GREAT LAKES FISHERY COMMISSION

2013 Project Completion Report[1]

Winter Warming Effects on Yellow Perch Reproduction and Recruitment

by:

Troy M. Farmer[2], Konrad Dabrowski[3], Elizabeth A. Marschall[2], and Stuart A. Ludsin[2]

[2] Aquatic Ecology Laboratory, Department of Evolution, Ecology & Organismal Biology, The Ohio State University, Columbus, OH 43212

[3] Aquaculture Laboratory, School of Environment and Natural Resources, The Ohio State University, Columbus, Ohio 43210

April 2013

---

[1] Project completion reports of Commission-sponsored research are made available to the Commission's Cooperators in the interest of rapid dissemination of information that may be useful in Great Lakes fishery management, research, or administration. The reader should be aware that project completion reports have not been through a peer-review process and that sponsorship of the project by the Commission does not necessarily imply that the findings or conclusions are endorsed by the Commission. Do not cite findings without permission of the author.

CONTACT INFORMATION:

Troy M. Farmer, 614-292-1613, farmer.147@osu.edu.

ABSTRACT:

Climate change is expected to affect fish populations worldwide through a number of mechanisms. To help understand consistent, failed Lake Erie yellow perch (*Perca flavescens*) year-classes following warm winters during 1975–2010, we used a combined laboratory-experimental and population-modeling approach. We hypothesized that climate change would negatively affect yellow perch by 1) increasing bottom hypoxia ($O_2 < 2$ mg/L) during summer, which can reduce energy reserves (fish condition) prior to winter, when ovaries develop for this species, and 2) increasing winter water temperature, which could increase basal metabolic rates during winter (i.e., reduce energy available for ovary development) and disrupt thermal requirements necessary for proper ovary development. Our laboratory experiment quantified the independent and interactive effects of winter duration (number of days < 5°C: levels = 50, 80, and 110 d) and energetic condition entering winter (high, low) on reproductive development, fecundity, spawning, egg hatching and quality, and larval quality of both domestic and wild adults. Results indicate that, relative to eggs produced by Lake Erie females in the short-winter treatment, those in in the long-winter treatment produced larger, higher quality eggs that contained more calories, total lipids, neutral lipids, and myristic acid (i.e., a saturated fatty acid) per egg. These higher quality eggs also experienced greater hatching success and produced larger larvae than eggs from Lake Erie females exposed to a short winter. While long winters positively affected egg and larval quality, we found no effect of female body-condition on reproductive output, quality, or hatching success in our experiment.

Using relationships among winter duration, female size, total fecundity, egg mass, and hatching success that were derived from our experiment, as well as historical adult yellow perch age-structure and winter temperature data, we developed a statistical population model to determine if winter temperature could explain historical (1975-2010) variation in Lake Erie yellow perch year-class strength, through its effects on total larval production. Finding that this annual index of total larval production was able to explain a significant amount of variation in observed year-class strength, we then used our model to forecast future year-class strength given predicted mid-century (2046–2065) winter temperatures under three commonly used scenarios (high, 1B; moderate, A2; and low, B1) of projected greenhouse gas emissions. Analysis of probability distributions generated for each future scenario suggests that continued winter warming would lead to reduced egg hatching success, with the largest decline in hatching success predicted under the highest emission scenario. Taken together, our experiment and modeling indicate a novel mechanism by which climate change can affect reproduction and recruitment of yellow perch in Lake Erie and potentially of other cool- and cold-water fishes that develop ovaries during winter.

INTRODUCTION:

As with other large aquatic ecosystems worldwide, both freshwater and marine, the Laurentian Great Lakes have experienced numerous anthropogenic perturbations, including cultural eutrophication, sedimentation, overfishing, heavy metal contamination, and species introductions. In turn, these perturbations have altered physicochemical and biological attributes of these ecosystems, including important recreational and commercial fisheries (e.g., Hartman 1972; Regier and Hartman 1973; Francis et al. 1979; Kelso et al. 1996; Ludsin et al. 2001). An emerging perturbation that should be of major concern to Great Lakes management agencies is climate change, which has the potential to directly and indirectly affect the species composition, productivity, and distribution of Great Lakes fishes (Meisner et al. 1987; Magnuson et al. 1997; Kling et al. 2003; Kerr et al. 2009).

Similar to marine (Grantham et al. 2004; Mackenzie et al. 2007; Smith et al. 2007; Kerr et al. 2009; Hoegh-Guldberg and Bruno 2010; Doney et al. 2012), estuarine (Genner et al. 2004; Willard and

Bernhardt 2011), and other freshwater (Schindler et al. 2005; Ficke et al. 2007) ecosystems across the planet, the Laurentian Great Lakes already have begun to experience warming trends (Assel et al. 1995; McCormick and Fahnenstiel 1999; Jones et al. 2006), which are predicted to continue in coming decades (Meisner et al. 1987; Magnuson et al. 1997; Kling et al. 2003). Further, in the case of the Great Lakes, water temperature has been increasing twice as fast as air temperature, due largely to a reduction in winter ice cover (Austin and Colman 2007).

While previous modeling studies have explored the effects of a changing climate on fish communities (Shuter and Meisner 1992; Stefan et al. 1996; Magnuson et al. 1997; Mackenzie-Grieve and Post 2006; Sharma et al. 2007), they have primarily focused on how warmer temperatures during the growing season would affect thermal habitat availability, expected growth rate, and species range. Because climate change also is anticipated to alter precipitation patterns (Kunkel et al. 2002; Kling et al. 2003), nutrient dynamics (Kerfoot et al. 2008), water levels (Hartmann 1990; Mortsch and Quinn 1996; Kling et al. 2003; Angel and Kunkel 2010; MacKay and Seglenieks 2013), nursery and spawning habitat (Mortsch 1998; Jones et al. 2006), as well as the timing, magnitude, and duration of thermal stratification (McCormick and Fahnenstiel 1999; Austin and Colman 2007), hypoxia (Fang et al. 2004; Hawley et al. 2006), and ice cover (Assel et al. 1995, 2003; Magnuson 2010; Wang et al. 2012), one should expect climate change to have interactive effects on fish populations and communities (Brook et al. 2008; Doney et al. 2012). The likelihood that climate change leads to "ecological surprises" (Paine et al. 1998, Doak et al. 2008) only increases when we consider that effects of climate change may interact with other anthropogenic stressors (e.g., effects of invasive species, eutrophication, overfishing, habitat loss) to influence species composition, distribution, and production.

Alteration of a population's demographic rates (e.g., birth, death) is one way that climate change may influence population dynamics and viability (Kerr et al. 2009; Ottersen et al. 2010). Further, given that the maximal number of potential future survivors (recruits) to a population in a year is set by the number of eggs produced that year (Houde 1987), those aspects of climate change that affect reproductive output (i.e., potential recruit production) may have a strong effect on a population's size and dynamics. Indeed, previous studies have investigated how climate change might affect fish populations via impacts on early life (e.g., eggs, larvae) survival (Svendsen et al. 1995; Casselman 2002; Köster et al. 2005; Vikebø et al. 2005).

Few studies, however, have investigated the link between climate change and fish reproductive biology and physiology (note the lack of such studies in the review by Drinkwater et al. 2010), which we view as a major gap in both the freshwater and marine climate change literature for two key reasons. First, temperature has been shown to be a key determinant of reproductive processes (e.g., vitellogenesis, ovulation) in temperate fishes (Dabrowski et al. 1996). Experimental and field-observational research in North American and European ecosystems have demonstrated that fecundity and spawning success of yellow perch (*Perca flavescens*) and its congener (Eurasian perch [*Perca fluviatilis*]) can decline when adult females do not experience a prolonged period of cold temperatures during winter (Jones et al. 1972; Hokanson 1977; Ciereszko et al. 1997; Sandstrom et al. 1997; Lukšienê et al. 2000; Migaud et al. 2002; Wang et al. 2006). Further, we (Ludsin 2000 and TMF, unpublished data) have documented a negative threshold relationship between winter temperature and an annual index of yellow perch juvenile (age-0) abundance in Lake Erie's western and central basin populations, which reveals that weak year-classes nearly always followed short, warm winters, whereas only after long, cold winters did the potential for a strong year-class exist. Thus, the effects of winter warming on reproductive success may scale up to the population level, even in systems as large as Lake Erie. Second, seasonal (mid-summer through early fall) hypolimnetic hypoxia (dissolved oxygen < 2 mg/L), which has re-emerged as a water quality impairment in Lake Erie during recent decades (Hawley et al. 2006; Rucinski et al. 2010) and is predicted to increase with continued climate warming (Kling et al. 2003; Fang et al. 2004; Ficke et al. 2007), may exacerbate the negative effects of warm winters on reproductive development by reducing female condition (i.e., energetic reserves) prior to winter. Indeed, poor energetic condition has been shown to reduce egg production (Bunnell et al. 2005, 2009; Kennedy et al. 2008; Gregersen et al. 2011) and increase the incidence of skipped spawning (Forney et al. 1965; Scott and Crossman 1973; Rideout et al. 2005) in several north-temperate fishes. Further, field and modeling data from central Lake Erie have shown that hypolimnetic hypoxia can reduce food consumption, energetic condition, and growth potential of several fishes in Lake Erie, including yellow perch (Roberts et al. 2009; Arend et al. 2010).

Despite much evidence to support our hypotheses that climate change can negatively affect north-temperate fishes that develop ovaries during winter by reducing 1) exposure of potential spawners to the thermal requirements necessary for proper ovary development during winter (Hypothesis 1 [H1]) and 2) the condition (i.e., energy reserves) of potential spawners prior to winter (Hypothesis 2 [H2]), the biological mechanisms underlying relationships between winter temperature, female condition, and reproductive success remain largely unexplored and no study to date has explored the population-level response of such relationships. Thus, we conducted an experimental and model-based study to quantify the independent and interactive effects of reduced body condition entering winter and winter duration on yellow perch reproductive success (*Objective 1*) and to assess the importance of both past and future winter temperature on Lake Erie yellow perch year-class strength (*Objective 2*), which we know is a good predictor of future recruitment to the fishery at age-2 (Ludsin 2000; YPTGR 2011). We used Lake Erie yellow perch, as a model organism because 1) it is a cool-water species that develops ovaries during winter, 2) it is ecologically, economically, and culturally important in the Great lakes region (and especially in Lake Erie), and 3) a wealth of historical data and research exists for this species.

OBJECTIVES:

Objective 1. *Evaluate the (possibly synergistic) effects of winter temperature and female body condition entering the winter on female reproductive output and quality (i.e., test H1 and H2), where female body condition represents the effect of extent and severity of hypoxia during the previous growing season.*

We successfully conducted a controlled laboratory experiment to assess the effects of winter temperature and energetic condition of females entering the winter on female reproductive output and progeny quality, which we briefly summarize below. For this experiment, we used both wild (central Lake Erie origin) and domesticated (hatchery origin from Lake Erie stock) yellow perch. For both types, we initially created two distinct levels of body condition entering winter by rearing fish under a high and low ration diet. We then exposed these fish to different levels of winter duration (short, medium, long) to assess the independent and interactive effects of condition of fish entering winter and winter duration on reproductive success. Results from this laboratory experiment indicate that, while female yellow perch across all winter-duration and body-condition treatments produced viable eggs, Lake Erie female yellow perch exposed to the long winter treatment produced larger eggs, with more total lipids, neutral lipids, and myristic acid (i.e., a saturated fatty acid) per egg than those females exposed to the short winter treatment. These higher quality eggs also experienced greater hatching success and produced larger larvae than eggs from Lake Erie females exposed to a short winter. No major problems were encountered en route to completion of Objective 1.

Laboratory studies have indicated that many cool-water fishes require an extended duration of cold temperatures to develop reproductively before being able to spawn during the spring (Hokanson 1977, Dabrowski et al. 1996, Ciereszko et al. 1997). As the induction of vitellogensis is dependent on both decreasing temperature and photoperiod (Dabrowski et al. 1996) and subsequent spring spawning is dependent on increasing temperature and photoperiod (Thorp 1977; Kayes and Calbert 1979; Dabrowski et al. 1996), it seems logical that an inadequate duration between the start of vitellogensis and spawning could result in incomplete reproductive development. In fact, this exact mechanism has been suggested to explain a lack a spawning in some cool-water fishes following abnormally short winters (Miller 1967; Clugston et al. 1978). Similarly, Dabrowski et al. (1996) found that female yellow perch on a manipulated photoperiod and temperature regime during winter (with long days and warm temperatures) did not develop viable eggs and also did not spawn the following spring. Ciereszko et al. (1997) also showed poor yellow perch gonadal growth and egg quality in response to warm winter temperatures, while Eurasian perch have been shown to experience incomplete ovarian development (Luksiene et al. 2000) and low egg survival (Sandstrom et al. 1997), owing to warm winter temperatures.

Female condition also can be expected to influence reproductive output, as the energy allocated to reproduction in percids can be extremely high (e.g., >86% of the energy stored in the soma; Craig 1977). Thus, any factor that has the capacity to limit condition prior to winter also could indirectly influence reproductive success. Such factors might include 1) hypolimnetic hypoxia in central Lake Erie, which is predicted to increase in intensity and duration as a result of climate change (Kling et al. 2003; Fang et al. 2004; Ficke et al. 2007) and has been shown to have a negative effect on Lake Erie yellow perch potential growth (Arend et al. 2011; but see Roberts et al. 2011) and condition entering the fall (Roberts et al. 2009), or 2) the loss of energetically rich prey (e.g., *Diporeia*, alewife [*Alosa pseudoharengus*]) in other systems (lakes Huron and Michigan), which has been shown to reduce condition of species such as lake whitefish (*Coregonus clupeaformis*) (Pothoven 2001, 2006). Because percids are capital breeders (i.e., use energy store accumulated during the preceding months to allocate to reproduction), female condition entering the winter is likely to affect allocation of energy to reproduction (Henderson et al. 1996; Henderson 2000). Indeed, Henderson and Nepszy (1994) identified a positive relationship between Lake Erie walleye (*Sander vitreus*) year-class strength and surplus female energy reserves the preceding fall, supporting the notion that a decline in female condition during autumn can result in a weak year-class the following year. This hypothesis was further supported by Madenjian et al. (1996), who showed that Lake Erie walleye year-class strength was positively related to the amount of clupeids available for consumption during the preceding summer.

In Barents Sea cod (*Gadus morhua*) stocks, Marshall et al. (1999) found positive relationships between liver mass and recruitment, suggesting that recruitment in these stocks was limited by the amount of energy stored in the liver. Marshall et al. (1999) also found that cod total lipid energy, which was positively related to prey (capelin *Mallotus villosus*) consumed, was correlated with total egg production. The suggestion by Marshall et al. (1999) that total lipid energy could potentially replace spawning stock biomass in stock-recruitment models indicates the importance of lipid reserves to successful recruitment.

While previous research has shown how winter temperature (Hokanson 1977; Dabrowski et al. 1996; Ciereszko et al. 1997; Sandstrom et al. 1997; Luksiene et al. 2000), photoperiod (Dabrowski et al. 1996), autumn cooling rates (Wang et. al 2006), female condition (Henderson and Nepszy 1994; Marshall et al. 1999), and prey availability (Madenjian et al. 1996) can influence the reproductive success of percids, no comprehensive research has been conducted to understand how winter temperature acting independently or interactively with female condition entering the winter can influence population-level demographics, including fecundity and recruitment. Thus, while we have empirical evidence to indicate that yellow perch recruitment may in part be driven by winter temperature, the exact mechanisms underlying these trends remain unknown.

Objective 2. *Use our findings from Objective 1 to determine the (possibly synergistic) effects of summer hypoxia (as reflected in female body condition) and winter temperature on historical and future YP recruitment (i.e., year-class strength) in Lake Erie.*

We successfully conducted the modeling described in Objective 2, generating probability distributions of yellow perch recruitment under both observed (historical) and predicted climate scenarios. Results indicate that experimental relationships (developed form Objective 1) helped to explain historical variation in recruitment, although, as expected, the data were highly variable. Using a stochastic model that used predicted regional winter temperature at mid-21st century as an input (under high, moderate, and low future greenhouse gas emission scenarios), we found that both the mean level of recruitment and frequency of very strong yellow perch year-classes declined under all future climate scenarios. No major problems were encountered en route to completion of Objective 2.

Field observations from Lake Erie suggest that winter temperature, in part, drives yellow perch year-class strength (as determined from annual indices of juvenile abundance in August and October), which is a strong predictor of future recruitment to the fishery at age-2 (Ludsin 2000; YPTG 2011). For example, during the period 1969–2004 , a negative threshold relationship was shown to exist between winter temperature and yellow perch year-class strength (Ludsin 2000; TMF, unpublished data), wherein yellow perch year-classes were consistently low after warm winters in both western and central Lake Erie. Additionally, Crane (2007) explored numerous abiotic (n = 13) and biotic (n = 7) correlates of yellow perch and walleye recruitment across four different habitat types in western Lake Erie, finding that the previous winter's temperature occurred in all of the best models for yellow perch recruitment and the majority of models for walleye recruitment. Similar to our own data, winter temperature was negatively related to year-class strength for both yellow perch and walleye with the strongest year-classes following long, cold winters (Crane 2007).

Using findings from Objective 1, which quantified the role of winter duration and female condition entering winter on yellow perch reproductive success, we sought to use a population-modeling approach to understand what effect, if any, the relationship between winter duration/female condition and egg quality might have on yellow perch recruitment in both western and central Lake Erie. More specifically, we used our model to both explain the previously documented historical (1975–2010) relationships between winter temperature and yellow perch year-class strength (Ludsin 2000; Crane 2007; TMF, unpublished data), as well as how predicted climate change would be expected to influence Lake Erie yellow perch recruitment through effects on reproduction.

METHODS:

Objective 1.

Overview

We conducted a controlled laboratory experiment with yellow perch during summer 2011 through spring 2012 to quantify the independent and interactive effects of winter duration and adult condition on ovarian development, gamete production and quality, female spawning success, egg hatching success, and the quality of eggs and larvae. For our experiment, we used domesticated (hatchery-reared) yellow perch (in all experimental treatments, owing to high availability) and wild (from Lake Erie) yellow perch (only used in 4 of 6 experimental treatments, owing to poor survival prior to the experiment). Details regarding each aspect of our experiment are given below. All animal handling procedures described below were in accordance with IACUC protocol #2009A0073 (SAL, PI).

Collection of live yellow perch

Domestic fish. Domestic male and female yellow perch were purchased from a commercial fish operation during September 2010 and housed in large (475-950 L) fiberglass tanks supplied with constant aeration and flow-through water in an indoor wet lab facility at The Ohio State University's Aquatic Ecology Laboratory (AEL) in Columbus, OH. These fish were believed to be age-1 at the time of purchase. All individuals experienced natural, seasonal variation in both temperature and photoperiod and were fed dry pelleted feed (Aqua-Max^{TM} Grower 500) from fall 2010 through spring 2011. During spring 2011, when sex could be determined visually, individuals were implanted with a passive integrated transponder (PIT) tags (Biomark$^{®}$ Boise, ID) so that individual growth and maturation could be monitored throughout the study.

Wild fish. Live male and female yellow perch were collected from Lake Erie during April-May 2011, (when sex could be determined by visual examination). Bottom trawling was conducted aboard the Ohio Department of Natural Resources – Division of Wildlife's R/V *Grandon* in central Lake Erie near

Fairport Harbor, OH. Immediately upon collection, all individuals were placed into live wells and 'fizzed' with a hypodermic needle to release air pressure from the gas bladder. Over-inflation of the gas bladder is a common occurrence in fish caught in deep water and brought to the surface. If not relieved, pressure from this over-inflation can result in mortality due to gas embolisms or internal organ damage (Kerr 2001). A previous study using yellow perch found that 'fizzing' reduced post-capture mortality and did not adversely affect long-term survival (Keniry et al. 1996). Indeed, we lost many fish prior to learning of this fizzing technique. After adopting this technique survival rates increased dramatically.

Live yellow perch were transported from Lake Erie to an outdoor pool facility at the AEL where they could experience natural, seasonal variation in temperature and photoperiod. These fish were held in 2,500-L circular tanks that were supplied with constant aeration and flow-through water and fed live fathead minnows (*Pimephales promelas*). All individuals were PIT-tagged to monitor individual growth and maturation.

Experimental Design and Procedures

Body-condition treatments. To create fish of varying condition (i.e., energetic reserves) prior to winter, so as to test the importance of adult condition on reproductive success, we exposed fish to 1 of 2 feeding regimes during late summer and early fall. During the third week of July 2011, all individuals, both domestic and wild, were briefly anesthetized in MS-222 (to reduce handling stress), measured (nearest 1 mm), weighed (nearest 0.1 g), scanned for PIT tags, and randomly assigned to 1 of 2 feeding treatments (maintenance ration or *ad libitum*). The low feeding level of our maintenance ration treatment was intended to simulate the effect of hypolimnetic hypoxia on yellow perch condition entering the winter (i.e., create individuals of low body condition), whereas the unlimited feeding level of our *ad libitum* ration treatment was intended to simulate to effect of a hypoxia-free environment (i.e., create individuals of high body condition), in which yellow perch foraging was not limited by low dissolved oxygen levels (per Roberts et al. 2009, 2011, 2012). Daily rations for our maintenance feeding treatment were calculated using a previously published bioenergetics model for yellow perch (Kitchell et al. 1977). Measurements of water temperature (recorded daily), yellow perch mass (recorded during the third week of July), and caloric density of yellow perch and their feed (i.e., fathead minnows or dry pelleted feed; TMF, unpublished data) were used to parameterize the model used to calculate daily maintenance rations (i.e., the amount of food that met all basal metabolic demands without allowing for growth or increased fat reserves). During summer/early fall feeding, domestic yellow perch continued to receive dry pelleted feed and Lake Erie yellow perch continued to receive live (or occasionally frozen) fathead minnows, both of which were consumed readily. During the first week of October 2011, at which time we concluded our feeding treatments, up to 15 Lake Erie and domestic male and female yellow perch from each feeding treatment were randomly selected and euthanized to measure condition (i.e., energy density, mesenteric fat mass, muscle tissue lipid content; see protocol details below in ***Sample Processing and Analysis***).

Winter-duration treatments. During October 2011 through June 2012, we conducted a controlled laboratory experiment to quantify the effects of 1) winter duration (number of days < 5°C: levels = 50, 80, and 110 d) and 2) body condition entering the winter (i.e., high, low) on ovarian development, gamete production and quality, female spawning success, egg hatching success, and the quality of eggs and larvae from both domestic and wild fish (Figure 1). The duration of winter and rates of fall cooling and spring warming (0.2°C/d) that were used in our experiment were based on historical (1990-2010) field measurements of water temperature collected from Lake Erie at a Cleveland, OH water intake (TMF, unpublished data). Our three winter-duration treatment levels were intended to simulate historical (110 d), present (80 d) and future (50 d) conditions for Lake Erie. All levels of winter duration modeled were observed in our historical range of winter durations (1990-2010), the shortest (50 d) being recorded during the warm El Niño winter of 2002.

Domestic yellow perch were assigned to all three winter-duration treatments. However, wild (Lake Erie) individuals were assigned only to the short (50 d) and long (110 d) winter duration treatment due to limited numbers. Domestic and wild fish were kept in separate tanks within treatments, with each treatment replicated in triplicate.

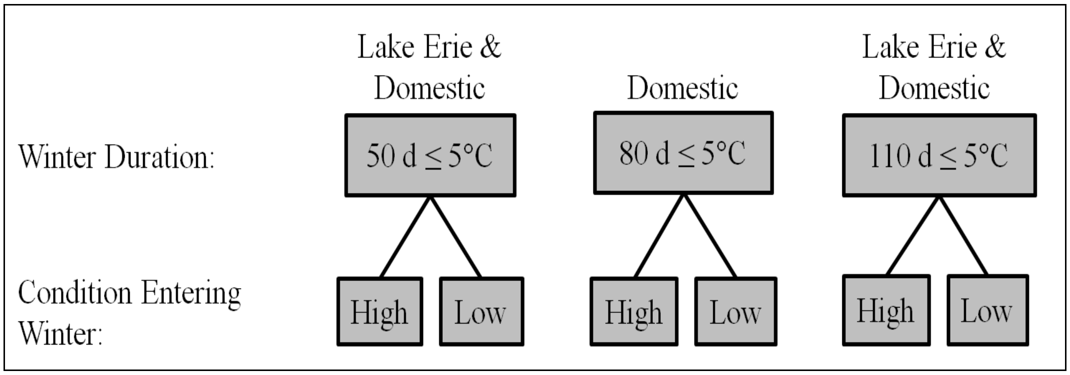

Figure 1*. Experimental design to test the effects of winter duration (number of days ≤ 5ºC) and adult body condition on yellow perch reproductive success. Domestic fish were used in all treatments, whereas wild fish were only used in the short (50 d) and long (110 d) winter-duration treatments. Each treatment was replicated in triplicate.*

During the first week of October 2011, prior to placement in winter-duration treatments, all individuals in our body-condition treatments were briefly anesthetized in MS-222, measured, weighed, and scanned for PIT tags. Subsequently, individuals were randomly assigned to a winter-duration treatment and placed into tanks inside walk-in, temperature-control rooms. Each room represented a single winter-duration treatment and contained a recirculating system with six 189 L tanks (3 tanks/body-condition treatment). Each individual tank contained 12 yellow perch (8-9 females and 3-4 males). The lighting in all rooms was provided by incandescent lights and controlled by a digital system that simulated daily reductions (during the fall) and increases (during winter and spring) in photoperiod so as to mimic the photoperiod at Cleveland, OH. Additionally, at dawn and dusk, 1 hour of increasing and decreasing light intensity preceded day and night periods, respectively. Recirculating systems were supplied with continuous aeration along with physical and biological filtration to maintain water quality. Ammonia, nitrite, nitrate, and pH were measured daily and water changes were conducted as needed to maintain high levels of water quality (i.e., unionized ammonia < 0.1 ppm; nitrates < 40 ppm). Hobo® loggers (Onset®) recorded water temperature every 2 hours in each recirculating system, and temperature and dissolved oxygen were measured daily with a YSI 550a handheld meter. During winter duration treatments, all yellow perch (both Lake Erie and domestic) were fed daily maintenance rations of live fathead minnows, determined from an existing bioenergetics model (Kitchell et al. 1977).

Spawning, fertilization, and euthanization. At the end of each winter-duration treatment, water temperatures were slowly increased to simulate spring warming and female yellow perch were watched closely (checked every 30 min from first light until 3 hours after last light) for external signs of ovulation. Once females showed signs of ovulation, they were removed from tanks, briefly anesthetized in MS-222, scanned for PIT tags, dried with a cloth, and gentle pressure was applied to the abdomen to strip ovulated egg ribbons. Eggs were expressed into a dry pan and their mass recorded. Females stripped of eggs were immediately euthanized and placed on ice for future dissection (see details in ***Sample Processing and Analysis*** below). From each female stripped of eggs, four 2-g egg masses were fertilized with a composite milt sample from three males. We collected subsamples of hand-stripped eggs for measures of reproductive development, fecundity determination, and several measures of egg quality (see ***Sample Processing and Analysis*** for details).

The milt was collected fresh for each fertilization event from three males within the same winter-duration/body-condition/fish-source treatment as the stripped female. As with females, males were briefly anesthetized in MS-222, scanned for PIT tags, dried with a cloth, and gentle pressure was applied to the abdomen to express milt. Milt from three males was composited into Moore's extender, where it was diluted 20-fold (Rinchard et al. 2005a). Each 2-g egg mass was subsequently fertilized with a concentration of 100,000 spermatozoa per egg (Kwasek 2012). We also analyzed both individual and composite milt samples from each fertilization event for percent sperm motility, duration of sperm motility, and sperm density (following Rinchard et al. 2005a).

Owing to the difficulty in assessing the final stages of ovulation from external signs, some females released egg ribbons spontaneously in their tanks. Upon finding ribbons in a tank, we removed, euthanized, and placed the spawner on ice for dissection (see details in ***Sample Processing and Analysis*** below). The water-hardened egg ribbons were then immediately collected from tanks, blotted to remove excess water, and weighed (nearest 0.01 g). We did not attempt to assess fertilization or hatching success of spontaneously released eggs, as in-tank egg ribbon release can cause highly variable male fertilization success rates (KD, personal communication).

Once three females in a winter-duration treatment had spawned or showed signs of ovulation, 1-3 females and 1-2 males per tank were sacrificed and placed on ice for dissection (see details in *Sample processing and analysis* below). These fish were used to assess reproductive development via histology and also provide a pre-ovulation measure of egg quality (e.g., energetic density, lipid concentration, egg size; see ***Sample Processing and Analysis***). In addition, these fish allowed us to determine if data collected from pre-spawning individuals in Lake Erie could be used to adequately assess post-spawning egg quality.

Sample Processing and Analysis

Fertilization and hatching success. Fertilized eggs were transported in fresh water to incubating and hatching facilities at The Ohio State University's Aquaculture Laboratory in Kottman Hall, where they were immediately placed into mesh-covered jars in upwelling California-style tray incubators. California trays were supplied with water from a partially recirculating system, equipped with a chiller to maintain water temperatures at optimal levels for yellow perch egg incubation (12-18°C) during the course of the experiment. Temperature and dissolved oxygen were recorded daily and eggs were watched carefully for presence of eyed-eggs. When fertilized eggs reached the eyed-egg stage (8-10 d, depending on water temperature), 2 of the 4 fertilized egg samples were removed from incubators and viewed under a dissecting microscope to quantify fertilization success. To quantify fertilization success, all eyed-eggs and dead eggs were counted in a single field of vision at 10x magnification (Dabrowski et al. 1996). This process was repeated up to 10 times for each egg mass, with each field of vision being randomly selected.

The remaining two fertilized egg samples were moved from California trays into hatching jars for hatching success determination. Clear, plastic 500-mL hatching jars were filled with water and sealed. An air stone in each jar provided vigorous aeration to assist with hatching. Hatching jars were held in a bath of flow-through water to maintain stable temperatures. Water temperature in the flow-through bath, measured daily, was13-20°C during the experiment. Eggs were checked every 12-24 hours for hatching. Once hatched larvae were visible, an 1800 µm sieve was used to separate hatched larvae from un-hatched eggs. All hatched larvae were immediately euthanized and preserved in 3% buffered glutaraldehyde. After collection of hatched larvae, all un-hatched eggs were returned to the hatching jar, with fresh water. The hatching success of each fertilized egg sample was determined by dividing the total number of hatched larvae collected by the total number of eggs in each sample (determined following methods for fecundity below).

All females sacrificed at all three end points (at the conclusion of the body-condition feeding treatments, prior to spawning during spring, and after hand-stripping of spontaneous release of eggs) had their total length (TL; nearest 1 mm), wet mass (nearest 0.1 g), ovary wet mass (nearest 0.001 g), liver wet mass (nearest 0.001 g), and mesenteric fat wet mass (nearest 0.001 g) measured, with otoliths being removed for age verification. After ovaries, livers, mesenteric fat, and otoliths were removed, a fillet of muscle tissue was removed from each female to determine the energy reserves stored in this tissue. The remaining soma of each female also was processed for total energetic content as a measure of female condition. The ovaries removed from females prior to spawning and the hand-stripped eggs were processed for a variety of data, including assessment of reproductive development, fecundity, and egg quality (see below).

Female body condition. While body-condition (high vs. low) was used as a class variable to investigate its effect on reproductive development, fecundity, and egg quality, additional measures of female body condition were taken at each end-point to quantify changes in condition throughout the winter period. Liver mass was used to calculate the hepatosomatic index (liver mass (g) x 100 / body mass (g); HIS), which has been used as an index of female body condition (Gauthier et al. 2008) and related to reproductive output in cod (Marshall et al. 1999). Mesenteric fat mass also was used as a direct measure of energy reserves. Finally, the total somatic energetic content of each female yellow perch was quantified as the ultimate indicator of body condition. Together these indices of female body condition (along with size) were regressed against measures of reproductive development, fecundity, and egg quality to assess if condition had any relationship with these variables within treatments. Also these measures of condition (particularly female energetic density) allowed us to evaluate if energy allocation patterns differed under different temperature and condition treatments. (e.g., Do females exposed to warm temperatures allocate energy to somatic growth at the expense of reproductive quality?).

Reproductive development. Ovarian development was measured, using several methods, including: 1) quantifying the percent of females that had ovulated during the experiment; 2) quantifying gonadosomatic index (gonad mass x 100 / body mass; GSI); and 3) conducting histological work on ovaries to determine mean size and developmental stage of eggs (see Dabrowski et al. 1996). A female was considered to be ovulating, if either she was able to be hand-stripped of egg or she spontaneously released eggs in her tank. The percentage of females ovulating in each treatment was recorded.

To characterize the stage of ovarian development, a subsample of each gonad was fixed in Davidson's solution for at least 48 hours. Gonads were then stored in 70% ethanol before being embedded in paraffin. Embedded gonads were sectioned on a rotary microtome (at 6 *u*m) and stained with hematoxylin and eosin (Shewmon et al. 2007). Stained sections were viewed and photographed using an image analysis system. State of ovarian development was classified as 1 of 6 stages (i.e., primary growth, early secondary growth, late secondary growth, vitellogenic growth, maturation and ovulation, and atretic; see West 1990; Shewmon et al. 2007), using specific criteria (e.g., appearance of cortical alveoli at the oocyte parameter, lipid droplets around the germinal vesicle).

Fecundity. Measured as the number of eggs per g of ovaries, fecundity was determined from ovaries of females sacrificed prior to spawning and from egg ribbons of females that were hand-stripped. Briefly, a subsample of each ovary or egg ribbon was collected and weighed, and the number of eggs in each subsample was counted under a dissecting microscope. In this manner, the total number of eggs produced by each female was estimated. While fecundity does not necessarily indicate fertility, which was tested with fertilization and hatching tests, it can provide an objective measure of reproductive output (Moyle and Cech 2000).

Egg quality. While our ultimate measures of egg quality were fertilization and hatching success, we also collected several additional measures of egg quality, including egg size, egg energetic density, egg total lipids, and egg fatty acids. These additional metrics of egg quality were intended to assist in our investigation of possible mechanisms underlying variation in fertilization and hatching success and also to determine if other, more easily collected, measures of egg quality could be used in future studies to accurately predict ultimate egg quality (i.e., fertilization and hatching success).

The number of eggs per g of ovaries was originally quantified to determine fecundity (as described above). The inverse of this metric gives the mass of an individual egg, which was subsequently used as measure of egg size, for each female. Egg size has been found to be an important predictor of egg quality, as larger eggs generally produce larger offspring that have higher rates of survival (see reviews by

Chambers and Leggett 1996 and Chambers and Waiwood 1996). While the effects of maternal traits, such as size and age, on egg size have been previously investigated (Heyer et al. 2001; Johnston et al. 2007; Venturelli et al. 2010), the effects of environmental variables, such as winter duration, have not.

Total energetic content of ovary subsamples was quantified with bomb calorimetry (following Collingsworth and Marshall 2011). Briefly, ovaries were dehydrated in a drying oven, homogenized into a fine powder, compressed into a small pellet, and 2-3 replicate samples for each ovary were combusted in a Parr bomb calorimeter. Total energy density was expressed as calories per g of wet mass.

Miller-Navarra et al. (2000) suggested that fatty acids of low melting point (e.g., eicosapenthaenoic acid; EPA) and ovarian phospholipids can be used as an indicator of egg quality in other organisms. Further, EPA in the phospholipid fraction of yellow perch ovarian lipids has been shown to vary inter-annually and between basins in Lake Erie (Rinchard et al. 2005b). As such, we quantified the percentages of total lipids, neutral lipids, and phospholipids in each hand-stripped egg mass. Additionally, we quantified fatty acid profiles of all neutral lipids in these egg masses, which provided a novel assessment of their use as a proxy for egg quality.

Total lipids were extracted from ovaries after homogenization in chloroform-methanol according to Folch et al. (1957). The organic solvent was evaporated under a stream of nitrogen and the lipid content determined gravimetrically. Total lipids were reported as mean ± SE for each treatment.

To measure fatty acids, total lipid extracts were separated into polar (phospholipids) and neutral (mostly triglycerides) fractions using silica sep-pak cartridges and determined gravimetrically. Fatty acid methyl ester mixtures were prepared from the neutral lipid fraction (Metcalfe and Schmitz 1961). Gas chromatograph analyses of the fatty acid methyl esters were performed with a Varian 3300 Gas Chromatograph (Varian Chromatography Systems, Walnut Creek, CA), using internal standard (C19:0) as detailed by Czesny and Dabrowski (1998). Mass-specific measures of fatty acids were measured.

Larval size and quality. To determine if larval size (TL) and quality differed among winter-duration and body-condition treatments, we measured five metrics of size and quality in preserved larvae: total length, eye diameter, yolk-sac volume, oil globule volume, and body depth at the insertion of the anal fin. Because previous research has found larval traits such as these to be correlated with female spawner size and/or age (Heyer et al. 2001; Berkley et al. 2004; Venturelli et al. 2010), we included female size and age as covariates in our analysis of winter-duration and female-condition effects.

Data Analysis

We used generalized linear models (PROC GLM, SAS v. 9.3) to test for effects of winter duration and female condition on each response variable for reproductive development, fecundity, and egg quality described above. Winter-duration and body-condition treatments were fixed categorical effects. Prior to using generalized linear mixed models, we assessed if response variables were related to female size (i.e., TL and/or mass). If significant relationships were found, we used residuals from size-specific relationships as our response variable in our generalized linear mixed models, to remove the effect of female size. Using data from our long winter treatment (as our replication was highest for this treatment), we tested for tank effects using tanks as random categorical effects (i.e., replicates nested within winter duration – body condition treatment combinations) in a generalized mixed model (PROC MIXED, SAS v. 9.3). Finding no tank effects ($P > 0.05$) for any of our variables, we calculated means of each response variable by tank (our experimental unit) and proceeded with testing for treatment effects. We also tested for an interaction between fixed categorical effects (i.e., winter duration*body condition). If the interaction term was not significant, it was removed from the model. In this manner, we tested for the effect of winter temperature by accounting for the effect of body condition on each of our response variables.

Additionally, in separate analyses, we used measures of female body condition as continuous covariates in generalize linear mixed models (substituting it for the fixed categorical predictor discussed above), to assess if these individual measures improved our ability to explain variation in our response variables. Finally, we used regression techniques (linear and non-linear) to evaluate the relationship between fertilization rates and hatching success with our metrics of egg quality (i.e., relative egg size, egg energetic density, egg total lipids, and egg fatty acids) to determine if a relationship existed between variables.

Prior to conducting statistical tests, we verified that each response variable was normally distributed. Additionally, we analyzed residuals from each model to verify that assumptions of normality, constant variance, independence, and (when appropriate) linearity were met. As needed, response variables were transformed to meet assumptions. For example, proportion data were arcsine-square root transformed prior to statistical analysis. In some cases, when transformations failed to meet assumptions, non-parametric statistics were used instead of generalized linear models.

Objective 2

Model Overview

Our goal was to derive a model that used annually varying environmental conditions to explain annually varying historical (1975-2010) yellow perch recruitment (as measured by year-class strength) and then to use the model to ask how projected changes in environmental conditions (e.g., winter temperature) might affect future (2046-2065) yellow perch recruitment. Initially, we planned to include the effect of summer hypoxia on fall female condition in this model. However, finding in our experiment that fall female condition was unrelated to reproductive output or quality (see **Results** section below for ***Objective 1***), our model only considered the effect of winter duration.

As a first step, we used recent Lake Erie adult yellow perch population size structure data, an index of juvenile yellow perch abundance (year-class strength), and winter temperature data to assess the ability of our model to explain annual variation in past recruitment. Afterwards, we used the model to forecast Lake Erie yellow perch recruitment under several predicted climate scenarios. This entire modeling process consisted of four steps:

1) We used our experimental data to relate Lake Erie agency-derived estimates of age-specific, adult yellow perch size distributions (in October; YPTG 2011) to predict spring egg production and quality (i.e., egg size, which was found to be important in our experiment). Our experimental data allowed us to use an index of annual winter duration (number of days with water temperature ≤ 5°C at the Cleveland, OH water intake; 1994 – 2010) to predict egg size the following spring (see Figure 13; *egg mass* = 1.55 + 0.014[*# d water temp ≤ 5°C*]; $R^2 = 0.50$). To obtain estimates of egg size for early years in our dataset (1975–1993), for which we did not have water temperature data, we developed a relationship between the number of days with mean daily air temperature ≤ 0°C each winter (derived from a regional index of mean daily air temperature averaged from Cleveland-Hopkins International Airport and Toledo Express Airport, OH) and the number of days water temperature was less than 5°C (*# d water temp ≤ 5°C* = 41.2 + 1.1[*# d air temp ≤ 0°C*]; $R^2 = 0.58$). With an annual measure of egg mass from 1975–2010 in hand, our experimental data allowed us to calculate annual hatching success as a function of egg mass (see Figure 19; *% hatching* = -0.50 + 0.37[*egg mass*]; $R^2 = 0.68$). Finally, by combining our estimate of total egg production with annual hatching success, we calculated an annual index of total larval production (TLP) for the period 1975-2010.

2) Using historical (1975-2010) annual estimates of TLP and estimates of year-class strength (i.e., age-0 yellow perch catch-per-unit-effort [CPUE] during October; YPTG 2011), we tested the hypothesis that high population TLP results in strong year-classes. Originally, we planned to test this hypothesis for both Management Unit 2 and 3 in Lake Erie, which are located in the central basin. However, due to a low frequency (and, in some cases, lack) of sampling in Management Unit 3 across years, this analysis was conducted only for Management Unit 2.

Previous research has demonstrated that abundance during August and October of the first year of life is a strong predictor of future recruitment to the fishery at age-2 (Ludsin 2000; YPTG 2011). Indeed, we found a positive relationship between TLP and recruitment in Management Unit 2 during 1975–2010 (Figure 28; *CPUE age-0 yellow perch* = 8.74 + 0.54(*TLP in millions*); $P = 0.02$; $R^2 = 0.16$). With this relationship added to our model, we gained the ability to predict recruitment the following year as a function of adult total egg production (based on adult size distributions in October) and winter duration. While we found a significant positive relationship between TLP and recruitment, this relationship had a great deal of variance associated with it (Figure 24); thus, we described it with a probabilistic model. In simulations with the resulting model, this part of the life cycle was assumed to have a stochastic relationship between the input of eggs and the output of recruitment (year-class strength).

3) The goal of this step was to produce a probability distribution of annual recruitment expected under current environmental conditions. Using our winter-duration index based on Lake Erie water temperatures (described above) and annual estimates of total egg production, we drew randomly from the observed distribution of winter conditions and from the observed distribution of total egg production. We applied the model that we derived in Steps 1-2 above to these input data to get recruitment as output. To model a stochastic representation of the transition from larvae to recruits, we used quantile regression (Cade et al. 1999) to define the 1st, 25th, 50th, 75th, 90th and 99th quantiles of the TLP to recruits relationship (Figure 24). Using these quantiles to give the probability of achieving specific levels of recruitment each year given TLP, we generated a recruitment probability distribution from 10,000 repetitions of this simulation process.

4) Ultimately, we used this model to ask how changes in environmental conditions predicted by climate models should change our expectations about yellow perch recruitment. We used downscaled and bias-corrected climate predictions of mean daily air temperature at mid-century (2046–2065) from three General Circulation Models used in IPCC (2007) (CCCMA: Canadian Centre for Climate Modeling and Analysis; GFDL: Geophysical Fluid Dynamics Laboratory; IPSL: Institute Simon Pierre Simon Leplace). We used downscaled air temperature predictions from each of the 1/8° grids that were nearest Cleveland-Hopkins International Airport and Toledo Express Airport. Exactly as we created a historical index of air temperatures in Step 1, we derived a regional index of future mean daily air temperature by averaging daily predictions from both of these grids for each model. We ran each model under three future greenhouse gas emissions scenarios (A1B: high; A2: moderate; and B1: low; IPCC 2007). Within each emissions scenario, daily regional predictions were averaged across all three models to generate a single index of the number of days with mean daily air temperatures < 0°C during 2046–2065. We altered our original distributions of Lake Erie winter water temperatures (using the previously defined relationship between air and water temperatures from Step 1) to reflect changes expected by 2046–2065 under each emission scenario. From these new distributions, we again drew randomly from winter environmental conditions and applied the model that we derived in steps 1-3 to these input data, exactly as done with the *current* environmental conditions in modeling Step 3 (using current levels of total egg production). We repeated this process for 10,000 repetitions to create probability distributions of expected annual recruitment under future climate conditions.

RESULTS:

Objective 1 Results

Fall Body Condition

Our feeding treatments were successful in creating two distinct levels of body condition entering the winter. We created TL - mass relationships for Lake Erie females ($\log_{10}[TL] = 3.20 \times \log_{10} [mass] - 5.40$; $P < 0.0001$; $R^2 = 0.94$), Lake Erie males ($\log_{10}[TL] = 3.11 \times \log_{10}[mass] - 5.17$; $P < 0.0001$; $R^2 = 0.94$), domestic females ($\log_{10}[TL] = 3.54 \times \log_{10} [mass] - 6.21$; $P < 0.0001$; $R^2 = 0.91$), and domestic males ($\log_{10}[TL] = 3.58 \times \log_{10} [mass] - 6.32$; $P < 0.0001$; $R^2 = 0.94$). Using the residual value for each individual as a relative index of body condition (i.e., positive residual indicates a higher than average mass for a given length), we determined that for all four groups, residual condition was higher in the ad libitum (high ration) treatment than in the maintenance (low) ration treatment (Lake Erie females: ANOVA $F_{1,99} = 27.6$, $P < 0.0001$; Lake Erie males ANOVA $F_{1,82} = 14.9$, $P = 0.0002$; domestic females: ANOVA $F_{1,221} = 61.2$, $P < 0.0001$; domestic males: ANOVA $F_{1,143} = 9.1$, $P = 0.003$; Figure 2).

Growth in mass from the start (late July) to the end of summer (early October) also was greater in the high (*ad libitum*) versus low (maintenance) ration treatments. This result was particularly straightforward for Lake Erie females and males (females ANOVA $F_{1,100} = 82.1$; $P < 0.0001$; males ANOVA $F_{1,82} = 56.2$; $P < 0.0001$; Figure 3), with fish TL having no effect on female ($P = 0.34$) or male ($P = 0.08$) growth in mass. The effect of daily ration (feeding treatment) on growth was more complex for domestic males and females. In the *ad libitum* treatment, growth increased with increasing TL for both domestic females ($growth = 1.2 \times TL - 236$; $P < 0.0001$; $R^2 = 0.38$; Figure 4) and males ($growth = 0.9 \times TL - 171$; $P < 0.0001$; $R^2 = 0.51$; Figure 5). By contrast, growth was unrelated to TL for domestic females ($P = 0.73$; Figure 4) or males ($P = 0.81$; Figure 5) in the low feed (maintenance ration) treatment. Furthermore, growth differences between high and low feeding treatments did not exist at the smallest TLs for domestic females (TL $\leq$ 215 mm; ANCOVA: $P = 0.16$) or males (TL $\leq$ 205 mm; ANCOVA: $P = 0.09$). However, at larger TLs, both domestic females (TL $\geq$ 220 mm; ANCOVA: $P < 0.01$) and males (TL $\geq$ 210 mm; ANCOVA: $P < 0.01$) in the high feeding treatment experienced more growth than those in the low feeding treatment.

Our summer feeding treatments also affected the initiation of reproductive development, although the direction of effects differed between Lake Erie and domestic yellow perch. In male and female domestic yellow perch that were sacrificed at the end of summer (first week of October), gonad mass increased with increasing fish mass, but the relationship between fish mass and gonad mass differed between feeding treatments (Figures 6-7). Both domestic males (ANCOVA $F_{2,22} = 3.9$; $P = 0.035$; $R^2 = 0.26$) and females (ANCOVA $F_{2,25} = 6.5$; $P = 0.005$; $R^2 = 0.34$) in the maintenance ration (low) feeding treatment experienced greater increases in gonad mass as fish mass increased, although a high degree of individual variation existed (Figure 6-7). Lake Erie female gonad mass also increased with fish mass, except that females in the high feed treatment had greater gonad mass than those in the low feeding treatment (ANCOVA $F_{2,6} = 13.4$; $P = 0.006$; $R^2 = 0.82$; Figure 6), which was inverse to the trend observed for domestic females. Lake Erie male reproductive development was strongly related to fish mass ($P < 0.0001$; $R^2 = 0.76$) although including the effect of feeding treatment as a class variable indicated a weak effect of feeding treatment on gonad mass ($P = 0.08$; Figure 7), with males of a given size in the high (*ad libitum*) feeding treatment having greater gonad mass than males in the low (maintenance ration) feeding treatment.

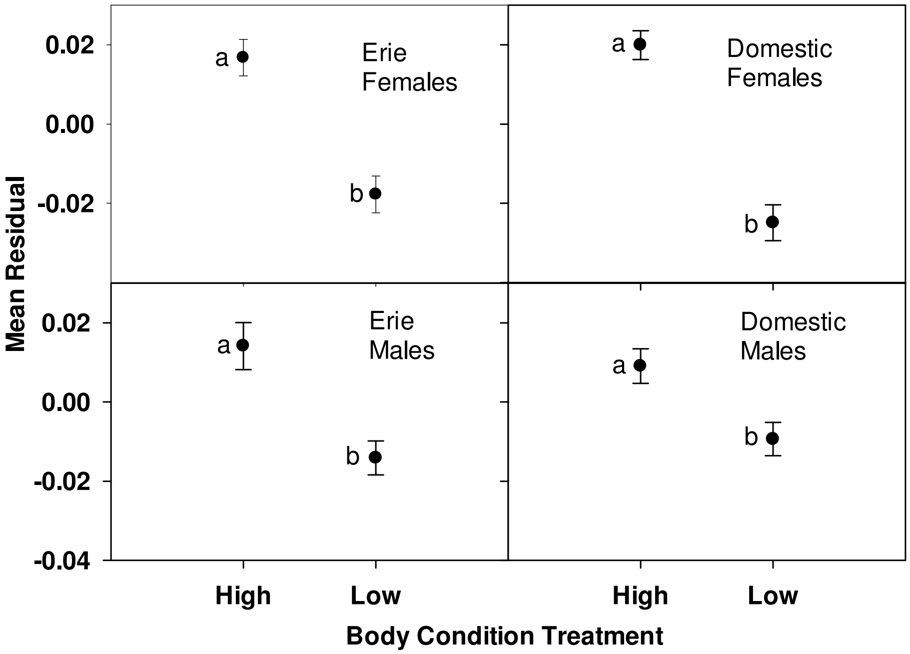

Figure 2. *Mean (± 1 SE) residuals (derived from total length – mass relationships) for high (*ad libitum*) and low (maintenance ration) body-condition treatments. Data are presented separately for Lake Erie and domestic male and female yellow perch. Means with different lowercase letters within a panel differed in a Tukey's honest significant difference post-hoc comparison.*

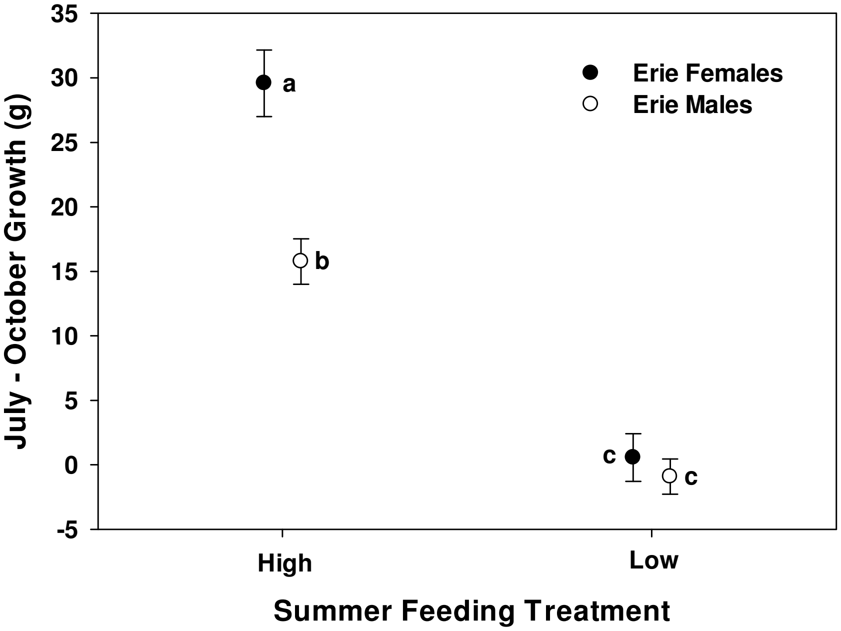

Figure 3. *Mean (± 1 SE) growth from late July through early October for male and female Lake Erie yellow perch in high and low summer feeding treatments. Means with different lowercase letters differed after correction for multiple comparisons.*

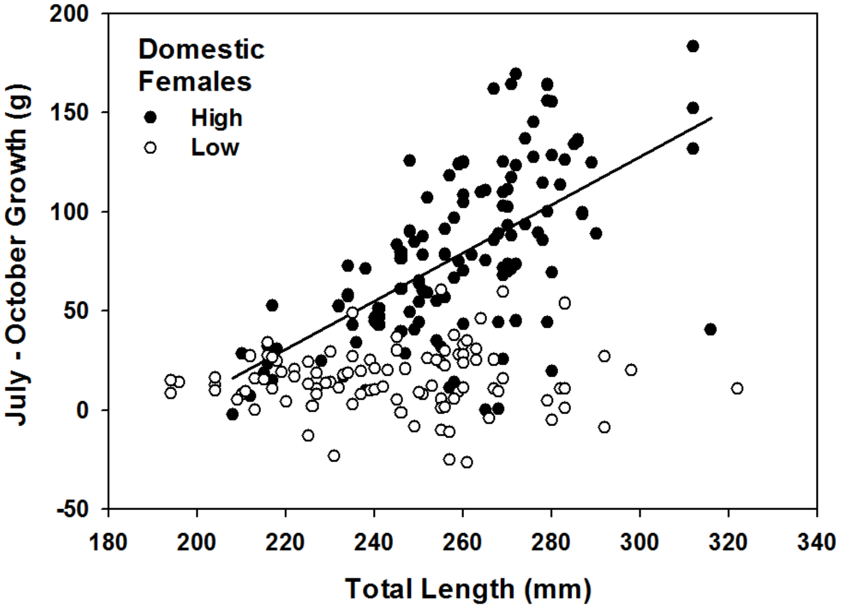

Figure 4. *Individual growth from late July through early October relative to total length (TL) for domestic female yellow perch in high (*ad libitum*) and low (maintenance ration) feeding treatments.*

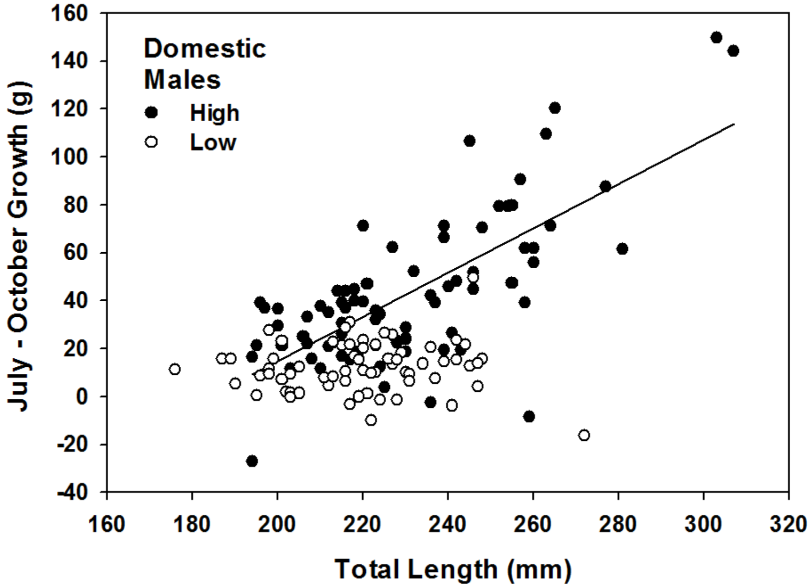

Figure 5. *Individual growth from late July through early October relative to total length (TL) for domestic male yellow perch in high (*ad libitum*) and low (maintenance ration) feeding treatments.*

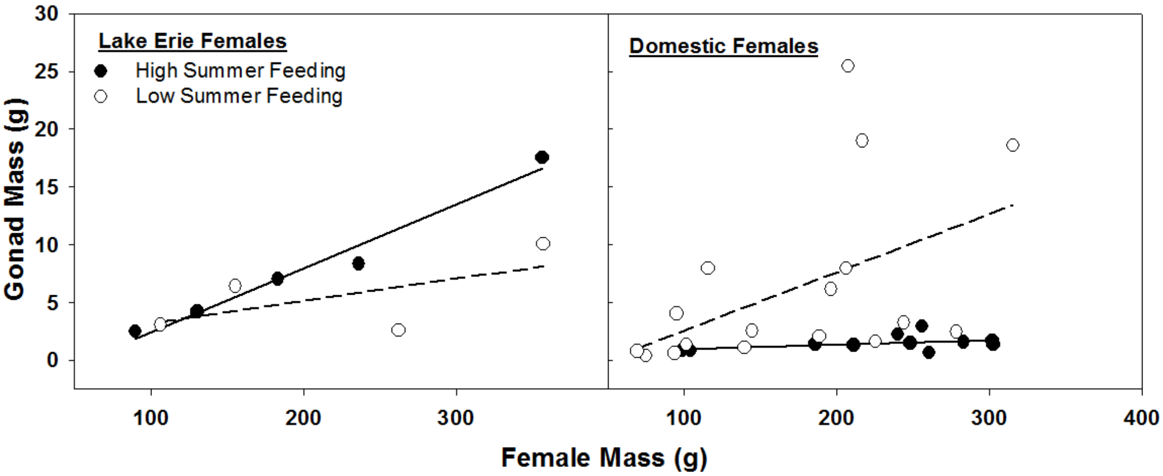

Figure 6. *Female gonad mass (g) during the first week of October (at the completion of our summer feeding regime) as a function of female mass (g) for Lake Erie and domestic yellow perch from high (*ad libitum*) and low (maintenance ration) feeding treatments.*

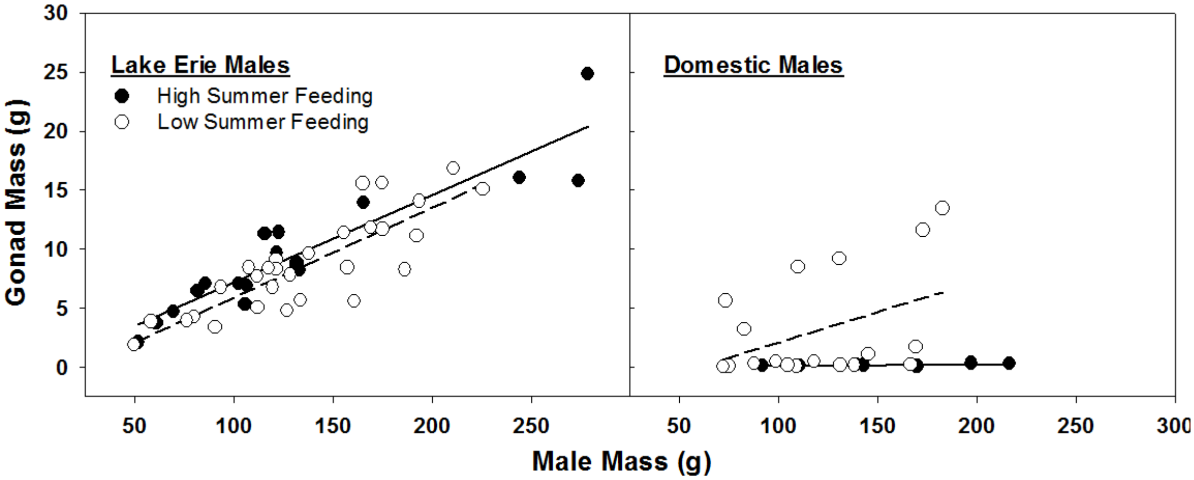

Figure 7. *Male gonad mass (g) during the first week of October as a function of male mass (g) for Lake Erie and domestic yellow perch from high (*ad libitum*) and low (maintenance ration) feeding treatments.*

Spawning, Fertilization, and Hatching Success

We successfully simulated winters of different duration and created conditions that allowed for apparently normal spawning. Observed winter duration in each of our treatments matched target durations at 4°C (i.e., short = 50 d, medium = 90 d, long = 110 d < 5°C; Figure 8). Likewise, yellow perch in all combinations of winter duration and female condition treatments spawned, and viable eggs were found in all treatments. However, important differences in the timing of spawning, quality of eggs and larvae produced, and hatching success of eggs existed among treatments.

Spawning phenology. Both the timing and temperatures at which spawning occurred differed across our winter duration treatments, with spawning being defined as either being hand stripped of eggs or eggs being spontaneously released in a tank (Table 1). Despite the fact that our short winter treatment began to warm 30 d prior to our medium winter treatment, periods of spawning for these two winter-duration treatments largely overlapped (from mid-April into May). As winter duration increased, the temperatures at which females spawned decreased. No obvious differences in the timing of spawning between females of high versus low body condition were found within each winter duration treatment. Also, Lake Erie and domestic females had similar responses in the short and long winter duration treatments.

Table 1. *Start and end dates (in 2012) and water temperatures of spawning in Lake Erie and domestic female yellow perch in our laboratory experiment.*

Winter Duration	Erie	Domestic
Short (50 d ≤ 5°C)	4/15 - 5/6 (15.1 - 15.3°C)	3/22* - 5/18 (13.5 - 15.2°C)
Medium (80 d ≤ 5°C)	-	4/19 - 5/26 (11.9 - 14.5°C)
Long (110 d ≤ 5°C)	5/9 - 6/3 (9.7 - 14.3°C)	5/6 - 5/30 (10.2 - 14.4°C)

*One female spawned on 3/22; next female spawned on 4/13, when temperature was 15.2°C

The percentage of spawning females was similar across winter-duration treatments for both domestic and Lake Erie females (Table 2). In both the short and long winter treatments, all Lake Erie females that were allowed to progress towards spawning eventually spawned. By contrast, about one-third (i.e., 21 – 35%; Table 2) of domestic females did not enter the final stages of ovulation and spawn across all winter duration treatments. Many of these females had low GSI (< 15%), and appeared never to complete reproductive development. Within each winter-duration treatment, the percentage of females that spawned did not appear to differ between female body-condition treatments.

Table 2. *Percentage of domestic and Lake Erie female yellow perch spawning in each winter-duration treatment.*

Winter Duration	**Erie**	**Domestic**
Short (50 d at 4°C)	100% (*N*=15)	70% (*N*=20)
Medium (80 d at 4°C)	-	79% (*N*=34)
Long (110 d at 4°C)	100% (*N*=20)	65% (*N*=26)

Of the females that entered the final stages of ovulation, ~50% were able to be hand-stripped of eggs, which were fertilized under controlled conditions (Erie: short N=7, long N=10; domestic: short N=10, medium N=14, long N=12). Fertilization and hatching success of these eggs was highly variable (Table 3). Furthermore, by regressing fertilization success against hatching success, we found that our index of fertilization success largely over-predicted hatching success (Figure 9). Therefore, in subsequent analyses that relate egg quality to egg survival, we used hatching success, as we believe this metric is a truer measure of egg viability. Neither winter duration (Erie P = 0.25; domestic P = 0.35) nor female condition (Erie P = 0.50; domestic P = 0.89) treatments affected hatching success.

Table 3. *Mean (and range of) fertilization (Fert) and hatching (Hatch) success (%) for domestic and Lake Erie female yellow perch eggs from each winter-duration treatment.*

	Erie		**Domestic**	
Winter Duration	**Fert**	**Hatch**	**Fert**	**Hatch**
Short (50 d at 4°C)	46% (6-80%)	37% (0-84%)	70% (33-85%)	22% (0-59%)
Medium (80 d at 4°C)	-	-	52% (0-89%)	28% (0-98%)
Long (110 d at 4°C)	82% (43-98%)	62% (14-100%)	68% (3-98%)	37% (0-87%)

Histological analysis. By conducting histological analysis of ovaries collected from euthanized pre-spawning female yellow perch in each treatment, we gained insight into the physiological state of reproductive development immediately prior to spawning. These collections allowed us to document that ovaries from domestic females typically had higher numbers of atretic oocytes than those from Lake Erie females (Figure 10). The occurrence of these atretic oocytes may provide insight into the lack of spawning for some domestic yellow perch females. However, in the females with low GSI (<15%), no obvious occurrence of atretic oocytes was found. These females instead showed a degenerating gelatinous layer (couche hyaline; *sensu* Malservisi and Magnin, 1968; incorrectly identified as "zona radiata externa" by Mansour et al. 2010) that might affect egg quality or prevent ovulation.

Egg Production and Quality

Fecundity. For both Lake Erie and domestic females, fecundity increased with female TL (Figure 11). Fecundity also was positively correlated with female residual condition entering the winter (*fecundity* = 479 x *total length* [*mm*] + 73821 x *residual condition* – 92599; $P < 0.0001$; $R^2 = 0.58$; see Figure 2). We used residual values from this relationship to assess if winter duration or body-condition treatments affected the total number of eggs produced, after accounting for the effect of female size. Neither winter duration (Lake Erie: $P = 0.44$; domestic: $P = 0.98$) nor body condition entering winter (Lake Erie: $P = 0.37$; domestic: $P = 0.44$) were related to total egg production.

Egg ribbon mass also increased with female TL, but Lake Erie females produced ribbons that were larger for a given TL than domestic females (Lake Erie: *ribbon mass* = 0.96 x *TL* [*mm*] – 163, $P < 0.001$, $R^2 = 0.62$; domestic: *ribbon mass* = 0.88 x *TL* [*mm*] – 158, $P < 0.001$, $R^2 = 0.48$; Figure 12). Using residuals from these regressions, we found that Lake Erie females in the long winter treatment produced larger ribbons than those in the short winter treatment (ANOVA $F_{1,6} = 22.1$, $P = 0.003$; $R^2 = 0.79$; Figure 13), although this same effect was not observed for domestic females ($P = 0.70$).

Egg mass. The increase in egg ribbon size was accompanied by an increase in the mass of individual eggs. Lake Erie females in the long winter treatment produced larger eggs than those in the short winter treatment (ANOVA $F_{1,6} = 6.1$, $P = 0.048$; $R^2 = 0.50$; Figure 14). However, this effect of winter duration on egg mass was not found for domestic females ($P = 0.27$). The energy density of egg ribbons declined with increasing winter duration in both Lake Erie (ANOVA $F_{2,5} = 27.6$, $P = 0.002$) and domestic (ANOVA $F_{2,12} = 5.8$, $P = 0.02$, $R^2 = 0.49$) females (Figure 15). Additionally, for Lake Erie yellow perch, energy density of egg ribbons was lower in the low-condition treatment (ANOVA $F_{2,5} = 27.6$, $P = 0.002$; Figure 15) than the high-condition treatment in both the short and long winter treatments.

Egg energy density. While the energy density of egg ribbons from Lake Erie individuals was *lower* in the long than short winter treatments (Figure 15), the mass of individual eggs showed an opposite effect (Figure 14). Because the increase in egg mass (~40%) was about double the decline in caloric density (~20%), the energy density *per egg* did not differ among winter-duration treatments for either Lake Erie or domestic females (Figure 16). Subsequently, we scaled lipid class data to the individual egg level (µg/egg wet mass), to account for changes in egg mass across winter-duration treatments (Figure 14).

Table 4. *Yellow perch lipid composition (µg) per egg (mean ± 1 SE) for Lake Erie and domestic females. (PUFA = polyunsaturated fatty acid, AA = Arachidonic acid, EPA = Eicosapentaenoic acid, DHA = Docosahexaenoic acid)*

Class		**Lake Erie**	**Domestic**
Total lipids		122.71 ± 0.009	89.08 ± 0.003
Neutral lipids		97.22 ± 0.007	70.80 ± 0.002
Fatty acids			
Saturated			
14:0		10.57 ± 1.70	7.41 ± 0.92
16:0		0.89 ± 0.13	0.66 ± 0.09
18:0		0.92 ± 0.43	0.95 ± 0.28
20:0		0.17 ± 0.05	0.10 ± 0.03
22:0		0.45 ± 0.07	0.40 ± 0.05
Monosaturated			
14:1		0.16 ± 0.04	0.12 ± 0.02
16:1(*n*-9)		5.64 ± 0.64	4.83 ± 0.23
18:1(*n*-9)		0.75 ± 0.06	0.53 ± 0.03
18:1(*n*-7)		0.01 ± 0.003	0.01 ± 0.001
20:1(*n*-9)		0.01 ± 0.002	0.01 ± 0.001
22:1		1.01 ± 0.19	0.59 ± 0.09
n-6 PUFA			
18:2(*n*-6)		4.54 ± 0.40	4.05 ± 0.19
20:2(*n*-6)		0.04 ± 0.008	0.06 ± 0.02
20:4(*n*-6)	AA	0.96 ± 0.16	0.56 ± 0.08
n-3 PUFA			
18:3(*n*-3)		0.12 ± 0.012	0.15 ± 0.008
20:3(*n*-3)		0.17 ± 0.03	0.09 ± 0.02
20:5(*n*-3)	EPA	1.18 ± 0.12	1.10 ± 0.06
22:6(*n*-3)	DHA	8.10 ± 0.53	6.65 ± 0.30

Egg lipids. A summary of lipid data from unfertilized yellow perch eggs is presented in Table 4. No effects of winter duration (Erie: $P = 0.13$; domestic: $P = 0.46$) or female condition (Erie: $P = 0.72$; domestic P: = 0.35) were found for the total lipid content of eggs in ribbons produced by Lake Erie or domestic females. Similarly, no differences in the neutral lipids per egg were found across winter-duration (Erie: $P = 0.11$; domestic: $P = 0.51$) and between body-condition (Erie: $P = 0.84$; domestic: $P = 0.39$) treatments for Lake Erie or domestic yellow perch. Of the 18 fatty acid classes quantified, only three (myristoleic acid 14:1 [a monosaturated fatty acid], stearic acid 18:0 [a saturated fatty acid], and eicosadienoic acid 20:2 [an *n*-6 polyunsaturated fatty acid (PUFA)]) differed among winter-duration and/or female body-condition treatments for Lake Erie eggs. In Lake Erie females, quantities of both myristoleic acid ($P = 0.01$) and stearic acid ($P = 0.02$) in eggs decreased as winter duration increased (Figure 17). Additionally, myristoleic ($P = 0.03$), stearic ($P = 0.02$), and eicosadienoic acid ($P = 0.04$) were lower in eggs produced from females in the low-condition treatments compared to those from high-condition females (Figures 17-18), although the relationship between stearic acid and female condition differed between winter-duration treatments (P = 0.01). For domestic females, docosahexaenoic acid (DHA; *n*-3 PUFA) was weakly negatively correlated with winter duration (P = 0.06; Figure 19). No other relationships between fatty acid classes and winter duration or female condition treatments were evident for eggs from domestic females.

Relating metrics of egg quality against hatching success, we found that egg mass was positively correlated with hatching success for Lake Erie (*hatching success* = - 0.5 + 0.37(*egg mass*), P = 0.01, R^2 = 0.68) and domestic yellow perch (*hatching success* = - 0.3 + 0.29(*egg mass*), P = 0.096, R^2 = 0.20) females, although the relationship was much stronger for Lake Erie yellow perch (Figure 20). Several other metrics of egg quality (i.e., energy density [cal/egg wet mass], total lipids [µg/egg wet mass], neutral lipids [µg/egg wet mass], and myristoleic acid [µg/egg wet mass]) also were positively correlated with hatching success (Figure 21). However, all of these latter egg quality metrics were also correlated with egg mass (Figure 21), making it difficult to determine the relative importance of each individual variable to hatching success. In contrast to eggs from Lake Erie females, domestic yellow perch eggs displayed a weak positive relationship between energy density (cal/egg wet mass) and hatching success (*hatching success* = - 0.5 + 0.44(*energy density*), P = 0.08, R^2 = 0.22), but mass of total lipids, neutral lipids, and myristoleic acid per egg were unrelated to hatching success (P > 0.1). Two different fatty acids, not found to be important in predicting Lake Erie hatching success, were found to be positively correlated with hatching success in domestic yellow perch. Behenic acid, 22:0 (a saturated fatty acid [*hatching success* = 0.03 + 0.62(*behenic acid*, P = 0.02, R^2 = 0.38]) and Erucic acid, 22:1 (an unsaturated fatty acid [*hatching success* = 0.09 + 0.32(*erucic acid*), P = 0.07, R^2 = 0.25]) were both positively related to hatching success. Unlike Lake Erie eggs, these lipids were not positively correlated with egg mass (benenic acid: P = 0.23 ; erucic acid: P = 0.12). These two fatty acids also did not differ between winter-duration treatments (benenic acid: P = 0.55 ; erucic acid: P = 0.31) or body-condition treatments (benenic acid: P = 0.86; erucic acid: P = 0.47). These results suggest that individual variability in egg fatty acid composition may have caused some of the variation in hatching success for domestic yellow perch.

Male Reproductive Quality

While some measures of male reproductive development and quality differed across winter-duration treatments, others appeared unaffected. Specifically, sperm motility (the percentage of milt that was activated by water contact) declined at the end of our long winter treatments for both Lake Erie (Figure 22) and domestic (Figure 23) males. By contrast, other measures of sperm quality (i.e., duration of motility) and production (i.e., sperm density) were unchanged throughout the experiment. To assess if repeated stripping of milt from males lowered sperm quality or production, we looked at how mean motility, the mean duration of motility, and mean sperm density changed through time for individuals that we had at least three measures of sperm quality. Finding no evidence that repeated stripping of males influenced any of these metrics, we averaged measures of sperm quality and production for each individual male to investigate treatment effects. The duration of motility did not differ between winter-duration or condition treatments and was similar between Lake Erie (35 ± 6 sec [mean ± 1 SD]) and domestic (37 ± 11 sec) males. Similarly, sperm density appeared unaffected by winter duration (P > 0.1) or condition treatments (P > 0.1), and was similar between Lake Erie (57.8 ± 7.9 % spermatocrit [mean ± 1 SD]) and domestic (54.2 ± 7.9) males. By contrast, sperm motility was lower in the long winter treatment than in the short winter one for Lake Erie males (Kruskal Wallis chi-squared = 6.33; *d.f.* = 1; P = 0.012), owing to a decline during the tail end of spawning in our long winter treatment. This decline in sperm motility, however, was unrelated to hatching success, and we found no correlation between hatching success and any other measure of sperm quality or production for either Lake Erie or domestic yellow perch. Additionally, including sperm motility as a covariate in the previously defined relationship between hatching success and egg mass did not explain any additional variation (P = 0.31).

Larval Size and Quality

We quantified the TL, body depth, and yolk-sac volume for a subsample of 1,197 larvae (out of 35,526 individuals) that were collected immediately after (within 12 hours of) hatching. Larval yellow perch TL did not vary across winter-duration (Erie: $P = 0.32$; domestic: $P = 0.41$) or between female condition (Erie: $P = 0.92$; domestic: $P = 0.72$) treatments. Larval body depth also was unaffected by winter duration (Erie; $P = 0.29$; domestic: $P = 0.32$) or female condition (Erie: $P = 0.81$; domestic: $P = 0.53$). Likewise, yolk-sac volume of recently hatched larvae did not differ across winter-duration (Erie: $P = 0.86$; domestic: $P = 0.32$) or female condition (Erie: $P = 0.48$; domestic: $P = 0.53$) treatments. However, larval TL was positively related to individual egg mass (TL [mm] = 4.38 + 0.27($egg\ mass$); $P = 0.04$, $R^2 = 0.52$) for Lake Erie females (Figure 24).

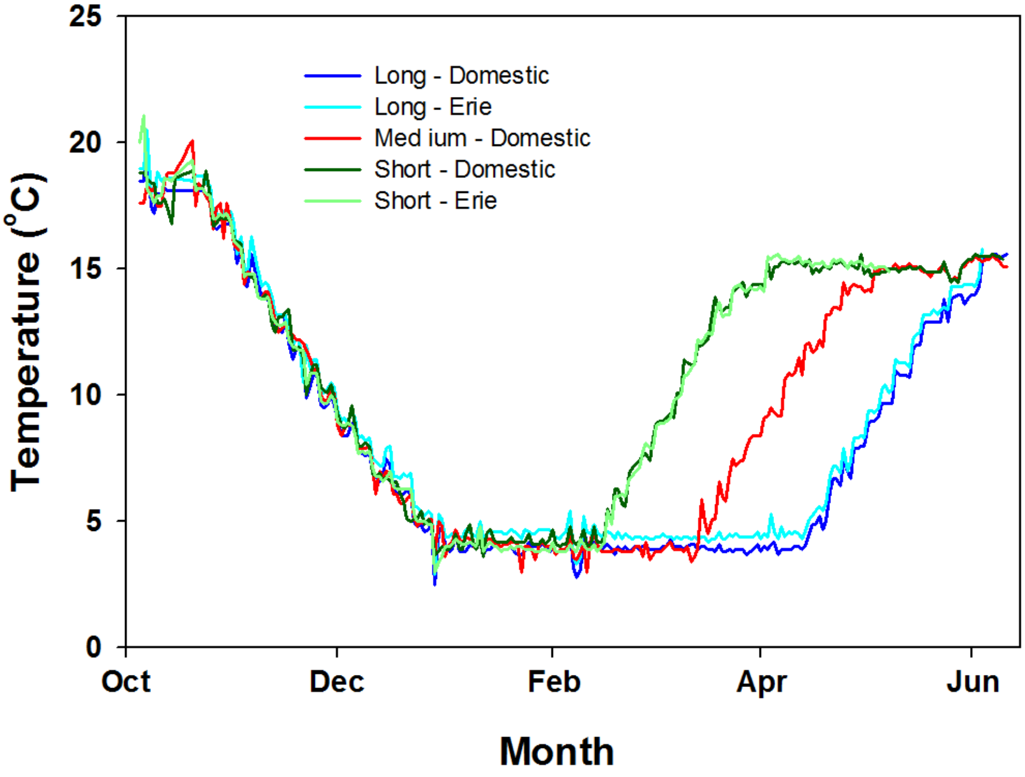

Figure 8. *Daily water temperature (°C) in the short (50 d < 5°C), medium (80 d < 5°C) and long (110 d < 5°C) winter-duration treatments for domestic and Lake Erie yellow perch.*

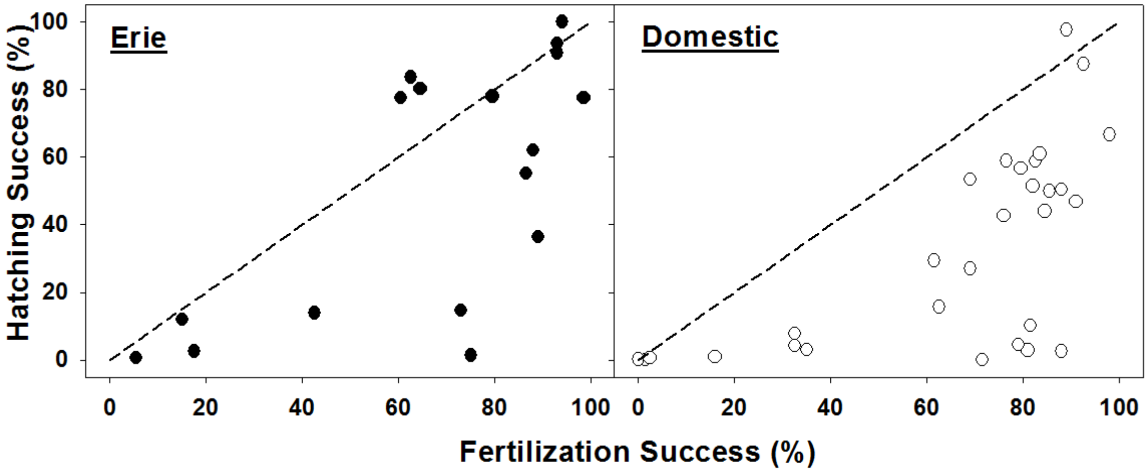

Figure 9. *Hatching success relative to fertilization success for Lake Erie and domestic female yellow perch eggs across all treatments. The dashed line indicates the 1:1 line.*

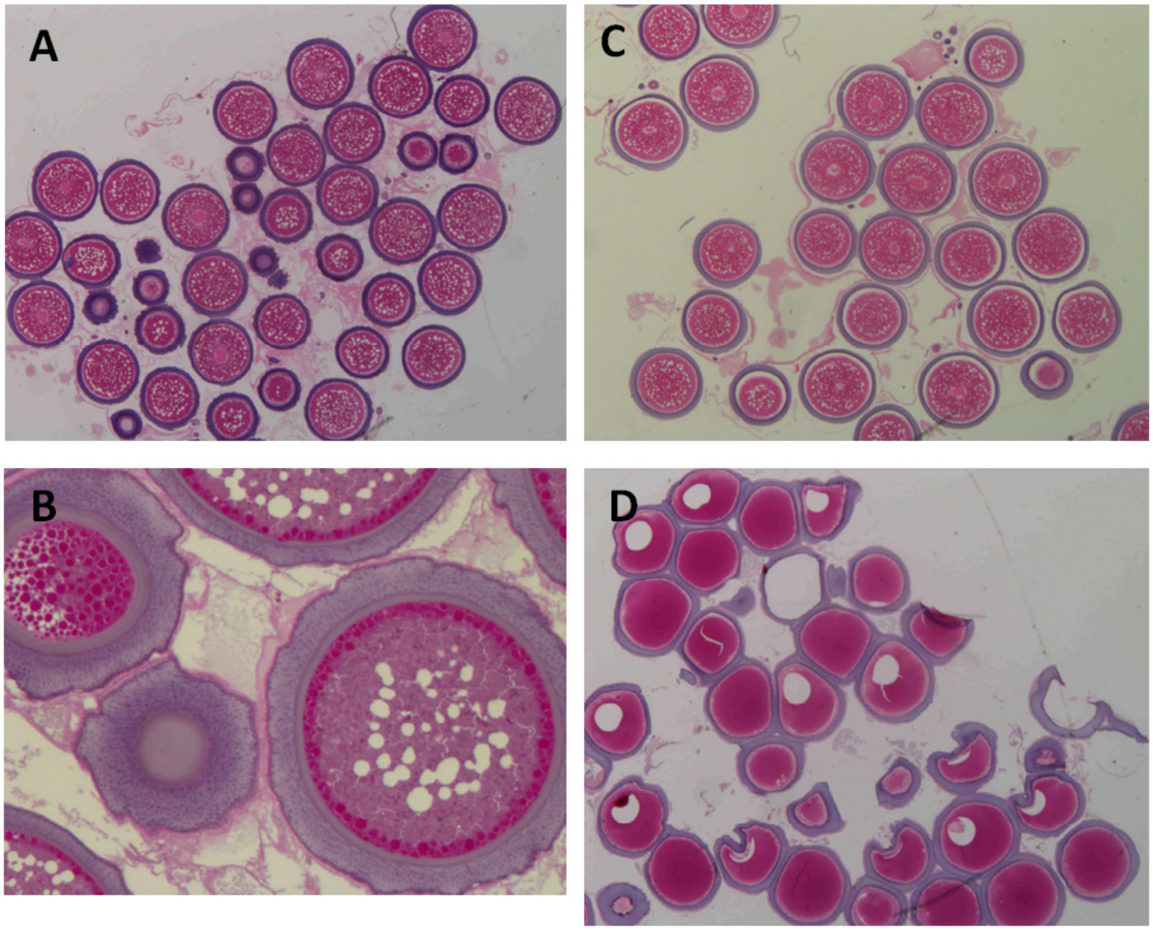

Figure 10. *A) Oocytes from a domesticated yellow perch female during April (GSI = 32%) with advanced stage of gelatinous layer formation and numerous atretic oocytes. B) Enlarged atretic oocyte with gelatinous layer and resorbed yolk (from image A above). C) Normal ovary of Lake Erie (wild) female yellow perch during April (GSI = 28 %) with centrally located nucleus and oil globules moving out of periphery. D) Ovulated oocytes of Lake Erie female yellow perch during May (GSI = 38%) with space from eluted oil globule; a few atretic oocytes are present.*

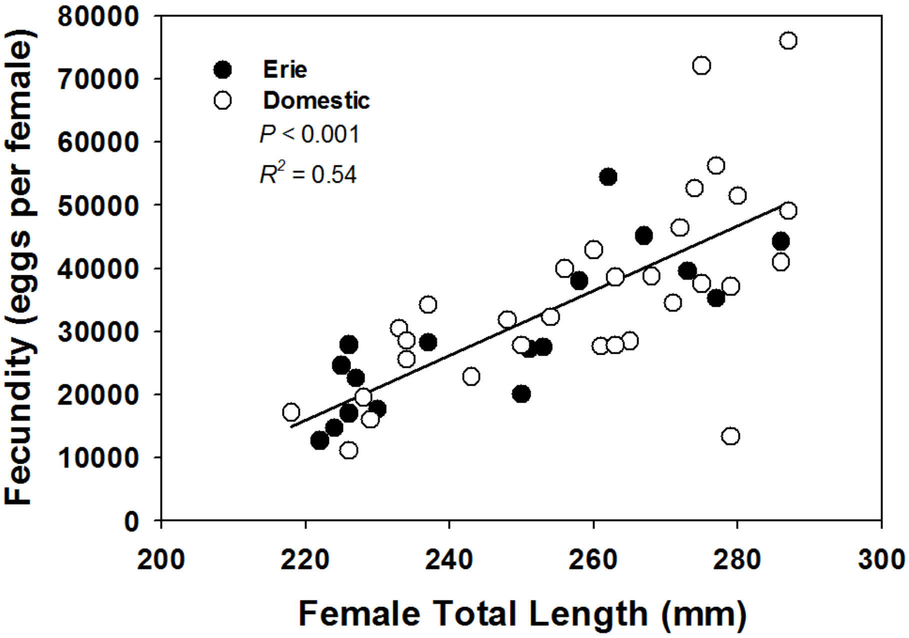

Figure 11. *Lake Erie and domestic yellow perch fecundity as a function of female total length (TL). A single relationship describes the number of eggs produced by both Lake Erie and domestic yellow perch of a given TL.*

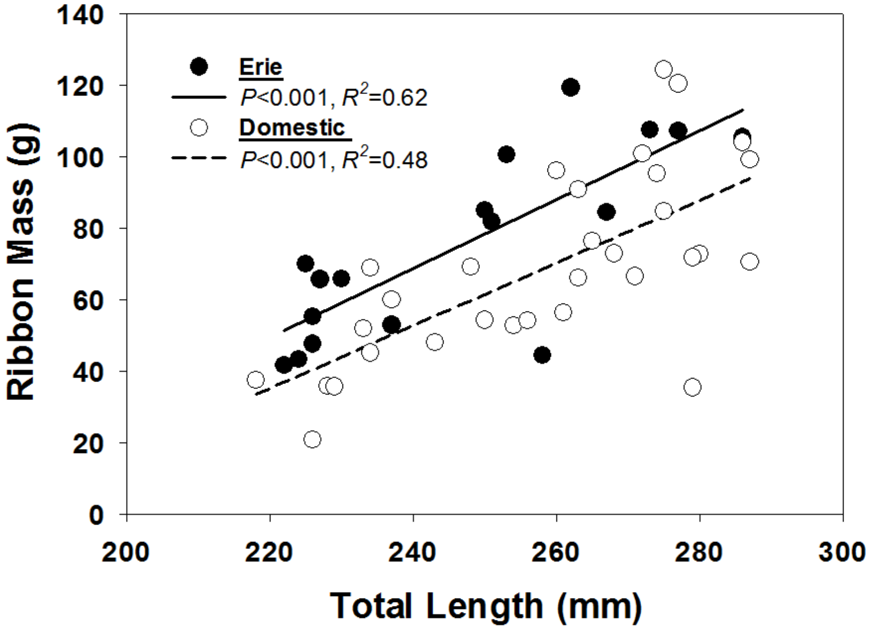

***Figure 12**. Yellow perch egg ribbon mass (g) plotted against female total length for Lake Erie and domestic individuals.*

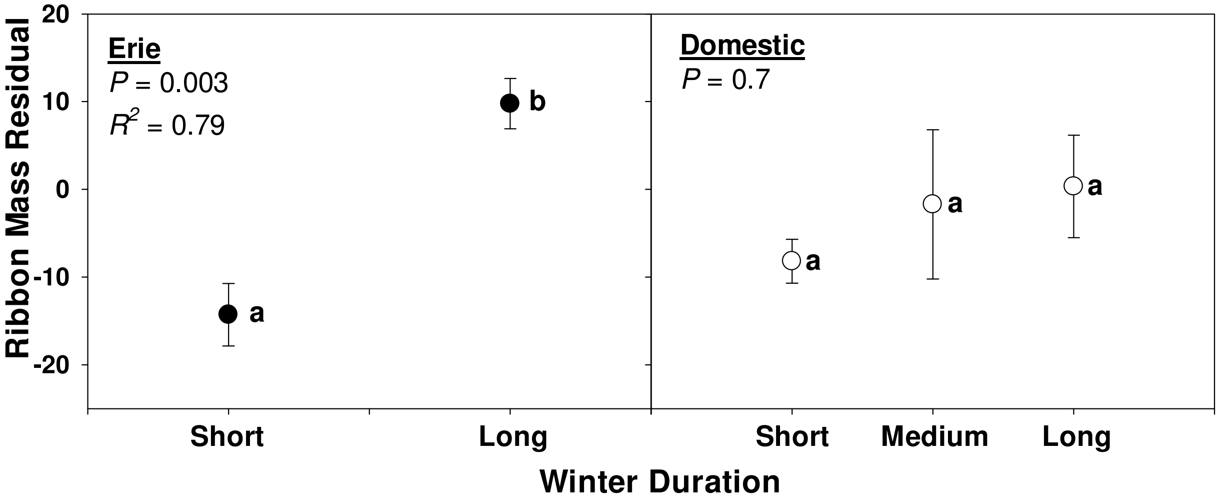

***Figure 13**. Mean (± 1 SE) residuals from the egg ribbon mass to total length (mm) relationship for Lake Erie and domestic winter-duration treatments. Means without lowercase letters in common within a panel differ after correcting for multiple comparisons.*

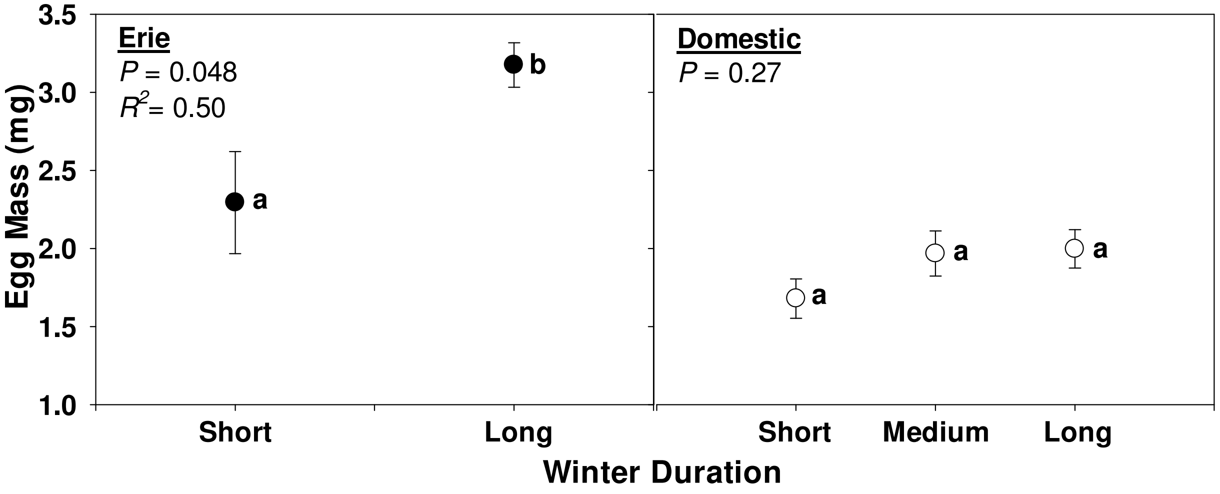

***Figure 14**. Mean (± 1 SE) egg mass in each winter-duration treatment for Lake Erie and domestic* females. *Means without lowercase letters in common within a panel differ after correcting for multiple comparisons.*

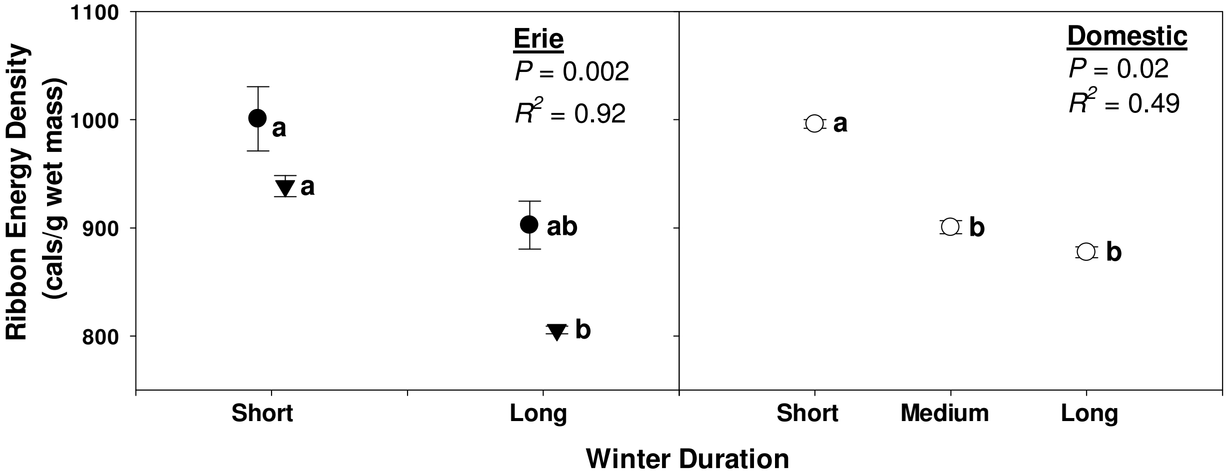

***Figure 15**. Mean (± 1 SE) egg ribbon energy density produced by yellow perch in each winter-duration treatment. Circles indicate females in the high-condition treatment, whereas triangles indicate females in the low-condition treatment (domestic females with low body condition did not produce egg ribbons). Means without lowercase letters in common within a panel differ after correcting for multiple comparisons.*

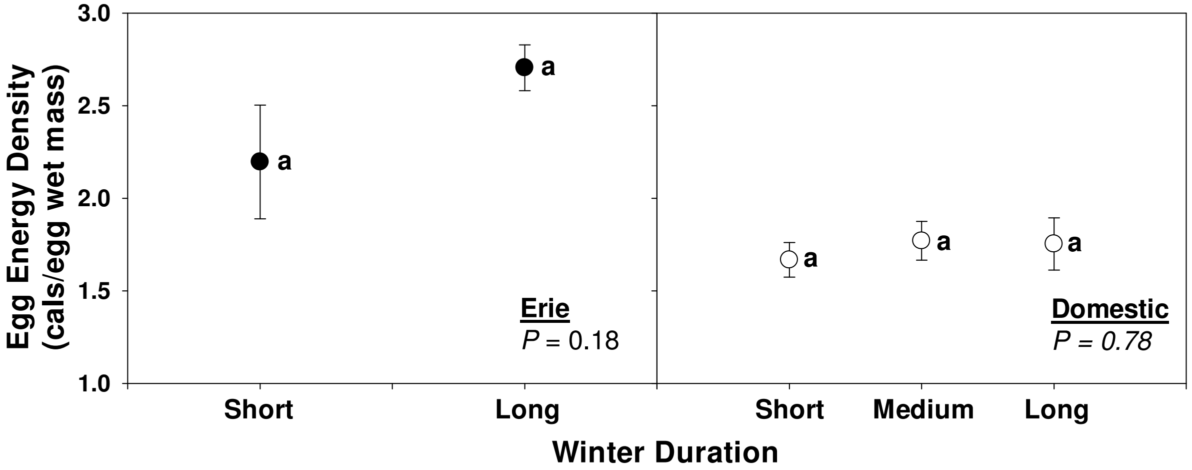

***Figure 16**. Mean energy density per egg (± 1 SE) in egg ribbons from Lake Erie and domestic yellow perch females in each winter-duration treatment. Means without lowercase letters in common within a panel differ after correcting for multiple comparisons.*

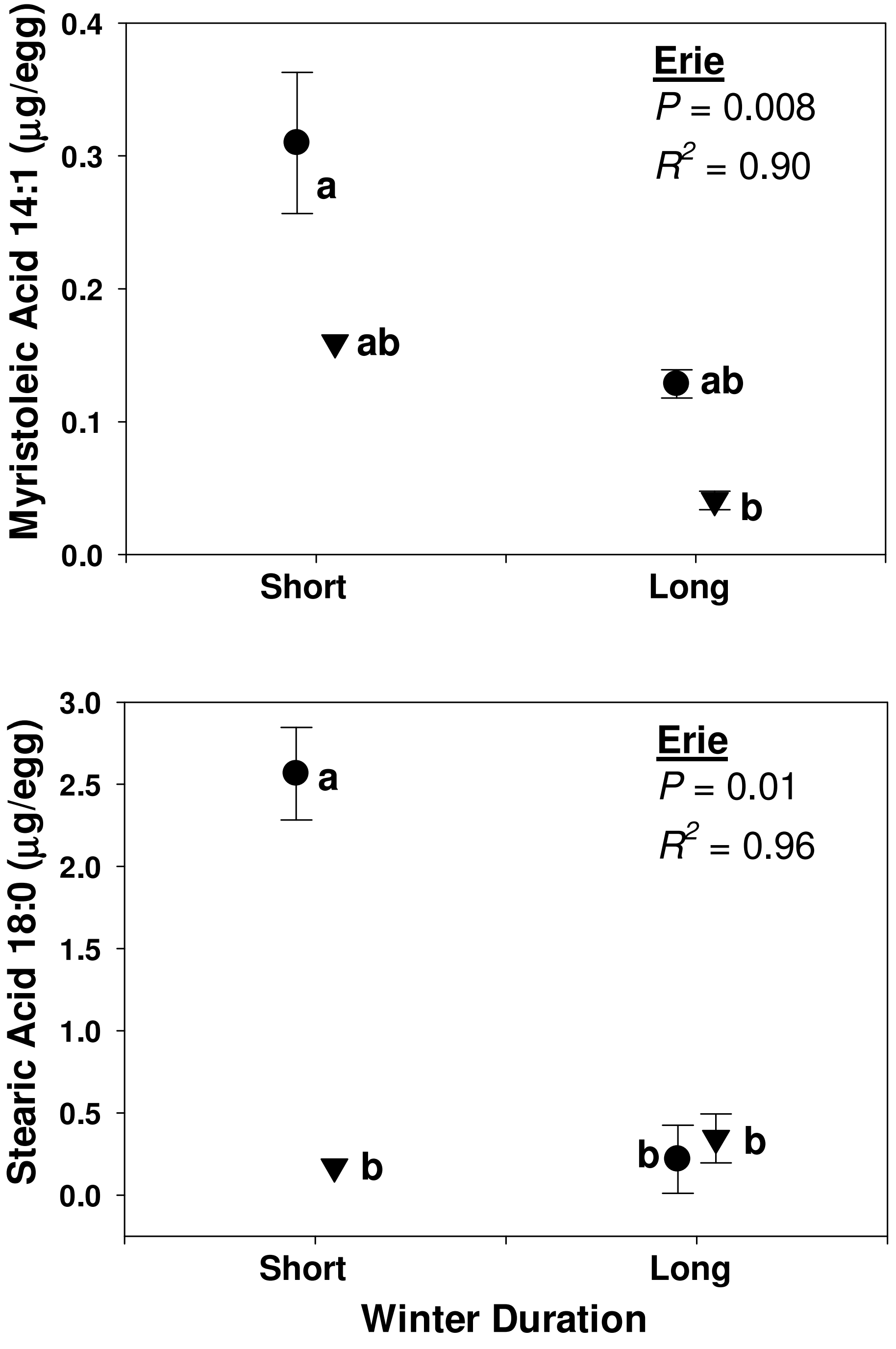

***Figure 17**. Mean myristoleic and stearic acid concentration (± 1 SE) for unfertilized eggs from Lake Erie female yellow perch. Circles and triangles represent females of high and low condition, respectively. Means without lowercase letters in common within a panel differ after correcting for multiple comparisons.*

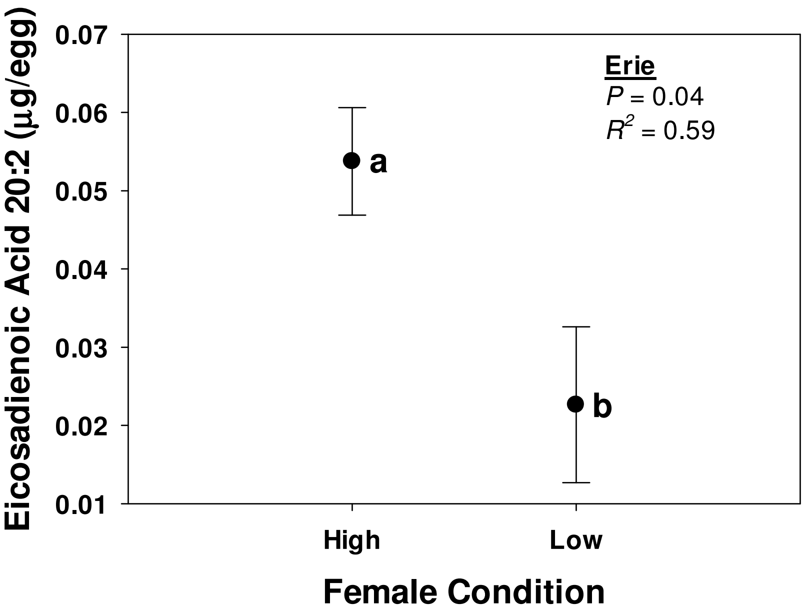

***Figure 18**. Mean eicosadienoic acid concentration (± 1 SE) for unfertilized eggs from Lake Erie yellow perch females in the low and high condition treatments. Means without lowercase letters in common within a panel differ after correcting for multiple comparisons.*

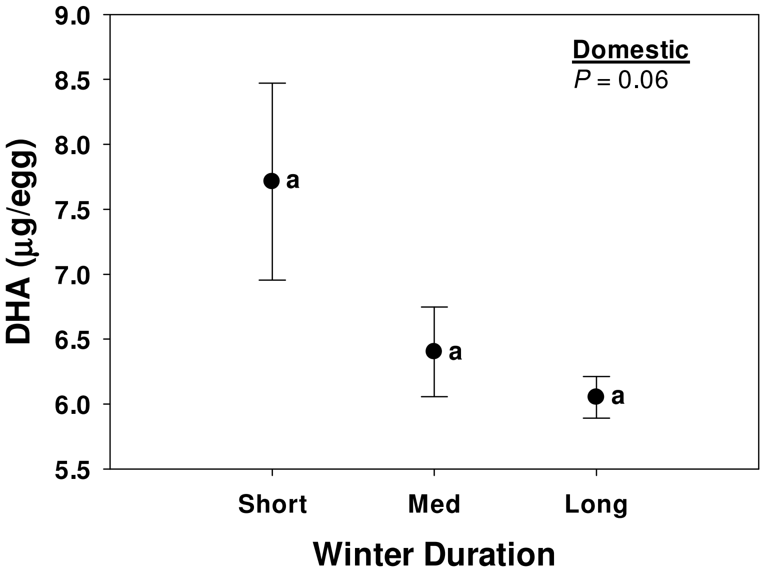

***Figure 19**. Mean docosahexaenoic acid (DHA) concentration (± 1 SE) for unfertilized eggs from domestic yellow perch females in each winter-duration treatment. Means without lowercase letters in common within a panel differ after correcting for multiple comparisons.*

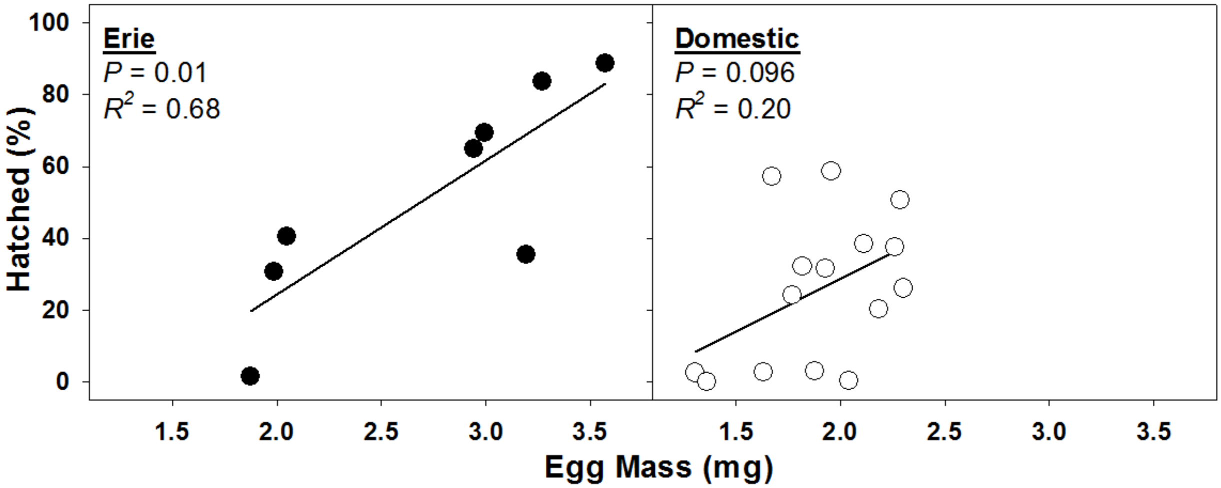

Figure 20. *Hatching success relative to average individual egg mass for Lake Erie and domestic female yellow perch across all winter-duration treatments.*

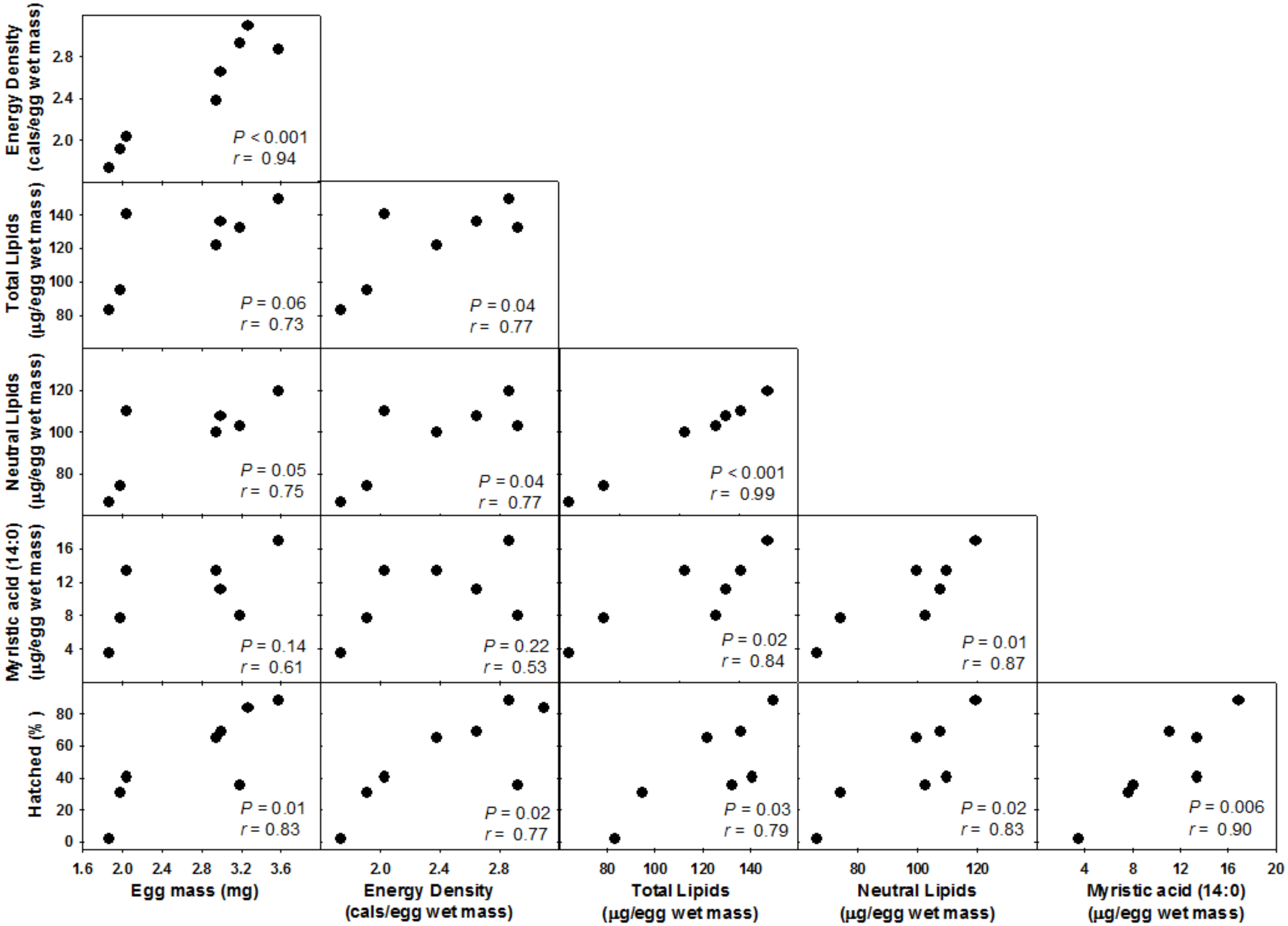

Figure 21. *Matrix scatterplot hatching success relative to five metrics of egg quality (egg mass, energy density, total lipids, neutral lipids, and myristic acid) for Lake Erie yellow perch eggs. Pearson correlation coefficients (r) and associated P-values are presented for each relationship.*

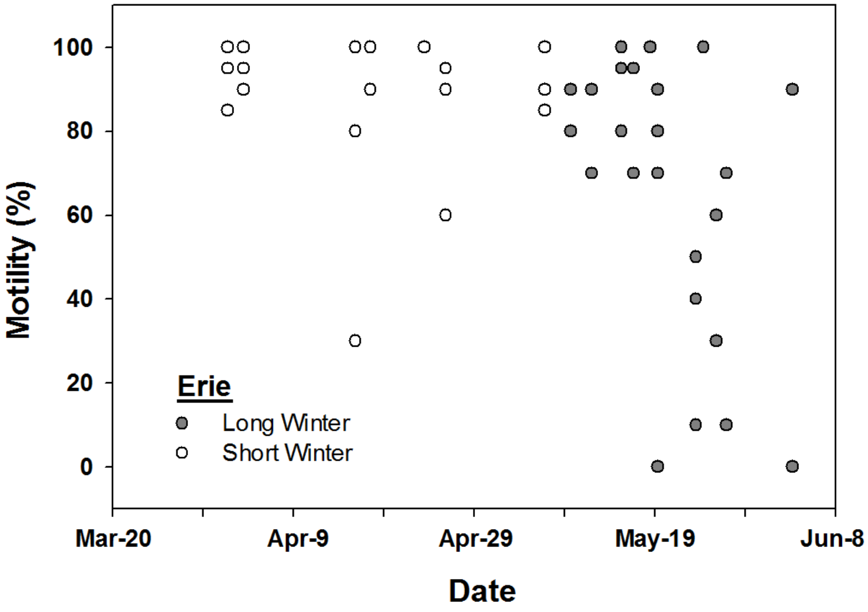

Figure 22. *Individual sperm motility measured for Lake Erie yellow perch males across winter-duration treatments (short winter N = 23 [12 males]; long winter N = 34 [18 males]).*

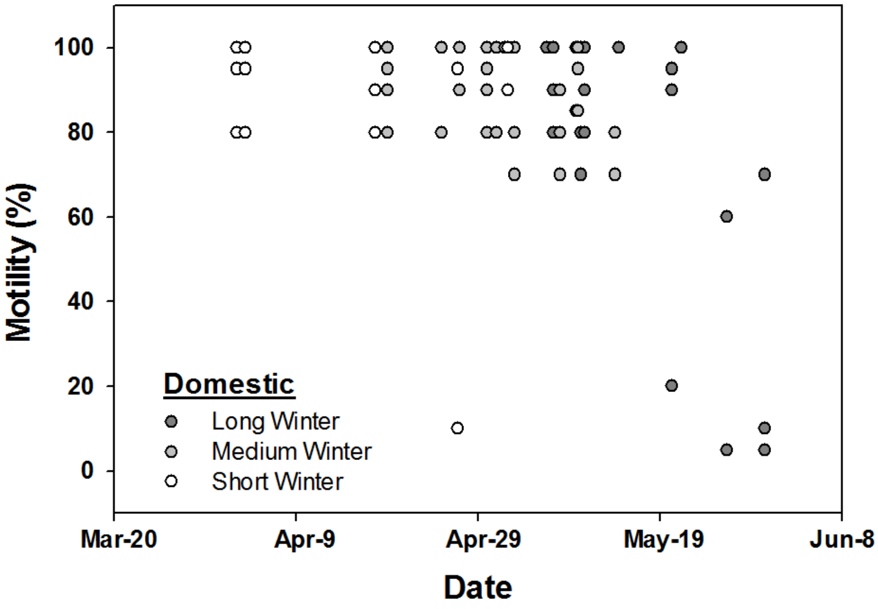

Figure 23. *Individual sperm motility measured for domestic yellow perch males across winter duration treatments (short winter N = 22 [13 males]; medium winter N = 36 [14 males]; long winter N = 28 [16 males]).*

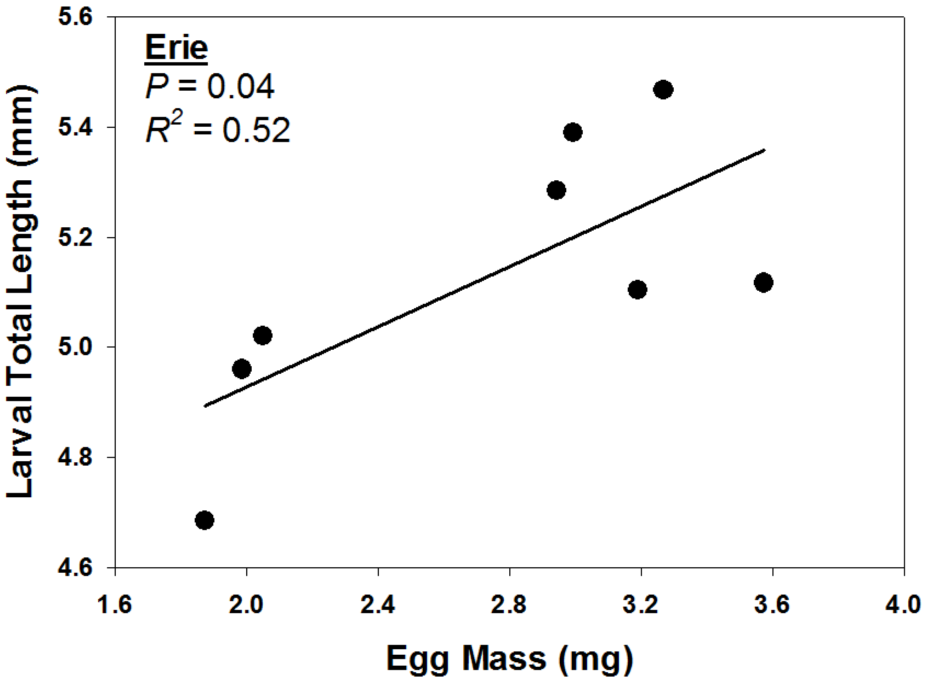

Figure 24. *Larval total length versus individual egg mass for Lake Erie yellow perch.*

Objective 2 Results

Our index of winter duration (number of days with water temperature ≤ 5°C) significantly differed from the current period (1975–2010) to all three mid-century scenarios (Figure 25). Winters were longer in the current time period than in any of the mid-century scenarios. Among mid-century scenarios, the highest emission scenario (A1B) had the shortest mean winter duration, whereas the moderate and low emission scenarios (A2 and B1, respectively) had similar mean winter durations (Figure 25).

Predicted hatching success (determined as a function of winter duration and egg mass) also differed between current and future scenarios (ANOVA $P < 0.0001$, $R^2 = 0.42$; Figure 26); being highest in the current period (64 ± 9% [mean ± std. dev.]) and lowest in the A1B scenario (47 ± 7%). Predicted hatching success was similar among the A2 (53 ± 7%) and B1 (54 ± 9%) emission scenarios, which was not surprising given the similar winter durations predicted for these emissions scenarios.

Distributions of TLP (generated from 10,000 repetitions using randomly selected values from distributions of winter duration and total egg production) were positively skewed for current and all predicted future mid-century scenarios (Figure 27). However, careful examination of these distributions reveals subtle differences. The current distribution of TLP (1975–2010) ranged from 0.5 to 158 million larvae and had a mode of 17.4 million. However, predicted distributions of TLP from all emissions scenarios had an abbreviated range, compared to the current distribution (A1B: 0.4 – 116; A2: 0.2 – 123; B1: 0.4 – 137 million larvae), with the smallest range occurring in the highest emissions scenarios (A1B; Figure 27). Also, the mode of the distribution shifted to lower values in all predicted future distributions of TLP (A1B: 12.5; A2: 10.6; B1: 11.8 million larvae), compared to the current distribution (Figure 27).

As evidence that high TLP is positively related to recruitment success, we documented a positive relationship between current annual estimates of TLP and recruitment in management unit 2 from 1975–2010 (Figure 28; *CPUE age-0 yellow perch* = 8.74 + 0.54(*TLP in millions*); $P = 0.02$; $R^2 = 0.16$), although this relationship was highly variable. Generally, the potential for strong year-classes increased as TLP increased. Specifically, the years with the highest recruitment followed springs with the highest levels of TLP. However, we found the potential for low recruitment across all levels of TLP (Figure 28).

Table 5. *Probability of achieving designated year-class strengths (Failed: CPUE age-0 yellow perch < 5; Weak: 5-14 CPUE; Moderate: 15-29 CPUE; Strong: 30-60; Very Strong: CPUE > 60) under current (1975-2010) and future (mid-century: 2046-2065) emissions scenarios (A1B: high, A2: moderate, B1: low; IPCC 2007) for management unit two in Lake Erie.*

Scenario	Failed	Weak	Moderate	Strong	Very Strong
Current	32%	19%	13%	24%	11%
Low	34%	19%	14%	25%	8%
Moderate	34%	19%	15%	25%	8%
High	35%	18%	16%	25%	6%

Using estimates of TLP generated under each of our 10,000 random repetitions for each climate scenario, we generated predicted recruitment using the stochastic transition from larvae to recruits (depicted by quantiles in Figure 28). Probability distributions of predicted recruitment are bimodal, with a high mode at extremely low CPUE and a lower mode at intermediate levels of CPUE (Figure 29). While distributions of predicted recruitment are qualitatively quite similar among current and future winter conditions, there is a slight truncation of recruitment probability distributions with increasing emissions scenarios. For example, under current climate conditions, mean recruitment is 27.6 CPUE with a range of 0 – 212 CPUE (Figure 29). In the high emissions scenario (A1B) the mean (20.2 CPUE) and range (0 – 185 CPUE) of predicted recruitment are lower, while in the moderate (A2: mean = 23.1; range = 0 – 190 CPUE) and low (B1: mean = 23.1; range = 0 – 205 CPUE) emissions scenarios, the mean and range of predicted recruitment are intermediate to those in the current and high emissions scenario. To further clarify the importance of these slight differences among probability distributions, we classified each predicted year-class as either failed (CPUE < 5), weak (CPUE = 5 – 14), moderate (CPUE = 15 – 29), strong (CPUE = 30 – 60), or very strong (CPUE > 60). These classifications were derived based on the observed relationship between age-0 CPUE and the resultant biomass of age-2 yellow perch produced two years later (1975 – 2010; YPTG 2011). In Management Unit 2, year-classes with a CPUE < 5 typically produced a mean age-2 biomass of 0.7 million kg (range = 0.15 – 1.13 million kg), and supported little commercial and recreational harvest in future years (YPTG 2011). Weak, moderate, and strong year-classes produced a mean age-2 biomass of 2.1, 2.9, and 3.1 million kg, respectively (ranges = 0.8 – 4.3, 0.9 – 5.4, and 1.6 – 4.9 mil kg). Very strong year-classes produced a mean age-2 biomass of 6.7 million kg (range 1.7 – 11.1 million kg). Further, these very strong year-classes typically dominated commercial and recreational harvest even after years of natural and fishing mortality (e.g., the 2003 year-class [age-0 CPUE = 91] dominated harvest in all four Lake Erie management units as recently as 2010; YPTG 2011). Results of these classifications for each scenario are presented in Table 5. Moving from current conditions to the high emission mid-century scenario (A1B), the probability of achieving failed and moderate year-class increased, slightly, whereas the probability of achieving very strong year-classes declined moving from current conditions to the high emission mid-century scenario (A1B).

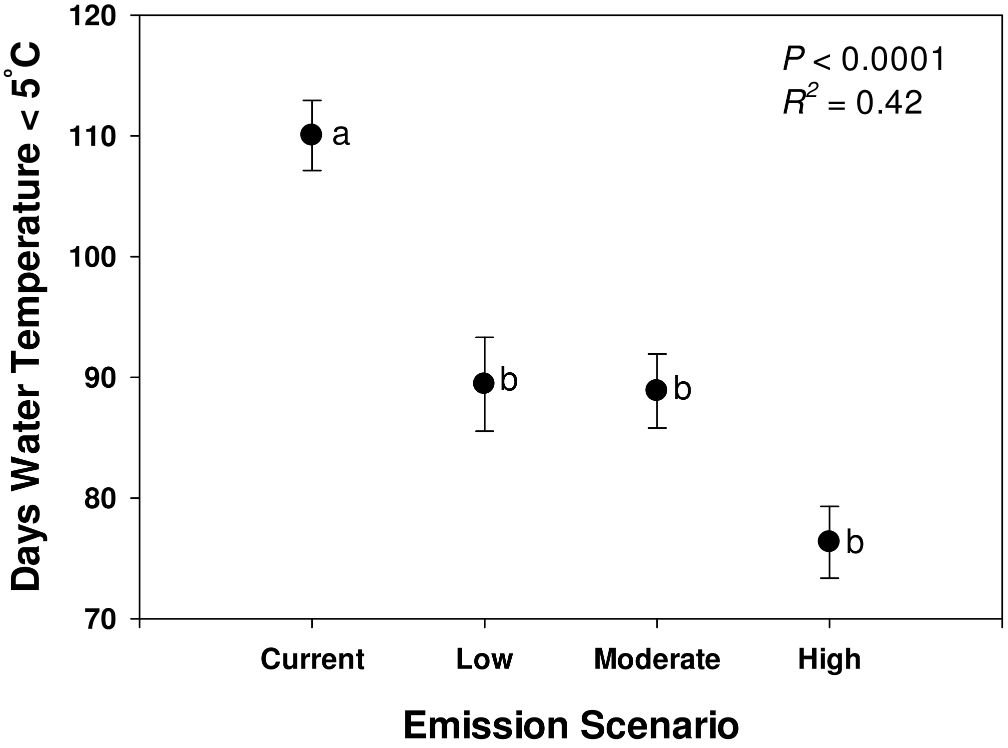

Figure 25. *Mean (± SE) number of days Lake Erie water temperature < 5°C under current (1975–2010) and predicted future environmental conditions at mid-century (2046–2065) under three emissions scenarios (A1B: high, A2: moderate; B1: low; IPCC 2007). Lowercase letters indicate means that differed significantly, after correcting for multiple comparisons.*

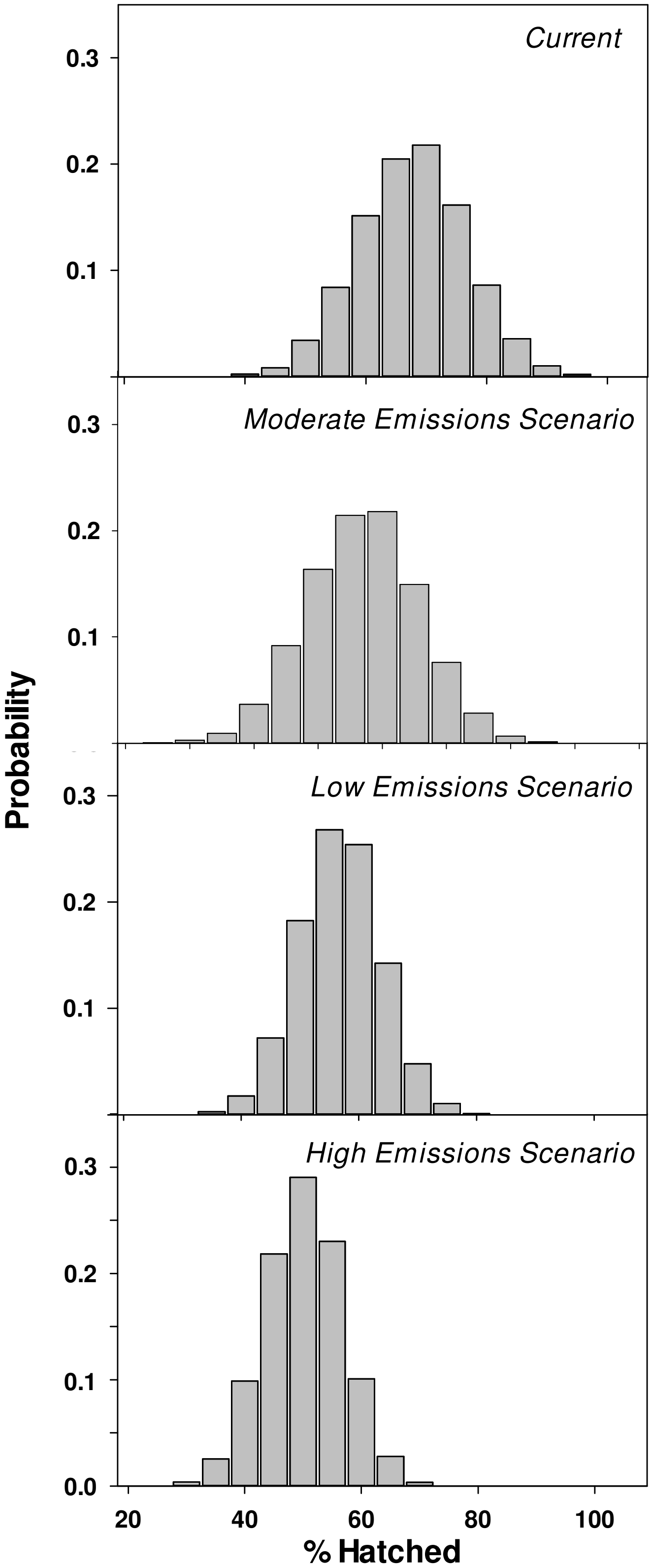

Figure 26. *Probability distribution of hatching success (% Hatched) for yellow perch eggs given current (1975 – 2010) and predicted future environmental conditions at mid-century (2046–2065) under three emissions scenarios (A1B: high, A2: moderate; B1: low; IPCC 2007).*

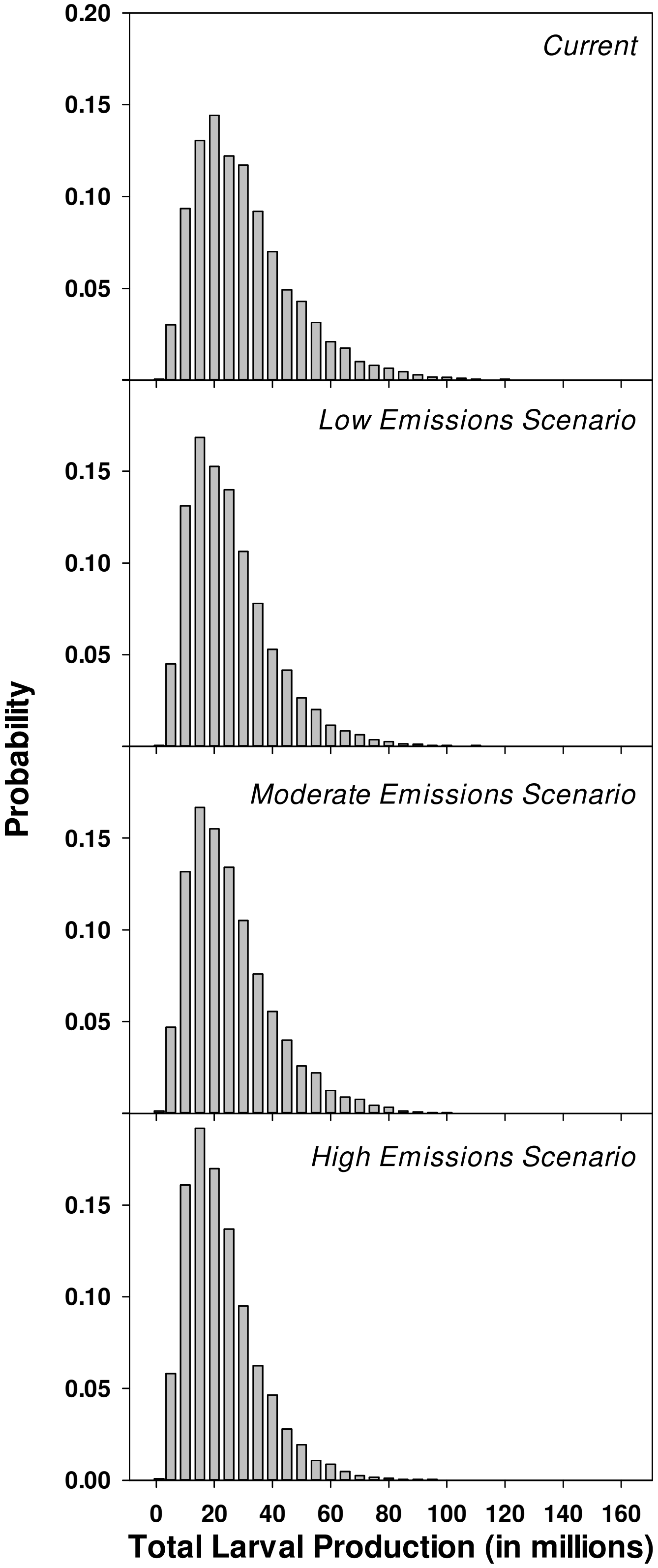

Figure 27. *Probability distribution of total larval production (in millions; estimated each spring from age-specific adult size distributions and relationships developed from our laboratory experiment) given current (1975 – 2010) and predicted future environmental conditions at mid-century (2046–2065) under three emissions scenarios (A1B: high, A2: moderate; B1: low; IPCC 2007).*

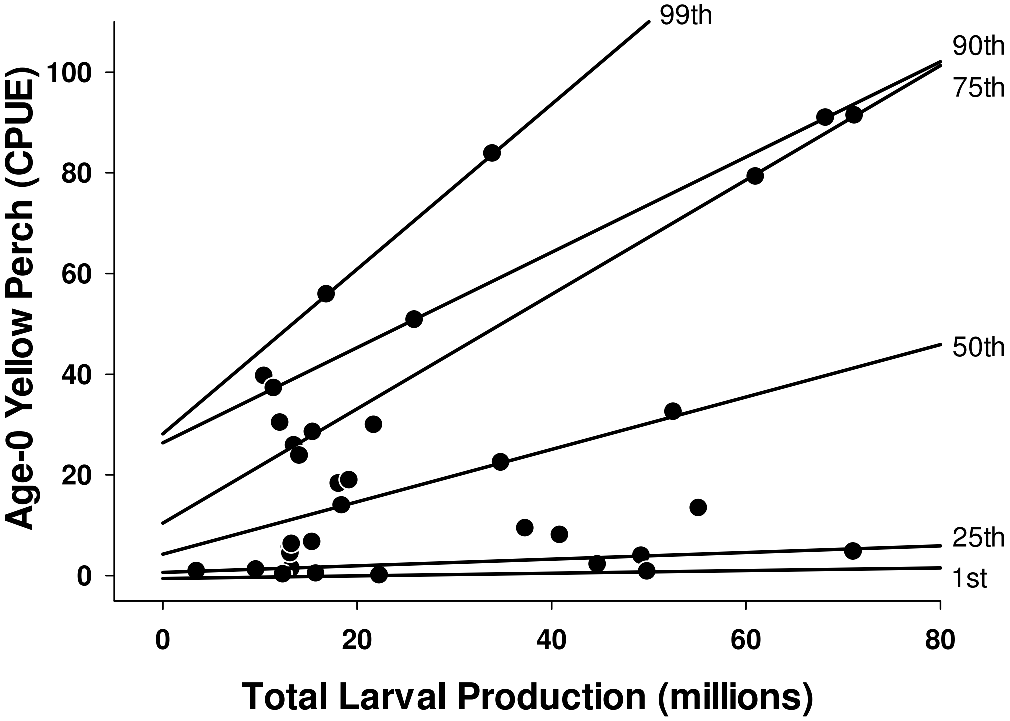

Figure 28. *Age-0 yellow perch catch-per-unit-effort (CPUE) during October 1975–2010 for central Lake Erie (management unit 2) versus total larval yellow perch production (in millions; estimated each spring from age-specific adult size distributions and relationships developed from our laboratory experiment). Lines plotted are for 99th, 90th, 75th, 50th, 25th, and 1st regression quantile estimates.*

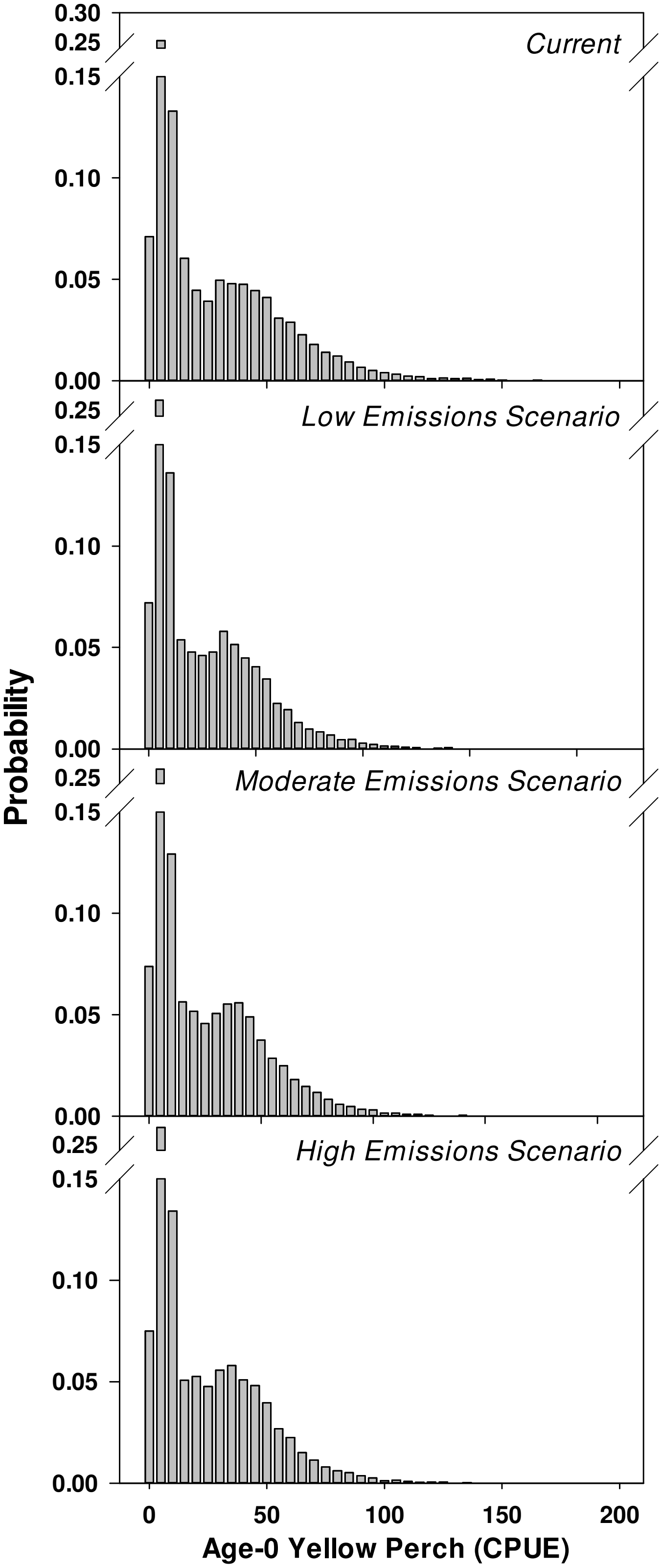

Figure 29. *Probability distribution of predicted yellow perch catch-per-unit-effort (PCUE) in October given current (1975–2010) and predicted future environmental conditions at mid-century (2046–2065) under three emissions scenarios (A1B: high, A2: moderate; B1: low; IPCC 2007).*

DISCUSSION:

Our experimental results indicate a novel mechanism by which climate change may influence yellow perch recruitment in the Laurentian Great Lakes. Lake Erie female yellow perch exposed to a long winter (i.e., 110 d of water temperature < 5°C) produced higher quality, larger eggs that contained more calories, total lipids, neutral lipids, and myristic acid (i.e., a saturated fatty acid) per egg. These higher quality eggs produced from females exposed to our long winter treatment hatched at higher rates and produced larger larvae than Lake Erie females exposed to a short winter (50 d of water temperature < 5°C). By incorporating our experiment results into a hind-casting model, we found that total larval production (a metric that included the effects of winter duration on egg quality and hatching success) was positively related to historical (1975–2010) variation in yellow perch recruitment in Lake Erie (although the relationship was highly variable). Next, by incorporating our results into a forecasting model that included future, predicted downscaled regional winter temperature data for the mid-20th century (2046-2065), we found evidence to suggest that hatching success of yellow perch eggs will decline under high (A1B), moderate (A2), and low (B2) greenhouse gas emission scenarios (IPCC 2007), with the largest decline predicted under the highest emission scenario. However, when future hatching success was combined with estimates of total egg production to obtain a probability distribution of total larval production, we found that the predicted effects of climate change on total larval production were less than those on hatching success alone. The results of those simulations were conservative, however, as we used current (1975-2010) estimates of age and size distribution of spawners to generate total egg production for all simulations, including those for mid-century total larval production estimates. We also did not allow the slight declines in year-class strength with climate change to translate into future declines in spawners. Inclusion of this feedback would have caused stronger negative effects of climate on simulated year-class strength.

Our results are significant in that they indicate a surprising, negative way in which winter warming may affect yellow perch recruitment across the Great Lakes. Previous modeling has indicated that warm-, cool- (including yellow perch), and even some cold-water fishes could benefit from climate change in the Great Lakes basin, owing primarily to an increase in thermal habitat available for growth (Minns et al. 1997; Stefan et al. 1996). Winter warming also would be expected to increase over-winter survival of juveniles of warm- and cool-water species such as smallmouth bass (*Micropterus dolomieu*), white perch (*Morone americana)*, and yellow perch (Johnson and Evans 1990; Shuter and Post 1990). Further, as the inability of smallmouth bass and yellow perch juveniles to grow large enough to survive winter temperatures sets the northern range limits of these species (Shuter and Post 1990), enhanced growth and reduced winter temperature, owing to expected climate warming, could result in range expansion (Magnuson et al. 1997). Expected increases in storm (precipitation) events and nutrient runoff during spring under future CO_2 emission scenarios (Magnuson et al. 1997; Kling et al. 2003) also would be expected to benefit yellow perch recruitment via river-induced nutrient and turbidity plumes that increase foraging opportunities and reduce predation risk for yellow perch larvae (Ludsin 2000; Reichert et al. 2010; Ludsin et al. 2011; Pangle et al. 2013).

Our results, and those of others, indicate that the anticipated effects of climate on Great Lakes fishes are not all positive, however. For example, in addition to affecting the total number of larvae produced, climate warming scenarios also predict increased nutrient loading (via enhanced spring precipitation events), increased summer temperature, and reduced summer water levels (due to decreased summer precipitation and increased evapotranspiration) (Magnuson et al. 1997; Lofgren et. al. 2002; Kling et al. 2003) that will lead to an increase in the intensity and duration of hypolimnetic hypoxia (Kling et al. 2003; Fang et al. 2004). This is problematic because hypoxia, which has been increasing in the central basin of Lake Erie during recent years (Burns et al. 2005; Hawley et al. 2006), has been shown to reduce consumption, the potential for growth, and condition (caloric value) of both cool-water and cold-water (e.g., rainbow smelt *Osmerus mordax*) fishes by both forcing these species into sub-optimal (warmer) surface and nearshore waters and reducing access to benthic food sources (e.g., chironomids) (Roberts et al. 2009, 2011; Vanderploeg et al. 2009; S. Ludsin, unpublished data). As percids are capital breeders that allocate energy reserves (lipids) accumulated during the summer and early fall to reproduction during late fall, when vitellogenesis (yolk formation) begins (Dabrowski et al. 1996), female condition entering the winter is likely to determine the amount of energy available for reproduction (Henderson et al. 1996; Henderson 2000). While we did not find evidence that female body condition in the fall affected reproductive output, egg quality, or hatching success, Lake Erie female yellow perch entering winter in relatively poorer body condition appeared to have delayed reproductive development in October, as compared to those in good body condition

Even if we conclude that hypoxia will not affect reproductive output by limiting energy reserves, we should also note that by reducing growth and, consequently, female size in the fall, hypoxia may have a secondary negative effect of reducing total egg production the following spring. As total egg production is a function of female size, smaller female yellow perch would produce fewer eggs than larger females. Herein, our experimental results did indicate that females with high fall body condition (measured as the TL-mass residual in October) produced more eggs than those with low fall body-condition, although this effect was small compared to the overall effect of length on egg production. Thus, consideration of these hypoxia-induced effects in our forecasting model likely would have resulted in stronger negative effects of climate on simulated year-class strength.

While our results suggest a possible mechanism through which climate change may affect yellow perch reproductive output and, subsequently, recruitment, we did not document complete reproductive failure in response to short, warm winters. This was particularly surprising given previous research that indicated yellow and Eurasian perch females would not spawn following abnormally short winters (Jones et al. 1972; Hokanson 1977; Ciereszko et al. 1997; Sandstrom et al. 1997; Lukšienê et al. 2000; Migaud et al. 2002). If female yellow perch have a minimum duration of cold winter temperatures that is required for proper reproductive development (as suggested by previous investigators; Jones et al. 1972; Hokanson 1977; Ciereszko et al. 1997), our experimental design did not breach this limit for yellow perch from Lake Erie. It should be noted that many of these previous studies exposed female yellow or Eurasian perch to minimum winter temperatures that were warmer (Hokanson 1977: 6, 8, and 10°C; Ciereszko et al. 1997: 7 and 11°C; Migaud et al. 2002: 6°C) than the minimum winter temperatures (4 – 5°C) used in our study, which mirrored those observed in Lake Erie over the past two decades. While our study did not replicate the dramatic effects observed in other studies (i.e., complete lack of spawning; Jones et al. 1972; Hokanson 1977; Ciereszko et al. 1997; Lukšienê et al. 2000), the finding that long winters produced larger eggs than shorter winters is supported by at least one previous study. Migaud et al. (2002) found that females exposed to 5 months 6°C water produced larger oocytes and had larger GSI than those exposed to only 3 months of 6°C water. While the exact mechanism causing larger, higher quality eggs to be produced after long winters is unknown, we speculate that longer winters allow for a prolonged period of low metabolic rates, which allow for a larger proportion of energy to be devoted to egg production. Future controlled laboratory experiments and/or bioenergetics modeling would be needed to appropriately test this hypothesis.

Other studies, which were not investigating winter effects on reproduction, also found that larger Eurasian perch eggs typically hatch at higher rates (Olin et al. 2012) and, for walleye, lead to higher juvenile survival rates (Venturelli et al. 2010) relative to their smaller counterparts. In a recent review, Kamler (2005) indicated that three primary periods of mortality exist for larvae prior to exogenous feeding: 1) early mortality associated with fertilization success; 2) mortality associated with hatching; and 3) starvation mortality that occurs when yolk reserves are depleted under absence of external food. Our hatching success metric quantified survival through the first two of these periods, and indicated that larvae from larger eggs (produced after long winters) survived these two periods at disproportionately higher rates than small larvae. Finally, large eggs also produced large larvae, which are more likely to survive the third period of elevated mortality than small larvae (Miller et al. 1988), as well as in the presence of larval yellow perch predators such as invasive white perch (Ludsin et al. 2013). Therefore, our experimental results suggest that eggs and larvae produced from long winters should have greater chances of surviving all three of these critical mortality periods, and be better positioned to survive to the juvenile stage than smaller eggs and larvae.

While our study documented a direct mechanism by which climate change may negatively affect reproduction and recruitment, other indirect effects of climate change on reproduction also may affect reproduction success, and subsequently, recruitment. One of these indirect effects of climate change could be on the timing of spawning. Previous research has shown that the timing of reproduction can have important consequences for early-life growth and survival in fish, which then can directly affect future growth, survival, recruitment, and population dynamics (Cushing 1990; Ludsin and DeVries 1997). During our experiment, across winter-duration treatments, both domesticated and Lake Erie female yellow perch spawned at warmer temperatures following short winters, but at colder temperatures following longer winters. This finding indicates that the timing of yellow perch spawning is not solely a function of spring temperature; it also may depend on photoperiod or require some set duration of time from the initiation of reproductive development the previous fall, as other have suggested (Kayes and Calbert 1979; Dabrowski et al. 1997). Along these lines, Abdulfatah et al. (2013) found strong evidence that the induction of reproductive development in the fall was due to a reduction in photoperiod, and that temperature only slightly modulated the initiation of gonadal development. Our experimental data certainly support the notion that yellow perch spawning also is relatively insensitive to changes in temperature. While future experiments would be required to determine the exact role of spring temperature in initiating yellow perch spawning, we find it likely that yellow perch have a minimum date before which spawning cannot occur that only partly depends on temperature. Given the warming trend that the Great Lakes region has experienced during the past several decades (Wang et al. 2012), along with the progressively earlier arrival of spring warming (Magnuson 2010), if prey species emerge earlier in response to warming temperatures, yellow perch offspring survival, and subsequently, recruitment may be low if the timing of larval and prey emergence do not match (sensu Hjort 1914; Cushing 1990).

Domesticated and Lake Erie females responded differently to similar winter-duration treatments. Lake Erie females produced larger and higher quality eggs after long winters than after short winters, whereas domesticated female egg size and quality were similar across winter-duration treatments. While natural variation in egg size and several fatty acid classes was found in domesticated yellow perch, and this variation was important in explaining hatching success, these factors were unrelated to either our female body-condition or winter-duration treatment. Different responses between Lake Erie and domesticated females could be due to a multitude of inherent differences. While our domesticated yellow perch were originally produced from Lake Erie broodstock, generations of intentional and unintentional selection in a hatchery environment may have resulted in females with a different suite of reproductive traits and/or energy allocation patterns than those maintained in wild, Lake Erie yellow perch. Regardless of the reasons for these differences, our results caution against using domesticated broodstock in experiments that seek to understand and predict how wild populations will respond to climate induced stressors. Our study adds to several recent studies that have noted important differences in reproductive traits and offspring survival between wild and domesticated stocks of the same species (Araki et al. 2007; Chittenden et al. 2010; Moore et al. 2012).

In contrast to the negative effects of short winters on female reproductive success, all measures of male reproductive success (sperm density, percent of motile sperm, and duration of motility) indicated that males were capable of fertilizing eggs following the shortest of our winter-duration treatments. However, at the end of our long winter-duration treatment, both Lake Erie and domestic males experienced a decline in sperm motility. This result was not surprising given that males typically show a readiness to spermiate in January. An extended period of low temperature (long winter) resulted apparently in sperm "aging" and deterioration of sperm quality. This finding is the first description of this phenomenon in yellow perch, although it has been documented rainbow trout (*Oncorhynchus mykiss*) following extended reproductive season (Ciereszko and Dabrowski 1995).

The lack of an effect of sperm quality on fertilization rate, and in turn, hatching success may be an artifact of our fertilization methods. The spermatozoa to egg ratio used in our study was 100,000 to 1, which was double the optimum level found for other fishes (e.g., walleye = 50,000 spermatozoa per egg; Rinchard et al. 2005a). We chose this high ratio so as to ensure maximal fertilization rates. Thus, our use of more spermatozoa per egg may have prevented the observed decline in male milt motility from negatively affecting fertilization and egg hatching success. What remains unknown, however, is if this physiological response of males to excessively long winters serves as a mechanism to limit the positive effect of long winters on yellow perch reproduction and recruitment in the wild.

Finally, understanding the effects of winter temperature on reproductive output and quality may allow Lake Erie fisheries managers to 1) better explain historically variable yellow perch recruitment in Lake Erie (YPTG 2011) and 2) better anticipate the effects of climate change so that they can manage user-group expectations, keeping them from exceeding the ability of Lake Erie to produce yellow perch. Our mechanistic study also should serve as an impetus for future research into the effect of climate change on reproductive output and recruitment both within and outside the Great Lakes basin, given that 1) yellow perch and its congener, Eurasian perch, are economically and ecologically important species across North America and Europe, and 2) numerous other species across the world have similar reproductive characteristics as yellow perch (i.e., spring spawners with winter ovary development, e.g., walleye, European pike-perch *Sander lucioperca*, alewife, rainbow smelt, white bass *Morone chrysops*, and white perch). While our study has identified one particular mechanism by which climate change can affect reproductive output and recruitment, we suspect many others exist that have yet to be explored. If so, the likelihood that climate change will lead to ecological surprises (Paine et al. 1998, Doak et al. 2008) will only increase, especially when considering that the effects of climate change may interact with other anthropogenic stressors. For this reason, we encourage integrative research approaches that combine controlled laboratory experiments, field observations, and modeling. Such approaches offer the best means not only to avoid major ecological surprises that can have devastating ecological and socioeconomic impacts, but also to provide critical ecological understanding that can increase the ability of mangers to overcome the complex challenge in sustaining fisheries in the face of a changing climate.

REFERENCES:

Angel, J.R., and K.E. Kunkel. 2010. The response of Great Lakes water levels to future climate scenarios with an emphasis on Lake Michigan-Huron. J. Gt. Lakes Res. **36**: 51-58.

Araki, H., B. Cooper, and M.S. Blouin. 2007. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. Science **318**: 100-103.

Arend, K.K., D. Beletsky, J.V. DePinto, S.A. Ludsin, J.S. Roberts, D.K. Rucinski, D. Scavia, D.J. Schwab, and T.O. Höök, T.O. 2010. Seasonal and interannual effects of hypoxia on fish habitat quality in central Lake Erie. Freshw. Biol. **56**: 366-383.

Assel, R., K. Cronk, and D. Norton. 2003. Recent trends in Laurentian Great Lakes ice cover. Clim. Change **57**: 185-204.

Assel, R.A., D.M. Robertson, M.H. Hoff, and J.H. Selgeby. 1995. Climatic-change implications from long-term (1823-1994) ice records for the Laurentian Great Lakes. Ann. Glaciol. 21: 383 - 386

Austin, J.A., and S.M. Colman. 2007. Lake Superior summer water temperatures are increasing more rapidly than regional air temperatures: A positive ice-albedo feedback. Geophys. Res. Lett. **34**: 1-5.

Berkeley, S.A., C. Chapman, and S.M. Sogard. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. Ecology **85**: 1258-1264.

Brook, B.W., N.S. Sodhi, and C.J.A. Bradshaw. 2008. Synergies among extinction drivers under global change. Trends Ecol. Evol. **23**: 453-460.

Bunnell, D.B., S.R. David, and C.P. Madenjian. 2009. Decline in bloater fecundity in Southern Lake Michigan after decline of *Diporeia*. J. Gt. Lakes Res. **35**: 45-49.

Bunnell, D.B., M.A. Scantland, and R.A. Stein. 2005. Testing for evidence of maternal effects among individuals and populations of white crappie. Trans. Am. Fish. Soc. **134**: 607-619.

Burns, N.M., D.C. Rockwell, P.E. Bertram, D.M. Dolan, and J.J.H Ciborowski. 2005. Trends in temperature, Secchi depth, and dissolved oxygen depletion rates in the central basin of Lake Erie, 1983-2002. Journal of Great Lakes Research **31**: 35-49.

Cade, B.S., J.W. Terrell, and R.L. Schroeder. 1999. Estimating effects of limiting factors with regression quantiles. Ecology **80**: 311-323.

Casselman, J.M. 2002. Effects of temperature, global extremes, and climate change on year-class production of warmwater, coolwater, and coldwater fishes in the Great Lakes Basin. *In* Fisheries in a Changing Climate. *Edited by* N.A. McGinn. pp. 39-59.

Chambers, R.C., and W.C. Leggett. 1996. Maternal influences on variation in egg sizes intemperate marine fishes. Amer. Zool. **36**: 180–196.

Chambers, R.C., and K.G. Waiwood. 1996. Maternal and seasonal differences in egg sizes and spawning characteristics of captive Atlantic cod, *Gadus morhua*. Can. J. Fish. Aquat. Sci. **53**:1986-2003.

Chittenden, C.M., C.A. Biagi, J.G. Davidsen, A.G. Davidsen, H. Kondo, A. McKnight, O.-P. Pedersen, P.A. Raven, A.H. Rikardsen, J.M. Shrimpton, B. Zuehlke, R.S. McKinley, and R.H. Devlin. 2010. Genetic versus rearing-environment effects on phenotype: hatchery and natural rearing effects on hatchery and wild-born Coho Salmon. PLoS One **5**.

Ciereszko, A., and K. Dabrowski. 1995. Sperm quality and ascorbic acid concentration in rainbow trout semen are affected by dietary vitamin C: an across season study. Biol. Reprod. **52**:982-988.

Ciereszko, R.E., K. Dabrowski, A. Ciereszko, J. Ebeling, and J.S. Ottobre. 1997. Effects of temperature and photoperiod on reproduction of female yellow perch *Perca flavescens*: plasma concentrations of steroid hormones, spontaneous and induced ovulation, and quality of eggs. J. World Aquacult. Soc. **28**: 344-356.

Clugston, J.P., J.L. Oliver, and R. Ruelle. 1978. Reproduction growth and standing crops of yellow perch in southern reservoirs. *In* Selected Coolwater Fishes of North America. *Edited by* R.L. Kendall. American Fisheries Society Special Publication **11**: 89-99.

Collingsworth, P.D., and E.A. Marschall. 2011. Identifying relationships between catches of spawning condition yellow perch and environmental variables in the western basin of Lake Erie. Trans. Am. Fish. Soc. **140**: 31-36.

Craig, J.F. 1977. The body composition of adult perch, *Perca fluviatilis*, in Windermere. Freshw. Biol. **8**: 59-68.

Crane, V. C. 2007. Lower trophic level and climate influence on western Lake Erie fish recruitment 1988 through 2005. M.S. thesis. The Ohio State University, Columbus, Ohio.

Czesny, S., and K. Dabrowski. 1998. The effect of egg fatty acid concentrations on embryo viability in wild and domesticated walleye (*Stizostedion vitreum*). Aquat. Living Resour. **11**: 371-378.

Dabrowski, K., R.E. Ciereszko, A. Ciereszko, G.P. Toth, S.A. Christ, D. ElSaidy, and J.S. Ottobre. 1996. Reproductive physiology of yellow perch (*Perca flavescens*): environmental and endocrinological cues. J. Appl. Ichthyol. **12**: 139-148.

Doak, D.F., J.A. Estes, B.S. Halpern, U. Jacob, D.R. Lindberg, J. Lovvorn, D.H. Monson, M.T. Tinker, T.M. Williams, J.T. Wootton, I. Carroll, M. Emmerson, F. Micheli, and M. Novak. 2008. Understanding and predicting ecological dynamics: Are major surprises inevitable? Ecology **89**: 952-961.

Doney, S.C., M. Ruckelshaus, J.E. Duffy, J.P. Barry, F. Chan, C.A. English, H.M. Galindo, J.M. Grebmeier, A.B. Hollowed, N. Knowlton, J. Polovina, N.N. Rabalais, W.J. Sydeman, and L.D. Talley. 2012. Climate change impacts on marine ecosystems. Ann. Rev. Mar. Sci. **4**: 11-37.

Drinkwater, K.F., G. Beaugrand, M. Kaeriyama, S. Kim, G. Ottersen, R.I. Perry, H.O. Portner, J.J. Polovina, and A. Takasuka. 2010. On the processes linking climate to ecosystem changes. J. Mar. Syst. **79**: 374-388.

Fang, X., H.G. Stefan, J.G. Eaton, J.H. McCormick, and S.R. Alam. 2004. Simulation of thermal/dissolved oxygen habitat for fishes in lakes under different climate scenarios - Part 1. Cool-water fish in the contiguous US. Ecol. Model. **172**: 13-37.

Ficke, A.D., C.A. Myrick, and L.J. Hansen. 2007. Potential impacts of global climate change on freshwater fisheries. Rev. Fish. Biol. Fish. **17**: 581-613

Folch J., M. Lees, and G.H. Sloane-Stanley. 1957. A simple method for the isolation and purification of total lipids from animal tissue. J. Biol. Chem. **226**: 497-509.

Forney, J. L. 1965. Factors affecting growth and maturity in a walleye population. NY Fish Game J. **12**: 217-232.

Francis G.R., J.J. Magnuson, H.A. Reiger and D.R. Talhelm. 1979. Rehabilitation of Great Lakes ecosystems. Technical Report No. 37. Gt. Lakes Fish. Comm., Ann Arbor, Michigan.

Gauthier, C., P.G.C. Campbell, and P. Couture. 2008. Physiological correlates of growth and condition in the yellow perch (*Perca flavescens*). Comp. Biochem. Physiol. A-Mol. Integr. Physiol. **151**: 526-532.

Genner, M.J., D.W. Sims, V.J. Wearmouth, E.J. Southall, A.J. Southward, P.A. Henderson, and S.J. Hawkins. 2004. Regional climatic warming drives long-term community changes of British marine fish. Proc. R. Soc. B **271**: 655-661.

Grantham, B.A., F. Chan, K.J. Nielsen, D.S. Fox, J.A. Barth, A. Huyer, J. Lubchenco, and B.A. Menge. 2004. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. Nature **429**: 749-754.

Gregersen, F., L.A. Vollestad, K. Ostbye, P. Aass, and O. Hegge. 2011. Temperature and food-level effects on reproductive investment and egg mass in vendace, *Coregonus albula*. Fish. Manag. Ecol. **18**: 263-269.

Hartman, W.L. 1972. Lake Erie – Effects of exploitation, environmental changes and new species on fishery resources. J. Fish. Res. Board Can. **29**: 899-912.

Hartmann, H.C. 1990. Climate change impacts on Laurentian Great Lakes Levels. Clim. Change **17**: 49-67.

Hawley, N., T.H. Johengen, Y.R. Rao, S.A. Ruberg, D. Beletsky**,** S.A. Ludsin, B.J. Eadie, D.J. Schwab, T.E. Croley, and S.B. Brandt. 2006. Lake Erie hypoxia prompts Canada-U.S. study. EOS Trans. **87**: 313-324.

Henderson, B.A., and S.J. Nepszy. 1994. Reproductive tactics of walleye (*Stizostedion vitreum*) in Lake Erie. Can. J. Fish. Aquat. Sci. **51**: 986-997.

Henderson, B.A., T. Trivedi, N. Collins. 2000. Annual cycle of energy allocation to growth and reproduction of yellow perch. J. Fish Biol. **57**: 122-133

Henderson, B.A., J.L. Wong, and S.J. Nepszy. 1996. Reproduction of walleye in Lake Erie: allocation of energy. Can. J. Fish. Aquat. Sci. **53**: 127-133.

Heyer, C.J., T.J. Miller, F.P. Binkowski, E.M. Caldarone, and J.A. Rice. 2001. Maternal effects as a recruitment mechanism in Lake Michigan yellow perch (*Perca flavescens*). Can. J. Fish. Aquat. Sci. **58**: 1477-1487.

Hjort, J. 1914. Fluctuations in the great fisheries of Northern Europe viewed in the light of biological research. Rapp p-v Réun Cons Int. Exp. Mer. **20**:1–228.

Hoegh-Guldberg, O., and J.F. Bruno. 2010. The impact of climate change on the world's marine ecosystems. Science **328**: 1523-1528.

Hokanson, K.E.F. 1977. Temperature requirements of some percids and adaptations to seasonal temperature cycle. J. Fish. Res. Board Can. **34**: 1524-1550.

Houde, E.D. 1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. **2**:17-29.

Intergovernmental Panel on Climate Change (IPCC). 2007. Climate change 2007: the physical science basis. Contribution of Working Group I to the 4th Assessment Report of the Intergovernmental Panel on Climate Change. Solomon S, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller, eds. Cambridge University Press, Cambridge, UK.

Johnson, T.B., and D.O. Evans. 1990. Size-dependent winter mortality of young-of-the-year white perch: climate warming and invasion of the Laurentian Great Lakes. Trans. Am. Fish. Soc. **119**: 301-313.

Johnston, T.A., M.D. Wiegand, W.C. Leggett, R.J. Pronyk, S.D. Dyal, K.E. Watchorn, S. Kollar, and J.M. Casselman. 2007. Hatching success of walleye embryos in relation to maternal and ova characteristics. Ecol. Freshw. Fish. **16**: 295-306.

Jones, B.R., K.E.F. Hokanson, and J.H. McCormick. 1972. Winter temperature requirements for maturation and spawning of yellow perch *Perca flavescens* (Mitchill). Towards a plan of action for mankind. Proc. World Conf. Vol. 3 Biological balance and thermal modification.

Jones, M.L., B.J. Shuter, Y.M. Zhao, and J.D. Stockwell. 2006. Forecasting effects of climate change on Great Lakes fisheries: models that link habitat supply to population dynamics can help. Can. J. Fish. Aquat. Sci. **63**: 457-468.

Kamler, E. 2005. Parent-egg-progeny relationships in teleost fishes: an energetics perspective. Rev. Fish. Biol. Fish. **15**: 399-421.

Kayes, T.B., and H.E. Calbert. 1979. Effects of photoperiod and temperature on the spawning of yellow perch (*Perca flavescens*). Proc. World Maricul. Soc. **10**: 306-316.

Kelso, J.R.M., R.J. Steedman, S. Stoddart. 1996. Historical causes of change in Great Lakes fish stocks and the implications for ecosystem rehabilitation. Can. J. Fish. Aquat. Sci. **53**: 10-19.

Keniry, M.J., W.A. Brofka, W.H. Horns, and J.E. Marsden. 1996. Effects of decompression and puncturing the gas bladder on survival of tagged yellow perch. North Am. J. Fish Manage. **16**: 201–206

Kennedy, B.P., K.H. Nislow, and C.L. Folt. 2008. Habitat-mediated foraging limitations drive survival bottlenecks for juvenile salmon. Ecology **89**: 2529-2541.

Kerfoot, W.C., J.W. Budd, S.A. Green, J.B. Cotner, B.A. Biddanda, D.J. Schwab, and H.A. Vanderploeg. 2008. Doughnut in the desert: late-winter production pulse in southern Lake Michigan. Limnol. Oceanogr. **53**: 589-604.

Kerr, L.A., W.J. Connelly, E.J. Martino, A.C. Peer, R.J. Woodland, and D.H. Secor. 2009. Climate change in the U.S. Atlantic affecting recreational fisheries. Rev. Fish. Sci. **17**: 267-289.

Kerr, S.J. 2001. A review of “fizzing”: a technique for swim bladder deflation. Ontario Ministry of Natural Resources, Peterborough, Ontario, Canada.

Kitchell, J.F., D.J. Stewart, and D. Weininger. 1977. Application of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. **34**: 1922-1935.

Kling, G.W., K. Hayhoe, L.B. Johnson, J.J. Magnuson, S. Polasky, S.K. Robinson, B.J. Shuter, M.M. Wander, D.J. Wuebbles, D.R. Zak, R.L. Lindroth, S.C. Moser, and M.L. Wilson. 2003. Confronting climate change in the Great Lakes region: impacts on our communities and ecosystems. Union of Concerned Scientists and Ecological Society of America, Cambridge, MA.

Köster, F.W., C. Mollmann, H.H. Hinrichsen, K. Wieland, J. Tomkiewicz, G. Kraus, R. Voss, A. Makarchouk, B.R. MacKenzie, M.A. St John, D. Schnack, N. Rohlf, T. Linkowski, and J.E. Beyer. 2005. Baltic cod recruitment - the impact of climate variability on key processes. ICES J. Mar. Sci. **62**: 1408-1425.

Kunkel, K.E., N.E. Westcott, and D.A.R. Kristovich. 2002. Assessment of potential effects of climate change on heavy lake-effect snowstorms near Lake Erie. J. Gt. Lakes Res. **28**: 521-536.

Kwasek, K.A. 2012. The nutritional and genetic effects on body growth, reproduction and molecular mechanisms responsible for muscle growth in yellow perch *Perca flavescens.* Ph.D. dissertation. The Ohio State University, Columbus.

Lofgren, B.M., F.H. Quinn, A.H. Clites, R.A. Assel, A.J. Eberhardt, and C.L. Luukkonen. 2002. Evaluation of potential impacts on Great Lakes water resources based on climate scenarios of two GCM’s. J. Gt. Lakes Res. **28**: 537-554.

Ludsin, S.A. 2000. Exploration of spatiotemporal patterns in recruitment and community organization of Lake Erie fishes: a multiscale, mechanistic approach. Ph.D. dissertation. The Ohio State University, Columbus.

Ludsin, S.A., and D.R. DeVries. 1997. First-year recruitment of largemouth bass: the interdependency of early life stages. Ecol. Applic. **7**:1024-1038.

Ludsin, S., K. Pangle, L. Carreon-Martinez, N. Legler, J. Reichert, D.D. Heath, B. Fryer, T. Johnson, J. Tyson, T. Höök, G. Leshkevich, D. Mason, D. Bunnell, C. Mayer, T. Johengen, H. Vanderploeg, and A. Drelich. 2011. River discharge as a predictor of Lake Erie yellow perch recruitment. Final completion report, Great Lakes Fishery Commission, Fisheries Research Program, Ann Arbor, MI. 166 pp

Ludsin, S.A., M.W. Kershner, K.A. Blocksom, R.L. Knight, R.A. Stein. 2001. Life after death in Lake Erie: Nutrient controls drive species richness, rehabilitation. Ecol. Appl. **11**: 731-746.

Luksiene, D., O. Sandstrom, L. Lounashelmo, and J. Andersson. 2000. The effects of thermal effluent exposure on the gametogenesis of female fish. J.Fish Biol. **56**: 37-50.

MacKay, M., and F. Seglenieks. 2013. On the simulation of Laurentian Great Lakes water levels under projections of global climate change. Clim. Change **117**: 55-67.

Mackenzie, B.R., H. Gislason, C. Mollmann, and F.W. Koster. 2007. Impact of 21st century climate change on the Baltic Sea fish community and fisheries. Glob. Change Biol. **13**: 1348-1367.

Mackenzie-Grieve, J.L., and J.R. Post. 2006. Projected impacts of climate warming on production of lake trout (*Salvelinus namaycush*) in southern Yukon lakes. Can. J. Fish. Aquat. Sci. **63**: 788-797.

Madenjian, C.P., J.T. Tyson, R.L. Knight, M.W. Kershner, and M.J. Hansen. 1996. First-year growth, recruitment, and maturity of walleyes in western Lake Erie. Trans. Am. Fish. Soc. **125**: 821-830.

Magnuson, J.J. 2010. History and heroes: the thermal niche of fishes and long-term lake ice dynamics. J. Fish Biol. **77**: 1731-1744.

Magnuson, J.J., K.E. Webster, R.A. Assel, C.J. Bowser, P.J. Dillon, J.G. Eaton, H.E. Evans, E.J. Fee, R.I. Hall, L.R. Mortsch, D.W. Schindler, and F.H. Quinn. 1997. Potential effects of climate changes on aquatic systems: Laurentian Great Lakes and Precambrian Shield Region. Hydrol. Process. **11**: 825-871.

Malservisi, A., and E. Magnin. 1968. Changements cycliques annuels se produisant dans les ovarires de *Perca fluviatilis flavescens* (Mitchill) de la region de Montreal. Nat. Can. (Que.) **95**: 929-945.

Mansour, N., F. Lahnsteiner, and R.A. Patzner. 2009. Ovarian fluid plays an essential role in the attachment of Eurasian perch*, Perca fluviatilis* eggs. Theriogenology **71**: 586-593.

Marshall, C.T., N.A. Yaragina, Y. Lambert, and O.S. Kjesbu. 1999. Total lipid energy as a proxy for total egg production by fish stocks. Nature **402**: 288-290.

McCormick, M.J., and G.L. Fahnenstiel. 1999. Recent climatic trends in nearshore water temperatures in the St. Lawrence Great Lakes. Limnol. Oceanogr. **44**: 530-540.

Meisner, J.D., J.L. Goodier, H.A. Regier, B.J. Shuter, and W.J. Christie. 1987. An assessment of the effects of climate warming on Great Lakes basin fishes. J. Gt. Lakes Res. **13**: 340-352.

Metcalfe, L.D., and A.A. Schmitz. 1961. The rapid preparation of fatty acid esters for gas chromatographic analysis. Analytical Chemistry **33**: 363–364.

Migaud, H., P. Fontaine, I. Sulistyo, P. Kestemont, and J.N. Gardeur. 2002. Induction of out-of-season spawning in Eurasian perch *Perca fluviatilis*: effects of rates of cooling and cooling durations on female gametogenesis and spawning. Aquaculture **205**: 253-267.

Miller, L.W. 1967. The introduction, growth, diet and depth distribution of walleye *Stizostedion vitreum* (Mitchill), in El Capitan Reservoir, San Diego County. Administrative Report California Resource Agency, Department of Fish and Game, Inland Fisheries Branch 67-10: 1-14.

Miller, T.J., L.B. Crowder, J.A. Rice, and E.A. Marschall. 1988. Larval size and recruitment mechanisms in fishes – toward a conceptual framework. Can. J. Fish. Aquat. Sci. **45**: 1657-1670.

Miller-Navarra, D.C., M.T. Brett, A.M. Liston, and C.R. Goldman. 2000. A highly unsaturated fatty acid predicts carbon transfer between primary producers and consumers. Nature **403**: 74-77.

Minns, C.K., J.A. Lane, and C.B. Portt. 1997. Analyses of the habitat requirements of Great Lakes fishes. 40th Conference of the International Association for Great Lakes Research: 98-98.

Moore, M., B.A. Berejikian, and E.P. Tezak. 2012. Variation in the early marine survival and behavior of natural and hatchery-reared hood canal steelhead. PLoS One 7(11): e49645.

Mortsch, L.D., and F.H. Quinn. 1996. Climate change scenarios for Great Lakes Basin ecosystem studies. Limnol. Oceanogr. **41**: 903-911.

Moyle, P.B., and J.J. Cech. 2000. Fishes: an introduction to ichthyology. 4th ed. Prentice Hall, Englewood Cliffs, New Jersey, USA.

Olin, M., J. Jutila, H. Lehtonen, M. Vinni, J. Ruuhijarvi, S. Estlander, M. Rask, A. Kuparinen, and J. Lappalainen. 2012. Importance of maternal size on the reproductive success of perch, *Perca fluviatilis*, in small forest lakes: implications for fisheries management. Fisheries Manag. Ecol. **19**: 363-374.

Ottersen, G., S. Kim, G. Huse, J.J. Polovina, and N.C. Stenseth. 2010. Major pathways by which climate may force marine fish populations. J. Mar. Syst. **79**: 343-360.

Paine, R.T., M.J. Tegner, and E.A. Johnson. 1998. Compounded perturbations yield ecological surprises. Ecosystems **1**: 535-545.

Pangle, K.L., T.D. Malinich, D.B. Bunnell, D.R. DeVries, and S.A. Ludsin. 2012. Context-dependent planktivory: interacting effects of turbidity and predation risk on adaptive foraging. Ecosphere **3**: art114.

Pothoven, S.A., T.F. Nalepa, P.J. Schneeberger, and S.B. Brandt. 2001. Changes in diet and body condition of lake whitefish in southern Lake Michigan associated with changes in benthos. North Am. J. Fish Manage. **21**: 876-883.

Pothoven, S.A., T.F. Nalepa, C.P. Madenjian, R.R. Rediske, P.J. Schneeberger, and J.X. He. 2006. Energy density of lake whitefish *Coregonus clupeaformis* in Lakes Huron and Michigan. Environ. Biol. Fishes **76**: 151-158.

Regier, H. A., and W.L. Hartman. 1973. Lake Erie fish community – 150 years of cultural stresses. Science **180**: 1248-1255.

Reichert, J.M., Fryer, B.J., Pangle, K.L., Johnson, T.B., Tyson, J.T., Drelich, A.B., and Ludsin, S.A. 2010. River-plume use during the pelagic larval stage benefits recruitment of a lentic fish. Can. J. Fish. Aquat. Sci. **67**: 987-1004.

Rideout, R.M., G.A. Rose, and M.P.M. Burton. 2005. Skipped spawning in female iteroparous fishes. Fish. Fish. **6**: 50-72.

Rinchard, J., K. Dabrowski, J.J. Van Tassell, and R.A. Stein. 2005a. Optimization of fertilization success in *Sander vitreus* is influenced by the sperm : egg ratio and ova storage. J. Fish Biol. **67**: 1157-1161.

Rinchard, J., K. Ware, and K. Dabrowski. 2005b. Evaluation of gamete quality in yellow perch collected from Lake Erie. Final Report to Lake Erie Protection Fund, Toledo, Ohio.

Roberts, J.J., S.B. Brandt, D. Fanslow, S.A. Ludsin, S.A. Pothoven, D. Scavia, D., and T.O. Höök. 2011. Effects of hypoxia on consumption, growth, and rna:dna ratios of young yellow perch. Trans. Am. Fish. Soc. **140**: 1574-1586

Roberts, J.J., P.A. Grecay, S.A. Ludsin, S.A. Pothoven, H.A. Vanderploeg, and T.O. Höök. 2012. Evidence of hypoxic foraging forays by yellow perch (*Perca flavescens*) and potential consequences for prey consumption. Freshw. Biol. **57**: 922-937.

Roberts, J.J., T.O. Höök, T.O., S.A. Ludsin, S.A. Pothoven, H.A. Vanderploeg, and S.B. Brandt. 2009. Effects of hypolimnetic hypoxia on foraging and distributions of Lake Erie yellow perch. J. Exp. Mar. Biol. Ecol. **381**: S132-S142.

Rucinski, D.K., D. Beletsky, J.V. DePinto, D.J. Schwab, and D. Scavia. 2010. A simple 1-dimensional, climate based dissolved oxygen model for the central basin of Lake Erie. J. Gt. Lakes Res. **36**: 465-476.

Sandstrom, O., I. Ambrahamsson, J. Andersson, and M. Vetemaa. 1997. Temperature effects on spawning and egg development in Eurasian perch. J. Fish Biol. **51**: 1015-1024.

Schindler, D.E., D.E. Rogers, M.D. Scheuerell, and C.A. Abrey. 2005. Effects of changing climate on zooplankton and juvenile sockeye salmon growth in southwestern Alaska. Ecology **86**: 198-209.

Scott, W.B., and E.J. Crossman. 1973. Freshwater fishes of Canada. Bulletin 184. Fisheries Research Board of Canada. 966 pp

Sharma, S., D.A. Jackson, C.K. Minns, and B.J. Shuter. 2007. Will northern fish populations be in hot water because of climate change? Glob. Change Biol. **13**: 2052-2064.

Shewmon, L.N., J.R. Godwin, R.S. Murashige, and H.V. Daniels. 2007. Environmental manipulation of growth and sexual maturation in yellow perch, *Perca flavescens*. J. World Aquacult. Soc. **38**: 383-394.

Shuter, B.J., and J.R. Post. 1990. Climate, population viability and zoogeography of temperate fishes. Trans. Am. Fish. Soc. **199**: 314-336.

Shuter, B.J., and J.D. Meisner. 1992. Tools for assessing the impact of climate change on freshwater fish populations. GeoJournal **28**: 7-20.

Smith, D.M., S. Cusack, A.W. Colman, C.K. Folland, G.R. Harris, and J.M. Murphy. 2007. Improved surface temperature prediction for the coming decade from a global climate model. Science **317**: 796-799.

Stefan, H.G., M. Hondzo, X. Fang, J.G. Eaton, and J.H. McCormick. 1996. Simulated long-term temperature and dissolved oxygen characteristics of lakes in the north-central United States and associated fish habitat limits. Limnol. Oceanogr. **41**: 1124-1135.

Svendsen, E., A. Aglen, S.A. Iversen, D.W. Skagen, and O. Smestad. 1995. Influence of climate on recruitment and migration of fish stocks in the North Sea. Canadian Special Publication of Fisheries and Aquatic Sciences **121**: 641-653.

Thorpe, J.E. 1977. Daily ration of adult perch, *Perca fluviatilis* during summer in Lock-Leven, Scotland. J. Fish Biol. **11**: 55-68.

Vanderploeg, H.A., S.A. Ludsin, S.A. Ruberg, T.O. Höök, S.A. Pothoven, S.B. Brandt, G.A. Lang, J. Liebig, and J.F. Cavaletto. 2009. Hypoxia affects spatial distributions and overlap of pelagic fish, zooplankton, and phytoplankton in Lake Erie. J. Exp. Mar. Biol. Ecol. **381**(Suppl. 1): S92-S107.

Venturelli, P.A., C.A. Murphy, B.J. Shuter, T.A. Johnston, P.J.V. de Groot, P.T. Boag, J.M. Casselman, R. Montgomerie, M.D. Wiegand, and W.C. Leggett. 2010. Maternal influences on population dynamics: evidence from an exploited freshwater fish. Ecology **91**: 2003-2012.

Vikebo, F., S. Sundby, B. Adlandsvik, and O. Fiksen. 2005. The combined effect of transport and temperature on distribution and growth of larvae and pelagic juveniles of Arcto-Norwegian cod. ICES J. Mar. Sci. **62**: 1375-1386.

Wang, J., X. Bai, H. Hu, A. Clites, M. Colton, and B. Lofgren. 2012. Temporal and spatial variability of Great Lakes ice cover, 1973-2010. J. Clim. **25**: 1318-1329.

Wang, N., J.-N. Gardeur, E. Henrotte, M. Marie, P. Kestemont, and P. Fontaine. 2006. Determinism of the induction of the reproductive cycle in female Eurasian perch, *Perca fluviatilis*: Identification of environmental cues and permissive factors. Aquaculture **261**: 706-714.

West, G. 1990. Methods of assessing ovarian development in fishes – a review. Aust. J. Mar. Freshwater Res. **41**: 199-222.

Willard, D.A., and C.E. Bernhardt. 2011. Impacts of past climate and sea level change on Everglades wetlands: placing a century of anthropogenic change into a late-Holocene context. Clim. Change **107**: 59-80.

Yellow Perch Task Group (YPTG). 2011. Report of the yellow perch task group. Great Lakes Fishery Commission, Ann Arbor, MI.

ACKNOWLEDGEMENTS:

We thank the students and staff of the OSU Aquatic Ecology Laboratory and Aquaculture Laboratory for their assistance in conducting this research. Specifically, Theo Gover, Alex Johnson, Jeramy Pinkerton, and Chelsea Schmit deserve special thanks for their dedication to all aspects of this project. We greatly appreciate assistance from biologists and research staff at both the Ohio Division of Wildlife (ODOW) Fairport Fisheries Station and the USGS Lake Erie Biological Station for their help in collecting live yellow perch for use in the laboratory experiment, with John Deller, Ann Marie Gorman, Carey Knight, Patrick Kocovsky, and Richard Kraus deserving special thanks. We are grateful to John Hageman for teaching us how to properly “fizz” live yellow perch and appreciate Matt Thomas and other staff at Ohio Sea Grant and OSU Stone Laboratory for providing lodging accommodations and assistance during field work. Thanks to Bill Lynch for assisting us in obtaining domesticated yellow perch for use in the laboratory experiment. We also appreciate technical assistance from supervisors and staff from the ODOW Hebron State Fish Hatchery, who modified the AEL pool facility so that this research could be conducted. Specifically, we would like to thank Elmer Heyob and Brian Kitchen for their assistance. Also, thanks to Mort Pugh and his staff at the ODOW St. Mary’s State Fish Hatchery for providing live minnows for our experiment. Special thanks to Jake Gilliland, Roy Stein, and Erich Williams for enduring one particularly grueling field expedition to Lake Erie. Finally, we would like to thank the numerous current and former OSU graduate students, post-doctoral researchers, undergraduate student volunteers, and staff who made this research possible by conducting field collections, caring for live yellow perch, processing samples, and providing helpful suggestions regarding logistical and analytical aspects of this project. Those deserving special thanks include Catherine Altemus, Mike Bahler, Luke Birk, Lindsey Boaz, Ben Bolam, John Boudouris, Chelsea Coble, Rachael Crane, Devin Crockett, Kristen DeVanna, Sarah Elliott, Chris French, Christine Grimme, Summer Hayes, Megan Helsinger, Breanna Humbarger, Joseph Hunt, Patrick Korn, Karolina Kwasek, Adam Luke, Anthony Moisinski, Kaelen Mortensen, Thomas Peterson, Gosia Korzeniowska, Kevin Pangle, Tim Parker, Logan Scheuermann, Austin Schnitzer, Tyler Stuebe, Melinda Varney, Willie Wilber, Devan Wolfe. Additional support for this research was provided by the Federal Aid in Sport Fish Restoration Program (F-69-P, Fish Management in Ohio), administered jointly by the U.S. Fish and Wildlife Service and the ODOW.

DELIVERABLES:

Publications

Farmer, T.M., K. Dabrowski, E.A. Marschall, and S.A. Ludsin. *in prep*. Negative effects of winter warming on offspring quality underlie observed declines in fish recruitment and fishery dynamics. Target journal: *Nature Climate Change*.

Farmer, T.M., S.A. Ludsin, K. Dabrowski, and E.A. Marschall. *in prep*. Winter warming expected to drive declines in a north-temperature, cool-water fish population through effects on reproduction. Target journal: *Global Change Biology*.

Departmental Seminars & Public Lectures

Ludsin, S.A. 2011. Climate change impacts on Fishes of the Great Lakes. Stone Laboratory Guest Lecture Series, Gibraltar Island, Put-in-Bay, OH. (public lecture).

Ludsin, S.A. 2012. Climate change impacts on fishes of the Great Lakes. Lakeside Chautauqua Environmental Stewardship Educational Seminar Series, Lakeside, OH (seminar).

Ludsin, S.A. 2011. Climate change impacts on Great Lakes fishes. Ohio State University Climate Change Webinar Series, Columbus. (webinar).

Oral Presentations

Dabrowski, K., M. Korzeniowska, T.M. Farmer, S.A. Ludsin, and E.A. Marschall. 2013. The function of neutral lipids in early life history of yellow perch: Transition from endogenous to exogenous nutrition. Lake Erie-Inland Waters Annual Research Review, The Ohio State University, Columbus.

Farmer, T.M, S.A. Ludsin, E.A. Marschall, and K. Dabrowski. 2013. What does climate change hold for Lake Erie yellow perch? Lake Erie-Inland Waters Annual Research Review, The Ohio State University, Columbus.

Ludsin, S.A. 2013. Lake Erie yellow perch recruitment mechanisms: a never-ending story of change. Lake Erie Committee annual meeting, Niagara Falls, NY.

Farmer, T.M., S.A. Ludsin, and E.A. Marschall. 2012. Meteorological effects on yellow perch recruitment in Lake Erie. American Fisheries Society, St. Paul, MN.

Farmer, T.M., S.A. Ludsin, and E.A. Marschall. 2012. Meteorological effects on yellow perch recruitment in Lake Erie. Lake Erie-Inland Waters Annual Research Review, The Ohio State University, Columbus.

Farmer, T.M., S.A. Ludsin, E.A. Marschall, and K. Dabrowski. 2011. Yellow perch spawning distributions, egg quality, and fecundity in Lake Erie's western and central basins. Lake Erie-Inland Waters Annual Research Review, The Ohio State University, Columbus.

Farmer, T.M, E.A. Marschall, and S.A. Ludsin. 2010. Energetic costs of climate change: winter temperature and hypoxia effects on reproduction of an iteroparous, cool-water fish. Ecological Society of America, Pittsburgh, PA.

Farmer, T., S. Ludsin, and E. Marschall. 2010. Meteorological effects on yellow perch reproduction and recruitment in Lake Erie. Lake Erie-Inland Waters Annual Research Review, The Ohio State University, Columbus.

Contributed Posters

Coble C., T. Farmer, E. Marschall, S. Ludsin, and K. Dabrowski. 2013. Climate change effects on the quantity and quality of eggs and larvae of a coolwater fish. Natural and Mathematical Sciences Undergraduate Research Forum, The Ohio State University, Columbus.

Coble C., T. Farmer, E. Marschall, S. Ludsin, and K. Dabrowski. 2013. Climate change effects on the quantity and quality of eggs and larvae of a coolwater fish. Denman Undergraduate Research Forum, The Ohio State University, Columbus, OH.

Humbarger, B., T. Farmer, C. Schmit, and E. Marschall. 2013. Climate change effects on spawning phenology in a coolwater fish, the yellow perch (*Perca flavescens*). Denman Undergraduate Research Forum, The Ohio State University, Columbus, OH.

Pinkerton, J. T. Farmer, J. Van Tassell, E. Marschall, and S.A. Ludsin. 2011. Understanding annual variation in female yellow perch age-at-maturity in Lake Erie. American Fisheries Society, Seattle, WA.

Theses and Dissertations

Farmer, T.M. *expected December 2013*. Climate change effects on Lake Erie yellow perch reproduction. PhD thesis. The Ohio State University, Columbus, OH.

Humbarger, B. 2013. Climate change effects on spawning phenology in a coolwater fish, the yellow perch *Perca* flavescens. Undergraduate Honor's Thesis. The Ohio State University, Columbus, OH.

High School and Undergraduate Students Trained

1. Catherine Altemus (The Ohio State University)
2. Michael Bahler (The Ohio State University)
3. Lindsey Boaz (The Ohio State University)
4. Ben Bolam (The Ohio State University)
5. Luke Birk (The Ohio State University)
6. John Boudouris (The Ohio State University)
7. Rachael Crane (The Ohio State University)
8. Chelsea Coble (The Ohio State University - Undergraduate Research Fellow)
9. Sarah Elliott (The Ohio State University)
10. Christine Grimme (The Ohio State University)
11. Summer Hayes (The Ohio State University)
12. Megan Helsinger (The Ohio State University)
13. Breanna Humbarger (The Ohio State University)
14. Joseph Hunt (The Ohio State University)
15. Patrick Korn (The Ohio State University)
16. Adam Luke (The Ohio State University)
17. Anthony Moisinski (The Ohio State University)
18. Kaelen Mortensen (Columbus Academy H.S.)
19. Thomas Peterson (The Ohio State University)
20. Logan Scheuermann (The Ohio State University)
21. Austin Schnitzer (John's Hopkins University)

22. Chelsea Schmit (The Ohio State University)
23. Tyler Stuebe (The Ohio State University)
24. Melinda Varney (The Ohio State University)
25. Willie Wilber (The Ohio State University)
26. Devan Wolfe (The Ohio State University)

Media Attention for Research

Cleveland Plain Dealer. "Changing Lake Erie, invasive white perch threaten popular yellow perch in Western Lake Erie". March 29, 2013.

http://www.cleveland.com/outdoors/index.ssf/2013/03/changing_lake_erie_invasive_wh.html

Ohio Outdoor News. "Winter affects fish in different ways". March 2012

http://www.outdoornews.com/March-2012/Winter-affects-fish-in-different-ways/.

PRESS RELEASE:

Previous research has suggested that that climate warming would benefit cool-water fish species in the North American Great Lakes Basin by providing good growth habitat for a longer portion of the year. While still potentially true, new research from a team of investigators at The Ohio State University suggests that warm, short winters, which have become common in Lake Erie during the past decade, can negatively affect reproduction in cool-water species such as yellow perch.

These researchers used a laboratory experiment and population model to quantify the potential effects of increased temperature during winter on yellow perch. They focused on the winter period because yellow perch develop ovaries during this time. They hypothesized that warm winters would cause yellow perch to use too much energy over winter, lessening energy available to produce offspring. They also hypothesized that warm winters would fail to provide yellow perch with the cold temperatures thought to be necessary for successful reproductive development.

In their experiment, these researchers exposed adult yellow perch that were captured in Lake Erie's central basin to simulated winter temperature conditions in the laboratory. Their experiment showed that the adult spawners that experienced a simulated long winter (110 days below 41°F) produced higher quality offspring than those fish exposed to a short winter (50 days below 41°F). The spawners exposed to a long winter produced larger eggs that hatched better and produced larger larvae than spawners exposed to a short winter. Because large larvae are believed to grow and survive better than small larvae during the first summer of life in Lake Erie, these observed differences in offspring quality may translate into differences in survival to the juvenile stage.

These researchers included their experimental findings on offspring quality in a population model that used winter temperature to predict the number of offspring surviving through their first summer. This model helped to explain the high frequency of failed yellow perch year-classes (low juvenile abundances) during the past two decades. In addition, when predicted winter temperatures for Lake Erie during the middle of this century were used in their model, these researchers showed that continued climate warming is likely to further reduce the frequency of strong year-classes.

This research ultimately identifies another way in which continued climate change is likely to negatively influence the Lake Erie ecosystem and its ecologically and economically important fish populations. In their Great Lakes Fishery Commission final report, these researchers also discuss the likelihood of winter warming interacting with the formation of areas of low oxygen availability ("dead zones") during summer to further reduce the reproductive potential of yellow perch in Lake Erie.

This research was conducted by Troy Farmer (a PhD candidate) and his graduate advisors (Drs. Elizabeth Marschall and Stuart Ludsin), who are in Ohio State's Aquatic Ecology Laboratory, as well as Dr. Konrad Dabrowski from Ohio State's Aquaculture Laboratory.

For more information, contact Dr. Stuart A. Ludsin, Aquatic Ecology Laboratory, Department of Evolution, Ecology, and Organismal Biology, The Ohio State University. ludsin.1@osu.edu, 614-292-1613.

APPENDICES:

Appendix A. *List of abstracts for oral presentations that required one.*

Farmer, T.M., S.A. Ludsin, and E.A. Marschall. 2012. Meteorological effects on yellow perch recruitment in Lake Erie. American Fisheries Society, St. Paul, MN.

Climate change is expected to alter numerous abiotic and biotic variables that are likely to influence fish recruitment. Before the response of fisheries to climate change can be predicted, however, we first must understand the mechanisms by which climate change can directly and indirectly affect fish populations. In Lake Erie, recent investigations have suggested the importance of several climate-influenced meteorological variables to yellow perch (*Perca flavescens*) year-class strength (an early predictor of recruitment to the fishery), including winter temperature, precipitation-driven tributary inflows, and temperature- and precipitation-driven hypolimnetic hypoxia. Using historical indices of yellow perch year-class strength, meteorological conditions, and two measures of stock size (total egg production, spawning stock biomass) in a multivariable model-building exercise, we sought to explain past (1987-2010) recruitment variation in western and central Lake Erie's yellow perch populations. We found a positive effect of long winters in both western and central Lake Erie populations. Additionally, in western Lake Erie, where conditions are heavily influenced by the large rivers flowing into it, we saw a positive effect of high river discharge in the spring. We found no support for including stock-recruit relationships in models, suggesting yellow perch populations in Lake Erie are driven largely by meteorological processes.

Farmer, T.M, E.A. Marschall, and S.A. Ludsin. 2010. Energetic costs of climate change: winter temperature and hypoxia effects on reproduction of an iteroparous, cool-water fish. Ecological Society of America, Pittsburgh, PA.

<u>Background/Question/Methods</u>**.** The frequency of hypoxic events and short, mild winters is expected to increase with continued climate change, potentially leading to unexpected consequences for aquatic ecosystems. In the North American Great Lakes region, historical field data suggest that such changes may in part be responsible for poor recruitment of several ecologically and economically important fishes. Herein, we test this hypothesis using Lake Erie yellow perch (*Perca flavescens*), a cool-water, iteroparous benthic species that develops ovaries during winter, as a model organism. We developed a dynamic state variable model within a bioenergetics modeling framework to test whether recent poor recruitment of yellow perch may be linked to a synergistic energetic effects of summer bottom hypoxia (i.e., reduced energy reserves available during winter for gonad growth, resultant of habitat shifts into sub-optimal thermal and feeding conditions) and winter warming (via increased metabolism and subsequent reduction in energy available for gonad growth) on reproduction.

<u>Results/Conclusions</u>. Our model calculated optimal energy allocation strategies for females representative of Lake Erie's spawning yellow perch population during historically typical distributions of summer hypoxia and winter conditions. We then simulated yellow perch energy allocation and reproductive potential using these strategies under both current and future (i.e., predicted by climate change models) environmental conditions, to gain insight into the potential bioenergetic costs of climate change. We modeled energy allocation to structural growth, fat reserves, and gonads during winter given (1) energetic condition entering the winter (a function of extent of hypoxia during the previous growing season), (2) winter temperature regime, and (3) prey availability during the winter. The optimal allocation pattern was that strategy that resulted in the highest expected lifetime fitness (i.e., total number of eggs produced). Preliminary results indicate that short winters result in similar amounts of energy allocated to ovaries as in long winters; however, when condition entering the winter is poor and winter prey resources are low, reproductive development is abandoned during both warm and cold winters.

Appendix B. *List of abstracts for contributed posters that required one.*

Coble C., T. Farmer, E. Marschall, S. Ludsin, and K. Dabrowski. 2013. Climate change effects on the quantity and quality of eggs and larvae of a coolwater fish. Denman Undergraduate Research Forum, The Ohio State University, Columbus, OH.

Understanding how the timing (or phenology) of important life history events, such as reproduction, are controlled by ambient temperature is a major focus of climate change research. Studies in terrestrial environments indicate many migratory bird species arrive earlier at spring nesting grounds and many plant species bloom earlier in response to early spring warming. Evidence suggests the timing of reproduction has important consequences for early-life growth and survival, which directly affect population dynamics. While many long-term phenology studies exist for terrestrial species, equivalent long-term studies of fish reproductive events are rare. Yellow perch *Perca flavescens* (economically and ecologically important across North America) is a coolwater fish species that typically spawns during April - May in Lake Erie, during a time when temperatures are highly variable from year to year. Previous laboratory studies indicate ambient spring temperature may have a minimal effect on the onset of yellow perch spawning; however, this hypothesis has not been tested in the field. Using data collected weekly during yellow perch spawning seasons on Lake Erie over three years (2010 – 2012), we quantified how the start, peak, and end dates of spawning correlated with weekly water temperatures. During this study, the percent of immature, gravid, flowing, or spent females was determined each week from a series of bottom trawls conducted across two nearshore-to-offshore transects in the western basin of Lake Erie. Spring air and water temperatures varied substantially during this study, which included the warmest spring on record for Ohio (i.e., 2012). Preliminary results indicate that yellow perch may not spawn earlier in response to warmer spring water temperatures. However, in response to cold spring water temperatures, spawning may be delayed. Ultimately, we discuss our results in context of other North American coolwater fish species, highlighting similarities, differences, and implications for management in a changing climate.

Coble C., T. Farmer, E. Marschall, S. Ludsin, and K. Dabrowski. 2013. Climate change effects on the quantity and quality of eggs and larvae of a coolwater fish. Natural and Mathematical Sciences Undergraduate Research Forum, The Ohio State University, Columbus.

Understanding how the timing (or phenology) of important life history events, such as reproduction, are controlled by ambient temperature is a major focus of climate change research. Studies in terrestrial environments indicate many migratory bird species arrive earlier at spring nesting grounds and many plant species bloom earlier in response to early spring warming. Evidence suggests the timing of reproduction has important consequences for early-life growth and survival, which directly affect population dynamics. While many long-term phenology studies exist for terrestrial species, equivalent long-term studies of fish reproductive events are rare. Yellow perch *Perca flavescens* (economically and ecologically important across North America) is a coolwater fish species that typically spawns during April - May in Lake Erie, during a time when temperatures are highly variable from year to year. Previous laboratory studies indicate ambient spring temperature may have a minimal effect on the onset of yellow perch spawning; however, this hypothesis has not been tested in the field. Using data collected weekly during yellow perch spawning seasons on Lake Erie over three years (2010 – 2012), we quantified how the start, peak, and end dates of spawning correlated with weekly water temperatures. During this study, the percent of immature, gravid, flowing, or spent females was determined each week from a series of bottom trawls conducted across two nearshore-to-offshore transects in the western basin of Lake Erie. Spring air and water temperatures varied substantially during this study, which included the warmest spring on record for Ohio (i.e., 2012). Preliminary results indicate that yellow perch may not spawn earlier in response to warmer spring water temperatures. However, in response to cold spring water temperatures, spawning may be delayed. Ultimately, we discuss our results in context of other North American coolwater fish species, highlighting similarities, differences, and implications for management in a changing climate.

Humbarger, B., T. Farmer, C. Schmit, and E. Marschall. 2013. Climate change effects on spawning phenology in a coolwater fish, the yellow perch (*Perca flavescens*). Denman Undergraduate Research Forum, The Ohio State University, Columbus, OH.

Understanding how the timing (or phenology) of important life history events, such as reproduction, are controlled by ambient temperature is a major focus of climate change research. Studies in terrestrial environments indicate many migratory bird species arrive earlier at spring nesting grounds and many plant species bloom earlier in response to early spring warming. Evidence suggests the timing of reproduction has important consequences for early-life growth and survival, which directly affect population dynamics. While many long-term phenology studies exist for terrestrial species, equivalent long-term studies of fish reproductive events are rare. Yellow perch *Perca flavescens* (economically and ecologically important across North America) is a coolwater fish species that typically spawns during April - May in Lake Erie, during a time when temperatures are highly variable from year to year. Previous laboratory studies indicate ambient spring temperature may have a minimal effect on the onset of yellow perch spawning; however, this hypothesis has not been tested in the field. Using data collected weekly during yellow perch spawning seasons on Lake Erie over three years (2010 – 2012), we quantified how the start, peak, and end dates of spawning correlated with weekly water temperatures. During this study, the percent of immature, gravid, flowing, or spent females was determined each week from a series of bottom trawls conducted across two nearshore-to-offshore transects in the western basin of Lake Erie. Spring air and water temperatures varied substantially during this study, which included the warmest spring on record for Ohio (i.e., 2012). Preliminary results indicate that yellow perch may not spawn earlier in response to warmer spring water temperatures. However, in response to cold spring water temperatures, spawning may be delayed. Ultimately, we discuss our results in context of other North American coolwater fish species, highlighting similarities, differences, and implications for management in a changing climate.

Pinkerton, J. T. Farmer, J. Van Tassell, E. Marschall, and S.A. Ludsin. 2011. Understanding annual variation in female yellow perch age-at-maturity in Lake Erie. American Fisheries Society, Seattle, WA.

Yellow perch *Perca flavescens*, an important commercial and recreational fish species in Lake Erie, exhibits high annual variability in demographic rates. For example, over the last 20 years (1990-2009), the annual percentage of age-2 female yellow perch that are mature has ranged from 6% to 94 %, and the contribution of age-2 yellow perch to population egg production has ranged from 1% to 70% of the total in a given year. To understand what drives this temporal variation in the reproductive contribution of age-2 fish, we 1) quantified the annual variation in age and size at maturation, 2) related age at maturation to annual growth rates of young ages, and 3) used environmental data to explain age-specific annual growth rates. Using length, age, and maturity data collected during annual Ohio Division of Wildlife fall bottom-trawl surveys from 1990-2003, we used logistic regression to estimate both the total length and age at which 50 % of females were mature for each year class. Total length at 50 % maturity across years ranged from 151 to 172 mm (164.94 ± 1.4 mm; mean ± SE), and age at 50% maturity ranged from 1.1 to 2.3 years (1.61 ± 0.1 years; mean ± SE). We found that percent mature at age-2 was strongly correlated to length at age-2 ($r^2 = 0.863$). Next, we used age-specific growth increments (calculated as differences in mean total lengths) for fish of age-0 (spring hatch through October of first year), 1 (October age-0 to October age-1), and 2 (October age-1 to October age-2) to explain age at maturation. Both age-0 ($r^2 = 0.259$) and age-2 ($r^2 = 0.568$) growth explained a significant proportion of the variation in age at maturation across years. Finally, we found that age-0 growth was positively correlated to annual growing degree days while age-2 growth was negatively related to average bottom dissolved oxygen (July-October). Our results suggest a link from abiotic effects (temperature and dissolved oxygen) through growth rate and age-at-maturation to reproductive contribution of age-2 yellow perch in Lake Erie.