which fish are collected and confined into ponds or cages within their “natural” environment. These studies provide an additional element of realism not available in the laboratory setting, and experimental results are often easier to relate to natural over-winter mortality. With the additional element of realism comes a loss of experimental control, and it is often more difficult in these settings to identify exact causes of mortality or track specific physiological responses to experimental treatments. Despite how informative experiments can be in identifying the potential responses of fish to different winter conditions, these studies often do not evaluate if a fish will encounter those types of conditions in the field. For instance, at low resource densities, smaller size may promote survival; however, there is no testing

of resource density in the field. Researchers must use caution when attempting to extrapolate experimental results to explain natural over-winter mortality.

Multiple temperatures

Exposing fish to several different temperature treatments and monitoring mortality and physiology can be a powerful tool to understand fish biology. Typically, fish perform the best at the warmest temperature, suffering the highest mortality in the coldest treatments (Johnson and Evans 1991; Johnson and Evans 1996; Lankford and Targett 2001; Ibarz et al 2007), however, fish adapted to cold temperatures may exhibit no difference between temperature treatments (Johnson and Evans 1991). Cause of mortality may also vary across temperature treatments. In many instances, mortality in the warmest treatments can be attributed to starvation, while those in colder treatments may die from cold-stress related mortality, including osmoregulatory failure (Johnson and Evans 1996; McCollum et al. 2003). Temperature has also been shown to affect size classes of fish differently, with smaller fish often impacted the most (Johnson and Evans 1991; Thompson et al. 1991; Bernard and Fox 1997; Pangle et al. 2004), however this is not always the case in fish which feed during winter (Lankford and Targett 2001; Connolly and Petersen 2003). Lower temperatures have been shown to increase mortality rates of fish infected with pathogens and parasites for several species including smallmouth bass (*Micropterus dolomieu*; Horning and Pearson 1973), gilthead sea bream (*Sparus aurata*; Domenech et al. 1997; Tort et al. 1998), and channel catfish (*Ictalurus punctatus*; Bly et al. 1993). In situ experiments have shown that temperature regimes (i.e. colder vs. warmer or constant vs. fluctuating) can influence energy use (Murphy et al. 2006) and immunosuppression (Lepak and Kraft 2008).

Fed vs un- Fed (multiple resource density levels)

Feeding and not feeding fish can provide valuable insights into the relative effect of feeding on survival. In these experiments, fed fish consistently have higher survival, condition, and energy content than starved fish (Thompson et al. 1991; Kirjasniemi and Valtonen 1997; Pangle et al. 2004). This is expected given that fish that are able to feed do not have to rely solely on their energy stores. Depending on the species, larger size may allow fish access to a wider suite of prey choices increasing consumption and subsequently survival. However, different prey densities may benefit smaller fish which require a smaller critical resource density to prevent decreases in size (Byström et al. 2006). Individual variability in activity and foraging rate can also influence survival, with prey availability determining the most appropriate strategy for survival (Micucci et al. 2003). In some instances, differences in the composition of food fed to experimental fish can influence survival by providing different essential nutrients or fatty acids which can increase the ability to acclimation to cold temperatures (Snyder and Hennessy 2003). Understanding how fish respond to starvation is also of critical importance, and substantial research has focused on how starvation and re-feeding disproportionately affects body composition and specific tissues across different temperatures (Kieffer and Tufts 1998; Larson et al. 2001; Van Dijk et al. 2005).

Acclimation rate

The rate of temperature decline to cold temperatures has been shown to have many effects on fish, commonly termed cold shock (Donaldson et al. 2008). If temperature declines at a fast rate, fish may be unable to acclimate physiological processes, resulting in a higher critical thermal minimum (Beitinger et al. 2000). Slower acclimation rates allow fish to acclimate physiological processes, thus

reducing the critical thermal minimum to a lower temperature (Reber and Bennett 2007). Temperature and acclimation tolerance can vary greatly within and across species and has been shown to be determined by such factors as latitude and geographic range, suggesting the potential for many fish species to demonstrate adaptations to local climatic conditions (Reber and Bennett 2007). Not all studies have documented an effect of acclimation rate on mortality (Lankford and Targett 2001).

Multiple treatments

In many cases, researchers attempt to address the response of fish to multiple stresses, for instance, they may have multiple temperature treatments and at each temperature they may separate treatments in which fish are fed and others where fish are starved. These experiments can be informative in how fish might respond to multiple stressors and illustrate synergistic effects on fish mortality and physiology. For instance, at lower temperatures, feeding rate may be reduced as metabolic rates decline, decreasing the importance of foraging. McCollum et al. (2003) looked at the effect of fish size, feeding regime, and temperature on over-winter mortality in white crappies (*Pomoxis annularis*), finding mortality was driven by different factors at different temperatures. By looking at multiple treatment effects, they were able to identify starvation as the driver of mortality at warmer temperatures ($>4^{\circ}$ C), but osmoregulatory failure appeared to drive mortality in the coldest treatments. Geographic origin may also influence survival and susceptibility of fish to over-winter mortality, suggesting over-winter mortality may exert substantial selection pressure (Fullerton et al. 2000; Garvey et al. 2003). Pratt and Fox (2002) looked at the interaction of size, prey availability, and predator presence/absence on survival of young-of-the-year walleye (*Stizostedion vitreum*), finding the presence of predators

increased the rate of energy use, increasing mortality of smaller individuals.

Documenting interactions between several treatments is common, suggesting survival of fish in the wild is likely driven by several interacting factors, making extrapolations from experimental results difficult unless field conditions are understood.

Field Data

Field data are commonly used in studies of overwintering fish because researchers can directly track mortality and physiology within a fish's natural habitat. These types of studies typically consist of tracking abundance, size or body composition over the course of the winter or pre- and post-winter. Often, these studies are conducted across two winters which differ in their duration and/or severity (i.e. a mild and severe winter). In contrast to experiments, analyses of field collections incorporate all winter stresses that fish are exposed to, providing a more realistic picture of fish responses to winter stresses. However, incorporation of multiple winter stressors makes it difficult to identify exact causes of mortality, and conditions, both of the fish and the environment, may not represent the average, may vary substantially across winters, and may not be closely monitored. The ability to accurately describe field conditions is especially challenging during winter, when cold temperatures and ice cover make sampling difficult and may lead to biased results. Additionally, the temporal scale of these studies may lead investigators to interpretation that is valid during the duration of their studies, but is not valid across multiple years. Given the many challenges associated with conducting field work during winter months, studies of this nature are often descriptive, providing interpretation based on observation alone.

Chronological sampling

Field studies will often track fish abundance and condition throughout or before and after the winter to gain an understanding of how fish physiological conditions change over time. Sampling before/after winter is used throughout the literature to demonstrate size-selective mortality of the smallest fish in the population over-the winter (Chevalier 1973; Toney and Coble 1979). Miranda and Hubbard (1994) were able to demonstrate shifting length-frequency distributions towards larger fish over the course of the winter, suggesting starvation of the smaller fish drove the shift, which was supported by reduced lipid content in smaller fish relative to larger ones. Identifying changes in body composition over winter is informative for identifying potential mortality drivers (Flath and Diana 1985; Pierce et al. 1980); however, it is difficult to determine timing of mortality events or when changes in body composition occurred. For instance, in some species, loss of lipids is minimal during the winter, and decreases the most as water temperatures warm following ice out (Pierce et al. 1980). By sampling fish multiple times over the course of a winter, researchers are able to identify more specific time trends in mortality and stored energy use, and offer more developed hypotheses about the relative importance of different sources of mortality (Eckmann 2004). Comparing collections of alive/healthy and dead/dying fish during winter months can also provide a powerful tool to explain mortality if differences between the two groups occur (Adams et al. 1985), however, these events can be rare and difficult to document.

Multiple winter comparisons

Comparisons across several winters, usually 2-3, differing in severity and/or duration are commonly used to assess interacting drivers of mortality under different conditions. Survival is typically higher during less severe, shorter winters, potentially

minimizing size-selective mortality (Morley et al. 2007). However, in some locations warmer winters result in fluctuating and/or colder water temperature resulting in a more stressful environment for fish, which are forced to constantly adapt enzymes and cellular membranes to function at several potentially colder temperatures (Murphy et al. 2006). In addition to monitoring climatic conditions across winters, these studies track the condition of fish entering winter and look at how this affects survival and subsequent recruitment to age-1 (Radke and Eckmann 1999; Sutton and Ney 2001; Morley et al. 2007). In almost all cases, years with larger, fatter fish experience higher survival, further supporting the importance of size in driving over-winter survival; however over-winter survival across years is likely driven by the interaction between fish condition and environmental factors. Within the growing season, additional prey resources available to larger, less-gape-limited fish may drive bimodal length distributions, influencing the relative proportions of large and small fish entering winter, and ultimately, the degree of over-winter mortality (Sutton and Ney 2001). However, effects of winter severity/duration may not influence survival if starvation is not a driving cause of mortality (Radke and Eckmann 1999; Fitzgerald et al. 2006).

Habitat sampling

An additional component of field sampling that has received less attention is the role of habitat in driving over-winter mortality of fish species. Habitat evaluation and sampling is difficult during winter months as cold temperatures, ice cover, and indirect relationships between air and water temperatures make it difficult to assess habitat heterogeneity and use by fishes across spatial and temporal scales. In many lakes, warmer winters as defined by air temperatures can actually result in colder water temperatures because a lack of ice formation results in constant heat lost to the atmosphere (Fitzgerald et al. 2006). Differences in temperature profiles of only a few

degrees can have substantial effects on mortality and physiological responses of fish (see above), however detection of potential temperature refugia is difficult.

Additionally, hypoxic conditions can be common during winter as consistent ice cover limits photosynthetic activity and atmospheric gas exchange, and can result in little oxygen being added to these habitats during winter months. “Fish kills” associated with anoxic conditions have been shown to drive community composition in small, shallow ponds (Tonn and Magnuson 1982). Larger systems may also be impacted if habitats providing temperature refuges are susceptible to hypoxia, resulting in death traps for fish seeking refuge in warm temperature (Bodensteiner and Lewis 1992). Model simulations of winter dissolved oxygen levels predict that the frequency of anoxia will decrease with continued climate warming, potentially reducing susceptibility of fish to winterkills (Fang and Stefan 1997; Fang and Stefan 2000).

Experiments and Field Data

Studies which combine laboratory/field experiments and field collections are widespread in studies of over-winter mortality in fish, and provide valuable insights not available in studies using only one approach. As discussed above, each of these approaches has limitations when used alone, however, by using both approaches researchers are able to realize the benefits of each approach and minimize limitations. Field collections allow researchers to validate experimental results which provide additional confidence in the interpretation of data. Additionally, discrepancies between the two approaches can be equally informative, highlighting differences between the conditions in the experiments and the field. These may arise for a variety of reasons, including confinement effects from experiments, feeding in wild fish, or use of different habitats than previously expected, which can be verified through stomach analysis of field collected fish or additional habitat

characterization/monitoring. By providing these multiple lines of evidence supporting or contradicting hypotheses, researchers are able to offer further discussion and understanding of the complexity of factors driving over-winter mortality and physiological responses in fish. Studies are usually short term, consisting of only one or two winters of data collection as conducting experiments and field collections can be resource intensive. As noted above, this may lead to interpretation that may not be valid across multiple years, however, by combining both experimental and observational results this can hopefully be avoided or minimized.

Experiment with field validation

Evaluating the response of fish to experimental conditions and then verifying results through field sampling is one of the most effective methods to increase our understanding of factors driving fish over-winter mortality and physiology. By implementing both methods researchers have been able to demonstrate the importance of temperature (Bodensteiner and Lewis 1992), energy stores (Hurst et al. 2000; Sogard and Olla 2000), and feeding (Dutil et al. 2003), on over-winter mortality in both laboratory settings and field collections. Inconsistencies between experimental results and field observations can also be informative, and have been used to demonstrate that fish in the wild are feeding (Dutil et al. 2003). Laboratory experiments on fish can be used to establish mortality thresholds based on energy content (Paul and Paul 1998), body composition (Dutil et al. 2003), and lipid reserves (Biro et al. 2004), and then extrapolated to field collections to infer the relative importance of different mortality sources. Field collections of fish with energy levels lower than the mortality threshold determined by a laboratory experiment, illustrates laboratory mortality may not be driven by starvation (Hurst et al. 2003).

Temperature experiment with habitat assessment

As discussed above, laboratory experiments can be used to identify differential responses of fish to different temperatures which can then be verified through a combination of field sampling and habitat characterization. Sampling fish from habitats with different temperature to identify effects of temperature on mortality and physiological responses would be challenging, and difficult to attribute to temperature alone. Interestingly, fish species adapted for cold temperatures may experience energetic benefits at lower temperatures, which reduce metabolism, prolonging the duration of time a fish can rely on limited energy stores (Kooka et al. 2007). Changes in habitat suitability for fish can also change over winter (Bodensteiner and Lewis 1992), and knowledge of these changes is necessary in extrapolating experimental results to field conditions experienced by fish. Understanding potential cost/benefits of different temperatures to over-wintering fish is important when trying to assess/identify quality habitat.

Long-term analysis

Correlation analysis of long-term patterns in fish size/condition, climate, and recruitment dynamics offer unique perspectives not available through experiments and field collections. Fish size/condition is commonly represented as length, energy content, or body composition of fish entering winter, and provides an index of a fish's ability to persist through the stress of winter conditions (see above). Climate is typically some measure of winter duration or severity, such as ice duration, average water temperature or a more complex representative of multiple climatic factors. Recruitment is often defined as the number of fish which recruit to age-1 or a standardized sampling protocol already established. These analyses provide valuable insights by incorporating multiple mortality drivers across years, which cannot be

tested using one or two years of data. Additionally, multiple years of data provide the opportunity to address density-dependent and density-independent processes across years. One must use caution when interpreting observed trends and relationships as this method is not well suited to assign specific causes of fish mortality. A more widespread application of this approach is also limited by the lack of adequate long-term datasets designed to assess the role of over-winter mortality on recruitment dynamics, requiring the use of less than ideal surrogates for more desired indices. For instance, climatic variability across years is often measured as air temperature which may not directly translate into water temperatures.

Long-term correlative trends:

Long-term fish and climate data have been used in several examples to assess the importance of winter in driving recruitment dynamics of fish. Post et al. (1998) looked at the entire first year of life, incorporating information on hatch date, growth rate, predation, and winter mortality of largemouth bass (*Micropterus salmoides*) to understand how density dependant and independent drivers of mortality can affect recruitment in fish. As adult and juvenile largemouth bass abundance decreased, the importance of predation in determining recruitment declined, and the importance of length entering winter and its effect on over-winter mortality drove recruitment (Post et al. 1998). Long-term datasets can also be informative for identifying the role of habitat in over-winter survival, by identifying how habitat availability and suitability vary under different climatic conditions and how this affects recruitment (Power et al. 2008). In most cases, studies are limited to the species of interest, as quality data set of multiple species are limited. Using a long-term data set for Oneida Lake, NY, Fitzgerald et al. (2006) were able to demonstrate how yellow perch (*Perca flavescens*), white perch (*Morone americana*) and gizzard shad (*Dorosoma cepedianum*) can

buffer each other from walleye predation, and drive recruitment dynamics. Through this data set, they were able to tease apart the relative importance of starvation and predation in driving recruitment dynamics for the prey species. In some cases, large scale shifts in winter conditions can alter community composition entirely (Jackson et al. 2007; Henriques et al. 2007); however, assessment of community wide responses to fluctuating climate conditions are typically rare (Massol et al. 2007).

DISCUSSION

There are a variety of methodologies used to address questions about fish over-winter mortality and physiology. Depending on the objectives of a particular study some methods may be more appropriate than others. Experimental approaches are ideal for understanding individual responses of fish to winter conditions, providing the opportunity to test research objectives in a controlled environment. Field observations can be used to identify how fish respond to the multiple stressors they experience in nature. Combining experimental and field data provides a valuable tool for researchers attempting to validate and extrapolate experimental results to field observations and conditions. Finally, long-term correlation analysis of fish and climatic conditions with recruitment dynamics provides a valuable tool for understanding how different factors drive over-winter mortality across multiple years. Though these methods have been instrumental in developing our current level of understanding of how winter conditions influence fish survival and ultimately recruitment, the increased application of multiple methods will be necessary to accurately predict the response of aquatic ecosystems and fish communities to projected climate change.

In a recent review of over-winter mortality in fish, Hurst (2007) calls for increasing attention to be paid to several drivers of winter mortality, including

causes/drivers of mortality, relationship between starvation and additional mortality stressors, predation as a source of mortality, and the role of habitat. Accomplishing these goals will require that researchers use unique combinations of current methods or explore new, creative methodologies in addressing over-winter mortality in fishes. For instance, laboratory experimentation of temperature effects on causes and rates of mortality should be related to measurements of habitat heterogeneity and dynamics. Further advances in this area will require that researchers overcome the obstacles to conducting winter investigations identified by Hubbs and Trautmann (1935) over 70 years ago.

Changes in winter duration and severity as a result of climate change will have major effects on the degree and causes of over-winter mortality in fishes. Detecting changing trends in over-winter mortality and subsequent effects on population dynamics will require innovative analysis of existing long-term datasets. Long-term datasets offer a unique opportunity to validate and extrapolate results from short term experimental and field studies and will provide a powerful tool for using information from short term studies to predict fish recruitment. If possible, modification of existing data sets or development of new long-term datasets should be designed to specifically address the causes and extent of over-winter mortality in fish populations.

One of the major challenges in studies of over-winter mortality in fish is the application of results to a broad range of species and systems. In many cases, drivers of mortality and physiological responses in fish are species-specific and may not provide insight into drivers of mortality in other species. In fact, applying results learned from a species in one location may not be applicable to the same species in wider range of locations, specifically at lower or higher latitudes. Additionally, interactions between multiple drivers of mortality may vary by system, making extrapolation of results extremely difficult. Researchers have demonstrated the

common occurrence/phenomena of size-selective mortality through starvation or starvation-related mortality and predation, and there is a greater need for additional “rules” with widespread applications. However, it seems widespread complexity may be the most unifying theme across species and systems, complicating prediction of future change.

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CHAPTER 2:

TEMPORAL AND SPATIAL VARIABILITY IN DRIVERS OF GIZZARD SHAD (*DOROSOMA CEPEDIANUM*) OVER-WINTER MORTALITY

ABSTRACT

Winter limits resource availability in temperate lakes, exerting a strong influence on the northern distributions of many temperate species by limiting the recruitment of age-0 fishes. Gizzard shad (*Dorosoma cepedianum*) are at the northern extent of their range in Oneida Lake, NY, and over-winter mortality of age-0 fish is high. Here I evaluate age-0 shad over-winter mortality through a combination of experiments and field sampling during the winters of 2005-6 and 2006-7. I designed two experiments to evaluate shad survival and stored energy usage before and after ice formation. In the first experiment, shad were placed into cages in Oneida Lake marinas during three time periods prior to ice formation. Shad experienced high mortality (>75%) in all cages as temperature dropped below 8° C. I observed no consistent patterns of length-dependant mortality or changes in percent dry weight. However, the visceral-somatic index (VSI) decreased during all time periods indicating shad were disproportionately using visceral tissues. In the second experiment, shad were exposed to three temperature-treatments of 1, 2 and 4° C in experimental cold rooms. Survival analysis indicated mortality of shad was highest in the coldest temperature treatments, with smaller fish dying at a faster rate. Logistic regression indicated VSI and percent dry weight are significant predictors of mortality, though the fit was weak. Field collected shad did not exhibit similar patterns of energy use as no change in VSI was observed indicating proportional use of visceral and somatic tissues. Results show that shad mortality during acclimation is

independent of size, but may become size-dependent as they exhaust limited energy reserves. Monitoring of physical and chemical conditions within Oneida Lake habitats indicated marinas as key temperature refuges for shad and large congregations of age-0 shad were observed in those areas. However, consistent ice cover can lead to anoxic conditions within these habitats. These observations suggest habitat selection plays an important role in shad over-winter survival, and the dynamics of these habitats influences recruitment of shad to age-1. Within any given year, shad survival is likely a function of length entering winter, rate of temperature decline preceding ice-on, and ice duration. Climate change projections for Oneida Lake (i.e. increasing summer water temperatures and decreasing winter severity/duration) should increase over-winter survival of gizzard shad.

INTRODUCTION

Over-winter mortality in fish can be a significant ecological force, affecting population dynamics (Hurst and Conover 1998; O’Gorman et al. 2004; Ward et al. 2006), and limiting geographic ranges (Shuter and Post 1990). Starvation and predation are commonly identified as major determinants of over-winter mortality (Adams 1985; Sogard 1997; Fitzgerald et al. 2006); however, research is increasingly identifying additional sources of mortality driven by a species’ inability to acclimate and/or function physiologically at cold temperatures (Hurst 2007; Donaldson et al. 2008). Over-winter mortality is most likely driven by several mechanisms interacting over spatial and temporal scales (White et al. 1987; Bodensteiner and Lewis 1992; Hurst 2007; Donaldson et al. 2008). The importance of over-winter mortality in driving population dynamics increases near a species’ northern distribution where winter conditions are often harshest (Shuter and Post 1990).

Over-winter mortality of many fish species can be size-selective (Toneys and Coble 1979; Sogard 1997; Hurst 2007) and is often attributed to decreased susceptibility to predation and starvation as fish reach larger sizes. Observation of size-selective predation on smaller individuals is common, as smaller fish are susceptible to greater predation risks due to decreased avoidance capabilities, higher risk-taking behavior and vulnerability to a greater suite of potential predators (Werner and Gilliam 1984; Sogard 1997). Energy depletion and starvation are also common during winter months, as many fish cease or reduce feeding, requiring dependence on energy stores. Smaller fish tend to have fewer energy reserves and metabolize at higher specific rates relative to larger fish (Oliver et al. 1979; Toneys and Coble 1979; Post and Parkinson 2001), limiting the duration of time they can survive on stored energy (Hurst and Conover 2003). Decreasing energy levels through winter have been observed for many species in both laboratory and field settings (Pierce et al. 1980; Flath and Diana 1985; Hurst et al. 2000; Hurst 2007). Though convincing evidence exist identifying predation and starvation as important causes of size-selective mortality, the two mechanisms are not independent. For instance, a starving fish may increase activity levels searching for food, resulting in greater risk of predation (Biro et al. 2003) and faster energy use. Similarly, starving or thermally stressed fish may have decreased predator avoidance capacity which can also increase susceptibility to predation (Ward and Bonar 2002; Smith and Hubert 2003).

Reduced fish physiological function can contribute to over-winter mortality in fish (Hurst 2007, Davidson et al. 2008). Physiological stress can take the form of decreased cell membrane fluidity (Snyder and Hennessey 2003), osmoregulatory failure (Stanley and Colby 1971, Johnson and Evans 1996), and immunosuppression (Lepak and Kraft 2008). At the northern extent of species' ranges, winter temperatures can frequently drop below those easily tolerated by all individuals,

resulting in mortality of fish that are unable to acclimate and function at extreme winter temperatures (Johnson and Evans 1996, Lankford and Targett 2001, Hurst and Conover 2002). Laboratory experiments exposing fish to controlled temperature treatments have revealed high levels of fish mortality seemingly unrelated to starvation in the coldest treatments, while fish in the slightly warmer treatments exhibit reduced mortality that has been linked to starvation (Johnson and Evans 1996, McCollum et al. 2003). Additionally, tolerance of extreme temperatures does not increase as the temperature range fish are exposed to increases (Currie et al. 2004). In many species, the rate of temperature change, or acclimation rate, can influence levels of mortality immediately or over time (Beitinger et al. 2000, Donaldson et al. 2008), though not always (Lankford and Targett 2001). Donaldson et al. (2008) summarize the current knowledge of primary, secondary, and tertiary responses of fish to cold shock in a recent review, highlighting the need for additional research to fully understand sub-lethal effects of cold shock to fish.

Recently, growing attention has focused on understanding the interaction between starvation and thermal stress in driving over-winter mortality (Hurst 2007). Starving fish may become increasingly sensitive to cold temperatures as reduced energy stores force fish to allocate limited resources to maintain critical life sustaining functions. Fish species store energy differently, and responses to starvation may vary depending on the particular energy storage strategy a species utilizes. Some species (e.g. salmonids and clupeids) accumulate lipid stores within muscle tissues, while others (e.g. percids, gadids, centrachids) accumulate lipid stores as visceral fat or within their livers (Shul'man 1974, Diana 2004). As a result, assessment of energy sources used by fish (i.e. liver; Power et al. 2000) or changes in body composition of different tissue types (i.e. visceral vs. somatic) during periods of starvation could help identify mechanisms of physiological stress-related mortality.

Gizzard shad (*Dorosoma cepedianum*) is a southern species whose northern range was historically southern Ohio. Over the past century, its range has expanded several hundred kilometers (White et al. 1987), with most expansion occurring during periods of warm winter temperatures. High over-winter mortality of age-0 shad likely sets the northern extent of their range (Bodola 1955, White et al. 1987). Shad are known to become disorientated at cold temperatures and have high mortality at temperatures below 4° C (Heidinger 1983; Adams et al. 1985; White et al. 1987). Reports of massive winter die-offs are common across northern portions of their range (Bodola 1955; Walburg 1964). Gizzard shad over-winter mortality has been observed to be size-selective, and is thought to be a function of cold stress, starvation, and predation. In southern Ohio, size-selective mortality of age-0 and adult gizzard shad has been attributed to starvation (Adams et al. 1985) based on observed over-winter decreases in whole fish dry weight, energy content, and percent lipid (Pierce et al. 1980). Shad over-winter mortality also appears to be related to winter duration, further supporting the importance of starvation (Walburg 1964; Heidinger 1983; White et al. 1987). Several studies conducted at the northern extent of the gizzard shad range have found evidence that other factors in addition to starvation may be driving shad mortality (Bodola 1955; White et al. 1987). In Lake Erie, White et al. (1987) observed no change in percent lipids of gizzard shad sampled throughout the winter, finding evidence that other factors in addition to starvation may be driving mortality, including inability to acclimate enzyme and biological membrane function, inability to mobilize stored lipids, and utilization of liver glycogen and tissue leading to liver failure. At higher latitudes where temperatures routinely drop below 4° C for extended periods of time, the relative importance of thermal stress in driving shad mortality is likely increased. At these latitudes, the importance of thermal refuges to survival during winter months would also be expected to increase.

In Oneida Lake, NY, shad over-winter mortality is high, and predicting the effect of climate change on over-winter mortality remains difficult. A hydrodynamic model for Oneida Lake predicts decreasing frequency and duration of ice cover over the next century (DeStasio et al. *submitted*), and forecasting the response of the gizzard shad population to these changes will require a better understanding of factors driving over-winter mortality. Here I combine the results of a series of experiments and field collections during the winters of 2005-06 and 2006-07 to explore spatial and temporal drivers of over-winter mortality in age-0 gizzard shad. Specifically, I test for differences in shad mortality during three time periods prior to ice formation to explore the effect of changing temperatures on shad mortality using *in situ* cage experiments. Additionally, I test the effect of different winter temperatures on shad survival and changes in dry weight composition in a controlled experimental setting at stable temperatures (1, 2, and 4° C). Observations from these experiments are compared to field collections during the winters of 2005-6 and 2006-7, and used to evaluate the use and suitability of different habitats for shad over-winter survival. The results are used to develop a conceptual model which identifies conditions promoting shad over-winter survival and can be used to predict the response of shad over-winter mortality to climate change.

METHODS

Study Site

Oneida Lake, NY is a large, shallow lake (area ~207 km², maximum depth ~16.6 m, mean depth ~6.5 m) located in the fertile plain of Lake Ontario. The Cornell Biological Field Station (CBFS) is located on Oneida Lake, and CBFS researchers have collected limnological and fisheries data for over 50 years. This dataset has been

instrumental in identifying biotic and abiotic drivers of aquatic ecosystem structure and function across trophic levels (Mills et al. 1978; Forney 1980). Gizzard shad are not native to Oneida Lake, and were first observed as large schools of age-0 fish during the mid-1950's (Forney 1980). During the following two decades shad were rarely observed in any of the CBFS's long-term monitoring, until the early 1980's when large schools of age-0 shad and catches of adult shad in standardized gillnet surveys became increasingly common (Rudstam and Jackson 2008; Figure 2.1). Over-winter mortality of age-0 gizzard shad is high in Oneida Lake (~100%), and it is suspected that changes in winter severity and duration related to climate change may decrease over-winter mortality.

Experimental Design

I designed two experiments to evaluate interactions between temperature and the importance of starvation as a source of mortality for gizzard shad during two winter time periods. The “acclimation” period is prior to ice formation, when temperatures decrease to near zero but continue to fluctuate and it is suspected shad mortality will be driven by an inability to acclimate to cold temperatures. The “starvation” period is after ice formation, when temperatures are near zero and relatively constant and mortality is suspected to be driven by starvation. The effect of changing temperatures on mortality and energy use during the “acclimation” period was tested *in situ* by placing gizzard shad into cages within the lake. The effect of different temperatures (1, 2, and 4° C) on mortality rate and energy use during the “starvation” period was tested in the laboratory. Physical and chemical conditions were monitored within Oneida Lake habitats to evaluate the suitability of different habitats for over-wintering shad as determined from the cage and tank experiments.

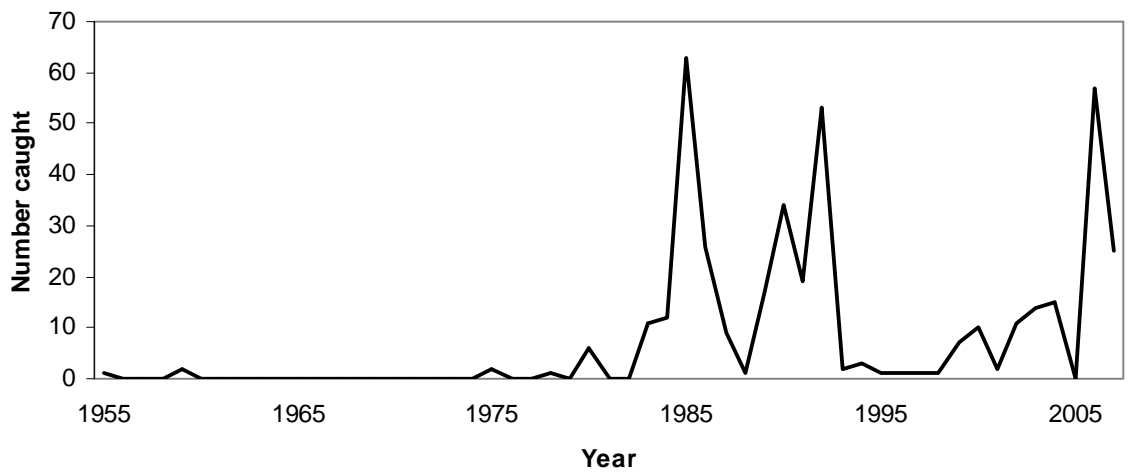


Figure 2.1. Catches of adult gizzard shad in Oneida Lake, NY. Temporal trends of the number of adult gizzard shad caught in gillnets on Oneida Lake, NY through the CBFS standardized long-term monitoring.

Field collections were made throughout the duration of both experiments to validate experimental observations and to evaluate gizzard shad habitat use during winter.

Cage experiment

Mortality was evaluated *in situ* during the “acclimation” period during the fall and winter of 2006-7. Cage experiments were conducted over three time periods, chosen to assess differences in shad energy use and mortality under different temperature regimes (Figure 2.2). Period 1 had warm, (~8° C) stable water temperatures. Period 2 had declining water temperatures, dropping from 8° C to below 2° C. Period 3 had cold, fluctuating water temperatures less than 4° C. Experimental sites (Table 2.1) changed each time period to reflect observed changes in shad habitat usage: Period 1- protected harbor; Period 2 - tributary deep hole and protected marina; Period 3 – two protected marinas. During Period 1, only one cage was moored, however, subsequent time periods had two cages moored at each of two sites (total of 4 cages/time period).

Cages were cylindrical (2 m diameter by 1 m height) and constructed from welded ground rods and landscaping fence (6.35 mm mesh). Each cage was stocked with approximately 200 YOY gizzard shad collected at each experimental site using an electro-fishing boat (Smith-Root electronics, 354 V pulsed DC current, pulse rate of 60 Hz, 6 A of current into water). During time period 1, the cage was stocked with ~800 shad. Upon capture, fish were immediately transported to cages. Once stocked, cages were lowered to the lake/tributary bottom and left undisturbed until the experiment was terminated (approximately 2-4 weeks). Sampling throughout the experiment was not possible, as any tampering with cages appeared to stress shad, potentially contributing to mortality and biasing results. Upon completion of each experiment, surviving shad were counted and a sample was saved for comparison with

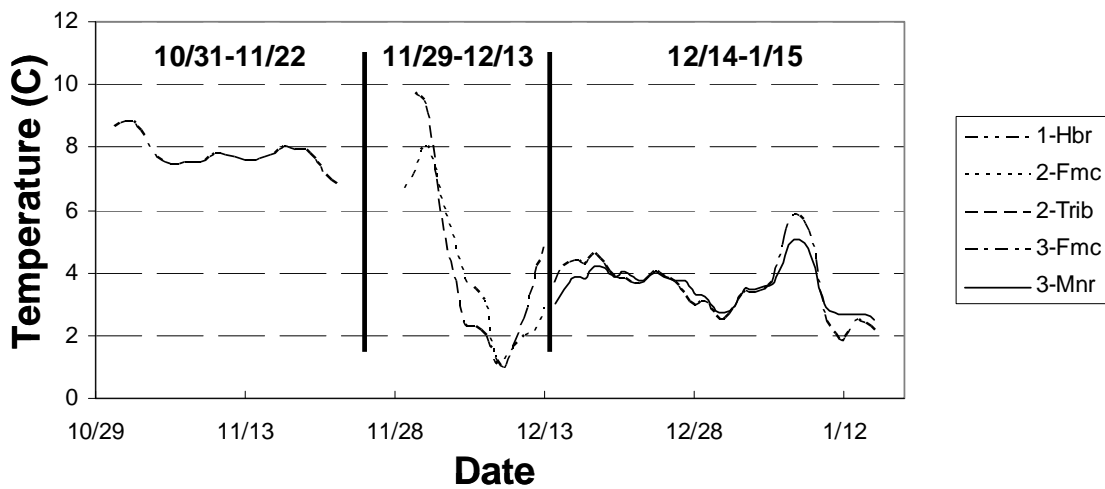


Figure 2.2. Cage experiment temperature profiles. Temperature profiles from different sites over duration of cage experiments. Sites and time periods are protected harbor – time period 1 (1-Hbr), tributary – time period 2 (2-Trib), protected marina – time period 2 (2-Fmc), and 2 protected marinas – time period 3 (3-Fmc; 3-Mnr).

Table 2.1. Cage experiments summary table. Dates, # days, percent mortality and mean (± 1 SE) length (mm), percent dry weight (% DW), relative somatic dry weight (Rela SOM), relative visceral dry weight (Rela VSC), and visceral-somatic index (Dry VSI) for initial reference and final surviving fish across time periods, sites and cages. Cage values significantly (Dunnett's test, $\alpha = 0.05$) different from the initial reference sample are indicated in bold.

Time period	I	II	II	III	III
Location	Harbor	Fremac	Tributary	Fremac	Mariner
Dates	10/31 - 11/22	11/29 - 12/13	11/29 - 12/13	12/14 - 1/15	12/14 - 1/15
# Days	22	14	14	32	32
Mortality (%)					
Cage 1	4.4	75.0	99.5	91.0	68.5
Cage 2	-	75.0	93.0	74.0	70.0
Length (mm)					
Start	95.2 (1.64)	99.7 (1.92)	95.8 (2.13)	100.1 (2.35)	89.3 (1.96)
Cage 1	89.7 (2.05)	100.5 (1.65)	101.9 (2.20)	85.3 (1.63)	91.0 (2.14)
Cage 2	-	98.5 (1.60)	-	92.4 (1.70)	86.5 (2.41)
% DW					
Start	18.2 (0.30)	17.3 (0.26)	17.9 (0.27)	17.1 (0.26)	17.9 (0.17)
Cage 1	17.4 (0.22)	16.5 (0.15)	16.0 (0.27)	16.8 (0.34)	17.3 (0.21)
Cage 2	-	17.8 (0.24)	-	17.2 (0.21)	16.4 (0.20)
Rela SOM					
Start	1.01 (0.03)	0.97 (0.02)	0.90 (0.02)	0.94 (0.02)	0.95 (0.02)
Cage 1	0.93 (0.02)	0.91 (0.01)	0.85 (0.02)	0.80 (0.03)	0.84 (0.02)
Cage 2	-	0.95 (0.01)	-	0.84 (0.02)	0.77 (0.02)
Rela VSC					
Start	1.02 (0.03)	0.84 (0.02)	1.14 (0.05)	0.86 (0.02)	0.84 (0.02)
Cage 1	0.74 (0.01)	0.73 (0.01)	0.77 (0.03)	0.69 (0.02)	0.57 (0.01)
Cage 2	-	0.80 (0.01)	-	0.72 (0.02)	0.52 (0.01)
Dry VSI					
Start	0.104 (0.002)	0.093 (0.001)	0.129 (0.005)	0.097 (0.001)	0.090 (0.001)
Cage 1	0.082 (0.001)	0.087 (0.001)	0.097 (0.002)	0.086 (0.002)	0.071 (0.001)
Cage 2	-	0.090 (0.001)	-	0.088 (0.001)	0.070 (0.001)

fish collected at the start of each experimental time period. All fish were frozen in water immediately following capture or termination of the experiment. Dead fish were counted to calculate percent survival, however, no dead shad were saved since they were highly deteriorated and time since mortality could not be determined. Water temperature profiles at each experimental location were recorded throughout with a continuously reading HOBO temperature recorder (Onset Computer Corporation, Bourne, Massachusetts, USA).

For analysis, fish were thawed, measured (total length) and weighed before being dried at 65° C until a constant weight was achieved, typically 120 hours. Visceral and somatic tissues were weighed and dried separately to calculate percent water, relative visceral and somatic dry weight, and visceral-somatic index (VSI). Visceral tissue is defined as all internal organs from the esophagus to the anus. VSI is the ratio of visceral to somatic dry weight (Kaufman et al. 2007). Relative visceral and somatic dry weights were calculated by the ratio of the observed tissue dry weight to a predicted tissue dry weight calculated from a standard length-dry weight equation. Visceral and somatic standard length-dry weight equations were established by fitting a regression through the log-transformed length and dry weight of fish collected from time period 1 before the experiments were started. Visceral and somatic standard length-dry weight equations generated during time period 1 were significant (visceral: $W = 0.001 * L^{2.98}$, $F_{1,28} = 79.97$, $p < 0.001$; somatic: $W = 0.008 * L^{2.50}$, $F_{1,28} = 75.78$, $p < 0.001$) and these equations were used across all subsequent time periods.

Analysis-of- variance (ANOVA) was used to test for significant differences between reference and final fish measurements at each site within each time period. The reference sample is the initial sample of fish collected at the start of each experimental site and time period. If a significant difference was detected, Dunnett's test was used to detect which final fish measurements were significantly different from

the reference sample collected at the beginning of each time period. A t-test was used during time period 1 (only one cage) and period 2 at the Anchorage site since cages were pooled due to low survival in both cages.

Tank experiment

Laboratory studies were conducted during the winter of 2006-7 to evaluate gizzard shad mortality rates and thresholds at different winter water temperatures (1, 2, and 4° C). Age-0 gizzard shad (72 – 133 mm) were collected from Oneida Lake, NY on November 19, 2006 using a beach seine (22.8 m x 1.5 m x 6.35 mm delta heavy duty 22 kg mesh), when the water temperature was 8° C. Fish were immediately transferred to the CBFS laboratory using a 600 L tank containing oxygenated lake water. At the laboratory, 100 fish were placed into each of nine 800-L flow-through tanks (total 900 fish) divided into three cold rooms (three tanks per room; Figure 2.3). Cold rooms were fed from a common source of 8° C dechlorinated groundwater to a reservoir tank within each room to attain desired temperature before being fed to individual tanks. Water flow-over from individual tanks was drained to the septic system. Tanks were maintained at 8° C while fish were allowed to acclimate to the tanks for three days, after which they were treated with a weak solution of formaldehyde to minimize disease related-mortality. Fish were treated once every 48 hours for a total of three treatments. Upon completion of the disease treatment, temperatures in the cold rooms were lowered at a rate of 0.33° C/day to allow fish adequate time to acclimate and avoid mortality associated with the temperature change. Individual cold rooms were lowered to 4, 2, and 1° C and maintained within \pm 0.25° C once final temperature was reached. Each cold room maintained a constant photoperiod of 10L:14D throughout the experiment. Fish were not fed as the literature indicates that shad do not feed at temperatures below 10° C (White et al. 1987).

Tank status was checked daily and temperature, dissolved oxygen and conductivity were recorded to assess similarity of conditions within tanks. Dead fish were removed, frozen in water, and the number remaining was recorded. Fish were grouped according to room and tank number to address location-specific differences in mortality. The experiment was continued until all fish were dead. In addition to removing dead fish, five live fish were removed from each tank, euthanized, and frozen in water when the temperature reached 4° C, and an additional 5 live fish were removed on days 10, 20, and 45, if numbers remaining were sufficient. In the two coldest rooms, fewer than five live fish were removed on multiple occasions due to a limited number of surviving fish.

For analysis, all fish (live and dead) were thawed and processed following the same protocol used in the cage experiments, providing individual fish length, wet weight (visceral and somatic), dry weight (visceral and somatic), percent dry weight, relative visceral and somatic dry weight, and VSI. Standard visceral and somatic length-dry weight equations were established from fish sacrificed at the beginning of the experiment (November 19, 2006) and were both significant (visceral: $W = 0.001 * L^{3.30}$, $F_{1,48} = 335.1$, $p < 0.001$; somatic: $W = 0.004 * L^{2.85}$, $F_{1,48} = 265.1$, $p < 0.001$)

Survival analysis, specifically the Cox Proportional-Hazard Model, was used to compare survival rates across rooms (Lankford and Targett 2001; Hurst and Conover 2002) using room, location, and length as input parameters. I used the Cox model so that the baseline hazard is unspecified, while the covariates enter the model linearly. Fish dying before the minimum temperature was reached were excluded from survival analysis as the treatment had not yet been applied. I assumed length was preserved throughout the experiment, and can therefore be used to predict survival duration. I use Akaike's Information Criterion (AIC) to select the most parsimonious

model, determined with the likelihood and number of parameters included for each candidate model. In the analysis, room and location are fixed. Logistic regression was used to evaluate mortality thresholds comparing fish collected alive to those which died during the experiment using input parameters: percent dry weight, relative somatic dry weight, relative visceral dry weight, and visceral-somatic index. All fish collected throughout the experiment were included in logistic regression analysis since I was not testing for a treatment effect on mortality thresholds. I used the stepAIC function in R (Version 2.8.1; Library – MASS; Venables and Ripley 2002) to perform stepwise AIC model selection to identify the most parsimonious model.

Field collections

YOY gizzard shad were collected throughout the fall and winter of 2005-6 and 2006-2007 at locations where shad were observed to congregate in high densities (i.e. protected harbors and marinas). During 2005-6, periods of open water throughout winter allowed us to collect samples of gizzard shad using a beach seine (described above in *tank experiment*). During the winter of 2006-7, consistent ice cover required that we employ a variety of gears to continue sample collections following ice on. Prior to ice formation, we use samples collected at the initiation of the cage and tank experiments. These samples were collected using an electro-fishing boat (cages; see above for description) or beach seine (tanks, see above for description). Following ice on in 2006-7, gizzard shad sampling was limited to small-mesh gillnets (21 m by 6 m, containing seven 3 m wide panels of bar mesh size 6.2, 8, 10, 12.5, 15, 18.7, and 25 mm) fished in marinas under the ice for four hours. Small-mesh gillnets were shortened to 1 m depth by wrapping bottom 5 m of net around the lead-line and tying with monofilament. Following capture, all samples were immediately frozen in water for later analysis. Frozen fish were processed identically to fish from the cage and

tank experiments, providing similar information on individual fish. Standard length-dry weight relationships of visceral and somatic tissues are the same as those used in the cage experiment since the initial sampling date and samples are identical.

I compared recruitment across 2005-6 and 2006-7 to evaluate conditions which promote over-winter survival. I define recruitment as adult gizzard shad being caught in the gillnet surveys conducted through the CBFS long-term monitoring program (Rudstam and Jackson 2008). If adult gizzard shad were collected, I used scales to back-calculate their length at age-0 (DeVries and Frie 1996). Length distributions of fish which survived the first winter are compared to length distributions collected prior to the 2005-6 and 2006-7 winters.

ANOVA was used to test for significant changes in length, percent dry weight, relative somatic dry weight, relative visceral dry weight, and dry weight visceral-somatic index across time for all sites during 2005-6 and at three sites during 2006-7. If a significant difference was detected, post-hoc Tukey's honestly significant differences (HSD) test was used to test which pair-wise comparisons were significantly different. A t-test was used to analyze the 2005-6 data for all indices except length.

Habitat characterization and monitoring

Habitat suitability for gizzard shad survival was assessed during the winters of 2005-6 and 2006-7. Habitats monitored represented potential over-winter habitats available to shad, and included the main lake, tributaries, and marinas. During the winter of 2005-6, a continuously reading HOBO temperature recorder was moored at the CBFS standard temperature station (10 m depth) which has been monitored since 1968 and in four major tributaries flowing into Oneida Lake. In the winter of 2006-7, the number of habitats monitored was expanded based on observations from the winter

of 2005-6. Temperature loggers were moored at three depths/locations within the main lake (nearshore- 2 m; offshore- 10 m (standard site), and in a deep hole- 16 m). Given the strong correlation observed across tributaries in 2005-6, only one tributary was monitored at two locations (0.5 km upstream from lake and 5 km upstream from lake). Temperature and dissolved oxygen profiles of marinas used in cage experiment were monitored following the observation of large numbers of shad congregating in these habitats during the winter of 2005-6. Temperature and dissolved oxygen profiles were measured at an additional seven marinas across the lake on February 20-21, 2007, to assess lake-wide variability of marina conditions.

Assessing habitat use by gizzard shad required a variety of gears be employed across habitats to overcome difficulties associated with sampling under winter conditions. In 2005-6, above average winter temperatures resulted in open water throughout much of the winter making it possible to use a beach seine (see description above) in nearshore habitats of the main lake during November, shifting to marinas as lake sampling became difficult. In 2006-7, pre-ice sampling of nearshore habitats and marinas was conducted with a bag seine and electrofishing boat (see above; *Field Collections*). Following ice formation, small-mesh gillnet sampling was limited to marinas (see above, *Field Collections*). Walleye diets were used to assess presence/absence of gizzard shad in offshore habitats in both years, as previous research on Oneida Lake has shown walleye continue to feed throughout the winter (S. Krueger, *pers. communication*) and will feed heavily on age-0 shad when available. Walleye diets were collected before and after ice formation through the use of three different gears. Gears used to assess walleye diets changed across the season (See Table 2.2) and included a 12.2 m bottom trawl (55 mm stretched-mesh cod end), an electro-fishing boat (see description above), and multi-mesh monofilament gillnets (45.7 m x 1.8 m, containing six 7.6 m wide panels of stretched-mesh size 89, 102, 114,

Table 2.2. Walleye diet survey summary table. Summary information of walleye diets surveys from main lake, including sampling date, site, gear, # nets (if applicable), # diets examined, and diet composition. Diet composition is broken into the number of fish with gizzard shad (Gizz), yellow perch (YP), other, unknown, and empty.

Date	Site	Gear	# Nets	# Diets	Stomach Contents				
					Empty	w/ Gizz	w/ YP	w/ Other	Unknown
10/18/2005	Three Mile Bay	TR	-	16	5	3	8	2	1
10/24/2005	Buoy 125	TR	-	34	15	1	5	7	10
10/27/2005	Buoy 117	TR	-	31	9	3	9	11	7
10/27/2005	Shackelton Point	TR	-	18	6	6	3	3	5
1/20/2006	Shackelton Point	GN	7	14	4	9	1	2	4
3/3/2006	North Bay	GN	2	7	7	0	0	0	0
3/10/2006	North Bay	GN	2	7	6	0	0	0	1
3/24/2006	Shackelton Point	GN	2	5	1	0	2	0	3
3/25/2006	Shackelton Point	GN	2	5	5	0	0	0	0
3/26/2006	Shackelton Point	GN	2	10	4	0	3	2	4
4/22/2006	Shackelton Point	GN	2	9	2	0	4	0	5
10/3/2006	Buoy 125	TR	-	10	8	1	0	1	1
10/3/2006	Shackelton Point	TR	-	4	3	0	0	0	1
10/11/2006	Buoy 117	TR	-	10	0	9	1	1	2
10/13/2006	Buoy125	TR	-	10	1	7	0	0	5
10/13/2006	Shackelton Point	TR	-	15	1	11	1	3	8
10/18/2006	Dutchmanns Island	EF	-	0	0	0	0	0	0
10/18/2006	Shackelton Point	EF	-	20	1	19	1	5	1
10/26/2006	Buoy 117	TR	-	16	4	10	1	6	4
10/26/2006	Buoy 125	TR	-	18	10	2	3	2	6
10/26/2006	Shackelton Point	TR	-	9	1	6	1	4	3
12/15/2006	Shackelton Point	GN	2	13	6	0	2	1	5
12/20/2006	Shackelton Point	EF	-	6	2	0	1	0	3
1/3/2007	Shackelton Point	EF	-	33	14	0	9	7	9
1/31/2007	Shackelton Point	GN	2	0	0	0	0	0	0
2/1/2007	Shackelton Point	GN	2	1	1	0	0	0	0
2/7/2007	North Bay	GN	2	28	24	2	1	0	3
2/14/2007	Shackelton Point	GN	2	1	1	0	0	0	0
2/16/2007	Shackelton Point	GN	2	1	1	0	0	0	0
2/20/2007	Shackelton Point	GN	2	2	2	0	0	0	0
3/1/2007	North Bay	GN	2	16	16	0	0	0	0
3/14/2007	North Bay	GN	2	25	24	0	0	0	1
4/28/2007	Shackelton Point	GN	2	22	13	0	1	0	8
5/2/2007	Erie Barge Canal	EF	-	44	36	0	1	1	7

127, 140, and 152 mm). Trawls were conducted during fall at four sites across Oneida Lake (see Fitzgerald et al. 2006 for description). Electrofishing surveys were conducted at sunset prior to ice formation during late fall and early winter near Shackelton Point, Oneida Lake. Gillnet surveys consisted of paired lines of two nets (4 nets total) fished within the same area unless otherwise noted for approximately 24 hours. Gillnet sites were selected based on ice cover during the 2005-6 winter and maintained during 2006-7.

RESULTS

Cage experiment

Gizzard shad mortality was low during time period I when temperatures were greater than 8° C, and high during time periods II and III when temperatures were lower than 8° C (Table 2.1). Within time periods II and III, mortality was highest in the tributary at 99.5 and 92.7% and lowest in the marinas, 69.5-91%. Across all time periods there was little evidence of size-selective mortality (Table 2.1, Figure 2.4), and three cages actually showed a shift towards a smaller length distribution. Percent dry weight showed inconsistent changes (Table 2.1, Figure 2.5). Relative somatic dry weight decreased significantly during time period 1 and 3 and showed inconsistent changes during time period 2 (Table 2.1, Figure 2.6). Relative visceral dry weight (Table 2.1, Figure 2.7) and VSI (Table 2.1, Figure 2.8) decreased across all time periods and sites except Cage 2 from Fremac during time period 2.

Tank experiment

The experimental set-up was successful in maintaining tanks at desired temperatures, and allowed gradual changes in tank temperatures. Gizzard shad

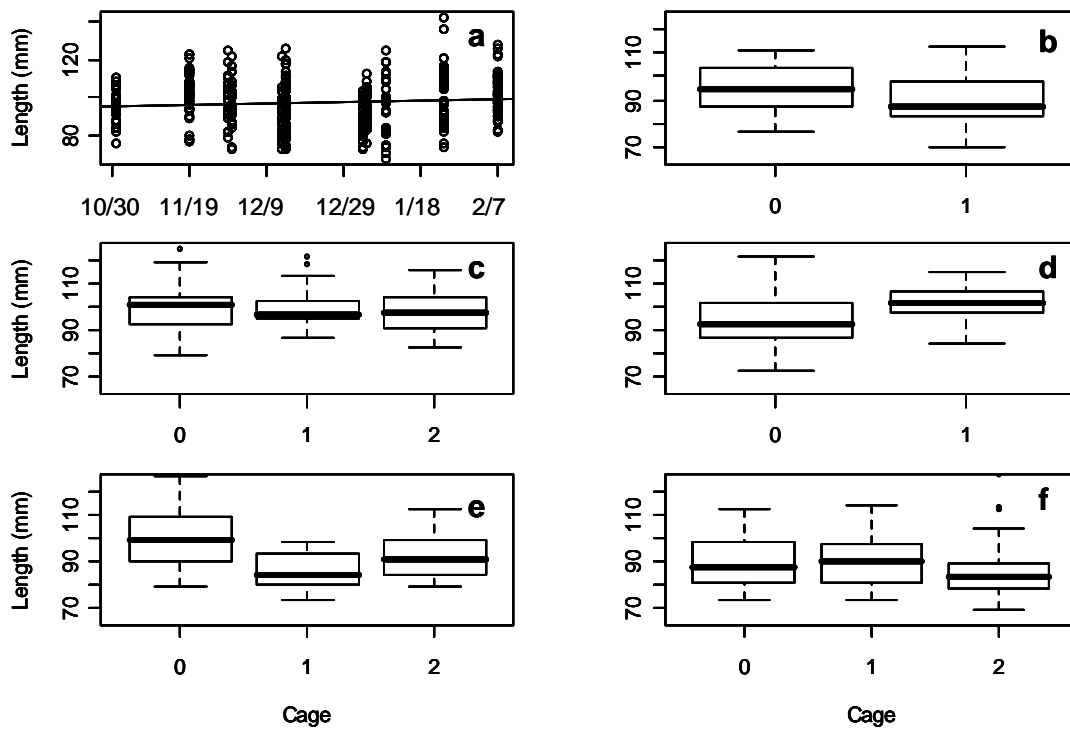


Figure 2.4. Length distributions from field collections and cage experiments. (a) Length over time from all field collections. (b-f) Boxplots of length distributions from cage experiments; 1-Hbr (b), 2-Fmc (c), 2-Trib (d), 3-Fmc (e), 3-Mnr (f). Initial reference sample indicated with 0; cages 1 and 2 indicated with 1 and 2, respectively.

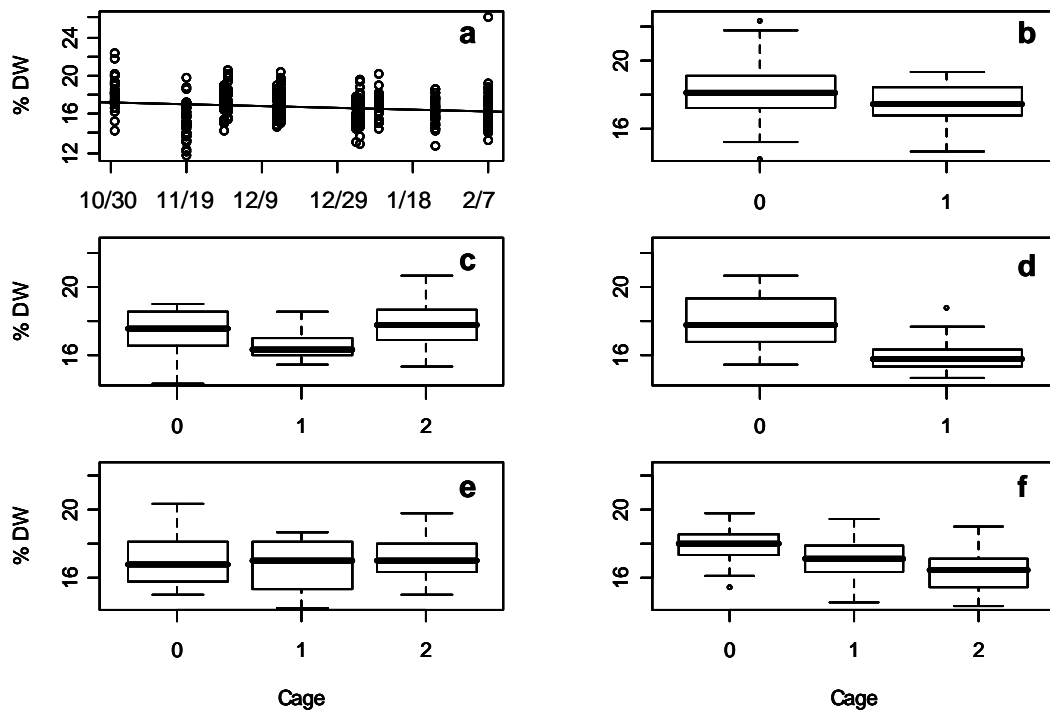


Figure 2.5. Percent dry weight (% DW) distributions from field collections and cage experiments. (a) Percent dry weight over time from all field collections. (b-f) Boxplots of percent dry weight distributions from cage experiments; 1-Hbr (b), 2-Fmc (c), 2-Trib (d), 3-Fmc (e), 3-Mnr (f). Initial reference sample indicated with 0; cages 1 and 2 indicated with 1 and 2, respectively.

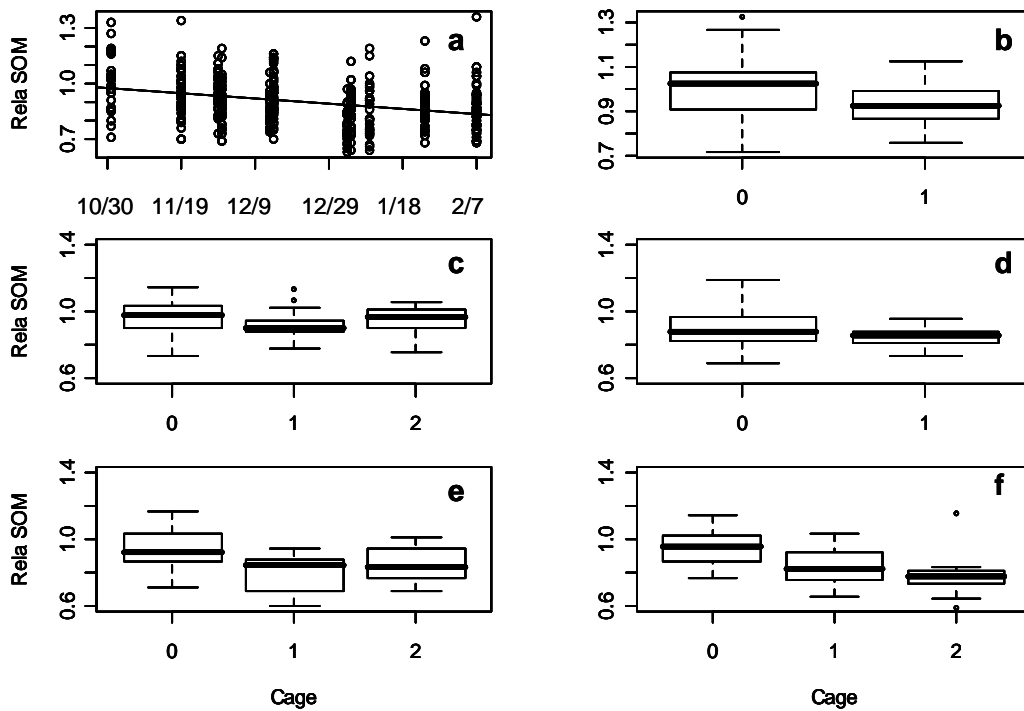


Figure 2.6. Relative somatic dry weight (Rela SOM) distributions from field collections and cage experiments. (a) Relative somatic dry weight over time from all field collections. (b-f) Boxplots of relative somatic dry weight distributions from cage experiments; 1-Hbr (b), 2-Fmc (c), 2-Trib (d), 3-Fmc (e), 3-Mnr (f). Initial reference sample indicated with 0; cages 1 and 2 indicated with 1 and 2, respectively.

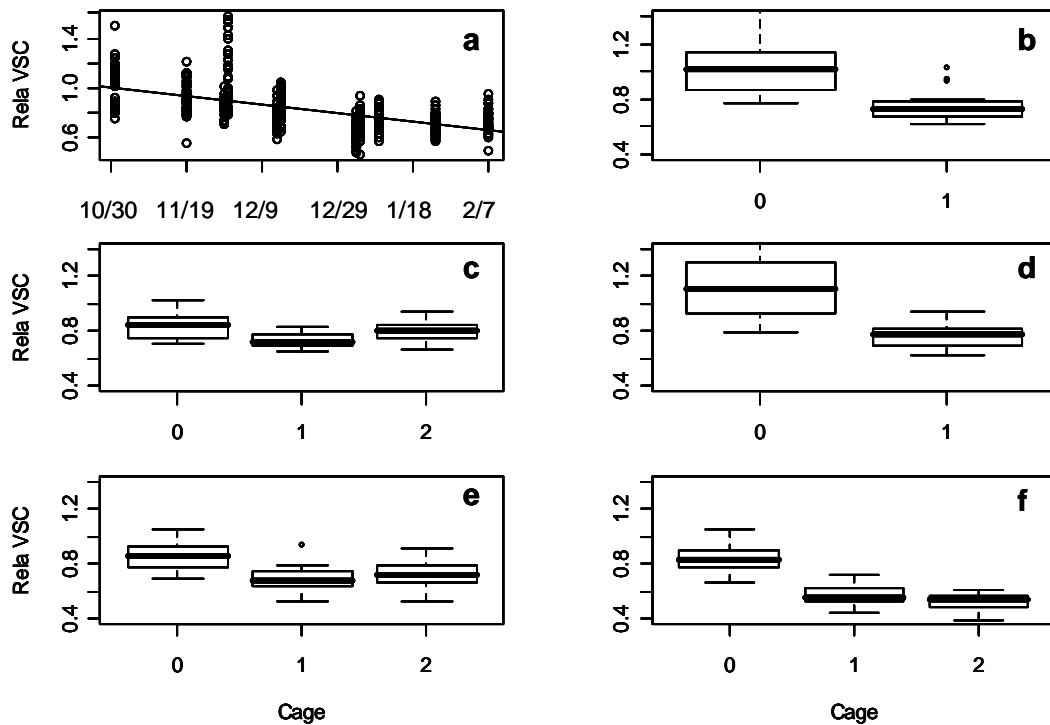


Figure 2.7. Relative visceral dry weight (Rela VSC) distributions from field collections and cage experiments. (a) Relative visceral dry weight over time from all field collections. (b-f) Boxplots of relative visceral dry weight distributions from cage experiments; 1-Hbr (b), 2-Fmc (c), 2-Trib (d), 3-Fmc (e), 3-Mnr (f). Initial reference sample indicated with 0; cages 1 and 2 indicated with 1 and 2, respectively.

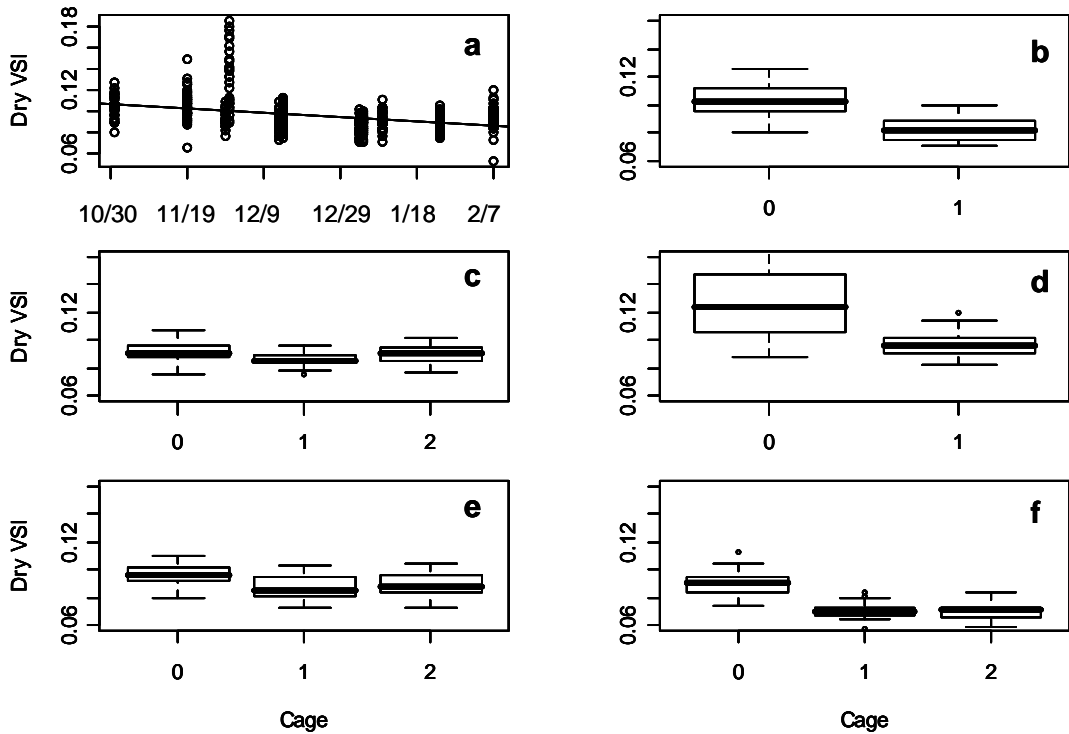


Figure 2.8. Dry weight visceral-somatic index (Dry VSI) distributions from field collections and cage experiments. (a) Dry weight visceral-somatic index over time from all field collections. (b-f) Boxplots of dry weight visceral-somatic index distributions from cage experiments; 1-Hbr (b), 2-Fmc (c), 2-Trib (d), 3-Fmc (e), 3-Mnr (f). Initial reference sample indicated with 0; cages 1 and 2 indicated with 1 and 2, respectively.

appeared to adjust to the tanks quickly and did not appear stressed during the acclimation process. Throughout the experiment, fish swam continuously, and were initially dispersed throughout each tank, but began to associate with the tank bottom as temperatures declined. Mortality during the acclimation period was minimal in all tanks in all rooms, peaking in all rooms as temperatures dropped below 4° C (Figure 2.9). In the coldest rooms, mortality remained high until all fish were dead. In the 4° C room, mortality slowed following the initial spike as temperatures dropped below 4° C.

Survival analysis and AIC indicated the model with room, location, and length was the most parsimonious in predicting shad mortality date. All other candidate models exhibited poor support. Room (temperature) explained the greatest variability, followed by location and length, respectively. Room and location coefficients are presented for room/location 2 and 3 (Table 2.3), and are relative to room/location 1. Negative coefficients in the selected model will increase survival time while positive coefficients decrease survival time. Therefore, room 1, the 4° C treatment, had the highest survival, followed by room 2 (2° C) and room 3 (1° C, Table 2.3, 2.4). Location 2 had the highest survival, followed by location 1 and location 3 (Table 2.3, 2.4). Length had a negative coefficient, and was the least important predictor of shad mortality (Table 2.3, 2.4).

Logistic regression and AIC indicated VSI and percent dry weight as significant predictors of mortality (Table 2.5, Figure 2.10). VSI explained the greatest amount of variation, followed by percent dry weight. Relative visceral and somatic dry weight did not significantly contribute to the model.

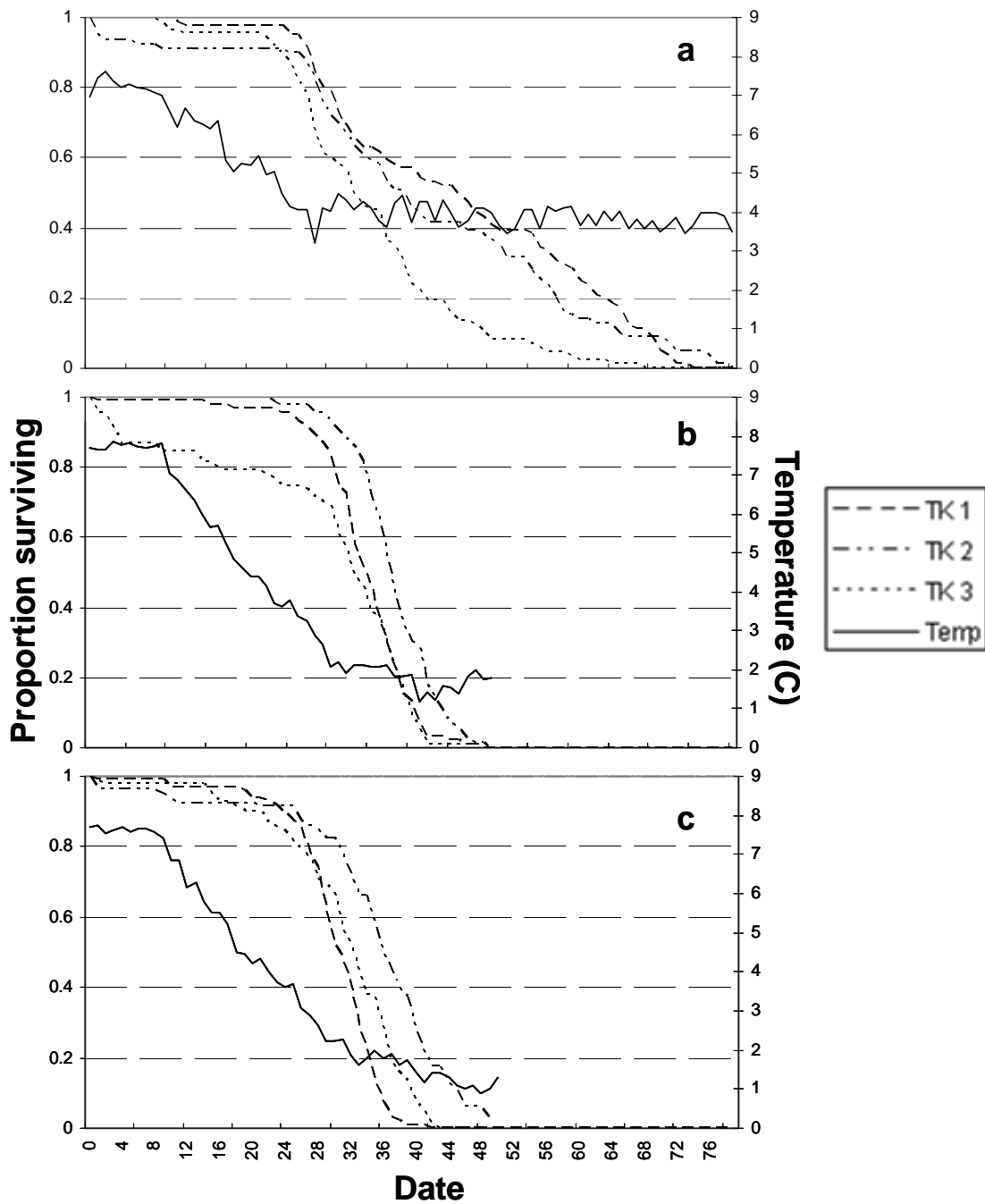


Figure 2.9. Proportion surviving and temperature ($^{\circ}$ C) over time from tank experiments. (a-c) Proportion of fish surviving and temperature over time across tanks from 4° C (a), 2° C (b), and 1° C (c) cold rooms.

Table 2.3. Survival model coefficients summary table. Survival analysis model coefficients and level of significance. Negative values increase survival time, while positive values decrease survival time.

Model Parameter	Coefficient	z value	p value
room 2	0.946	8.610	< 0.001
room 3	1.220	10.820	< 0.001
location 2	-0.480	-4.920	< 0.001
location 3	0.156	1.620	0.110
length	-0.012	-3.070	< 0.01

Table 2.4. Survival analysis predictions. Model predictions of number days to reach 20, 10, 5, and 2.5 % of initial population under different conditions. Temperature predictions are based on a 100 mm fish in location 1. Location predictions are based on a 100 mm fish in room 1. Length predictions are based on 75, 100, and 125 mm fish in room and location 1.

Parameter	Value	Survival Level			
		0.2	0.1	0.05	0.025
Temperature	4	32	41	47	49
	2	18	22	26	30
	1	15	18	21	25
Location	1	31	40	46	48
	2	43	48	49	50
	3	29	35	43	46
Length	75	27	33	41	45
	100	32	41	47	49
	125	39	47	49	50

Table 2.5. Logistic model coefficients summary table. Logistic regression model coefficients and level of significance.

Parameter	Estimate	Standard Error	z value	p value
intercept	14.43	2.13	6.8	< 0.001
% DW	-20.58	10.42	-1.98	0.048
Rela VSC	-4.53	1.15	-3.94	< 0.001
Dry VSI	-58.46	12.03	-4.86	<0.001

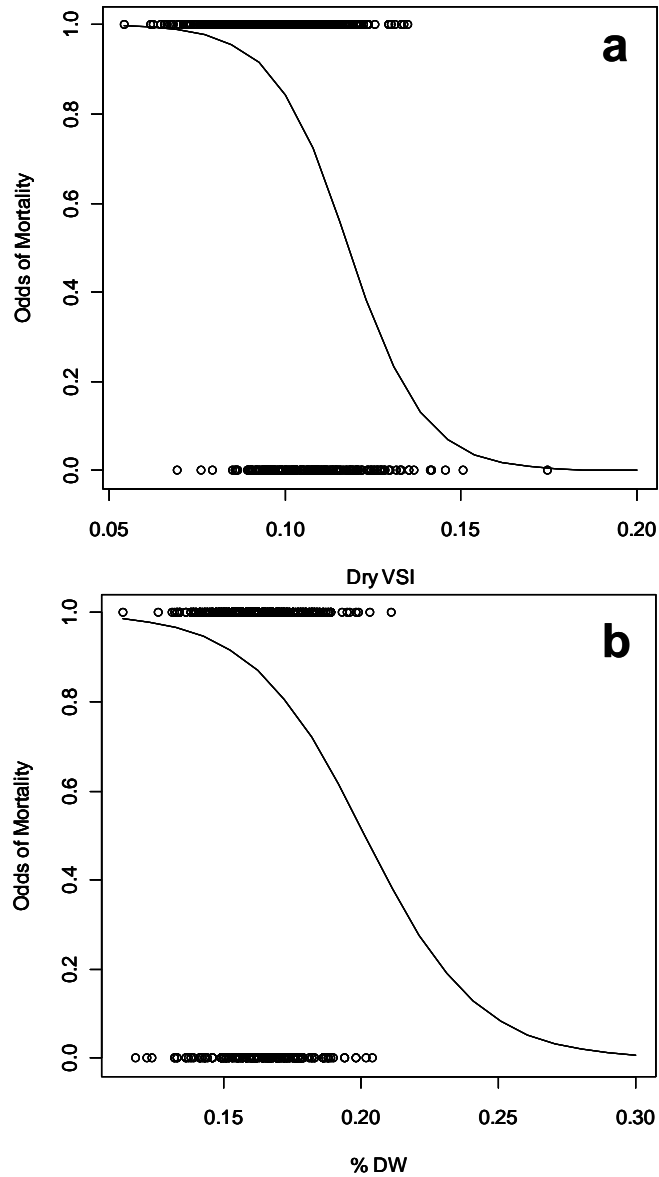


Figure 2.10. Logistic regression model predictions. Logistic regression model predictions for visceral-somatic index (Dry VSI; a) and percent dry weight (% DW; b). Lines represent model fit to particular parameter of interests while setting other parameter equal to its mean.

Field collections

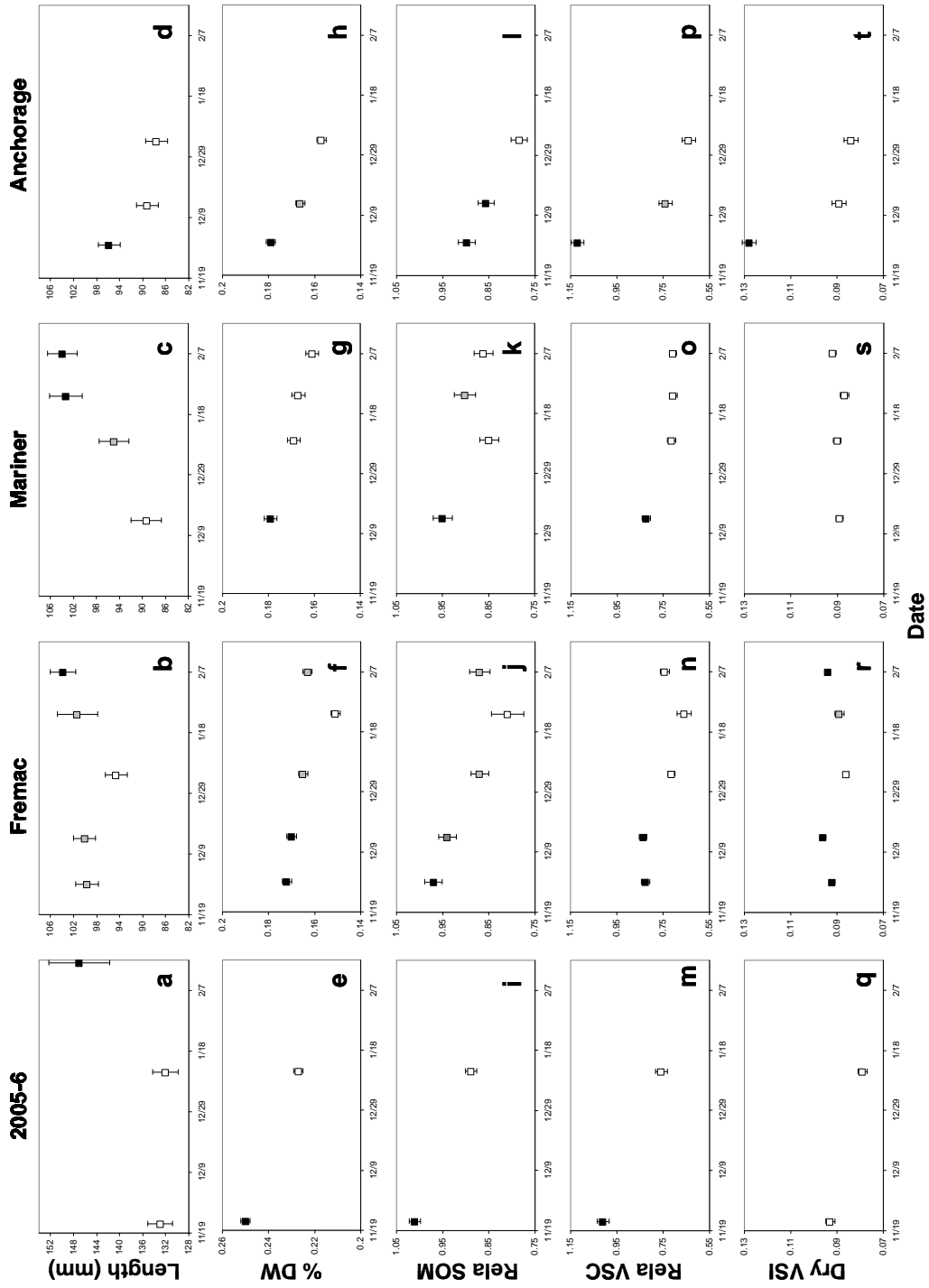
Gizzard shad collected during the 2005-6 and 2006-7 winters showed similar patterns of length-selective mortality as the cage and tank experiments (Figure 2.11). Fish collected from November through January showed no significant changes in length distribution. However, in late January and early February of both years, shad length became significantly larger (Figure 2.11). These patterns follow those observed in the experiments, further demonstrating that mortality was only size-selective during the later part of the winter. Percent dry weight, relative somatic dry weight, and relative visceral dry weight show inconsistent patterns of change across the season. In most cases, these indices are higher early in winter and decrease over time (Figure 2.11). There was little consistent change in VSI over winter (Figure 2.11).

Recruitment to age-1 differed across years. In 2005-6, fish were large entering winter (range 104-152, mean = 133) and age-1 fish were consistently caught in the CBFS long-term monitoring program. In 2006-7, fish were smaller entering winter (range 72-133, mean 103) and no recruitment to age-1 was documented. Back-calculated lengths from the 2005-6 year class collected at age-2 indicated size-selective mortality had occurred (range 129-194, mean = 154). I could not evaluate if size-selectivity occurred during the 2006-7 winter since no age-1 or older gizzard shad were collected from this year class.

Habitat characterization and monitoring

Temperature profiles were different across habitats and years in Oneida Lake, NY. The winter of 2005-6 had warmer air temperatures with inconsistent ice cover, while 2006-7 had colder air temperatures and consistent ice cover. Patterns of ice cover directly influenced water temperature and potentially oxygen profiles across habitats. In 2005-6, initial ice formation occurred on December 10th, broke-up

Figure 2.11. Fish indices versus time from field collections. Mean and standard error of fish indices presented over time from all sites during 2005-6 (column 1) and three sites during 2006-7: Fremac (column 2), Mariner (column 3), and Anchorage (column 4). Significantly different means are indicated using different colors (black/white), gray color indicates the mean is not significantly different from black or white. (a-d) Length (mm) over time from 2005-6 (a), Fremac (b), Mariner (c), and Anchorage (d). (e-h) Percent dry weight (% DW) over time from 2005-6 (e), Fremac (f), Mariner (g), and Anchorage (h). (i-l) Relative somatic dry weight (Rela SOM) over time from 2005-6 (i), Fremac (j), Mariner (k), and Anchorage (l). (m-p) Relative visceral dry weight (Rela VSC) over time from 2005-6 (m), Fremac (n), Mariner (o), and Anchorage (p). (q-t) Dry weight visceral-somatic index (Dry VSI) over time from 2005-6 (q), Fremac (r), Mariner (s), and Anchorage (t).



January 14th, froze again February 9th, broke up in the main lake on February 17th, and completely broke up on April 1st. In 2006-7, initial ice formation occurred on January 23rd and persisted until April 4th (Rudstam and Jackson 2009). The dynamics of main lake temperature profiles follow those of ice cover. When ice is consistent, temperature is consistent and warmer; when ice is inconsistent, temperature is inconsistent and colder (Table 2.6). In 2006-7, nearshore temperatures were cooler than the standard temperature buoy, while the deep hole temperatures were warmer.

Temperature profiles from additional Oneida Lake habitats differed across years (Table 2.6). During 2005-6, tributary temperature profiles fluctuated rapidly between 0 and 6° C. Across the five tributaries sampled, temperatures followed similar patterns and appeared to respond similarly to weather patterns. In 2006-7, temperatures were stable but consistently at or near 0° C in both sites monitored. Marina temperatures were stable and warm relative to the nearshore temperature buoy. During 2006-7, marina dissolved oxygen decreased over the season across sites, eventually becoming anoxic after approximately 5-6 weeks (Table 2.7). On February 20-21, 2007, 6 out of 8 marinas sampled for dissolved oxygen showed evidence of declining levels of dissolved oxygen demonstrating development of winter anoxia can be widespread during years with consistent ice cover. Dissolved oxygen levels increased quickly following ice out in marinas.

Gizzard shad habitat use shifted over the course of the winter but was consistent across years (Table 2.8). Shad were observed throughout the main lake in early fall of both years, shifting to nearshore areas, marinas, and tributaries by late fall. By early winter, shad were only observed in high densities at marinas. By mid-February, catches of shad in marinas ceased, and corresponded to low dissolved oxygen conditions. Shad were uncommon in predator diets collected in the main lake

Table 2.6. Habitat specific temperature profile summary table. Mean monthly temperature (± 1 SE) and number of days below 1° C, 2° C, and 4° C from Oneida Lake habitats. *Site monitored from January 1, 2006- March 31, 2006. Average temperature from Dec-Mar. and number of days below 1, 2, and 4° C are only calculated from this time period. **Site monitored from December 15, 2006- March 31, 2007. Average temperature from Dec-Mar. and number of days below 1, 2, and 4° C are only calculated from this time period.

Year	Habitat	Location	Average Temperature				Winter Average			Number of days		
			December	January	February	March	Dec. - Mar.	< 1 C	< 2 C	< 4 C		
2005	Main Lake Tributary	Standard Site	1.93 (0.04)	1.20 (0.03)	0.53 (0.01)	1.21 (0.03)	1.23 (0.02)	63	104	120		
		Chittenango Creek*	-	2.12 (0.04)	1.75 (0.06)	3.26 (0.08)	2.40 (0.04)	23	39	73		
		Erie Canal (East)*	-	0.84 (0.02)	0.55 (0.02)	1.87 (0.07)	1.11 (0.03)	54	76	84		
		Erie Canal (West)*	-	0.93 (0.02)	0.44 (0.01)	1.40 (0.05)	0.94 (0.02)	58	85	87		
2006	Main Lake	Fish Creek*	-	0.83 (0.03)	0.41 (0.03)	1.76 (0.07)	1.02 (0.03)	53	75	85		
		Deep	4.08 (0.04)	1.92 (0.04)	2.19 (0.01)	3.04 (0.01)	2.82 (0.02)	9	33	136		
		Shallow	3.99 (0.04)	1.71 (0.05)	0.62 (0.00)	1.25 (0.01)	1.92 (0.03)	50	87	125		
		Standard Site	4.01 (0.04)	1.69 (0.04)	1.07 (0.01)	1.46 (0.03)	2.08 (0.03)	34	78	136		
		Fremac	3.67 (0.05)	2.50 (0.05)	2.15 (0.01)	2.68 (0.02)	2.76 (0.02)	1	41	122		
Tributary	Marina	Marian Manor**	3.53 (0.07)	1.72 (0.07)	0.20 (0.00)	0.93 (0.06)	1.38 (0.04)	73	78	99		
		Marinel**	3.67 (0.02)	2.62 (0.04)	1.47 (0.01)	1.69 (0.02)	2.22 (0.02)	7	59	109		
		Downstream	4.13 (0.07)	1.95 (0.09)	-0.11 (0.00)	1.82 (0.08)	2.00 (0.04)	61	71	103		
		Upstream**	4.44 (0.09)	2.07 (0.09)	-0.10 (0.00)	1.86 (0.08)	1.81 (0.05)	60	66	91		

Table 2.7. Habitat specific dissolved oxygen summary table. Mean dissolved oxygen measurements from marinas sampled during the winter of 2006-7.

Site	Date	Temperature (° C)	Dissolved Oxygen (mg/L)
Fremac	1/9/2007	4.30	15.50
	1/15/2007	2.00	12.30
	1/24/2007	1.80	7.79
	1/31/2007	1.70	5.13
	2/1/2007	1.80	5.10
	2/6/2007	1.70	1.44
	2/21/2007	2.02	0.44
	3/28/2007	1.95	4.92
	4/7/2007	2.40	11.65
Mariner	1/9/2007	4.30	15.30
	1/15/2007	2.00	10.00
	1/24/2007	1.70	8.73
	2/1/2007	1.00	8.20
	2/6/2007	1.10	5.22
	2/21/2007	2.20	0.33
	3/28/2007	2.91	4.10
Marion Manor	1/9/2007	3.50	15.80
	2/21/2007	0.01	9.43
AeroMarine	2/20/2007	2.40	4.73
Anchorage	2/21/2007	1.05	0.70
Fisher Bay	2/21/2007	2.95	0.49
Float-UR-Boat	2/20/2007	2.58	0.49
Snug Harbor	2/21/2007	0.82	3.64
Yacht Club	2/20/2007	0.27	11.10

Table 2.8. Gizzard shad habitat use. Summary information from gizzard shad habitat use surveys, including year, date, habitat type, site, gear, number caught, number measured, and average length (± 1 SE).

Winter	Date	Habitat Type	Site	Gear	# Caught	# Measured	Ave. Length (± 1 SE)
2005-6	11/22	Main Lake	Shackelton Point	BS	> 1000	30	132.96 (1.83)
	1/11	Marina	Fisher Bay	BS	29	29	132.03 (2.54)
	1/11	Marina	Fremac	BS	0	-	-
	2/16	Marina	Fisher Bay	BS	5	5	147 (5.23)
2006-7	10/31	Main Lake	Shackelton Point	EF	> 1000	30	95.2 (1.64)
	11/19	Main Lake	Shackelton Point	BS	> 1000	50	102.56 (1.51)
	11/29	Marina	Fremac	EF	> 1000	29	99.66 (2.13)
	11/30	Tributary	Anchorage	EF	> 1000	30	95.8 (2.13)
	12/13	Tributary	Anchorage	EF	> 100	30	89.23 (2.06)
	12/14	Marina	Fremac	EF	> 1000	30	100.06 (2.35)
	12/14	Marina	Mariner	EF	> 1000	30	89.33 (1.96)
	12/20	Main Lake	Shackelton Point	EF	0	-	-
	1/3	Tributary	Anchorage	EF	> 100	30	87.63 (1.46)
	1/3	Main Lake	Shackelton Point	EF	0	-	-
	1/4	Marina	Fremac	EF	> 100	31	94.58 (1.64)
	1/9	Marina	Mariner	EF	> 100	30	94.90 (2.93)
	1/24	Marina	Fremac	GN	9	9	101.33 (3.13)
	1/24	Marina	Mariner	GN	25	25	103.28 (3.53)
	2/7	Marina	Fremac	GN	22	22	103.86 (1.76)
	2/7	Marina	Mariner	GN	30	30	103.97 (2.17)
2/21	Marina	Fremac	GN	0	-	-	
2/21	Marina	Mariner	GN	0	-	-	

throughout the winter, suggesting shad are present in the main lake but at low levels (Table 2.2).

DISCUSSION

Experimental tests of gizzard shad over-winter mortality indicate mechanisms causing mortality vary temporally throughout winter and across winters. Prior to ice formation, as temperatures decline to near zero, mortality is size-independent and is not driven by starvation but rather inability to fully acclimate to cold temperatures. Following ice formation when temperatures stabilize, mortality becomes size-selective and is driven by starvation and associated complications, however the importance of cold stress increases at lower temperatures. These observations are supported by field collections of gizzard shad which do not show a shift towards larger size distributions until later in the winter, despite observations of large numbers of dead and dying shad throughout the early sampling period. Habitat heterogeneity in the Oneida Lake ecosystem indicated that drivers of mortality are also likely to vary spatially.

Cage Experiment

Results from cage experiments demonstrate gizzard shad mortality varies during the acclimation period and is not directly driven by starvation but rather thermal stress related to cold, changing temperatures. Across time periods, mortality was greatest when temperatures were decreasing to or fluctuating at cold temperatures, and minimal at warm stable temperatures. The complete lack of shifts towards larger size distributions in the pre- to post-experimental samples illustrates starvation is not the cause of mortality within cages as smaller fish would be expected to exhaust limited energy reserves faster than larger fish. Acclimation stress associated with changing temperatures is the most likely cause of gizzard shad mortality, since high

mortality rates were not observed until temperatures began to decline. Inability to acclimate to changing temperatures is known to cause mortality in many fish species during early winter (White et al. 1987, Beitinger 2000, Hurst 2007, Donaldson et al. 2008), while little evidence has identified starvation as the driving cause of mortality as temperatures decline. These observations are not surprising, as the acclimation to cold temperatures occurs at the onset of winter, and age-0 fish have only recently begun to utilize energy stores accumulated throughout the growing season.

Despite the lack of size-selective mortality or evidence supporting starvation as the driver of mortality, lack of available energy reserves may still be contributing to shad mortality. Inability to acclimate physiological functions at low temperatures could limit their ability to access stored energy reserves (lipids) forcing them to utilize emergency energy stores (liver). Within their native range, shad are rarely exposed to temperatures below 4° C for prolonged periods of time, and may be physiologically maladapted to access all energy reserves at these temperatures. I found supporting evidence that shad may not be able to utilize all available energy reserves. Changes in relative somatic dry weight were consistently smaller than those observed in relative visceral dry weight, which was clearly evident by the large decreases in shad VSI. Shad store lipids within their muscle tissues; therefore, I would expect somatic tissue to show the greatest decrease. Additionally, as muscle lipid decreases, I would expect shad percent dry weight to also decrease, which was not consistently observed. Observations demonstrate despite high levels of energy reserves, these may be inaccessible to shad at low temperatures. If shad are using emergency energy stores (e.g. liver tissue), this could decrease physiological function and potentially lead to mortality (White et al. 1987). Therefore, despite high levels of stored lipids, shad may be functioning physiologically similar to a fish with exhausted energy reserves.

Previous research on shad suggests the inability to access traditional stored energy reserves may drive mortality during acclimation and prolonged exposure to cold temperatures. White et al. (1987) observed little change in shad percent lipids over the winter, but observed declines in liver tissue and function. They suggest shad are unable to mobilize lipids at temperatures below 8° C and will instead utilize emergency energy sources, such as liver glycogen and tissue. As liver and other organ functioning decreases, shad begin to suffer complete physiological failure eventually leading to mortality. White et al. (1987) suggest gizzard shad are unable to acclimate enzyme function, specifically, lactate dehydrogenase, until January, resulting in frequent size-independent mortality events during periods of rapid temperature change common in early winter. Results from this experiment support the interpretations presented in the report by White et al. (1987).

Inconsistent results across sites suggest suitability of habitats for shad survival varies. During the time period 2, shad in cage 2 at Fremac marina did not show changes in relative somatic or visceral dry weight, and were the only samples throughout all time periods where some shad had stomach contents. Site-specific variability can promote shad feeding and potentially increase survival at low temperatures if feeding prevents reliance on limited energy stores (e.g. liver). These conditions appear to be highly localized since cage 1 was moored within 5 meters, but followed similar patterns as those observed throughout other time periods and locations. The high mortality in the tributary cages during time period 2 is difficult to interpret. I suspect it was driven by the additional stress associated with maintaining position within flowing water, which increased the rate shad exhausted already limited energy reserves. Though moored in a tributary deep hole (~6 m) with a low flow rate where confinement stress should be limited, I cannot definitively say if experimental shad are representative of fish within the tributary. Evaluation of tributaries as

potential shad refuges remains difficult; however, temperature profiles (see below) did not identify these habitats as refuges for over-wintering shad.

Tank Experiment

Gizzard shad demonstrated clear differences in mortality rates across temperatures. In all rooms, mortality was minimal during the acclimation period, allowing fish to acclimate and avoid acclimation-related mortality observed in the cage experiment. As temperatures declined below 4° C, however, the mortality rate increased rapidly across cold rooms indicating 4° C is a threshold of shad temperature tolerance. Within the coldest rooms, the mortality rate was maintained at a high rate as temperatures dropped to 2° and 1° C, resulting in 100% mortality after only 25 days in the coldest rooms, compared to 50 days in the warmest room. Within the warmest room, the initial spike in mortality as the temperature dropped below 4° C eventually declined. Mortality rates and potential mortality drivers are temperature-dependent and vary across temperature as indicated by the significance of room in the survival analysis. If mortality were driven by starvation, the fish in the warmest room should experience higher mortality rates since fish metabolize limited energy reserves faster at higher temperatures. Since the highest mortality was observed in the coldest room, these fish are unlikely to be dying from starvation but are dying from cold-stress related complications. In the warmest room, the gradual rate of mortality indicates these fish are less impacted by cold stress and could be dying from starvation or complications associated with starvation.

Survival analysis indicated room, location and length all made significant contributions to predicting survival duration. As indicated above, the warmest temperature treatment promoted the longest survival duration relative to the two coldest rooms (Table 2.4, Figure 2.10). These observations provide clear experimental

evidence of prior claims throughout the literature that mortality increases rapidly below 4° C (Heidinger 1983; White 1987). Differences in mortality across temperatures show temperature refuges could play an important role in driving shad over-winter survival, especially in systems where winter temperatures consistently drop below 2° C. The significance of location in the survival model is likely driven by location-specific conditions within cold rooms where experiments were conducted. Cold room chillers blow air downward and out across the room, which likely led to faster and more dramatic temperature fluctuations in locations 1 and 3. Finally, the significance of length in the model demonstrates size-selective mortality in over-wintering shad, predicting longer survival duration for larger shad (Table 2.4). This provides experimental evidence that mortality is related to time (Walburg 1964; White et al. 1987) and size (Heidinger 1983; White et al. 1987). However, it does not prove mortality is driven by starvation nor does it identify energy sources used by shad.

Prior research has shown that gizzard shad are unable to mobilize lipids at cold temperatures, forcing them to mobilize emergency energy stores, such as liver and muscle glycogen and tissue (White et al. 1987). As a result, liver function decreases, resulting in jaundice and subsequent mortality. Additionally, shad are unable to fully adjust membrane function at cold temperatures, forcing them to compensate by elevating serum glucose by ten times the normal level. Over time, shad deplete energy stores and are unable to maintain elevated serum glucose. As serum glucose declines, glucose is no longer transported to the brain, resulting in “brain starvation”, which eventually leads to the disoriented, comatose behavior observed prior to shad mortality. Experimental results and logistic regression analysis support previous research as shad VSI explained the greatest amount of variation in the model. Additionally, percent dry weight, a metric of available lipid reserves, explained the least amount of variation in the model, suggesting starvation is likely not driven by

decreasing lipid reserves, but rather depletion of emergency energy sources such as liver and muscle tissue. Disproportionate use of visceral tissues, such as the liver, likely decreases liver function and leads to physiological failure discussed above. Thus, over-wintering shad energy allocation strategies reflect those of starving fish despite having lipid reserves, which appear to be inaccessible at cold temperatures.

In addition to starvation and physiologically driven mortality discussed above, the disorientated and confused behavior of shad observed at cold temperatures undoubtedly makes them highly susceptible to predation. Though not evaluated in this experiment, predation may be an additional source of mortality in over-wintering gizzard shad, and the need to minimize predation risk could influence shad over-winter habitat selection.

Field collections

Time trends in field collected fish support results from cage and tank experiments. Prior to ice formation, when temperatures were declining towards 4° C, we observed no changes in size distributions across sites or years. Following ice formation and temperature stabilization, size distributions began to shift towards larger fish, suggesting smaller fish in the population were suffering higher mortality rates. During the 2006-7 winter, the observed increase in length distributions corresponded with a shift in sampling gear from electro-fishing to under-the-ice gillnets, suggesting differences in size selectivity between the two gears could be driving the length distribution shift. I suspect this is not the cause. First, sampling in 2005-6 was conducted using a beach seine throughout the winter, and time trends of length distribution changes correspond to similar time periods as 2006-7. Second, previous research has demonstrated limited selectivity of these nets for catching a similar clupeid species (alewife -*Alosa pseudoharengus*) for the lengths sampled (Warner et

al. 2002). Finally, at the temperatures I am sampling, gizzard shad are highly disorientated, swim at very slow speeds, and are not “gilled” but rather became tangled in the net, which should prevent size-selectivity of the gillnets.

Despite consistent trends in size-dependent mortality in experiments and field collections, patterns of energy use were not consistent between experiments and field collections. Experimental fish showed disproportionate use of visceral tissues relative to somatic tissues, as evidenced by the decrease in VSI over time across experiments, while field collected fish showed little change in VSI. These discrepancies could be due to confinement stress associated with experiments or feeding by fish in the field. Confinement stress seems unlikely and does not explain why confined fish would disproportionately rely on visceral energy stores. The most likely explanation is that fish in the wild are feeding at a minimal maintenance level, while those in the experiments were not fed. Several field collected fish had minimal stomach contents suggesting modest feeding by shad may minimize stress associated with starvation and prolong survival. Changes in fish visceral and somatic dry weights indicate that shad are still losing weight, but feeding may be enough to minimize reliance of shad on emergency energy stores such as liver and other visceral tissues.

The high recruitment of the 2005-6 year class provides additional proof that size is an important factor in determining over-winter survival of gizzard shad. The mean length of fish that survived the 2005-6 winter increased by over 50 mm, indicating size-selective mortality of the smaller individuals in the population. Several fish from the 2006-7 year class were within the range of fish which survived the 2005-6 winter; however, this does not mean these fish should have survived as the minimum length required to survive through winter likely varies annually. I suspect the complete lack of recruitment of the 2006-7 year class is driven by the interaction

between smaller length entering winter and the development of anoxia limiting availability of temperature refuges (see below).

Habitat characterization and monitoring

Habitat monitoring during the winters of 2005-6 and 2006-7 showed high spatial heterogeneity within Oneida Lake. Yearly variation in ice cover is likely the most important factor driving winter habitat availability. During years with consistent ice cover, temperature profiles across habitats are relatively stable, and identified marinas and offshore areas of the main lake as the best habitat for shad survival. Tributaries and nearshore habitats are likely too cold or fluctuate too rapidly for shad survival. During years with inconsistent ice cover, habitat profiles across the Oneida Lake system are highly variable, with only marina and backwater slough habitats promoting shad survival. Inconsistent ice cover in the main lake and tributaries results in temperatures that fluctuate rapidly and are often near 0° C for extended periods of time. Both of these characteristics will likely lead to high over-winter mortality. Ice dynamics can also influence dissolved oxygen profiles during winter months, which can affect habitat availability for shad. Consistent ice cover in marinas can lead to development of anoxia across these habitats, resulting in high mortality for over-wintering shad. Inconsistent ice cover and mid-winter snow melt prevents the development of anoxia in marinas, allowing shad to persist in these habitats throughout winter. Given the role both temperature and dissolved oxygen play in defining shad habitat availability during winter, it seems optimal shad habitat likely varies across years.

Monitoring of shad habitat use is consistent with what one would predict based on experimental results and habitat characterization. During late fall, shad are distributed throughout nearshore bays, marinas and tributaries. By early winter, large

congregations of shad are limited to marinas. As winter progresses, shad remain in marinas and other protected areas despite declining levels of dissolved oxygen. As hypoxia/anoxia develops, shad either stay in marinas and die or leave the marinas for nearshore habitats. Colder temperatures and the presence of predators likely results in additional mortality for shad once they leave marinas. Interestingly, predators were not observed within marinas during winter electro-fishing or gillnet surveys. During years when shad are forced to leave marinas for the main lake, I suspect mortality is extremely high due to thermal stress, starvation and predation. Inconsistent ice cover and mid-winter snowmelt prevent the development of anoxia in marinas and shad likely remain within these habitats throughout the winter, avoiding additional thermal stress and predation. Difficulties in monitoring the main lake, specifically the deep hole, limit our ability to interpret the importance of this habitat for over-wintering shad. During years with inconsistent ice cover, this habitat appears to be too cold to promote shad survival; however, consistent ice cover and the development of a deep hole temperature refuge could provide an additional habitat for over-winter shad.

Synthesis/summary

Across experiments, temperature and the rate of temperature change affected the mortality rate and was potentially the driver of gizzard shad mortality. During the acclimation period, mortality appeared unrelated to starvation, as evidenced by the lack of size-selective mortality in the cage experiment and field collections prior to ice formation. Tank experiments also demonstrated fish can minimize mortality during acclimation to lower temperatures if the rate of change is slow enough to allow adequate physiological adaptation to function at cold temperatures. During the starvation period, the tank experiment and field collections identified cold stress and potentially starvation as a likely source of mortality, especially if shad are unable to

utilize stored lipids. Interestingly, the importance of starvation as a driver of mortality appears to vary by temperature, with additional sources of mortality related to thermal stress becoming increasingly important at colder temperatures. These results highlight that the cause of gizzard shad mortality likely varies across temporal and spatial scales in heterogeneous systems.

Differences between energy usage patterns observed in the experiments and field collections suggest different responses of experimental and field collected fish to starvation. Several studies have documented that during starvation, many fish will utilize liver energy stores as an emergency energy source (Pastoureud 1991; Power et al. 2000; Rios et al. 2007). Results from both experiments demonstrated that shad viscera was changing disproportionately to somatic tissue, supporting the literature. Field collections show proportional changes in viscera and somatic tissues, and no changes in VSI were observed. These results suggest that shad response to cold temperatures and starvation were not consistent between experiments and field collections. Stomach content analysis on field collected fish identified that a minimal level of feeding was occurring, which may help maintain liver size and function. Evidence of feeding at temperatures below 4° C contradicts literature values which suggest shad cease feeding at 10° C (White et al. 1987).

The importance of temperature and potential feeding on the ability of gizzard shad to survive winter suggests that shad may experience different spatial patterns of recruitment. In several species and systems, over-winter survival is linked to contributions from geographically small refuge habitats (Magnuson et al. 1985; Bodensteiner et al. 1992). Refuge habitats may buffer fish from stresses associated with temperature, predation, and starvation, and dynamics of habitat availability may influence fish over-winter survival and subsequent recruitment. In this research, I have demonstrated a major effect of temperature on survival rates and physiological

responses of gizzard shad. In Oneida Lake, gizzard shad appear to select for marinas and backwater sloughs, interestingly these areas generally have higher temperatures and large amounts of organic material which shad can feed on. Further research should assess temperature and dissolved oxygen dynamics of these habitats within and across winters to evaluate their suitability as refugia for over-wintering gizzard shad.

Relating experimental results and field observations of over-winter mortality in fishes to patterns of recruitment and population dynamics remains difficult. In this chapter, I identify acclimation rate, winter water temperature, and cold-stress related starvation as potentially important drivers of shad over-winter mortality. Given these observations, we predict shad recruitment will be highest in years with large length entering winter, gradual temperature declines, short winter duration and large amounts of habitat refuges where shad can find warm water temperatures and food resources (Figure 2.12). These results support prior research which showed shad recruitment is highest at low age-0 shad-abundance, warm summer water temperatures, and warm winters (Ward et al. 2006). These conditions lead to larger fish entering winter and reduce the risk of starvation. Here I provide an additional source of mortality, availability of refuge habitats to explain shad over-winter survival.

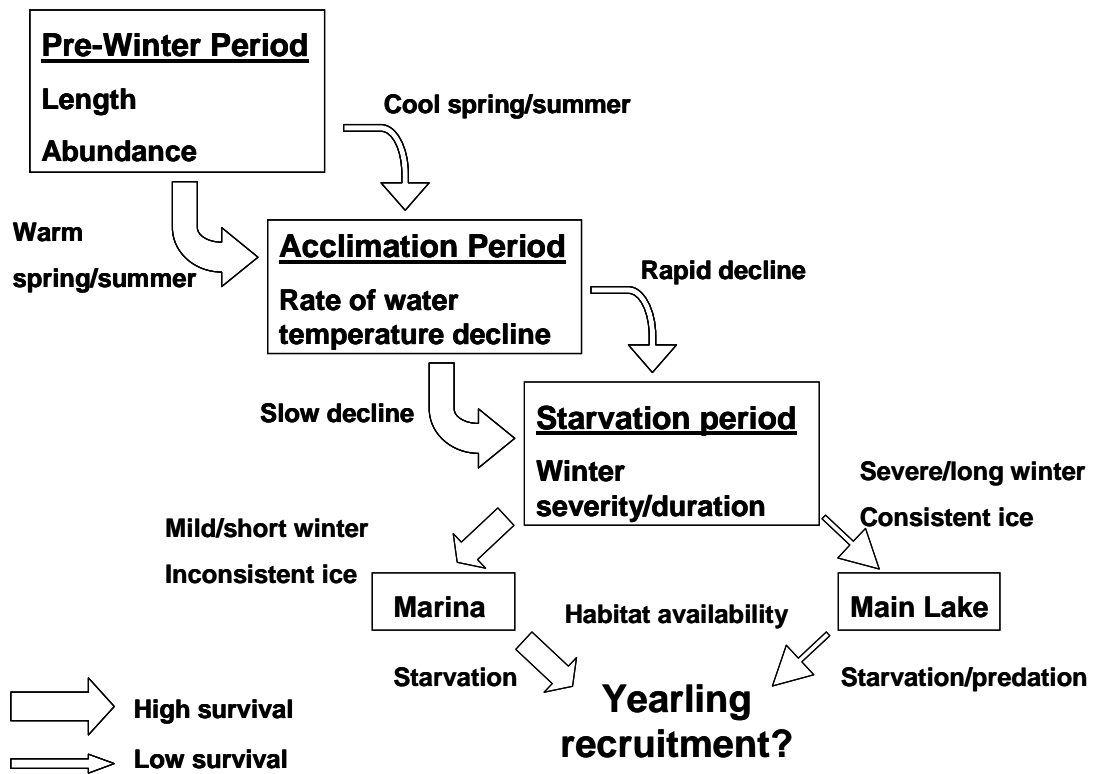


Figure 2.12. Routes to gizzard shad over-winter survival. Conceptual model of potential routes to yearling recruitment. Large arrow indicate conditions leading to high survival, while small arrows indicate conditions leading to low survival.

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