THE EFFECT OF FOOD RATION ON GROWTH, REPRODUCTION AND MUSCLE LIPID STORAGE IN MATURE FEMALE LAKE TROUT FROM DIFFERENT POPULATIONS RAISED IN A COMMON ENVIRONMENT

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ABSTRACT

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This study examined the differences in growth rates, percent lipid, and reproductive output between hatchery and wild individuals from lake trout (*Salvelinus namaycush*) stocks that show very different life history strategies in efforts to characterize energy allocation along life history considerations, and responses to a food limitation stressor. This study monitored individuals raised in a common environment for two years for growth rates, percent muscle lipid storage and reproductive output under different feeding regimes from the Killala, Manitou, Michipicoten, and Kingscote stocks and their wild counterparts. For the course of this study, some fish were maintained on a high ration, some fish on a low ration, and some fish were switched from a high ration to a low ration, and the remaining fish were switched from a low ration to a high ration. Robust reaction norms between egg number and percent lipid were identified within all stocks across rations within both years, but this relationship changed shape between years. These results suggest that there are differences between lake trout stocks in the range of phenotypic expressions, based on genetics, and that the relationship between lipids and egg number may be predictable within each stock at a given age. This increased understanding of stock-specific phenotypic expressions in limiting environments and energy allocation patterns, in light of specific life history adaptations such as population mortality, may eventually be used by managers to predict egg production, growth and storage of stocks in natural environments.

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INTRODUCTION

Study Rationale

The allocation of energy to different physiological processes in individual lake trout (*Salvelinus namaycush*) is determined by a combination of both environmental conditions present, and the genetics of the individual; the underlying genetic makeup (alleles) are usually selected for based on long-term environmental conditions in the local environment (Comstock and Moll 1963). Local adaptations to prevailing environmental conditions, as well as reproductive, behavioral, and geographic isolation allow separate populations (or stocks) to genetically diverge and develop unique life history strategies (Loftus 1958; Goodier 1981; Marsden et al 1995; Wilson and Mandrak 2004). Optimally, these stock-specific life history strategies maximize lifetime reproductive output in specific environments (Stearns 1989; Roff 1992). Energy allocation towards physiological processes, such as growth and reproduction, are of interest for management of this natural resource because both contribute to survival and abundance. In this thesis, I explore the relationship between energy acquisition, growth, storage, and reproduction in four lake trout stocks from different populations with varying life histories. These stocks were raised in similar hatchery conditions to determine if such allocations fit into a conceptual model that accommodates life history. More specifically, I explore how each stock responds, in a common controlled environment, to a changed food ration and evaluate how energy is reallocated towards growth, storage, and reproduction.

Life History Theory and Optimal Energy Allocation

Life history theory predicts that there will be intra-specific differences in energy allocation towards maintenance, growth, and reproduction to maximize lifetime reproductive output in a given environment (e.g. Jokela 1997; Heino and Kaitala 1999). The general model used to express energetic demands in an individual at a given point in time is:

$$G + R = C - (R_{met} + F + U + A)$$

where G = growth, R = reproduction, C = consumption, R_{met} = respiration (standard metabolism), F = fecal egestion, U = excretion, and A = locomotion (Diana 1982).

All excess energy not accounted for in the equation is presumably allocated to storage, in the form of lipid reserves. Energy is usually assumed to be first allocated toward maintenance costs (standard metabolism, fecal egestion, excretion, and locomotion), while the remaining energy is selectively allocated toward growth, reproduction and storage (Kozlowski 1992). How the remainder of this energy is allocated and what factors affect this allocation is one of the most important topics in life history theory and optimal resource allocation theory (Stearns 1992, Jokela 1997). In this study, I evaluate stock-specific energy allocation in lake trout to growth, reproduction, and percent lipid which I assume is a measure of energy allocated toward storage.

. Storage of energy in the form of lipid reserves is widespread across species that live in seasonably variable environments as these reserves serve as a way for individuals to take advantage of times when food is abundant (Schultz and Conover 1997; Hurst 2007; Jonsson and Jonsson 2009). This stored energy can then be selectively allocated towards growth, reproduction, or maintenance when food is more limiting and also allows more flexibility in energy allocation priorities. This model of the role of storage in energy allocation is summarized in a conceptual model in Jokela (1997) that explains storage as a way to cope with seasonal differences in food consumption and to deal with times when required energy does not reflect energetic demands.

Given the importance of storage discussed above, why not put all energy from food consumption towards storage to maximize flexibility in energy allocation throughout the season? Perhaps there are benefits to putting energy towards reproduction and growth immediately. In iteroparous species, reproductive output is typically highly correlated with spawner length (Roff 1992). This means that immediate allocation of energy toward growth will increase maximum reproductive potential in following years, likely at the expense of reproductive output in that year (Heino and Kaitala 1999; Jokela 1997). Although the goal is to maximize lifetime reproductive output, allocating all energy toward growth would not be advantageous because maintaining critical levels of storage is required for over-winter survival (Gardiner and Geddes 1980; Biro et al. 2004).

Lake trout inhabit a wide variety of environments including deep water lakes, arctic lakes, and rivers across their wide geographic range that stretches across most of Canada and the Northern United States (Scott and Crossman 1973). Lake trout stocks show differences in life history strategies across their range which reflect local conditions and theoretically maximize lifetime reproductive output of individuals in a given area. In this study, I make predictions of how variations in lifespan, growth rate, and diet in the wild influence the prioritization of allocation of energy to lipid reserves, growth, and reproductive output. My ultimate goal is to apply a conceptual framework to make predictions regarding the energy allocation of four lake trout stocks, relying on information collected from a literature review and data gathered in the wild.

Stocks with long lifespans are expected to come from environments with low mortality which is expected in systems that have no sea lamprey, low fishing mortality, low predation rates on young lake trout as well as enough food resources. In these long-lived stocks, fish will allocate a relatively low amount of energy to reproductive output on an annual basis because they have a relatively long amount of time to maximize lifetime reproductive output, and will prioritize energy allocation to growth in younger years (Table 1; Williams 1966; Charnov 2005). Short-lived stocks are expected to come from environments with high adult mortality (due to fishing pressure, sea lamprey, etc.) or high predation rates on young lake trout. These short-lived stocks are expected to prioritize allocation of energy to reproduction because they have a smaller amount of time to maximize lifetime reproductive output (Table 1; Williams 1966; Charnov 2005).

Tracking growth rates of individuals in the field is logistically difficult, therefore insight into stock-specific growth rates can be gained through analysis of length-at-age curves. Differences in the slopes of these curves between stocks indicate differences in growth rates between stocks. In stocks with steeper length-at-age curves, more rapid growth is expected to be seen in stocks with high adult mortality (high fishing pressure, sea lamprey), or gape-limited predators that prey on smaller lake trout (Table 1; Hutchings 1993; Chivers et al. 2008). For the purposes of this study, growth is defined as the change in fork length between two points in time.

In this study, diet is defined as the quantity and quality (energy density) of food that stocks have access to in their natural environments. While diet is ultimately going to drive all aspects of energy allocation in individuals because it determines energy intake, I hypothesize that natural diet is going to be the most predictive of percent lipid. I predict that stocks with a high quality diet in the wild (piscivorous, abundance of smaller bodied fishes, little competition, etc.) will have higher percent lipid than those stocks that have lower quality diets (lack of smaller bodied fishes, low productivity, high levels of competition, etc; Table 1).

Table 1. Conceptual model of energy allocation in lake trout to reproduction, growth, and storage and the hypothesized effects of stock-specific lifespans, local environmental conditions (fishing pressure, predation, etc.), and diet on the amount of energy allocated to each energetic category.

Energetic Category	**Description**	**Energy Allocation Priority**
Reproduction	Short-lived (i.e., 10-20 Years)	High
	Long-lived (i.e., 20-40 Years)	Low (especially in younger ages)
Storage	Piscivorous, high productivity	High
	Planktivorous, low productivity	Low
Growth Rate	High fishing pressure, sea lamprey presence, high predation	High
	Low fishing pressure, no sea lamprey, low predation	Low

Seasonal Energy Allocation

Lake trout are an iteroparous species found in temperate zones (Wilson and Mandrak 2004) and only have one spawning episode per year (Esteve et al. 2008; Muir et al. 2012). This life history strategy is usually a result of adaptations to local environments that select for low annual reproductive potential, and delayed maturation to allow increased adult survival and reproductive success in sub-optimal environments (Winemiller and Rose 1992; Shuter et al. 1998). How such life history adaptations would refine my conceptual model is that I predict that part of the year will prioritize energy allocation towards gonadal growth, where more energy will be shunted towards building eggs, and towards spawning events (Quince et al 2008; Table 2). However, once the fish spawns eggs, she will then spend energy on growth processes. Any excess energy accumulated (in storage) will also be allocated towards somatic growth after spawning (Quince et al 2008). Growth has been shown to be highly correlated with seasonal shifts in food availability and reproductive demands (Mangel and Clark 1988; Houston and McNamara 1999) in organisms, such as lake trout, that live in seasonally variable environments (Power 2002). Growth is expected to slow over the winter and also during the spawn because of these influences; however, excess storage can help jump start growth and maintain fish over lean winter months when lipid levels are depleted (Swift 1955; Josrgensen et al. 2005) (Table 2). Lake trout start to build gonads in March (Henderson and Wong 1998) and will put some energy towards lipids, but the majority of energy is expected to go towards growth as gonads are still very small, especially in the spring. This trend is expected to continue throughout the summer when metabolism and food consumption is high, until periods of final gonad growth (late summer and Fall), where most energy will be devoted towards final gonadal growth and very little energy will be put towards somatic growth and storage (Table 2).

Table 2. Conceptual model of energy allocation in lake trout to reproduction, growth, and storage and the hypothesized effects of time of year on the amount of energy allocated to each energetic category.

Season	Growth	Storage	Reproduction
Post-Spawn: Winter and Early Spring	High	Converted to Growth	High
Pre-Spawn: Spring and Early Summer	High	Low	Low
Summer	Medium	Medium	Medium
Spawn	Low	Converted to Reproduction	High

Age-Specific Energy Allocation

Lake trout tend to be long-lived but have a wide range of maximum sizes across their wide geographic range (McDermid et al. 2010) and will spawn over several years as a form of bet hedging (Winemiller and Rose 1992; Donaldson-Matasci et al. 2008) The relatively long life span of lake trout makes them a good candidate for life history studies because it allows long-term monitoring of growth, storage, reproduction, and other characteristics tied to life history strategy. As they age and approach the end of their lifespan, they devote much less energy towards growth and storage and allocate more energy to reproduction (Hutchings 1993; Quince et al. 2008a; Quince et al. 2008b). Most growth trajectories of fish are modeled to simulate initial periods of rapid growth followed by a slowing down which is attributed to slowing to reproduction, but rarely is mechanistically modeled as such (Figure 1) (von Bertalanffy 1938; Cox 2010). Some researchers also suggest that lake trout may also show evidence of senescence (Foster 1984; Lantry et al. 2008) and as a result, will show less reproduction as they enter old age (Table 3). I build this effect of age into my conceptual model (Table 3). In my model, based on other published models (e.g. Quince et al. 2008), I predict that immature fish put more energy into growth and storage to maximize growth and survival during the winter months. In immature fish, the relatively small amount of energy allocated to reproduction is used for gonadal development, while energy allocated toward growth is maximized.

Mature fish that have not yet reached the age of maximum reproduction (Table 3) are expected to allocate energy equally between growth, storage and reproduction. These fish are expected to put more energy towards reproduction than immature fish because they are actively spawning, which reduces the energy available for growth and storage.

However, in these young spawning fish, energy allocated towards growth and lipids is still critical, as the fish are in the period of rapid growth (Figure 1). Fish that are at the age in which reproductive output is maximized are expected to put high amounts of energy towards reproduction, at the expense of growth and storage (Figure 2). This age also corresponds with the maximum point of the growth rate curve (Figure 1).

Mature fish that have passed the age at maximum reproduction (Table 3) and may be in senescence are expected to show a decrease in energy allocation towards both growth and reproduction, with increased amounts of energy being put towards lipid reserves, representing a general inefficiency and shutting down associated with age (Lantry et al. 2008; Gunderson and Dygert 1988). Basal metabolism and maintenance costs are also increased in larger, older fish, especially in food-limited environments (Paterson et al. 2005). This increased energy demand reduces the amount of energy available to allocate towards growth, storage, and reproduction.

The age at which reproductive output is maximized was hypothesized to differ between stocks with overall adult mortality for the population driving this life history adaptation. Annual variability in environmental conditions that drive eventual year-class success are variable from year to year so it is unlikely that these lifetime reproductive maximum values are highly dependent on environmental conditions during the lifetime of an individual fish. There are tradeoffs involved in the “decision” to spawn earlier in life versus later in life. When individuals spawn early in life, they are sacrificing energy that could have been put towards growth and reducing future survival and reproduction (Williams 1966a; Williams 1966b). When fish delay maturation and spawn later in life, they run the risk of not surviving long enough to spawn (Stearns 1989).

Table 3. Conceptual model of energy allocation in lake trout to reproduction, growth, and storage and the hypothesized effects of age on the amount of energy allocated to each energetic category.

Age	Growth	Storage	Reproduction
Immature Fish	High	Medium	Low
Young, Mature Fish	Medium	Medium	Medium
Mature Fish (Maximized Reproduction)	Low	Low	High
Old, Mature Fish	Low	Medium	Medium

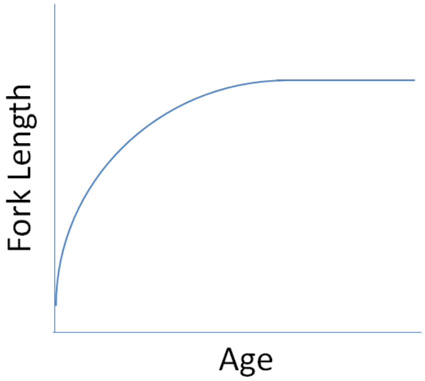

Figure 1. General von Bertalanffy model of length vs. age in lake trout under natural conditions. For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this thesis.

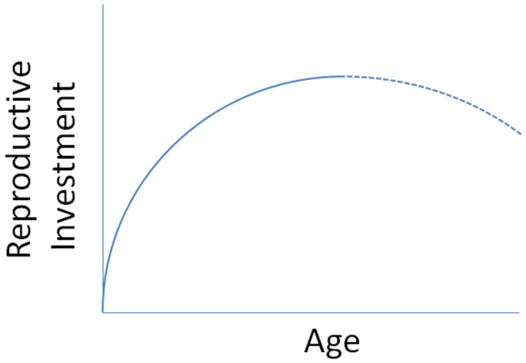

Figure 2. Hypothetical curve of potential relationship between age and reproductive investment in lake trout stocks.

Because lake trout stocks are adapted to different environments, it is likely that there are some genetic limitations for each stock in terms of their abilities to respond to environmental conditions, which would indicate that the response to the environment has a heritable component. However, there is strong evidence that there are general environment-based responses that are similar between stocks (McDermid et al. 2007), as a result of phenotypic plasticity. Phenotypic plasticity is the ability of an individual organism to use a single, fixed genotype to express multiple phenotypes, based on environmental conditions (Bradshaw 1965). It is critical to understand the stock-specific abilities of lake trout to adjust their energy allocation patterns based on local conditions. Lake trout stocks that overlap in the plasticity of a phenotypic expression in a given environment will have the same ability to respond to, and succeed, in that specific environment. However, understanding the limitation of each stock in their plasticity of growth, storage, and reproduction will allow discovery of the non-overlapping potential phenotypic expressions between stocks. These stock-specific differences in the range of phenotypes will drive differences in reproductive performance and survival of these stocks under specific environmental conditions, especially when resources are limiting. The plasticity, or scope for adaptation, within lake trout stocks will determine how far each stock can be pushed before growth or reproduction fall to the point where the stock will not be successful, based on the prevailing environmental conditions that could be altered due to a number of reasons, such as direct anthropogenic influences (e.g., harvesting), invasive species, or global climate change. Furthermore, establishing a link between growth, storage, and reproduction will serve as a powerful tool for stock-specific population models, as the environment and foraging success of an individual will directly affect its reproductive output.

Because of the economic and ecological significance of lake trout in the Great Lakes region, many management programs and research efforts have focused on their restoration through stocking programs and investigation of the factors that led to their decline. A more specific understanding of the scope for adaption in lake trout stocks will allow managers to make more meaningful predictions of how lake trout will respond to changes in their environment, whether it be an introduction to a new environment via stocking, such as in rehabilitation programs, or changes in their existing environment through introductions of non-native species, loss of critical habitat, changes in prey base, or other human-induced changes.

Study Approach - Common Environment Experiment

In this study, a common environment experiment is used to evaluate the responses of growth, storage, and reproduction of lake trout stocks to multiple feeding regimes. The term "common environment" refers to a type of experiment in which genetically-distinct organisms, or in this case fish stocks, are housed under common conditions in a controlled environment to determine the phenotypic response of each respective stock. Because reproductive traits in fish are influenced by both the environment and genetics, common environment experiments allow me to determine the response of individuals to changes in the environment, based on genetics (i.e., heritable constraints and phenotypic plasticity) and the scope for adaptation of each stock. Common environment experiments have been used to determine genetic differences in many organisms such as: amphibians (Urban 2008), plants (Williams et al. 2008), insects (Armbuster and Conn 2006), mammals (Dobson and Baudoin 2002), fish (Piche et al. 2008), and have been used to track physiological (Strimbeck et al. 2007), morphological (Piche et al. 2008), reproductive (Dobson and Baudoin 2002), and behavioral (Dobson and Baudoin 2002) responses of these various species to environmental conditions.

In this study, lake trout from the Killala, Michipicoten, Manitou, and Kingscote stocks were held in a common environment experiment for 2.5 years to see how energy allocation towards growth, storage, and reproduction changes throughout the year and across years. These stocks show different life history adaptations and I compared data collected from the field to characterize the life history strategies employed by stocks. Percent lipid, length, and fecundity (egg number and egg size) data taken from wild individuals from the stocks studied in this experiment provide an overall view of each stock's life history in terms of life span, growth rate, and age-specific fecundity. This allows me to speculate on how percent lipid, growth and reproduction will change in hatchery fish as they age on year. This data informed my conceptual model of energy allocation, and I manipulated the food ration of the hatchery fish and explored how changing food ration affected storage (percent lipid), growth and reproductive output (total, egg number and egg size) to see if patterns fit into what I would expect based on their life history. I also compared the relationship between egg size and egg number across the stocks in both the field and the hatchery to determine how this relationship is affected by environmental conditions and fish age.

I explored whether physiological reaction norms, in the form of egg production in response to food availability, changes as a function of stock. Specifically, can egg production be predicted from a given percent lipid measurement? Reaction norms examine the change in a variable in response to a range of environmental conditions. The term "reaction norm" refers to all the possible phenotypes that can be potentially expressed when an organism is exposed to a range of environmental conditions, or alternatively, what changes occur in a phenotypic trait as environmental conditions (e.g. food availability) change (Stearns and Koella 1986, Barot et al. 2004). The possible existence of reaction norms was explored to determine the response of egg number to percent lipid in four lake trout stocks to determine how individuals will respond when energetic intake is altered (for example, when stocked into a new, and potentially food limiting environment). Although referred to as a reaction norm in this study, I evaluated multiple individuals from the same stock under different environmental conditions, rather than evaluating a single organism under different environmental conditions which constitutes a “true” reaction norm. A reaction norm exists when the relationship between two variables is predictable and robust, meaning that fecundity can be reliably predicted based on percent lipid, even after an environmental change occurs. Reaction norms can be powerful predictive tools, and in this case, could be used to predict how fecundity of multiple lake trout stocks with different life history adaptations responds to food availability.

WORKS CITED

WORKS CITED

Armbuster, P. and J. E. Conn. 2006. Geographic Variation of Larval Growth in North American *Aedes albopictus* (Diptera: Culicidae). Annals of the Entomological Society of America 99: 1234-1243.

Barot, S., M. Heino, L. O'Brien, and U. Dieckmann. 2004. Long term trend in the maturation norm of two cod stocks. Ecological Applications 14: 1257-1271.

Bradshaw, A.D. 1965. Evolutionary significance of phenotypic plasticity in plants. *Adv. Genet.*, 13: 115–155.

Charnov, E. L. 2005. Reproductive effort is inversely proportional to average adult life span. Evolutionary Ecology Research ember 7: 1221-1222.

Chivers, D. P., Zhao, X., Brown, G. E., Marchant, T. A., and M. C. Ferrari. 2008. Predator-induced changes in morphology of a prey fish: the effects of food level and temporal frequency of predation risk. Evolutionary Ecology 22: 561-574.

Comstock, R.E., and R.H. Moll. 1963. Genotype-environment interactions. In: W.D. Hanson and H.F. Robinson, editors, Statistical genetics and plant breeding. National Academy of Sciences-National Research Council (U.S.) Publ. 982. National Academies, Washington, DC. p. 164–196.

Cornelius, F. C., K. M. Muth and R. Kenyon. 1995. Lake Trout Rehabilitation in Lake Erie: A Case History. Journal of Great Lakes Research 21:65-82.

Cox, B. 2010. Assessment of an invasive lake trout population in Swan Lake, Montana. Master of Science Thesis, Montana State University.

Dobson, F.S., and C. Baudoin. 2002. Experimental tests of spatial association and kinship in monogamous mice (Mus spicilegus) and polygynous mice (Mus musculus domesticus). Canadian Journal of Zoology-Revue Canadienne de Zoologie 80: 980-986.

Donaldson-Matasci, M. C., M. Lachmann, and C. T. Bergstrom. 2008. Phenotypic diversity as an adaptation to environmental uncertainty. Evolutionary Ecology Research 10: 493-515.

Edwards, C. J., R. A. Ryder, and T. R. Marshall. 1990. Using Lake Trout as a Surrogate of Ecosystem Health for Oligotrophic Waters of the Great Lakes. Journal of Great Lakes Research 16: 591-608.

Eschmeyer, P.H., and A. M. Phillips Jr. 1965. Fat content of the flesh of siscowets and lake trout from Lake Superior. Transactions of the American Fisheries Society 94: 62-74.

Eshenroder, R. L., N. R. Payne, J. E. Johnson, C. Bowen II and M. P. Ebener. 1995. Lake Trout Rehabilitation in Lake Huron. Journal of Great Lakes Research 21:108-127.

Esteve M, McLennan D. A., and J. M. Gunn. Lake trout (*Salvelinus namaycush*) spawning behaviour: the evolution of a new female strategy. Environmental Biology of Fishes 2008: 69-76.

Fleming, I. A. and M. R. Gross. 1990. Latitudinal clines: a trade-off between egg number and size in Pacific salmon. Ecology 71: 1-11.

Foster, N.R. 1984. Physiology and behavior. In Strategies for rehabilitation of lake trout in the Great Lakes: proceedings of a conference on lake trout research, August 1983, R.L. Eshenroder, T.P. Poe, and C.H. Olver, eds., pp 22–27. Great Lakes Fishery Commission Technical Report 40.

Goodier JL (1981) Native lake trout (Salvelinus namaycush) stocks in the Canadian waters of Lake Superior prior to 1955. Can J Fish Aquat Sci 38:1724–1737.

Gregersen, F., Haugen, T. O., and N. Larsen. 2006. Egg size differentiation among sympatric demes of brown trout: possible effects of density-dependent interactions among fry. Ecology of Freshwater Fish 15: 237-246.

Gunderson, D. R., and P. H. Dygert. 1988. Reproductive effort as a predictor of natural mortality rate. Journal Du Conseil 44: 200-209

Heino, M., and V. Kaitala. 1999. Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. Journal of Evolutionary Biology 12: 423-429.

Henderson, B. A., and J. L. Wong. 1998. Control of lake trout reproduction: role of lipids. Journal of fish biology, 52: 1078-1082.

Houston, A. and J. McNamara. 1999. Models of Adaptive Behaviour. New York, NY: CambridgeUniversity Press.

Hutchings, J. A. 1993. Adapted life histories effected by age-specific survival and growth rate. Ecology 74: 673-684.

Jastrebski, C. J., and Y. E. Morbey. 2009. Egg Size Variation in Lake Trout: Phenotype–Habitat Correlations Show an Effect of Rearing Environment. Transactions of the American Fisheries Society 138: 1342-1351.

Jokela, J. (1997). Optimal energy allocation tactics and indeterminate growth: Life-history evolution of long-lived bivalves. In Evolutionary Ecology of Freshwater Animals (pp. 179-196). Birkhäuser Basel.

Jonsson, N. and B. Jonsson. 1999. Trade-off between egg mass and egg number in brown trout. Journal of Fish Biology 55: 767-783.

Josrgensen, E. H., Johanse, J. H. S., and M. Jobling. 2005. Seasonal patterns of growth, lipid deposition and lipid depletion in anadromous Arctic charr. Journal of Fish Biology 51: 312-326.

Krueger, C. C., M. L. Jones and W. W. Taylor. 1995. Restoration of lake trout in the Great Lakes: Challenges and strategies for future management. Journal of Great Lakes Research 21: 547-558.

Lantry, B. F., O'Gorman, R., and L. S. Machut. 2008. Maternal Characteristics versus Egg Size and Energy Density: Do Stocked Lake Trout in Lake Ontario Experience Premature Reproductive Senescence. Journal of Great Lakes Research 34: 661-674.

Lienesch, P. W., M. E. McDonald, A. E. Hershey, W. J. O'Brien, and N. D. Bettez. 2005. Effects of a whole-lake, experimental fertilization on lake trout in a small oligotrophic arctic lake. Hydrobiologia 548: 51-56.

Lobon-Cervia, H., Utrilla, C., Rincon, P., and F. Amezcua. 2003. Environmentally induced spatio-temporal variations in the fecundity of brown trout *Salmo trutta* L.: trade-offs between egg size and number. Freshwater Biology 38: 277-288.

Loftus, K. H. 1958. Studies on River-Spawning Populations of Lake Trout in Eastern Lake Superior. Transactions of the American Fisheries Society 87: 259-277.

Mangel, M. and C. W. Clark 1988. *Dynamic Modeling in Behavioral Ecology.* Princeton, NJ: Princeton University Press.

Marsden J. E., Casselman J. M., and T. A.Edsall 1995. Lake trout spawning habitat in the Great Lakes—a review of current knowledge. Journal of Great Lakes Research 21(Supplement 1):487–497.

McDermid, J. L., P. E. Ihssen, W. N. Sloan, B. J. Shuter. 2007. Genetic and Environmental Influences on Life History Traits in Lake Trout. Transactions of the American Fisheries Society 136: 1018-1029.

McDermid, J. L., Shuter, B. J., and N. P. Lester. 2010. Life history differences parallel environmental differences among North American lake trout (*Salvelinus namaycush*) populations. Canadian Journal of Fisheries and Aquatic Sciences 67: 314-325.

Muir, A. M., Blackie, C. T., and C. C. Krueger. 2012. Lake charr Salvelinus namaycush spawning behaviour: new field observations and a review of current knowledge. Reviews in Fish Biology and Fisheries 22: 575-593.

Paterson, G., Huestis, S. Y., Whittle, D. M., Drouillard, K. G., and G. D. Haffner. 2005. In situ measurement of tissue turnover and energy conversion efficiencies in lake trout (Salvelinus namaycush) using a novel toxicokinetic approach. Canadian Journal of Fisheries and Aquatic Sciences, 62: 464-471.

Piche, J., J.A. Hutchings, and W. Blanchard. 2008. Genetic variation in threshold reaction norms for alternative reproductive tactics in male Atlantic salmon, Salmo salar. Proceedings of the Royal Society B-Biological Sciences 275: 1571-1575.

Power, G. 2002. Charrs, glaciations and seasonal ice. Environmental Biology of Fishes 64: 17–35.

Quince, C., Abrams, P. A., Shuter, B. J., and N. P. Lester. 2008(b). Biphasic growth in fish I: theoretical foundations. Journal of Theoretical Biology 254: 197-206.

Quince C, Shuter BJ, Abrams PA, Lester NP. 2008. Biphasic growth in fish II: empirical assessment. J. Theor. Biol. 254(2): 207-214.

Roff, D. A. 1992. The evolution of life histories: theory and analysis. Chapman and Hall, New York.

Scott, D. P. 1962. Effect of Food Quantity on Fecundity of Rainbow Trout, Salmo gairdneri. Journal of the Fisheries Research Board of Canada 19: 715-731.

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

Simons, A. M. 2007. Selection for increased allocation to offspring number under environmental unpredictability. Journal of evolutionary biology, 20: 813-817.

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

Shuter, B. J., M. L. Jones, R. M. Korver, and N. P. Lester. 1998. A general, life history based model for regional management of fish stocks: The inland lake trout (Salvelinus namaycush) fisheries of Ontario. Canadian Journal of Fisheries and Aquatic Sciences 55: 2161-2177.

Smith, S. H. 1972. Factors of ecologic succession in oligotrophic fish communities of the Laurentian Great Lakes. Journal of the Fisheries Research Board of Canada 29: 717-730.

Smith, C. C., and S. D. Fretwell. 1974. The Optimal Balance between Size and Number of Offspring. The American Naturalist 108:499-506.

Stearns, S. C. 1989. Trade-Offs in Life-History Evolution. Functional Ecology 3: 259-268.

Strimbeck, G. R., T. D. Kjellsen, P. G. Schaberg, and P. F. Murakami. 2007. Cold in the common garden: comparative low-temperature tolerance of boreal and temperate conifer foliage. Trees- Structure and Function 21: 557-567.

Swift, D. R. 1955. Seasonal Variations in the Growth Rate, Thyroid Gland Activity, and Food Reserves of Brown Trout (*Salmo trutta* linn.). Journal of Experimental Biology 32: 751-764.

Urban, M.C. 2008. Salamander evolution across a latitudinal cline in gape-limited predation risk. Oikos 117: 1037-1049.

von Bertalanffy L. 1938. A quantitative theory of organic growth (inquiries on growth laws. 11.). Human Biology 10: 181-213.

Wilberg, M. J., M. J. Hansen, and C. R. Bronte. 2003. Historic and Modern Abundance of Wild Lean Lake Trout in Michigan Waters of Lake Superior: Implications for Restoration Goals. North American Journal of Fisheries Management 23:100-108.

Williams, G.C. 1966a. Adaptation and Natural Selection. Princeton University Press, Princeton.

Williams, G.C. 1966b. Natural selection, the cost of reproduction, and a refinement of Lack's principle. American Naturalist 100: 687-690.

Williams, J.L., H. Auge, and J.L. Maron. 2008. Different gardens, different results: native and introduced populations exhibit contrasting phenotypes across common gardens. Oecologia 157: 239-248.

Wilson, C. C., and N. E. Mandrak. 2004. Chapter two: History and evolution of lake trout in Shield Lakes. Pages 21-35 in J. M. Gunn, R. J. Steedman, and R. A. Ryder, editors. Boreal Shield Watersheds: Lake Trout Ecosystems in a Changing Environment. CRC Press LLC.

Winemiller, K.O., and K.A. Rose. 1992. Patterns of life history diversification in North American fishes: implications for population regulation. Canadian Journal of Aquatic Sciences 49: 2196-2218.

Chapter 2: Characterization of Hatchery Fish in Context of Wild Counterparts

INTRODUCTION

Understanding how managed species, like lake trout, allocate energy towards reproduction and growth is important for stock rehabilitation and restoration (Mason et al. 1998). Many theoretical and empirical studies suggest that populations of organisms will allocate energy towards growth and reproduction in a way that will maximize reproductive output in face of their prevailing environmental conditions (Hutchings 1993; Quince et al. 2008), resulting in heritable life history traits. The goal of my study is to determine if particular stocks alter energy allocation towards growth, reproduction and storage as part of their life history strategy, in both hatchery and field, because if so, then I have the potential to develop powerful predictive tools that can be incorporated into population models (Shuter et al. 1998; Quince et al. 2008). In this study, I tracked growth, reproduction and storage of energy in lipid reserves in sexually mature female lake trout (Ages 8 and 9 during Year 1 of the study) from four different populations that were raised in a common environment. These hatchery fish were fed known rations (see Chapter 3), and if the allocation patterns were completely plastic and dependent on the environment, then I would expect every stock to show similar responses in growth, reproduction and storage. However, my hypothesis is that some characteristics will be heritable and I will see differences. Therefore, to make sense of any observed patterns and to determine what factors could be contributing to life history adaptations, I first had to determine how percent lipid, reproductive output, and fish length compare to their wild counterparts, and how these characteristics vary with age. This chapter is a comparison of the characteristics we can measure in wild fish related to life history (growth, reproduction, percent lipid), to similar characteristics measured in hatchery fish, under controlled conditions.

There are differences between hatchery-reared individuals and wild individuals that make it difficult to predict responses of wild fish to changes in environmental conditions from observation of hatchery-reared individuals. Several differences observed between hatchery fish and their wild counterparts, that could be due to genetic or environmental influences, include the following: the level of aggressive behaviors (Deverill et al. 1999), morphology, osmoregulatory system performance (Hill et al. 2006), predator avoidance behavior (Beamish et al. 1992, Olla et al. 1994), and growth (Hindar et al. 1991; Fleming et al. 1997; Fleming et al. 2002). These differences affect the survival and reproduction of hatchery fish in the wild and impair my ability to extrapolate hatchery studies to general conclusions about wild populations. The main concern with stocking hatchery fish into wild environments for restoration purposes is that hatchery fish come from different geographic areas and may not be adapted to the new environment (Weber and Fausch 2003). In recent years, more care has been taken to stock individuals into the wild that are of the same stock, or genetic strain, of the wild fish that naturally occur in the area by spawning wild individuals to create progeny raised in hatcheries. However, sometimes a particular genetic strain has been extirpated as was the case with the native lake trout in Lake Michigan, and as a result, restoration is only possible with a different strain (Dexter et al. 2010; Hanson et al. 2012).

Hatchery individuals may also substantially diverge from the genetics of their wild counterparts if offspring of wild fish are not consistently brought into the hatchery system. The progeny of the breeding hatchery fish will become more domesticated with each generation, and will not have normal natural selection processes that determine which individual survives and reproduces. Divergences between hatchery and wild individuals may also occur due to conditions in the hatchery that are not consistent with natural conditions, such as fish density, food availability, food type, and water quality (Weber and Fausch 2003). While responses to these different conditions may be a result of short-term phenotypic responses or long-term genetic adaptations, these differences in environmental conditions affect the behavior and ultimately the probability of survival and reproduction of these hatchery fish when they are stocked into natural waters (Olla et al. 1994). The purpose of this chapter specifically is to compare the reproduction, lipid storage and growth between hatchery and wild fish within four lake trout stocks and year classes and to use what is known about the natural environment of each stock to explain why these trends were observed.

Background of Hatchery Stocks

In this study I tracked 1999 and 2000 year-class lake trout from stocks derived from 4 different environments. I studied lake trout from Michipicoten Island in Lake Superior, lake trout from Killala Lake, which is a protected lake north of the Neys Provincial Park in Ontario, lake trout from Kingscote Lake, a small, inland lake in Algonguin Provincial Park in Ontario, Canada, and lake trout from Lake Manitou on Manitoulin Island in Lake Huron (Figure 3). The fish available for study at the time of this experiment were spawned at different times (1999 for Manitou, 2000 for Michipicoten and Killala), however both 1999 and 2000 year classes were available for Kingscote so I included them to tease out environment, tank effects and age differences.

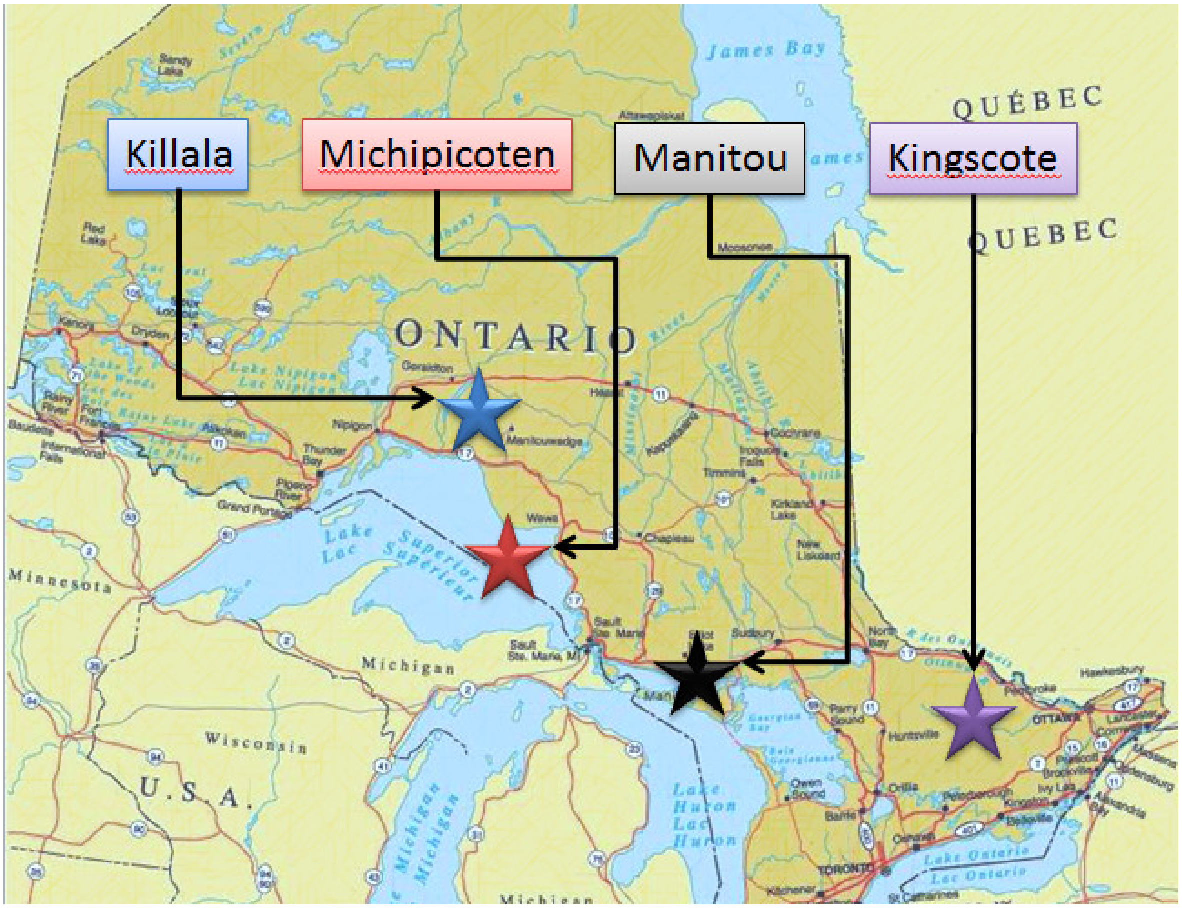

Figure 3. Map of locations of source populations for stocks used in a common environment study in OMNR hatchery.

The Michipicoten Island lake trout stock spawn in the shoals near Michipicoten Island in the Canadian waters of Eastern Lake Superior. The Michipicoten stock grows relatively slowly, is piscivorous, and has adapted to a Great Lakes system which has smaller-bodied fish such as sculpins, lake whitefish, and rainbow smelt (Gamble et al. 2011a; Gamble et al. 2011b) available as a food source. This stock is being used for restoration of native lake trout to the Canadian portion of Lake Huron, primarily in areas where there is minimal sea lamprey abundance and low amounts of fishing pressure (Ebener 1998).

The Killala stock are progeny from individuals from Killala Lake, Ontario, which is a fish sanctuary for lake trout and fishing is not permitted. Killala lake trout are relatively long-lived and are used for stocking of inland lakes (Ontario Ministry of Natural Resources Policy Report).

The Kingscote stock are progeny of individuals from Kingscote Lake in southern Algonquin Park, Ontario. The Kingscote lake trout are distinct in appearance because they exhibit a uniform silver color and lack the characteristic markings observed on other lake trout stocks (Wilson and Mandrak 2004). These differences in appearance may be due to genetic differences, unique diets, or a combination of these two factors. Another key characteristic is that the Kingscote stock is planktivorous in its natural habitat, due to the lack of smaller-bodied forage fish (Martin and Olver 1976).

The Lake Manitou stock originated from an inland lake located on the Manitoulin Island of Lake Huron (Ebener 1998). Lake Manitou lake trout are a short-lived, fast-growing stock that have been used for restoration in Lake Huron since 1981 and have shown higher survival rates when stocked in areas that have low fishing pressure and limited sea lamprey abundance (Ontario Ministry of Natural Resources Policy Report 2005).

METHODS

Wild Collections

Lake trout from the Michipicoten, Killala, Kingscote, and Manitou stocks were collected from their natural habitats during sampling trips with the Ontario Ministry of Natural Resources (OMNR). The following stocks were sampled during the fall the following years: Michipicoten (2008, Benjamin Felt and OMNR), Killala (2006, Cheryl Murphy with OMNR), Kingscote (2006, Cheryl Murphy with OMNR), and Manitou (2007, Cheryl Murphy with OMNR). Fish were captured using a combination of gill nets and trap nets, with set durations and effort being specific to a site based on lake trout size and abundance. Fish were euthanized immediately on site, using a concentrated dose of MS-222. Mature females were scanned with a non-invasive fat meter to measure percent lipids (described below), measured for length and weight, the ovary was removed and stored for future enumeration and egg diameter measurements, and the otoliths were removed for ageing by the OMNR.

Hatchery

Individually-marked lake trout from four stocks were held in a common garden environment in an Ontario Ministry of Natural Resources (OMNR) hatchery in Codrington, Ontario and were fed tank-specific rations to evaluate fecundity, growth, and percent lipids in 2008 and 2009. Lake trout from each stock used in this study were maintained separately in the hatchery early in life, but with similar densities, water temperature, dissolved oxygen, and food regimes. As adults, the fish were individually branded and moved to circular tanks that received high quality water at ambient temperatures from a nearby stream. Fish were fed high quality salmonid brood pellets formulated specifically for the OMNR by Corey Aquafeeds. The reared fish consisted of individuals from the following stocks and year classes (with year class in parentheses): Kingscote (1999, 2000), Michipicoten (2000), Manitou (1999), and Killala (2000). The Killala, Manitou, and Michipicoten individuals used in this study were two generations removed from the wild. Both year classes of the Kingscote stock used in this study were first generation hatchery fish. Only fish from the 2000 Kingscote stock were used for the purposes of this chapter; two year classes of the Kingscote stock allowed analysis of the effects of age and ration in Chapter 3. Including both year classes in this chapter was unnecessary because differences in percent lipid, growth and reproductive output between the year classes in the ration combined data were negligible and comparison of the 2000 Kingscote year class across two years allowed me to evaluate the effects of age and tank effects in the next chapter.

Fish were maintained at similar densities in each tank during rearing and the densities were continually adjusted due to minimal mortality rates of approximately 1-2 fish per tank per year. During the first two spawning seasons, about half of each stock were maintained on a high ration (0.4% of tank biomass per day) or a low ration (0.2% of tank biomass per day) to determine stock-specific patterns relating body percent lipid to fecundity (Murphy et al., in prep). This study monitored reproductive investment and percent lipids for an additional 2.5 years, with some fish remaining on a high food ration, and others remaining on a low food ration. This study added an additional treatment by creating “switchers”, or fish that were previously maintained on a low ration and switched to a high, and vice versa. A minimum of eighteen fish from each stock were maintained under a constant ration to track the effects of age alone on the relationship between percent lipids and fecundity when held in a constant environment (Table 4). In addition to allowing me to look at responses of stocks to changing ration levels, another goal of manipulating ration levels in the hatchery was to represent variability in available food that would somewhat mimic natural environments.

Table 4. Summary of initial fish densities and composition of lake trout stocks housed in a common environment experiment in OMNR hatchery in Codrington, Ontario.

Tank No.	**Ration**	**Total Fish**	**2000 Kingscote**		**2000 Michipicoten**		**2000 Killala**		**2000 Slate**		**1999 Manitou**		**1999 Kingscote**	
			Male	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**
1	High-High	30	1	8	1	10	1	9						
2	High-Low	31	2	7	4	8	0	2	2	6				
3	Low-Low	28	1	8	2	7	1	9						
4	Low-High	28	2	8	2	8	1	0	2	5				
5	High-High	29									2	12	3	12
6	High-Low	30									3	11	6	10
7	Low-Low	30									2	12	2	14
8	Low-High	30									2	11	4	13

Fish were processed approximately every eight weeks to determine weight, total length, fork length and fat content using a non-invasive fat meter (Distell Inc.). The fat meter was calibrated prior to each measurement period and was used to measure the fat content of each fish at four locations on the body (Figure 4). The fat meter uses low-power microwaves to penetrate through the skin and measure the attenuation of the microwaves by water in the flesh which is negatively correlated with fat content, allowing a reliable lipid estimate (www.distell.com). The fat meter was calibrated in a previous study by Claus (2011), and the following equation was used where Muscle Lipid Concentration was a function of the raw fat meter reading:

$$\text{Muscle Lipid Concentration} = [e^{(1.9436 + \ln(\text{Fat meter Reading})) - 9.5022}] \times 100$$

$$(r^2 = 0.6117)$$

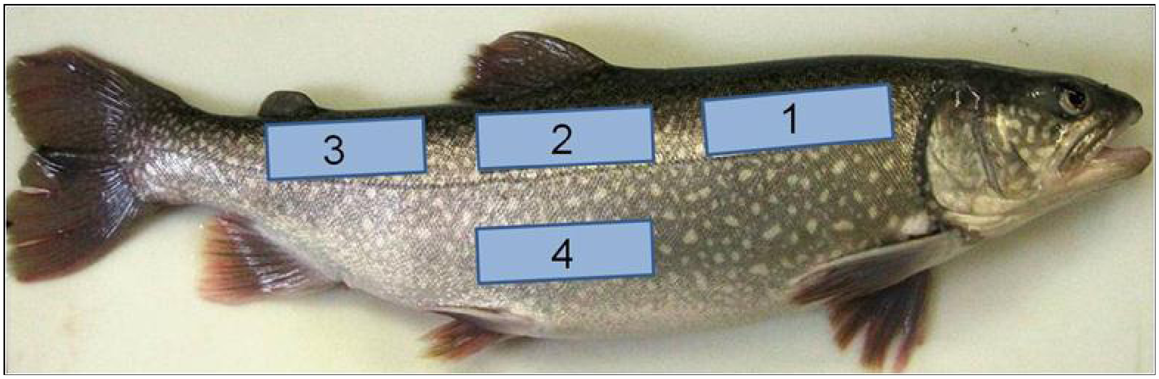

Figure 4. Locations of lipid measurements taken on lake trout using non-invasive fat meter at OMNR hatchery in Codrington, Ontario (Photograph Courtesy of Sara Smith).

During the Fall of 2008 and 2009, females were checked weekly to determine if they had ovulated by lightly applying pressure to the urogenital region. If eggs were easily extruded, the entire volume of eggs was stripped from the females into a volumetric flask to determine total volume. One 30-mL egg sample was preserved in a 5% formalin solution to measure the diameter of the eggs at a future date using digital microscope pictures of the eggs and analysis using Leica Application Suite ®. When measuring eggs, thirty total eggs from each female were measured and each egg measured six times for average egg diameter, to determine average egg size for a female.

Data Analyses

I standardized the number of eggs collected from each female by dividing by the female's length. The correlation between spawner size and fecundity is well documented and corrections of fecundity based on spawner length are common (Blanchard et al. 2011; Downs et al. 1997; Lobon-Cervia et al. 1997). For my analyses, egg production was corrected for length of the spawner because of the strong linear correlation between these two variables (Figure 27). Additionally, lipid levels were averaged across all lipid measurement locations within each individual to approximate mean muscle lipid content of the fish across the entire body.

To determine how length, percent lipid, egg size and egg number were influenced by age, I modeled the best functions to describe these relationships using linear, quadratic, hyperbolic, and logarithmic functions to choose the model that had the lowest Akaike's Information Criterion (AIC) value. AIC values were found using the following formula:

$$AIC = n \times \ln\left(\frac{RSS}{n}\right) + 2k$$

The parameter, k, represents the number of parameters within the model; the parameter, n, represents the number of observations, and the parameter, RSS, represents the Residual Sum of Squares (Burnham and Anderson 2002). I then used the model with the lowest AIC value to estimate stock-specific length, percent lipid, egg size, and egg number of wild individuals at age 8.5 years, which is the average age of hatchery fish during the study. In cases where the linear model, or another model with fewer parameters than the selected model, had an AIC difference of ≤ 2 (Burnham and Anderson 2002) compared to the "best" model, the simpler model was selected. A general guideline proposed in Burnham and Anderson (2002) is that models with a difference of AIC less than or equal to two ($AIC_{Initial} - AIC_{Alternate} \leq 2$) have strong support to show there is no difference between models in terms of their ability to describe the data (Burnham and Anderson 2002; Stylianou et al. 2013). Selection of simpler models allows for a more straightforward comparison of metric values across stocks.

I grouped all the hatchery data across rations for the hatchery-field comparison because variability in ration levels simulates differences in foraging success in the hatchery and the exact ration that most closely approximates natural feeding conditions in each stock is unknown. A post-hoc Tukey-Kramer test ($\alpha = 0.05$) was used to determine the significance of differences in length, mean percent lipid, egg size, and egg number between hatchery years.

RESULTS

Characterizing the Wild Populations

Fork Length

A linear relationship was used to predict length at age for the wild caught fish in all stocks based on AIC values for model selection (Figure 5, Table 6, Table 7, Table 8, and Table 9). These stock-specific linear relationships in age vs. fork length were plotted on one figure for comparison (Figure 7). All stocks increased in length with age, but the short-lived Kingscote and the long-lived Killalas were the slowest growing. The short-lived Manitou had a much higher rate of growth (steeper slope), while the long-lived Michipicoten grew the fastest (Figure 5, Figure 6).

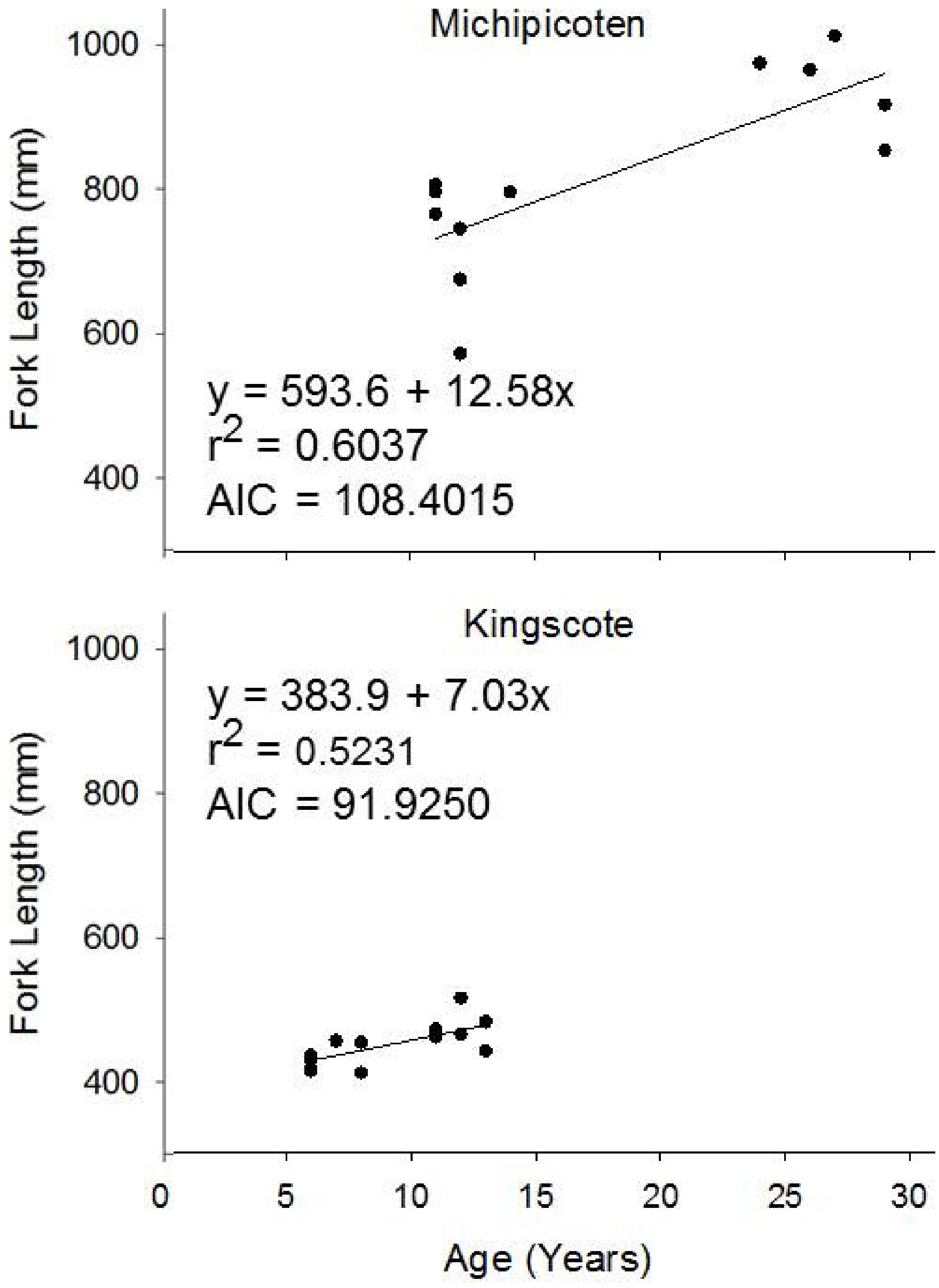

Figure 5. Relationship between fork length and age from Michipicoten and Kingscote lake trout stocks sampled in their natural environments. Line shows model of best fit to predict how length changes as function of age, based on AIC values.

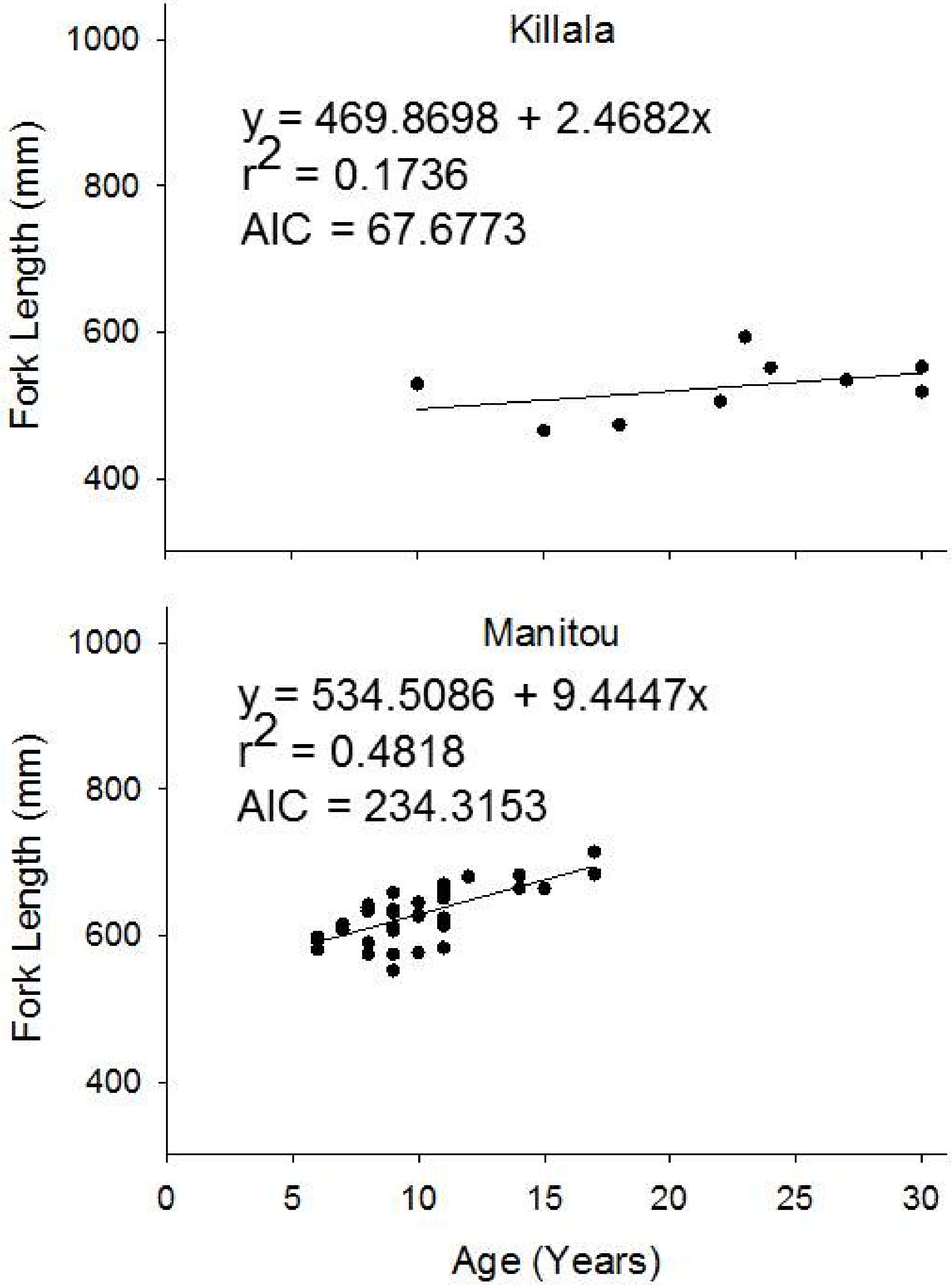

Figure 6. Relationship between fork length and age from Killala and Manitou lake trout stocks sampled in their natural environments. Line shows model of best fit to predict how length changes as function of age, based on AIC values.

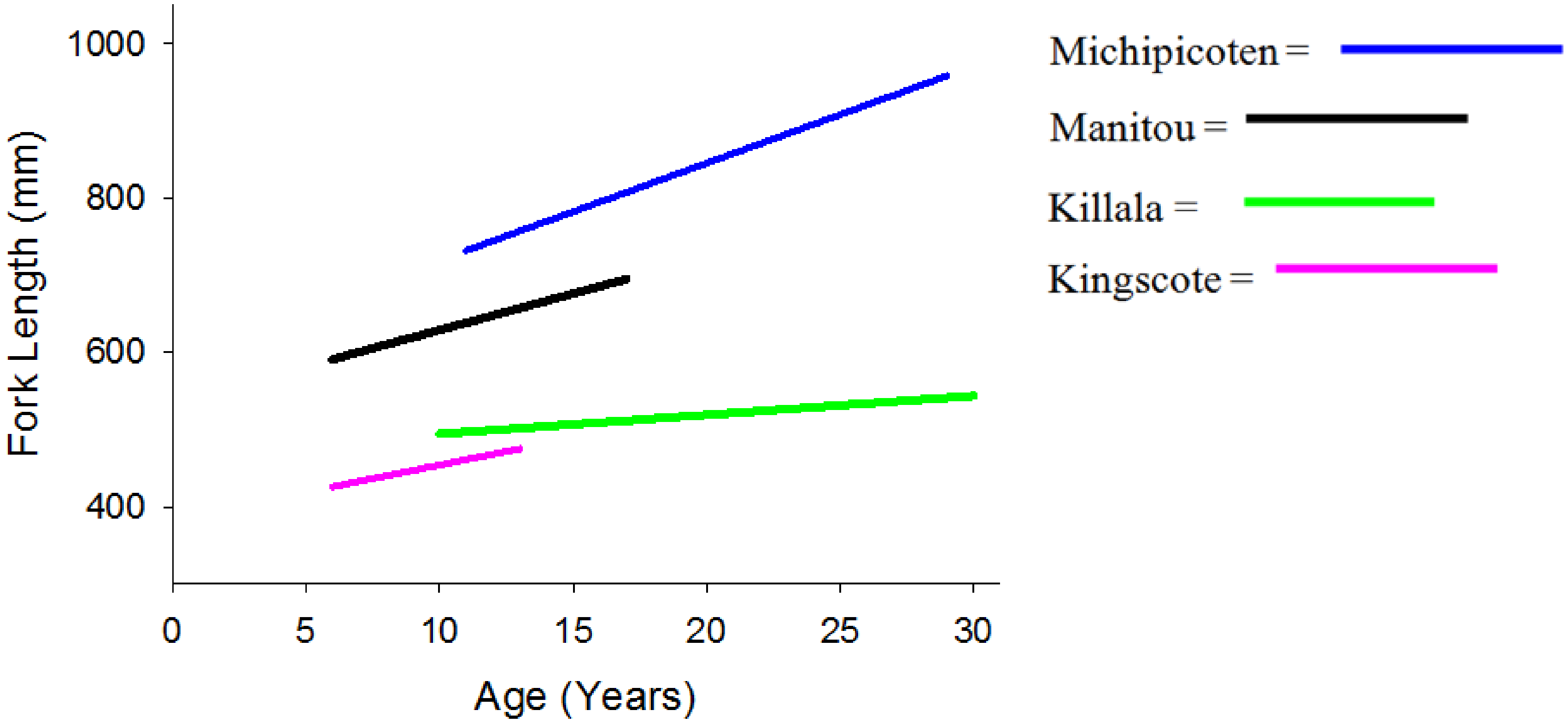

Figure 7. Stock-specific modeled relationship between fork length and age of four lake trout stocks in natural environments. The age range of the curve shown indicates the age range of individuals sampled in the field.

Percent Lipids

Linear models were used to predict changes in percent lipid as a function of age in the Michipicoten, Killala, and Manitou stocks. However, the Kingscote stock showed a quadratic relationship between mean percent lipid and age because the AIC value showed a difference of greater than 2, relative to the linear model (Figure 8, Figure 9, Table 6, Table 7, Table 8, and Table 9). I created a generalized stock-specific figure that plotted the lipids against age regression for all stocks on one graph to ease comparisons between stocks (Figure 10). Both Kingscote and Killala had very low percent lipid values, across all ages, while Manitou and Michipicoten had higher percent lipids, with maximum values occurring at the youngest ages in the Manitou stock while Michipicoten mean percent lipids showed a gradual increase with age. The stocks with low lipids did not show any change with percent lipid across ages, except for a slight decline with age in the Kingscotes. However, the two stocks with high percent lipids showed opposite patterns with age. The long-lived Michipicoten stock gradually increased percent lipid with age, while the short-lived Manitou showed a rapid decline in percent lipid with age (Figure 10).

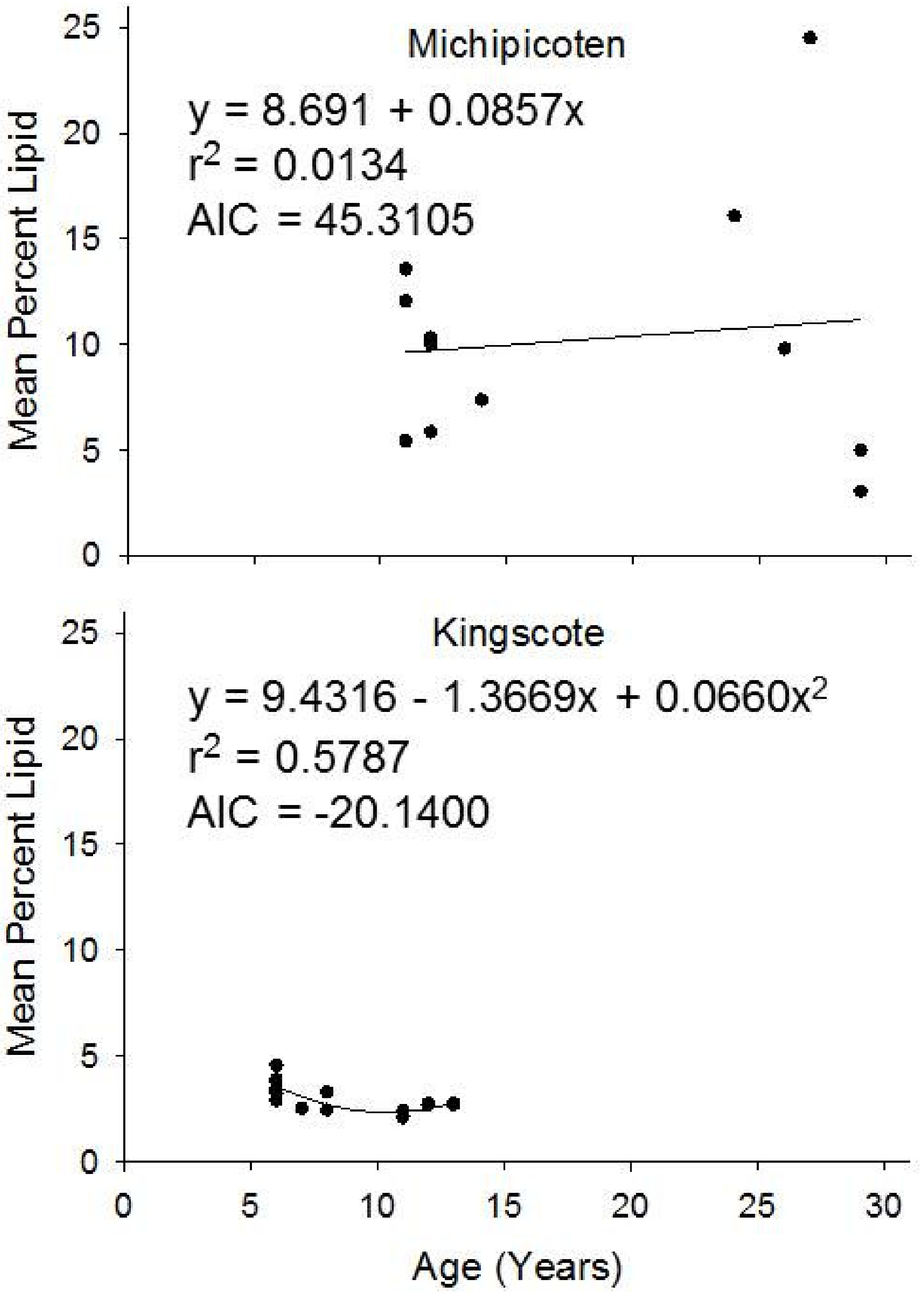

Figure 8. Relationship between mean percent lipid and age from Michipicoten and Kingscote lake trout stocks sampled in their natural environments. Line shows model of best fit to predict how percent lipid changes as function of age.

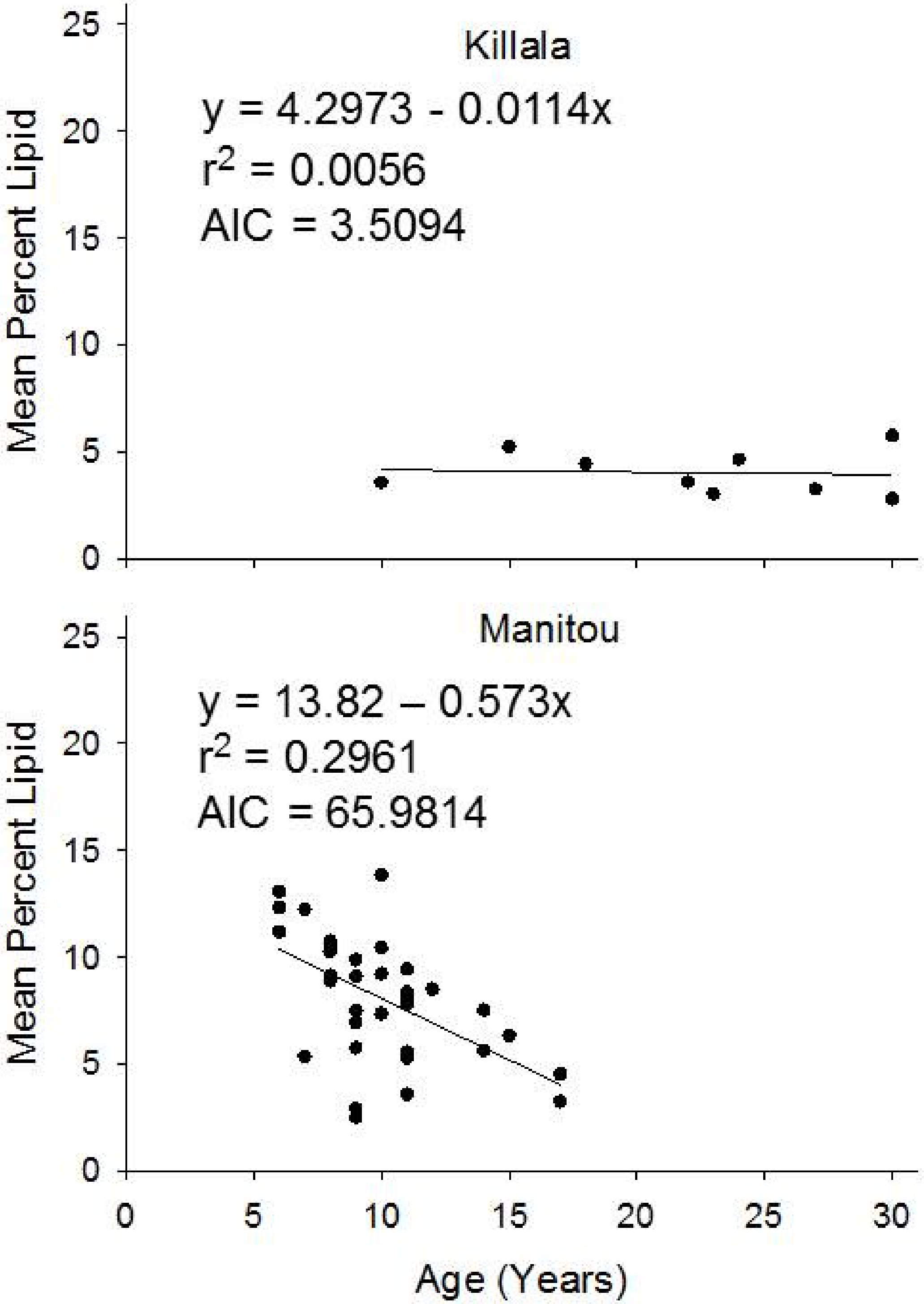

Figure 9. Relationship between mean percent lipid and age from Killala and Manitou lake trout stocks sampled in their natural environments. Line shows model of best fit to predict how percent lipid changes as function of age.

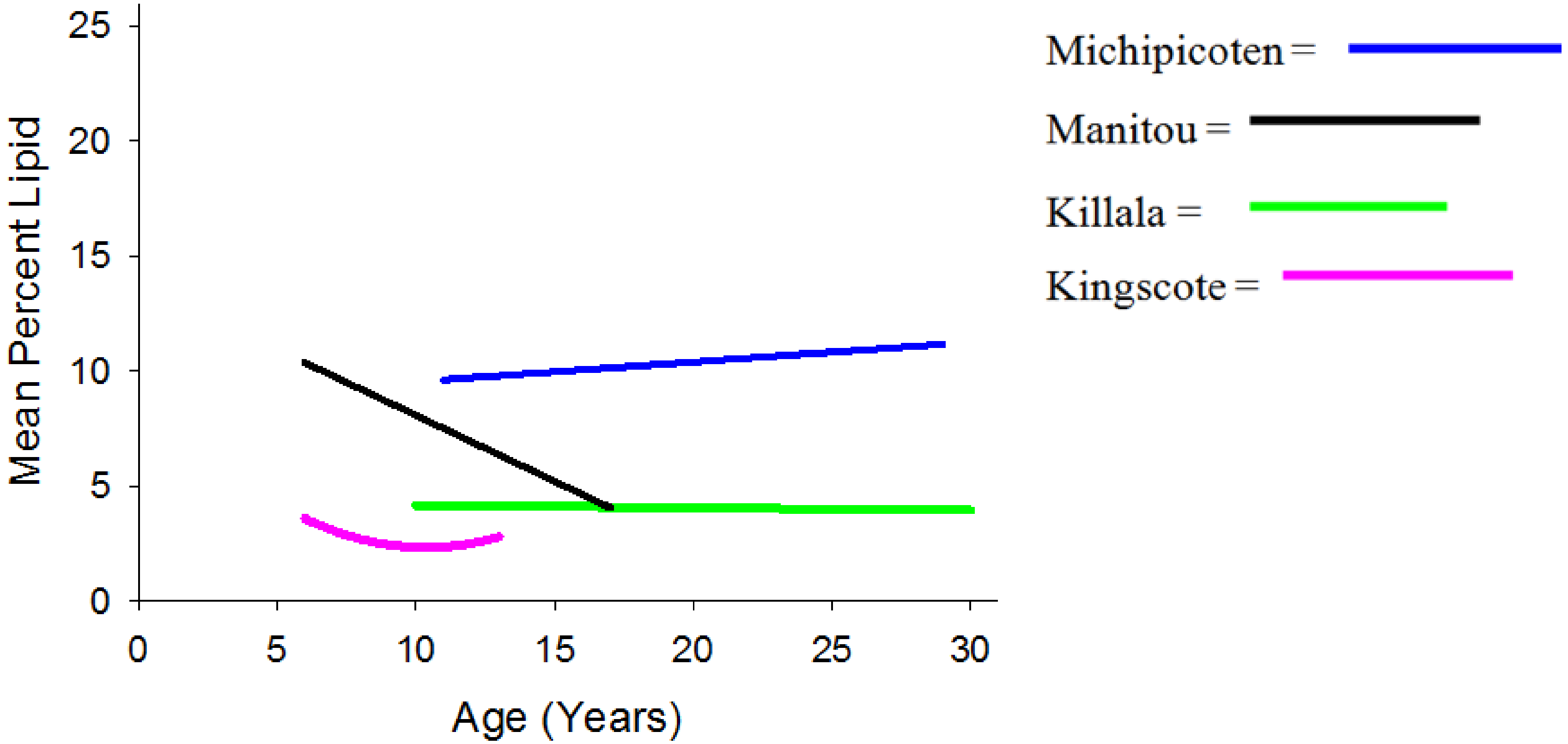

Figure 10. Stock-specific modeled relationship between mean percent lipid and age of four lake trout stocks in natural environments. The age range of the curve shown indicates the age range of individuals sampled in the field.

Egg Size

Linear relationships were used to model the relationship between age and egg diameter (Figure 11, Figure 12) in all four stocks, based on AIC values (Figure 11, Figure 12, Table 6, Table 7, Table 8, and Table 9). All stocks showed an increase in egg diameter as fish age (Figure 11, Figure 12). The Kingscote and Manitou stocks had the smallest eggs and also showed a rapid increase in size with age (Figure 11, Figure 12). In contrast, the Killala had the largest eggs, followed by the Michipicoten stock, but both showed a more gradual increase in size with age (Figure 13).

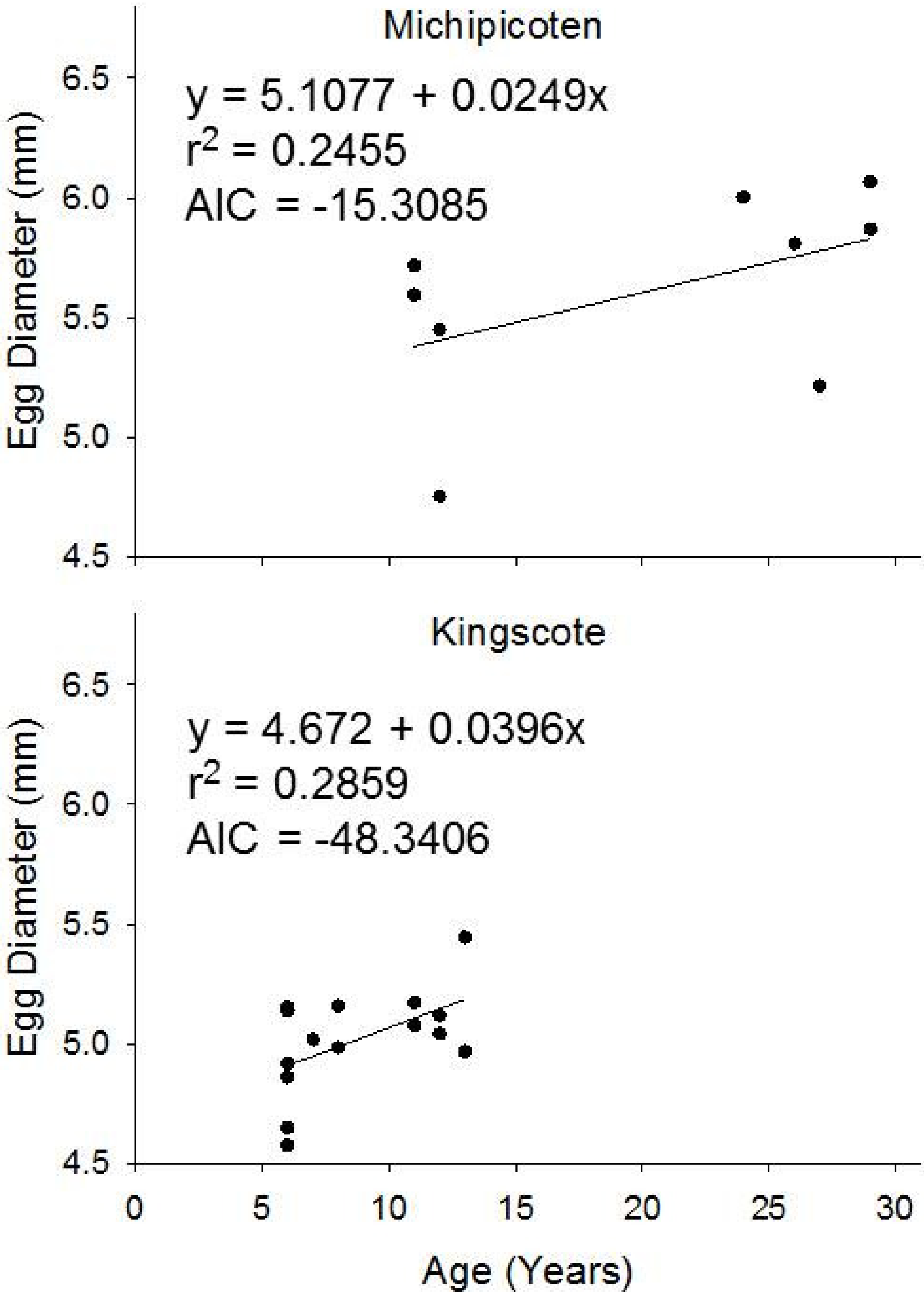

Figure 11. Relationship between egg diameter and age from Michipicoten and Kingscote lake trout stocks sampled in their natural environments. Line shows regression of best fit based on AIC values.

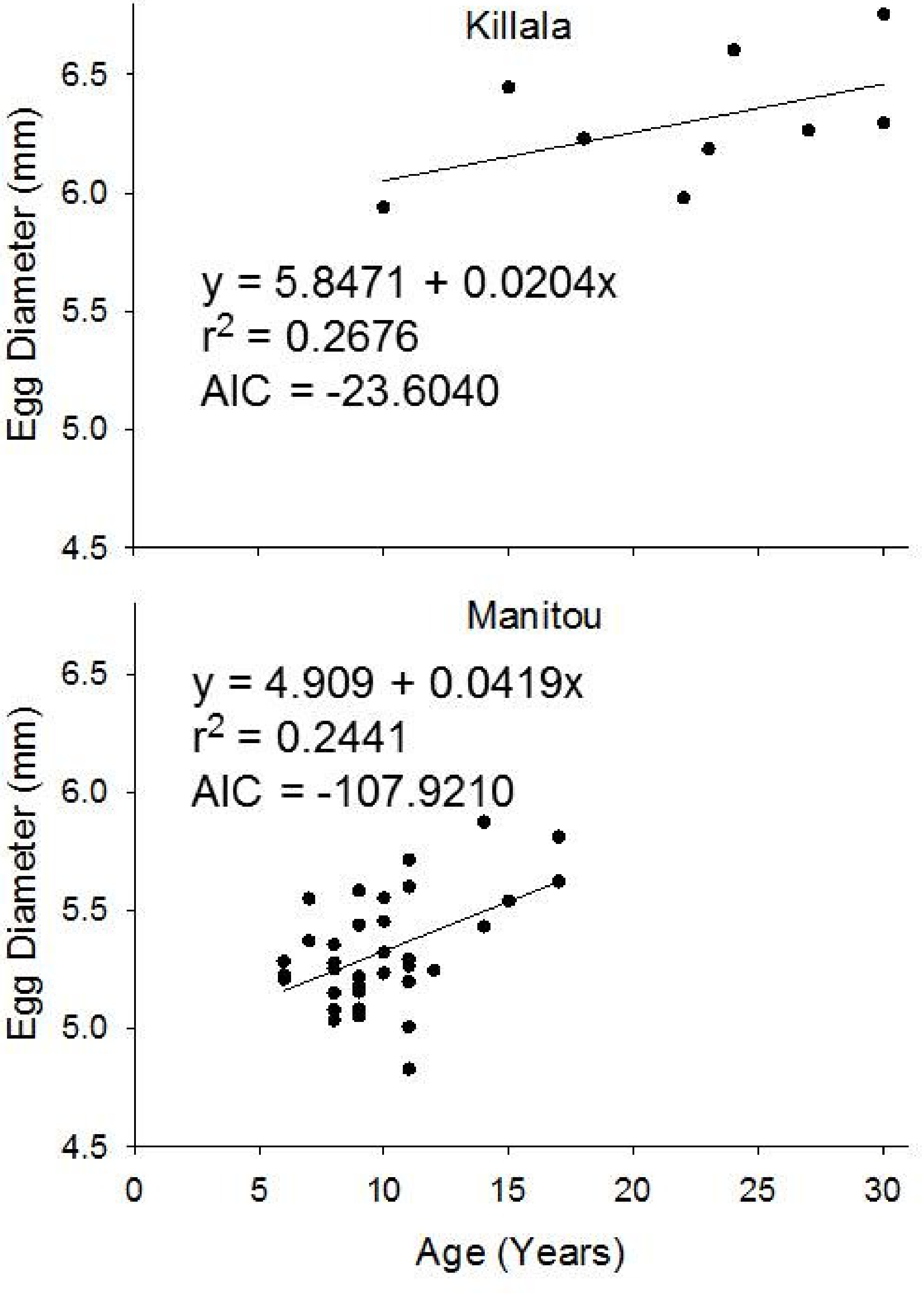

Figure 12. Relationship between egg diameter and age from Killala and Manitou lake trout stocks sampled in their natural environments. Line shows regression of best fit based on AIC values.

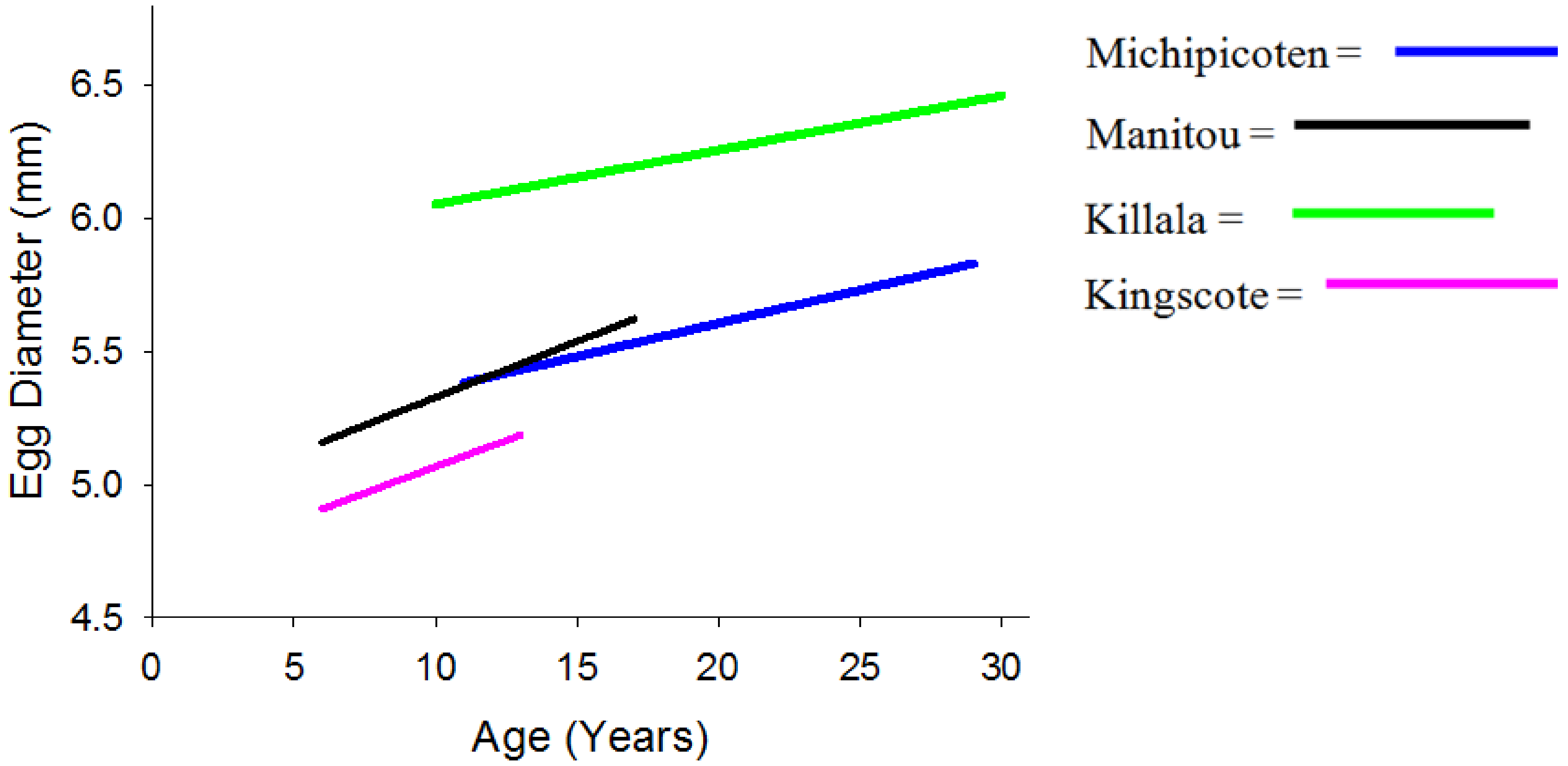

Figure 13. Stock-specific modeled relationship between egg diameter and age of four lake trout stocks in natural environments. The age range of the curve shown indicates the age range of individuals sampled in the field. Lines show regression of best fit in each stock, based on AIC values.

Egg Number

Linear models were used to model the relationship between age and egg number (in eggs/mm) in the Michipicoten, Kingscote, and Manitou stocks, based on AIC values. However, a quadratic relationship was assigned to the age-egg number relationship in the Killala stock because of a difference in AIC values that exceeded 2 between the quadratic and linear models (Table 6, Table 7, Table 8, and Table 9). The stocks with the higher percent lipids (Manitou and Michipicoten) had the highest egg number. There was an increasing trend in egg number with age in the Michipicoten stock while the Manitou stock showed a gradual decrease in egg production with age (Figure 11, Figure 12). The Killala stock showed decreasing egg production as fish age while the Kingscote stock showed increases in egg production with age. At the youngest ages, which are the most comparable to the hatchery stocks, the Manitou and Michipicoten stocks appear to produce the most number of eggs per mm of fish, followed by Killala and Kingscote, respectively (Figure 14, Figure 15, Figure 16).

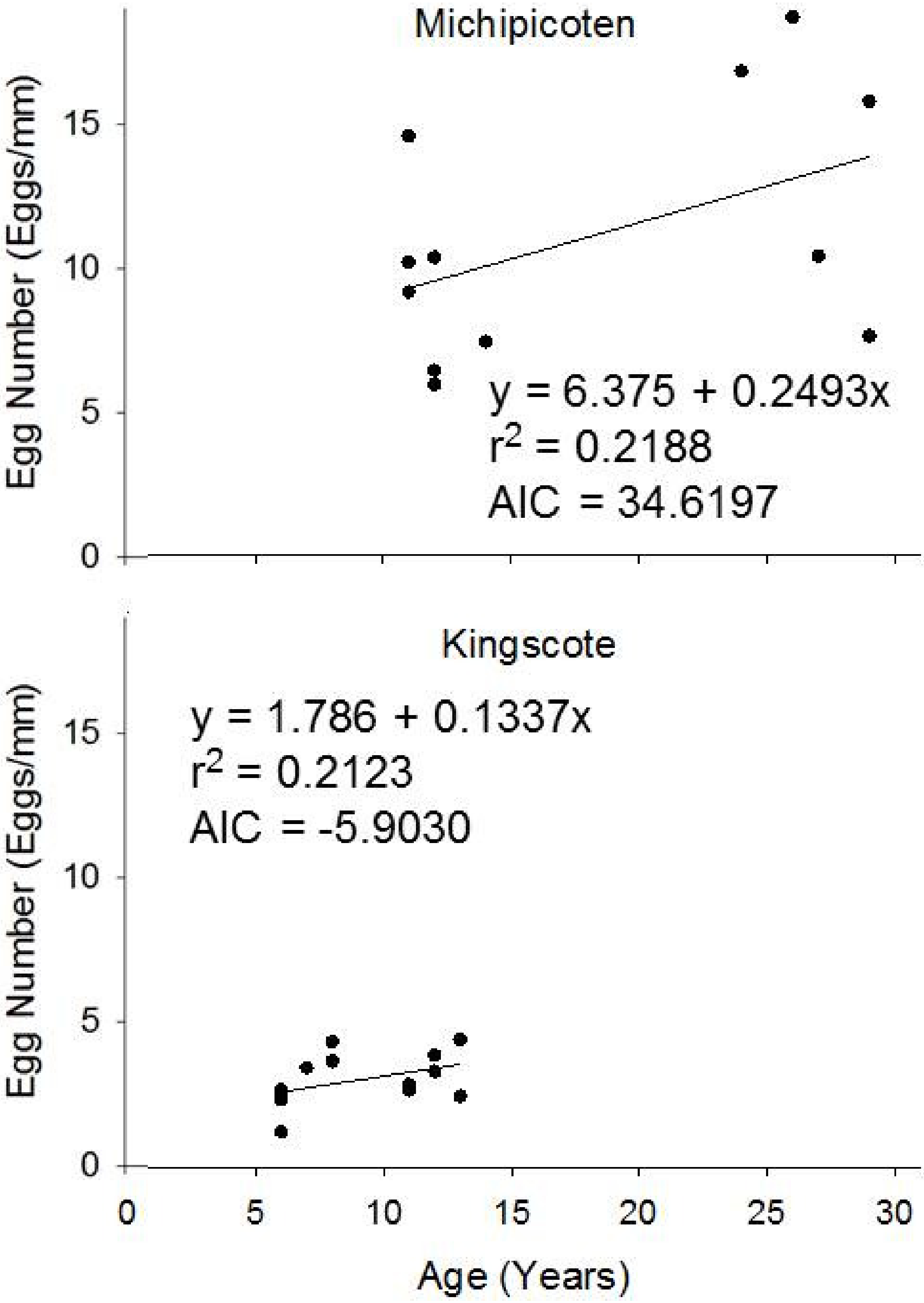

Figure 14. Relationship between egg diameter and age from Michipicoten and Kingscote lake trout stocks sampled in their natural environments. Lines show regression of best fit in each stock, based on AIC values.

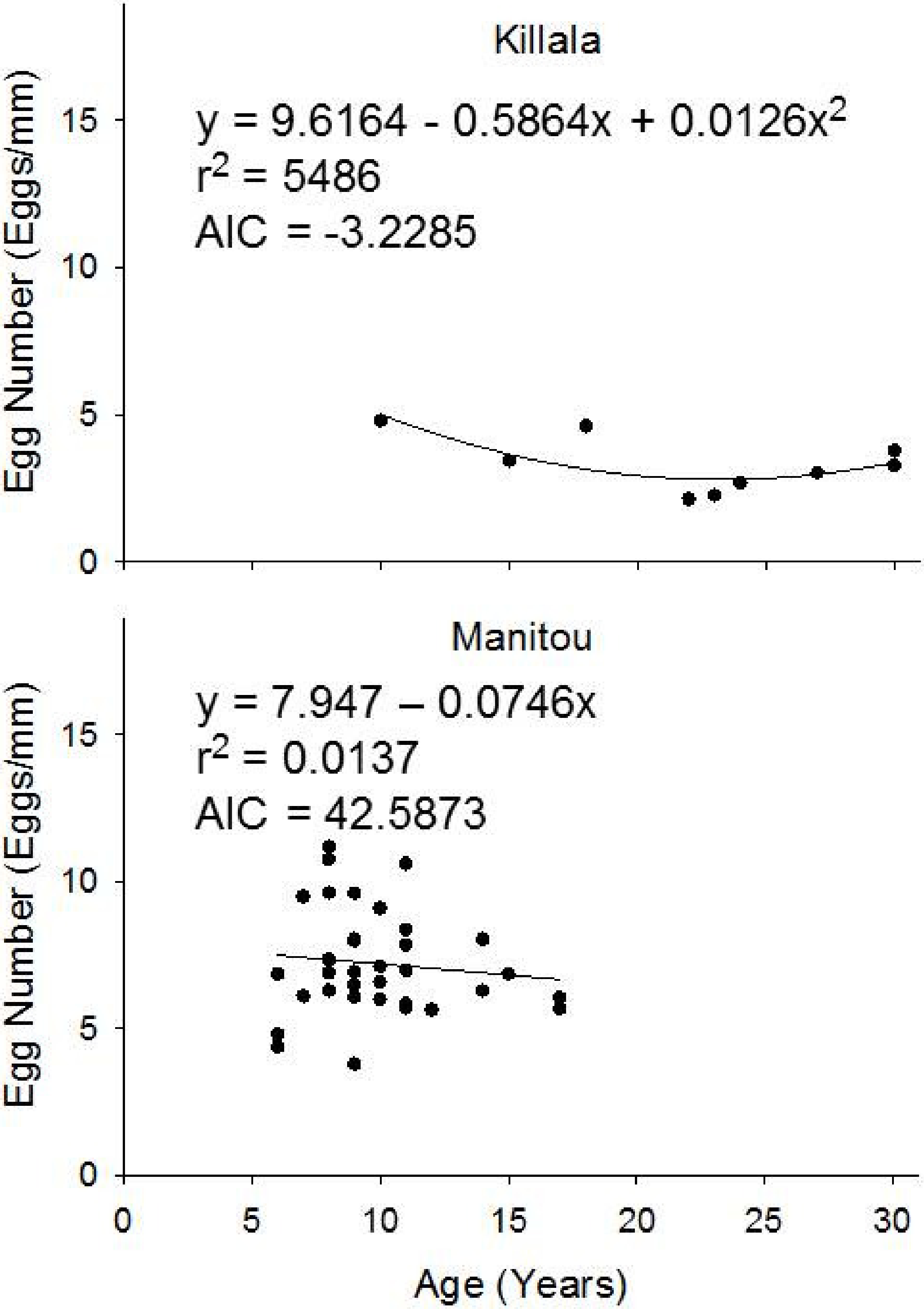

Figure 15. Relationship between egg diameter and age from Killala and Manitou lake trout stocks sampled in their natural environments. Lines show regression of best fit in each stock, based on AIC values.

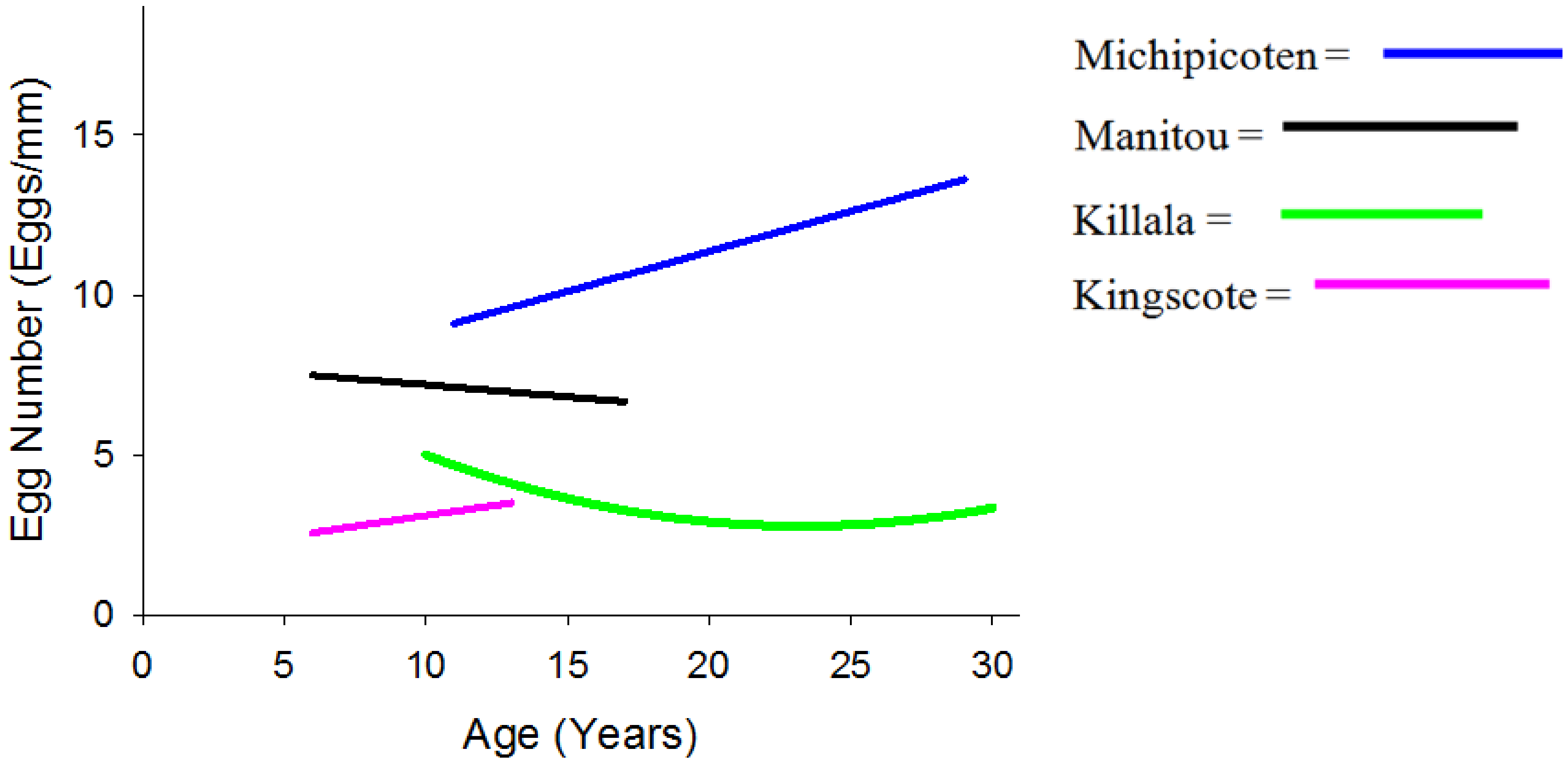

Figure 16. Stock-specific modeled relationship between eggs/mm (number of egg produced / length of individual) and age of four lake trout stocks in natural environments. The age range of the curve shown indicates the age range of individuals sampled in the field. Lines show regression of best fit in each stock, based on AIC values.

Comparison of Field and Hatchery Data within Stocks

To compare wild fish to hatchery fish, I used the modeled equations for predicting length, percent lipid, egg size, and egg number by age to calculate these metrics for an 8.5-year-old fish. I compared these simulated values to what I observed in the Year 1 and Year 2 of my hatchery study (Figure 17, Figure 18, Figure 19, and Figure 20). I also determined if length, percent lipid, egg size and egg number differed between years of the hatchery study.

Results suggest that my hatchery fish grew significantly each year (Figure 17), and that the stocks that have low percent lipid in the wild (i.e., Kingscote and Killala) were bigger in the hatchery than their wild counterpart, at the same age. The Manitou and Michipicoten stocks were smaller in the hatchery than what I would expect to see from a wild fish of the same age (Figure 17).

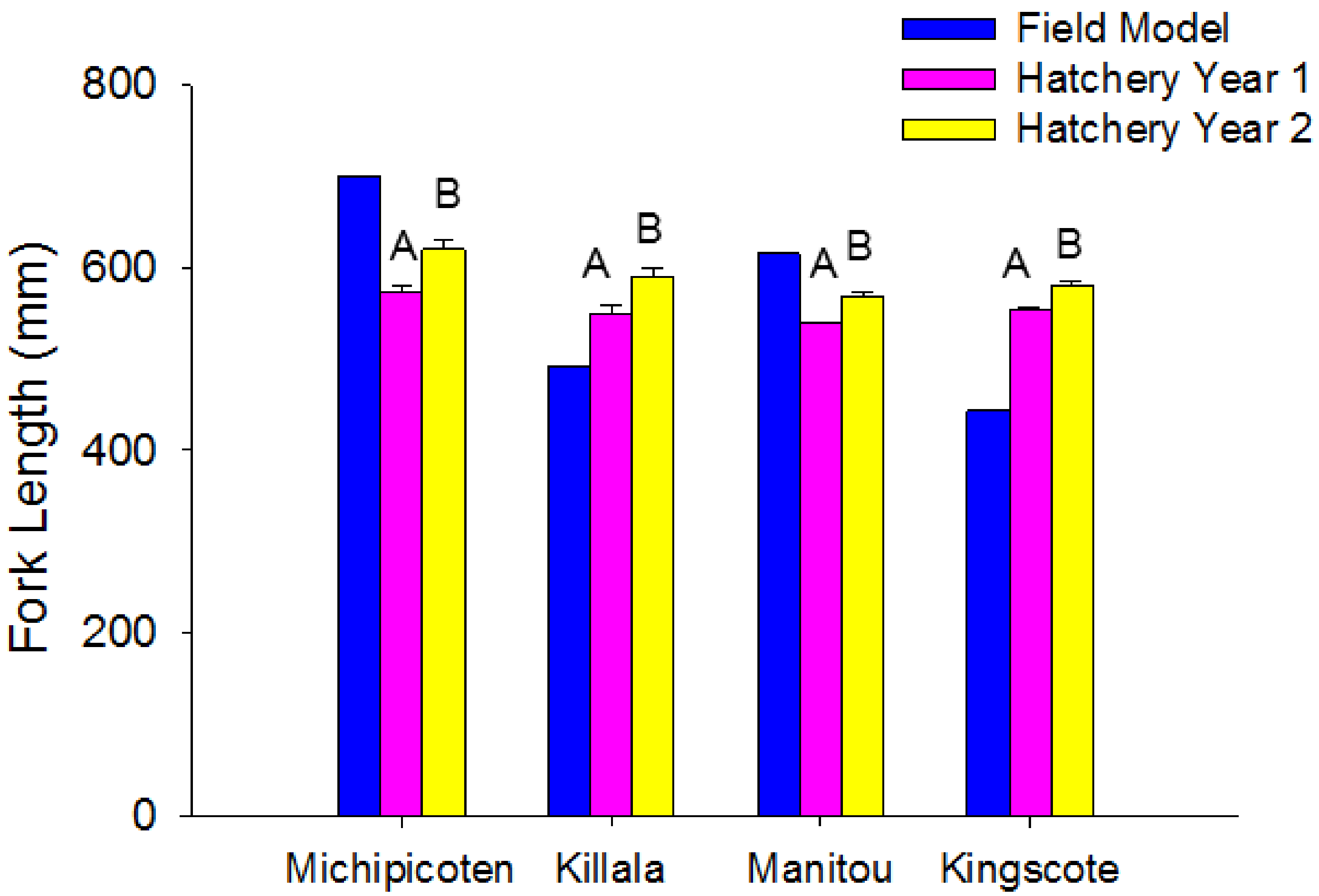

Figure 17. Comparison of fork length of four stocks of lake trout sampled in the wild to hatchery individuals held in a common garden environment during the 2008 and 2009 spawning seasons. The letters “A” and “B” above each data column indicate statistical groupings within a stock based on Tukey’s test ($p<0.05$). Field values based on model and are not included in statistical comparison.

The percent lipid in hatchery fish greatly differed from the percent lipid observed in their wild counterparts in the Kingscote and Killala stocks. The hatchery-held Kingscote and Killala had much higher percent lipid than the wild-caught individuals, while the hatchery-held Michipicoten and Manitou stocks had slightly higher percent lipid as wild fish at the same age (Figure 18).

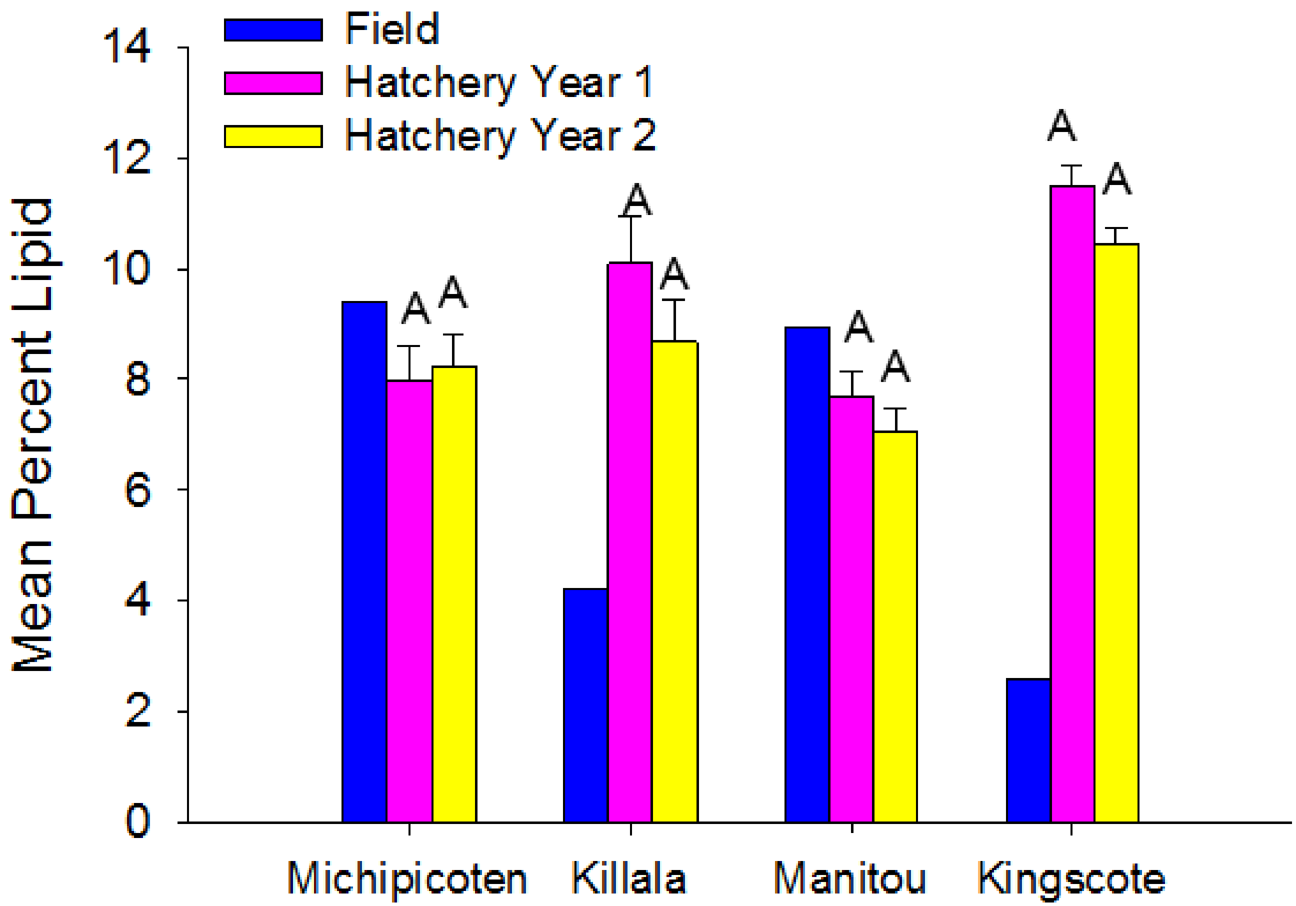

Figure 18. Comparison of percent lipids of four stocks of lake trout sampled in the wild to hatchery individuals held in a common garden environment during the 2008 and 2009 spawning seasons. The letters “A” and “B” above each data column indicate statistical groupings within a stock based on Tukey’s test ($p<0.05$). Field values based on model and are not included in statistical comparison.

Egg size in hatchery fish was very comparable to the values measured/estimated from wild fish. However, the long-lived stocks (i.e., Michipicoten and Killala), for which I could only use estimated data for an age comparison, had smaller eggs in the hatchery than what would be expected in the wild (Figure 19). The egg size in the hatchery appeared to decrease with age for the Manitou, Kingscote and Killala stocks (Figure 19), which is opposite of what I found in wild fish (Figure 13).

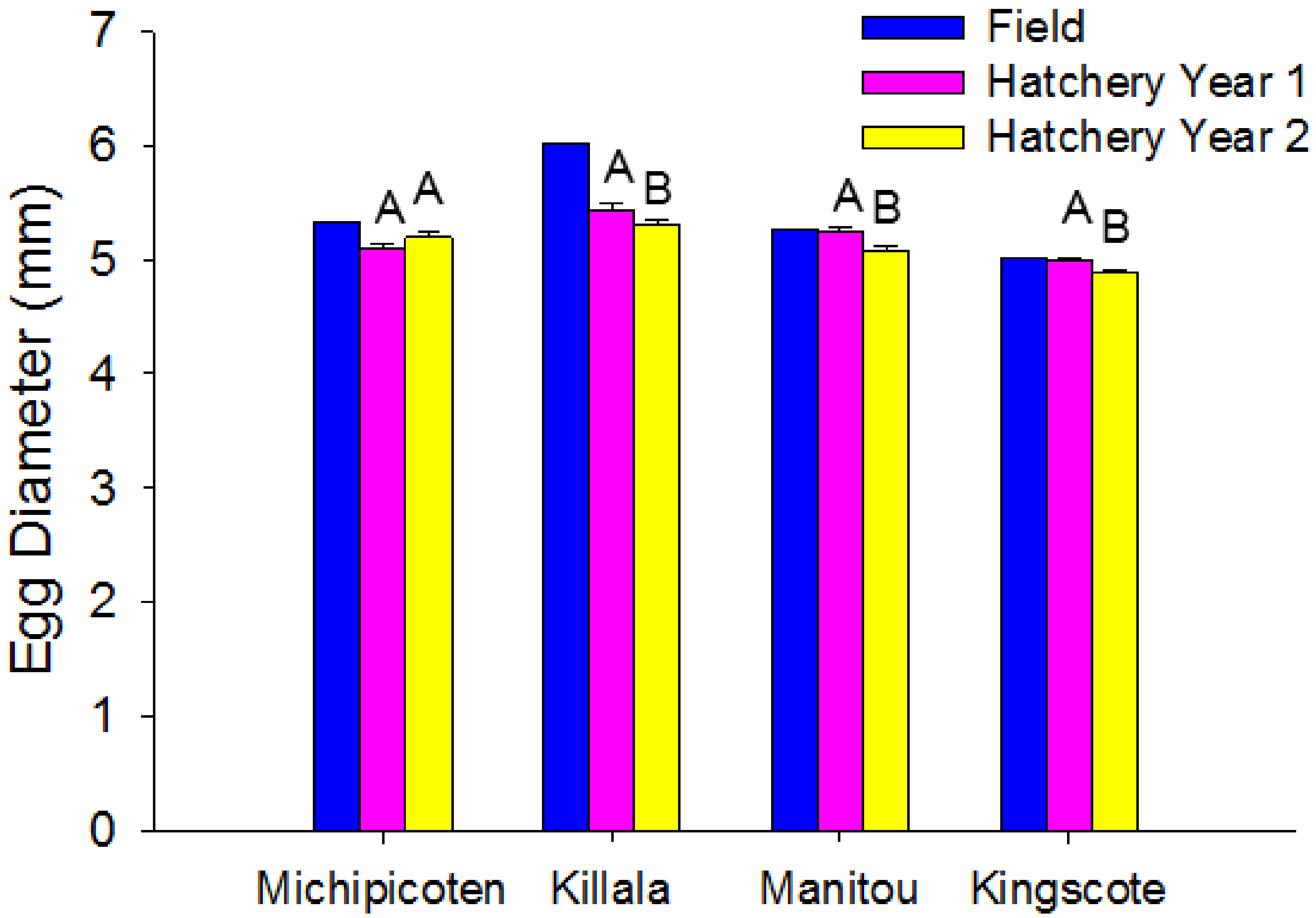

Figure 19. Comparison of egg size of four stocks of lake trout sampled in the wild to hatchery individuals held in a common garden environment during the 2008 and 2009 spawning seasons. The letters "A" and "B" above each data column indicate statistical groupings within a stock based on Tukey's test ($p<0.05$). Field values based on model and are not included in statistical comparison.

Egg production was similar between hatchery fish and wild fish in the Manitou and Killala stocks (Figure 20). However, wild Kingscotes had lower egg production than seen in the hatchery while wild Michipicotens had increased egg production in the wild relative to their hatchery counterparts.

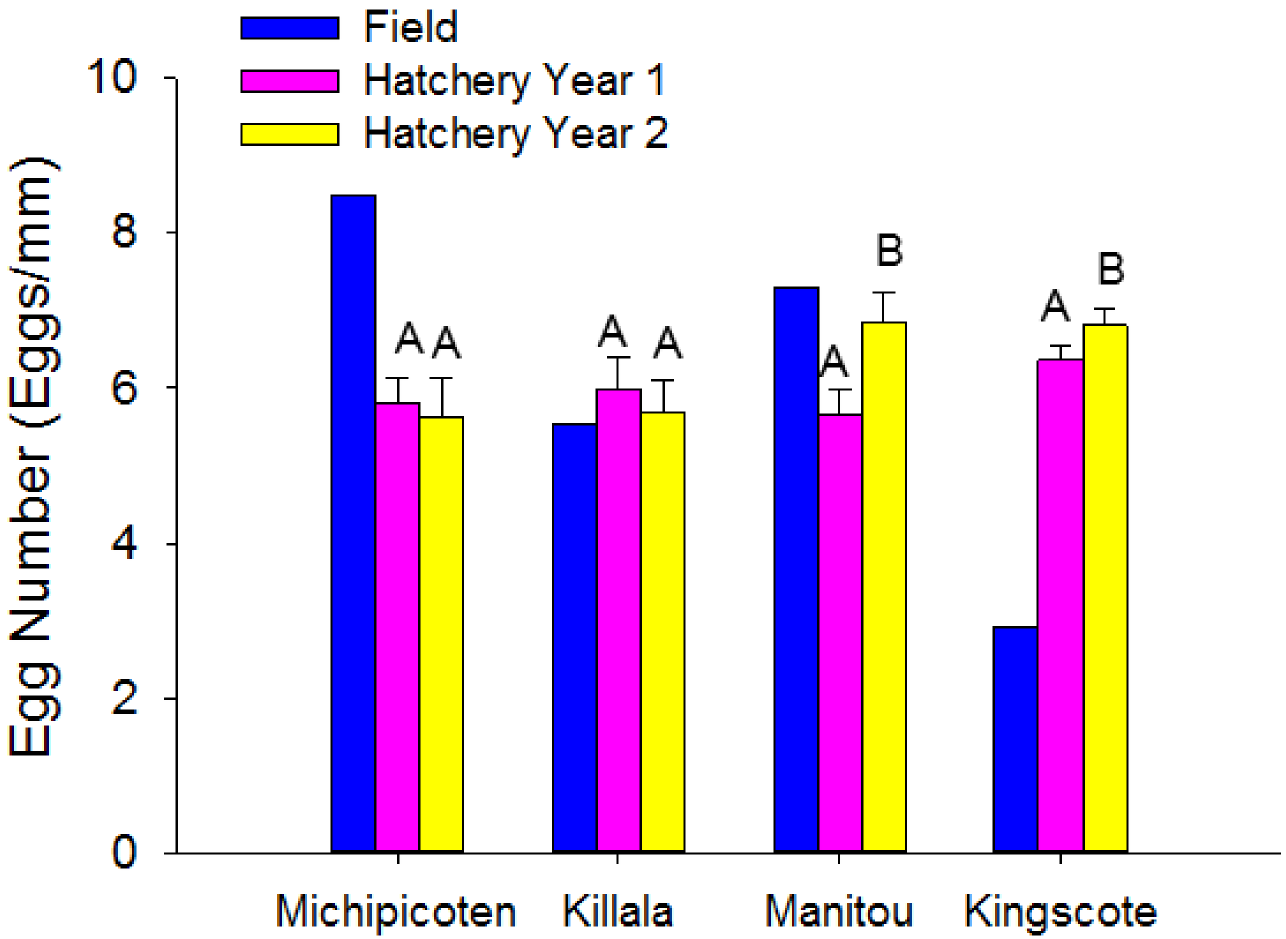

Figure 20. Comparison of egg number of four stocks of lake trout sampled in the wild to hatchery individuals held in a common garden environment during the 2008 and 2009 spawning seasons. The letters “A” and “B” above each data column indicate statistical groupings within a stock based on Tukey’s test (p<0.05). Field values based on model and are not included in statistical comparison.

Comparison of Field and Hatchery Data between Stocks

Michipicoten fish were consistently larger than the other stocks, when compared across stocks within years (Figure 21 and Table 10), which was consistent with modeled predictions, in which I predicted Michipicoten to be the longest, followed by Manitou, Killala, and Kingscote, respectively. However, the differences in length in the hatchery fish from the other stocks did not differ much from each other.

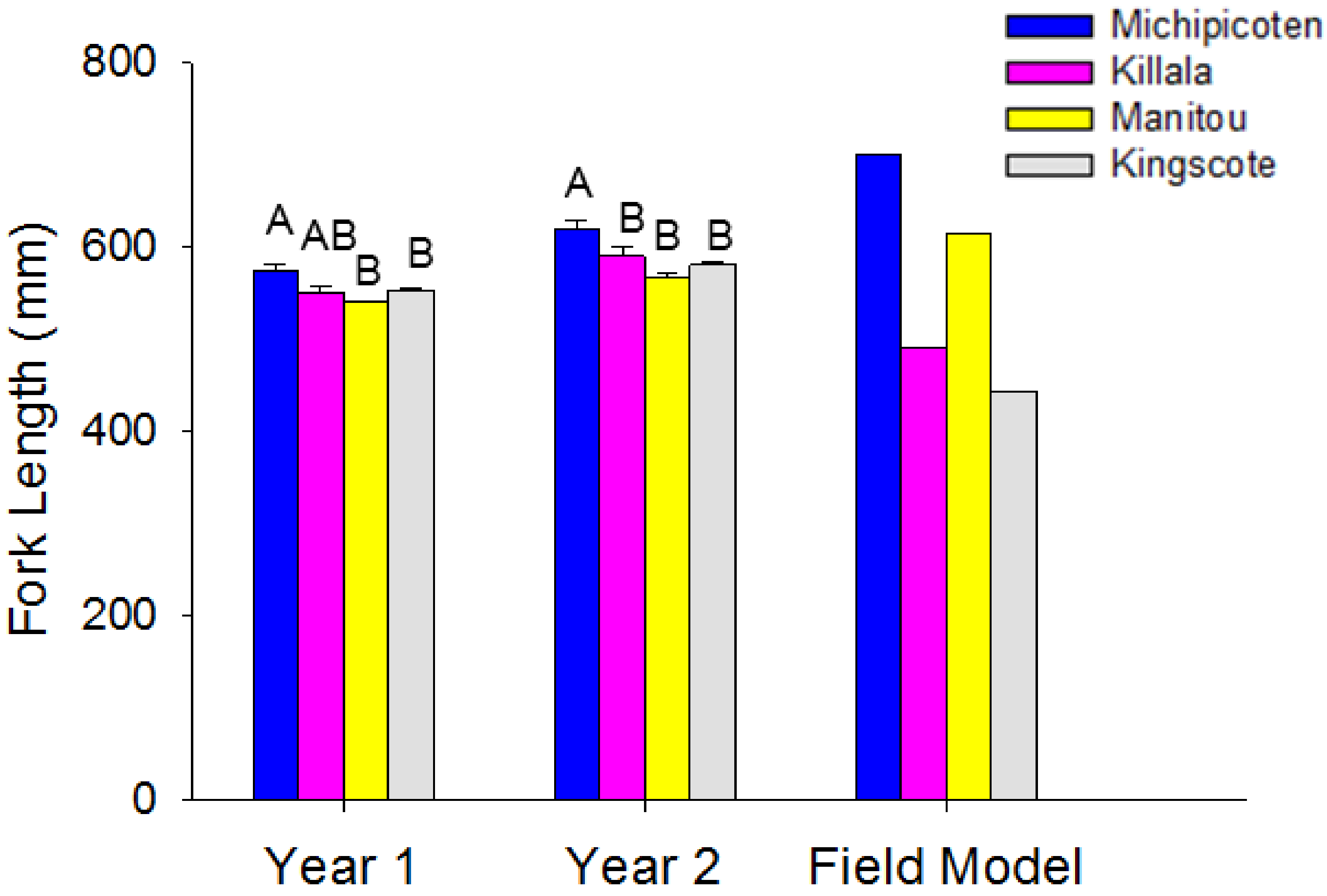

Figure 21. Comparison of Fork Length of four stocks of lake trout during: Year 1 of the hatchery study, Year 2 of the hatchery study, and modeled field value at 8.5 years old. The letters “A” and “B” above each data column indicate statistical groupings within a year based on Tukey’s test ($p<0.05$). Field values based on model and are not included in statistical comparison.

Percent lipid differed significantly between stocks in the hatchery, with the fish from stocks that show low percent lipid in the wild exhibiting the highest percent lipids in Year 1 of the hatchery study (Figure 22 and Table 11). By Year 2, however, only the Kingscote had significantly higher percent lipids than the other stocks. The percent lipid observed in the hatchery fish did not compare well to wild counterparts, where the Michipicoten and Manitou had the highest percent lipid, followed by the Killala stock, and the Kingscote stock, respectively (Figure 22).

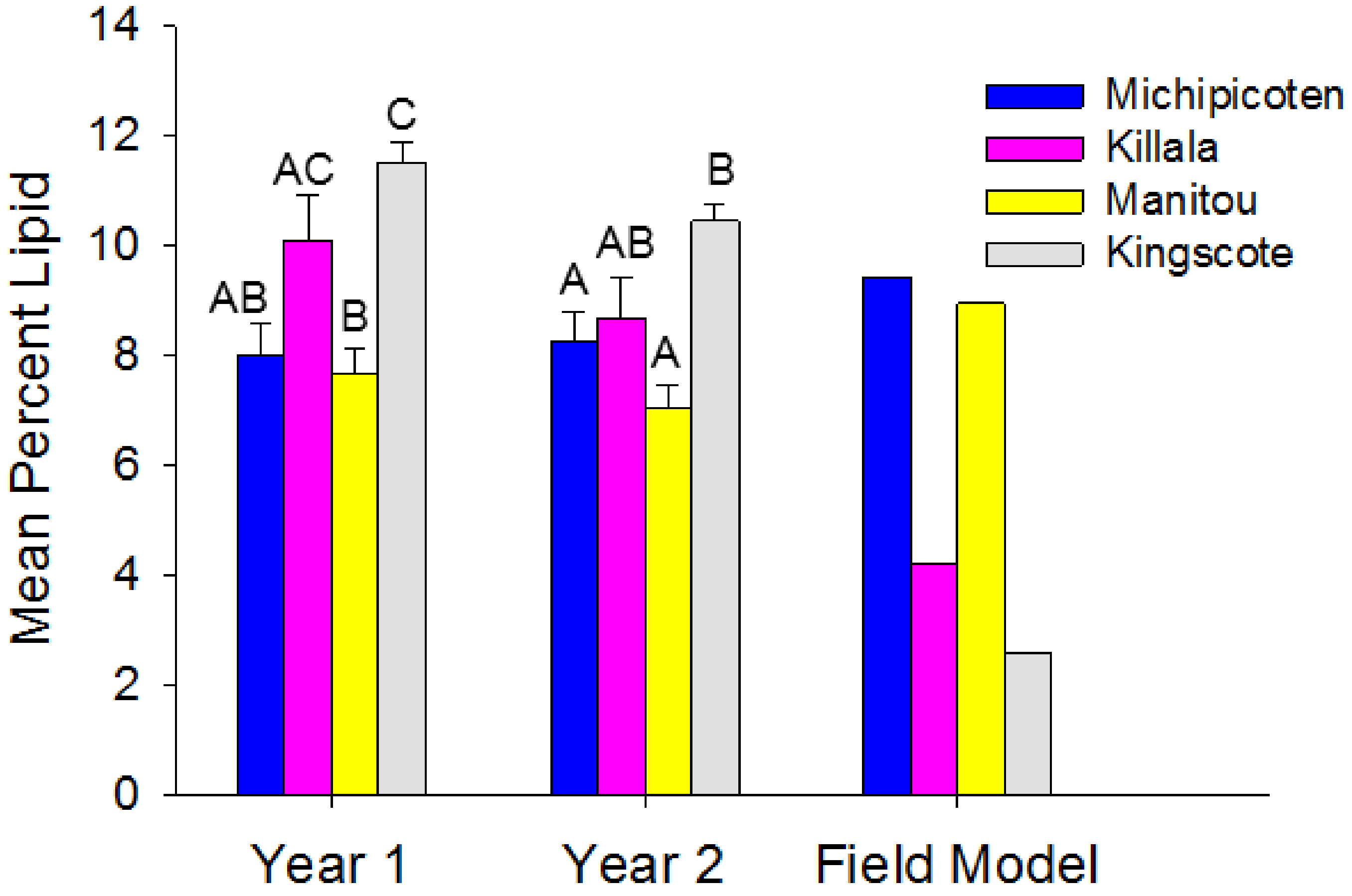

Figure 22. Comparison of mean percent lipids of four stocks of lake trout during: Year 1 of the hatchery study, Year 2 of the hatchery study, and modeled field value at 8.5 years old. The letters "A" and "B" above each data column indicate statistical groupings within a year based on Tukey's test ($p<0.05$). Field values based on model and are not included in statistical comparison.

Egg sizes across stocks were consistent from Year 1 to Year 2 and were comparable to that predicted from their wild counterparts (Figure 23 and Table 12) The Kingscote were significantly smaller than most of the stocks (except Michipicoten) in Year 1, and significantly smaller than all stocks in Year 2. The Killala consistently had larger eggs than the other stocks in Year 1, and in Year 2 (except Michipicoten).

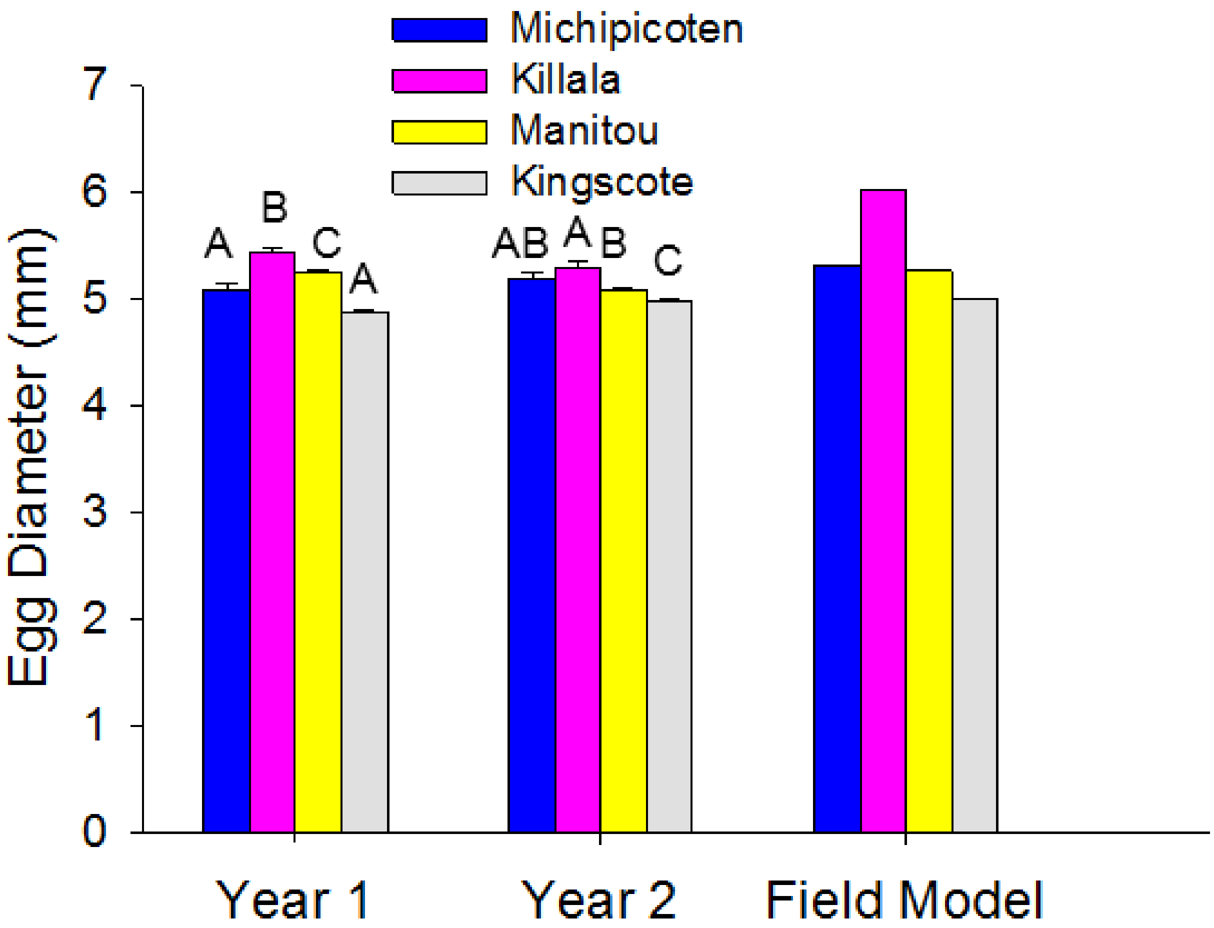

Figure 23. Comparison of egg size of four stocks of lake trout during: Year 1 of the hatchery study, Year 2 of the hatchery study, and modeled field value at 8.5 years old. The letters “A” and “B” above each data column indicate statistical groupings within a year based on Tukey’s test ($p<0.05$). Field values based on model and are not included in statistical comparison.

The number of eggs produced per millimeter (eggs/mm) of hatchery fish showed a lot of variability, and there were no statistically significant differences between stocks each year (Figure 24 and Table 13). The modeled field data suggested that the Michipicoten and Manitou stocks should produce the most number of eggs, while the Kingscote would produce the least. The hatchery data from Year 2 suggested a trend that Manitou fish would produce more eggs/mm. The hatchery Kingscote, on the other hand, did not show any indication that these stocks would produce the lowest number of eggs/mm and seemed most divergent from their wild counterparts.

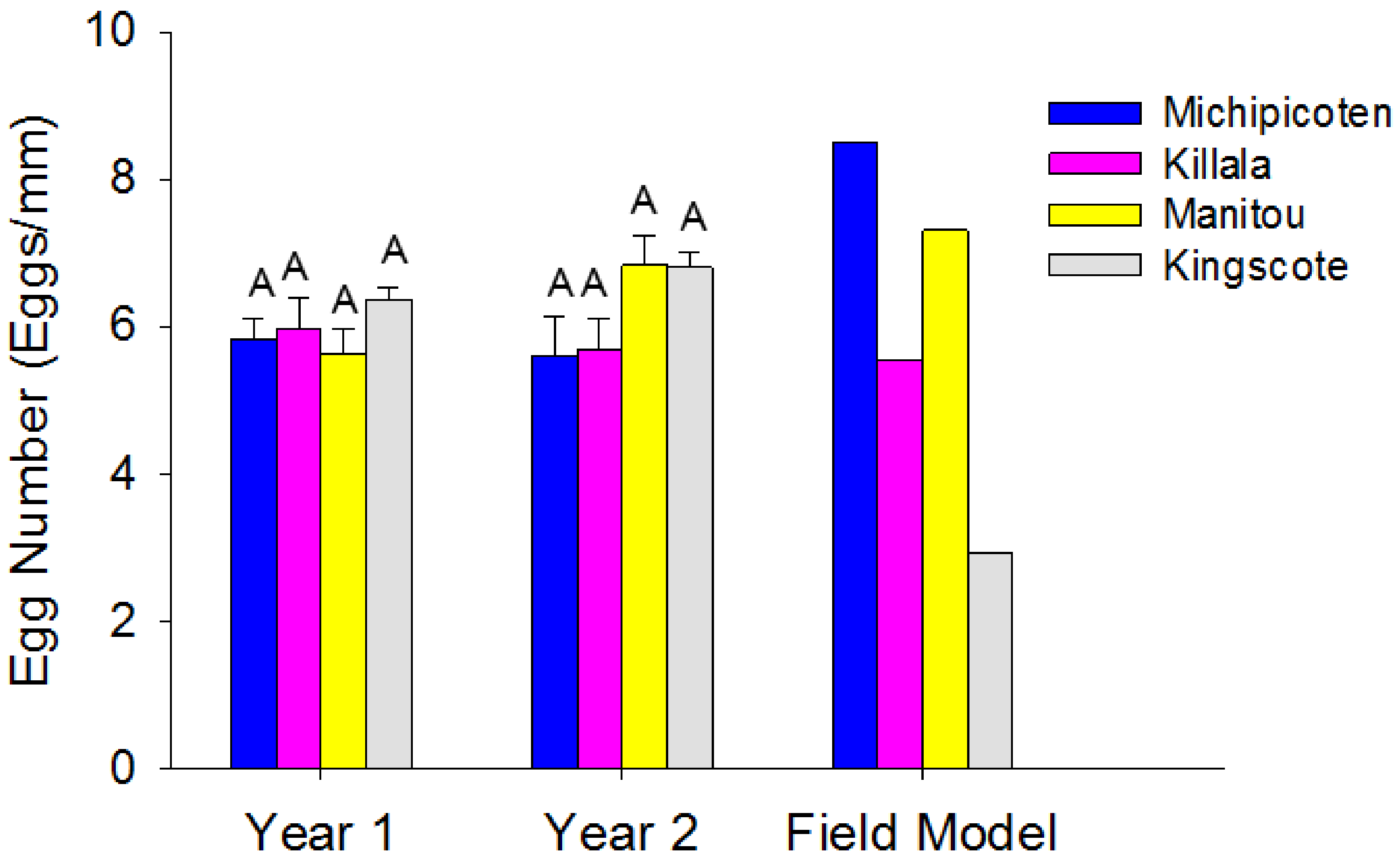

Figure 24. Comparison of eggs number of four stocks of lake trout during: Year 1 of the hatchery study, Year 2 of the hatchery study, and modeled field value at 8.5 years old. The letters “A” and “B” above each data column indicate statistical groupings within a year based on Tukey’s test ($p<0.05$). Field values based on model and are not included in statistical comparison.

DISCUSSION

Lake trout appear to allocate energy towards growth, reproduction and storage in ways that may be explained by inherited life history traits, but the artificial environment of the hatchery makes comparisons more complicated. The most interesting result from this study is that each stock shows differences in some metrics when raised in common environment, and these patterns can be explained, in part, by comparison to wild counterparts.

Stock Differences in Hatchery and Wild Fish

The most conserved trait between wild and hatchery fish was egg size, while the other traits showed variation between wild and hatchery fish. This is consistent with the results found in Jastrebski and Morbey (2009) that show the heritability of egg size in lake trout causes egg size to remain relatively stable in a wide variety of environments within a given stock.

The more divergent of the two reproductive traits between the hatchery and wild individuals appears to be egg number. This finding suggests that the local environment (presumably ration), has a larger effect on egg number than egg size. This is consistent with previous studies that have found egg number to be variable, depending on environmental conditions (Scott 1962; Lobon-Cervia 2003).

Percent lipid showed a large difference between the wild and hatchery in the Kingscote and Killala stocks which are adapted to low-energy diets. This suggests that percent lipid of individuals is sensitive to local conditions and that environmental differences between hatchery and wild conditions drive these differences, specifically energy intake.

Growth, as measured by modeled fork length at age 8.5, also showed differences between hatchery and wild which indicates it is influenced by hatchery conditions and is likely dependent on food availability in the hatchery.

Insight into Stock-specific Life Histories from Field and Hatchery Data

Four distinct life history strategies resulted in some differences in percent lipid, growth, and reproductive output between stocks in their natural environments as well as when held in a common environment.

The wild fish showed differences in relative percent lipid between stocks (Figure 18). The Kingscote fish had lowest lipid levels in the field, and Killala had slightly more lipid storage. The Michipicoten and Manitou fish had the highest lipid levels in the wild, both of which were on par with lipid levels observed in the hatchery. These data, combined with data showing similar growth in the Manitou and Michipicoten stocks between the hatchery and field, suggest that energy intake in the hatchery is similar to that in the natural environment for these two stocks.

Kingscote individuals in the hatchery had much higher levels of lipids than the other stocks, followed by Killala. These two stocks that have limited access to energy rich food sources in the wild and appear to be adapted to those environments because in the hatchery, even though they are fed the same as the other stocks, they may be overfed and put the excess into storage.

The percent lipid appeared to vary considerably between the hatchery and the wild fish, and may be sensitive to ration. Percent lipid also appears to be influenced by stock-specific food-conversion efficiencies. This finding shows that percent lipid is sensitive to environmental conditions, and presumably food consumption, and that changes in food availability in a given environment has the potential to influence the amount of energy allocated to growth and reproduction because of the importance of lipid reserves in the flexibility of energy allocation in an individual (Jokela 1997).

Within the hatchery, fork length was very consistent between stocks (Figure 17), which suggests that there are not strong stock-specific differences in growth rates in a common environment. However, there are large differences between stocks in length-at-age in the wild fish which is likely a result of differences in energy intake based on the natural environments of the stocks. Only the Manitou stock showed similar lengths in the hatchery and field which suggests energy intake in the hatchery is on par with their natural environment.

Egg size was more variable between stocks within the hatchery, but less variable within a stock across environments (hatchery vs. field), which suggests that egg size has a strong genetic component, while ration level and local environment play a lesser role (Figure 19). This trend of consistent egg size within a lake trout stock across a range of environments was also observed in Jastrebski and Morbey (2009). In my study, egg size was consistent from Year 1 to Year 2 in the hatchery and was comparable to the wild fish. However, the modeled estimate of the egg size of the long lived stocks, Michipicoten and Killala, is larger than that observed in the hatchery. The size difference could be due to the model extrapolating beyond the available data. Results from this study confirm other studies that suggest egg size is an inherited trait, which is somewhat conserved. In natural environments, there are a multitude of strong selection pressures on egg size including predation, resource availability and oxygen levels (Chambers et al.

1989; Reznick et al. 2001; Einum et al. 2002) which would dictate such a rigid life history trait.

Because egg size appeared to be fixed within a stock, the only other thing that can vary substantially and adjust to a common environment situation is egg number. There were no significant differences in egg number between the stocks in the hatchery (Figure 16). However, there seemed to be a trend to suggest that Manitou would produce the most eggs in Year 2, which is consistent with the pattern observed in wild fish. The stock that showed a highly divergent pattern in the hatchery compared to the wild was the Kingscote stock. Kingscotes produced equal numbers of eggs as other stocks, but in the field, they produce far fewer eggs. This result suggests that energy intake in the hatchery was driving the egg production. This effect of ration on reproductive output is explored further in Chapter 3.

Stock-Specific Conceptual Models

The stock-specific conceptual model (Table 5), based on the energy allocation criteria presented in Chapter 1, would suggest that wild Michipicotens have higher lipid reserves because they eat more energy-dense forage fish. The conceptual model also predicts that Michipicotens will devote high amounts of energy towards growth because of the relatively steep line in the length-at-age data from the wild (Figure 5, Figure 7). Lastly, the model predicts a relatively low amount of energy allocated towards reproduction because of the relatively long lifespan of the stock. These predictions, based on environmental conditions and field data, are consistent with previous studies that suggest a high investment to storage and growth in much larger environments (such as the Great Lakes) where it may be beneficial to grow faster and bigger and have readily available energy to survive sparse food or winter (Post and Parkinson 2001; Biro et al. 2004).

The conceptual model of energy allocation in the Killala stock (Table 5) predicted that they would have a relatively low amount of energy put towards reproduction in a given year because of their long lifespan. The Killalas are expected to have a low amount of energy put towards growth because the length-at-age curve had a shallow slope and also because of limited fishing pressure (OMNR Report). Lastly, the model predicted that the Killala stock would have a low amount of energy allocated toward reproduction because of the stock's relatively long lifespan. In this case, the Killala stock is expected to have low amounts of energy allocated to growth, storage, and reproduction relative to the other stocks. Within the Killala stock, I predicted a relatively equal allocation of energy toward each factor.

The conceptual model for the Kingscote stock (Table 5) predicted that they would have a relatively high amount of energy put toward reproduction in a given year because of their short-lived life history strategy. They were predicted to have a low amount of energy allocated towards storage because of their planktivorous diet and were predicted to allocate a small amount of energy to growth, based on the length-at-age data gathered.

The Manitou stock, a short-lived stock, derived from an ecologically rich aquatic community with ample forage fish, was expected to feed on energy-dense food items (Table 5). The stock is short-lived and has high natural rates of mortality in its natural environment (Budd et al. 1968; Shuter et al. 1998) which, according to life history theory (Murphy 1968; Budd et al. 1968) suggests that much energy will be devoted towards reproduction in both hatchery and wild stocks so that reproduction is successful before the end of life. Indeed, anecdotally, the Manitou strain is known in the hatchery system as "egg machines"; however, the size of eggs produced by the stock is expected to be smaller because of the tradeoff between egg size and egg number (Smith and Fretwell 1974). Also, because Lake Manitou has a rich community structure and presumably high quality prey, they are expected to have a relatively high percent lipid.

Table 5. Conceptual model of energy allocation in lake trout stocks to reproduction, growth, and storage based on field data gathered and conceptual models summarized in Tables 1-3 (Chapter 1).

Stock	**Growth**	**Storage**	**Reproduction**
Michipicoten	High	High	Low
Killala	Low	Low	Low
Kingscote	Low	Low	High
Manitou	High	High	High

Study Limitations

While I found interesting results that could be related to life history, I only studied stocks that were from divergent life histories. This study would be enhanced if I could explore multiple stocks showing same life history strategy (i.e. long lived, low lipid) in a common environment. Therefore, this study is more descriptive of these specific stocks because there is little overlap in the life history strategies between these stocks.

An additional limitation of this study was the sample size and age range of wild individuals collected that formed the basis of comparisons. It was difficult to acquire samples of females encompassing a wide range of ages for the long-lived Michipicoten and Killala stocks. In the case of the Michipicoten stock, there was a gap in data between ages 15 and 25 which may have resulted in an inaccurate prediction of variables based on age in intermediate-aged fish. There were no samples of individuals at younger ages in the Michipicoten and Killala stocks which forced me to extrapolate beyond the range of my wild datasets to predict percent lipid, growth, egg size, and egg number at age 8.5.

Also, the Kingscote stock had a gap from 8 to 11-years-old in the wild dataset. These sample size and age range limitations in my wild dataset could be a result of a limited number of individuals in certain size classes in a given stock, or the bias of gears used when sampling lake trout with the OMNR.

One possible implication of this potential bias caused by limited sampled sizes and missing ages in the field samples is seen in the effects of age on egg size between the hatchery and the field data. Although it is possible that differences between the hatchery and natural environments are affecting this change in egg size as fish age, it is also possible that limited sample sizes in younger fish biased my models and resulted in inaccurate predictions in the extrapolated data.

Implications

A comparison of hatchery and wild individuals from lake trout stocks with a wide range of life histories permitted exploration into the differences between hatchery fish and wild fish and what traits are most influenced by environmental differences. A common environment resulted in similar length at age and egg number between stocks, while egg size was relatively fixed within each stock at a given age, regardless of environment. Percent muscle lipid storage showed differences between stocks and also showed differences within stock between the hatchery and the wild. This indicates that when fish from energy-limited environments in the wild are exposed to an energy-rich environment, they take advantage of this environment by moving excess energy to lipid reserves. Given that the stocks from energy-rich environments grew less than wild fish when in a hatchery setting, these stocks are not saturated with food in the lab. However, these stocks still showed allocation of energy to lipid storage. This suggests that there may be a limit to what fraction of their overall intake of energy can be allocated to growth and that “excess” energy will still be selectively allocated to storage despite a lack of food. This result is consistent with other studies that show a tradeoff between growth and storage and also predict that there will be allocation of energy to lipid reserves, even in limiting environments, to maintain lipids at a minimum critical level to allow over-winter survival (Henderson and Wong 1998; Berg et al. 2011). Given the high importance of lipids in over-winter survival, growth would then be more indicative of limiting environments, which was seen in my study as evidenced by differences in length-at-age between the hatchery and wild fish. The implications of this strategy of maintaining critical lipid levels despite food abundance in a given year is that growth, and the associated reproductive output in following years is going to be reduced due to the energy allocated to lipid reserves for over-winter survival. In the next chapter, I quantitatively explore the role of these lipid reserves on reproductive output within each stock to determine the stock-specific responses to multiple rations, and in particular, to explore the effect of low food ration on egg production, storage and growth to determine if this stressor is mediated by life history.

APPENDIX

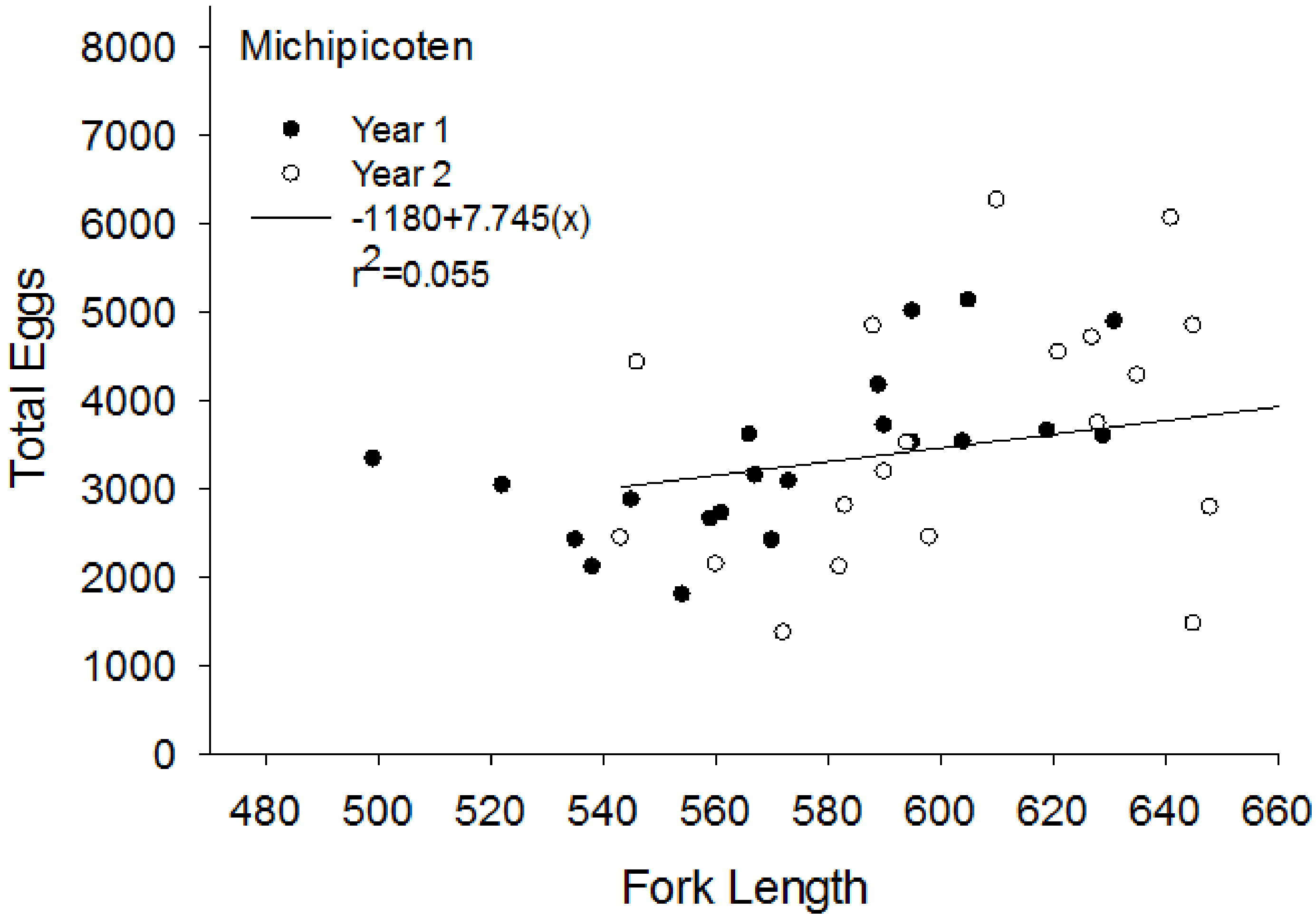

Figure 25. Figure showing relationship between egg number and fork length of spawning female Michipicoten lake trout held in a common environment in OMNR hatchery in Codrington, Ontario. Regression is linear, the linear equation fit to each relationship and corresponding r^2 value are shown.

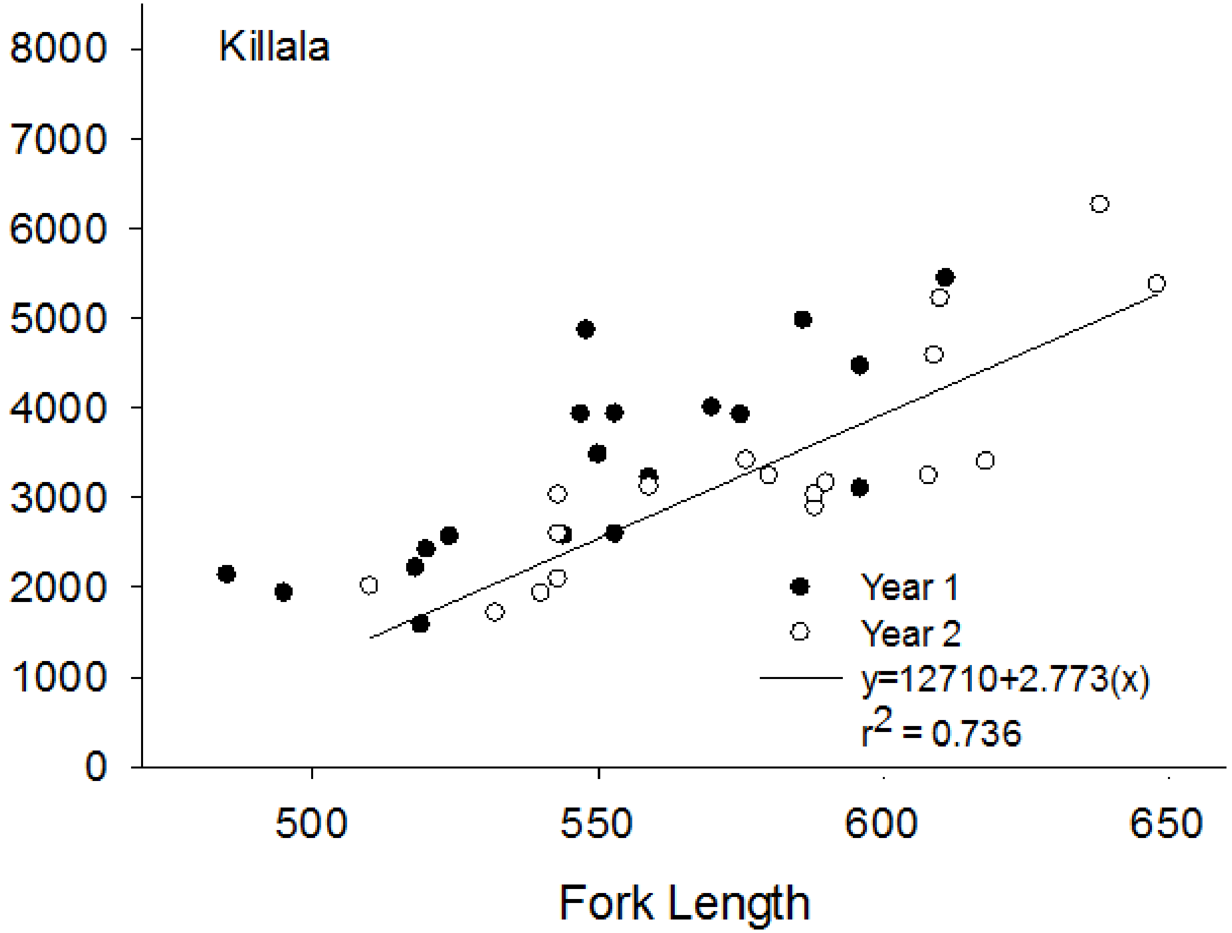

Figure 26. Figure showing relationship between egg number and fork length of spawning female Killala lake trout held in a common environment in OMNR hatchery in Codrington, Ontario. Regression is linear, the linear equation fit to each relationship and corresponding r^2 value are shown.

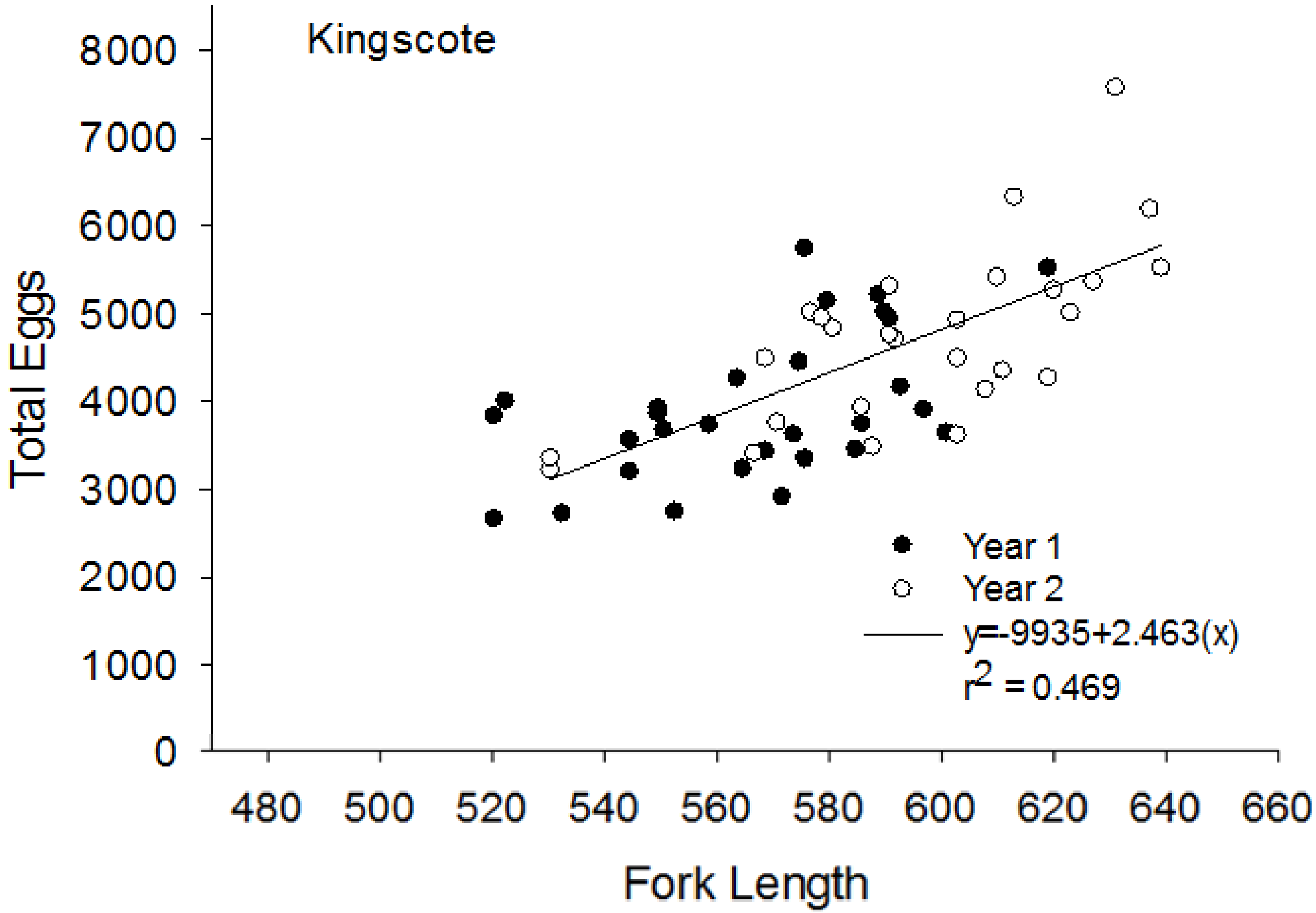

Figure 27. Figure showing relationship between egg number and fork length of spawning female Kingscote lake trout held in a common environment in OMNR hatchery in Codrington, Ontario. Regression is linear, the linear equation fit to each relationship and corresponding r^2 value are shown.

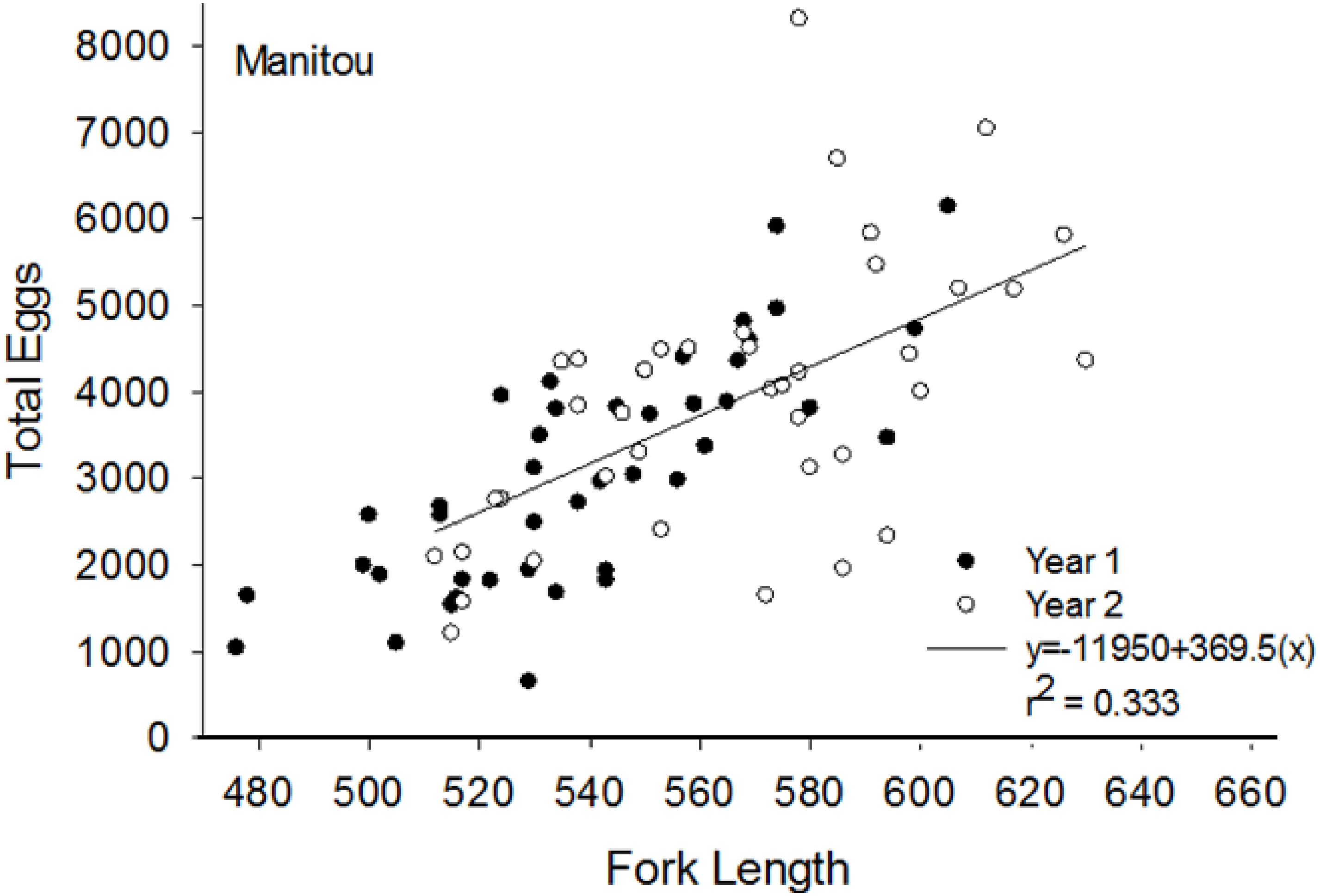

Figure 28. Figure showing relationship between egg number and fork length of spawning female Manitou lake trout held in a common environment in OMNR hatchery in Codrington, Ontario. Regression is linear, the linear equation fit to each relationship and corresponding r^2 value are shown.

Table 6. AIC values and Residual Sum of Squares (RSS) of linear, quadratic, logarithmic, exponential, and hyperbolic relationships assigned to data age vs.: egg number, egg diameter, length, and percent lipid in wild Manitou stock lake trout.

Metric	Relationship	No. of Parameters (k)	No. of Observations (n)	Residual Sum of Squares (RSS)	Akaike Information Criterion (AIC)
Egg Number (Eggs/mm)	Linear	2	35	105.4089	42.5875
	Quadratic	3	35	99.3365	42.5108
	Logarithmic	2	35	106.3809	42.9087
	Exponential	1	35	560.3061	99.0597
	Hyperbolic	2	35	106.865	43.0676
Egg Diameter (mm)	Linear	2	35	1.4299	-107.9210
	Quadratic	3	35	1.3161	-108.8236
	Logarithmic	2	35	1.5184	-105.8192
	Exponential	1	35	154.4907	53.9675
	Hyperbolic	2	35	1.6025	-103.9324
Length (mm)	Linear	2	35	25229.8815	234.3153
	Quadratic	3	35	25072.8706	236.0968
	Logarithmic	2	35	26850.0535	236.4936
	Exponential	1	35	10312561.5	442.7734
	Hyperbolic	2	35	28256.8704	238.2810
Percent Lipid	Linear	2	35	205.6643	65.9814
	Quadratic	3	35	202.0699	67.3643
	Logarithmic	2	35	200.1567	65.0313
	Exponential	1	35	1121.8716	123.3592
	Hyperbolic	2	35	200.3428	65.0639

Table 7. AIC values and Residual Sum of Squares (RSS) of linear, quadratic, logarithmic, exponential, and hyperbolic relationships assigned to data age vs.: egg number, egg diameter, length, and percent lipid in wild Killala stock lake trout.

Metric	Relationship	No. of Parameters (k)	No. of Observations (n)	Residual Sum of Squares (RSS)	Akaike Information Criterion (AIC)
Egg Number (Eggs/mm)	Linear	2	9	5.5226	-0.3954
	Quadratic	3	9	3.2279	-3.2285
	Logarithmic	2	9	4.9491	-1.3822
	Exponential	1	9	19.3958	8.9105
	Hyperbolic	2	9	4.3835	-2.4744
Egg Diameter (mm)	Linear	2	9	0.419	-23.6040
	Quadratic	3	9	0.4179	-21.6276
	Logarithmic	2	9	0.4206	-23.5697
	Exponential	1	9	45.8561	16.6546
	Hyperbolic	2	9	0.4234	-23.5100
Length (mm)	Linear	2	9	10641.129	67.6773
	Quadratic	3	9	10541.8695	69.5930
	Logarithmic	2	9	11056.6562	68.0221
	Exponential	1	9	1197382.605	108.1858
	Hyperbolic	2	9	11569.2501	68.4299
Percent Lipid	Linear	2	9	8.5225	3.5094
	Quadratic	3	9	8.5225	5.5094
	Logarithmic	2	9	8.5418	3.5297
	Exponential	1	9	23.6218	10.6845
	Hyperbolic	2	9	8.5659	3.5551

Table 8. AIC values and Residual Sum of Squares (RSS) of linear, quadratic, logarithmic, exponential, and hyperbolic relationships assigned to data age vs.: egg number, egg diameter, length, and percent lipid in wild Michipicoten stock lake trout.

Metric	Relationship	No. of parameters (k)	No. of observations (n)	Residual Sum of Squares (RSS)	Akaike Information Criterion (AIC)
Egg Number (Eggs/mm)	Linear	2	12	153.9383	34.6197
	Quadratic	3	12	145.3113	35.9277
	Logarithmic	2	12	153.0786	34.5525
	Exponential	1	12	462.6192	45.8240
	Hyperbolic	2	12	152.711	34.5237
Egg Diameter (mm)	Linear	2	9	1.0532	-15.3085
	Quadratic	3	9	1.042	-13.4047
	Logarithmic	2	9	1.0673	-15.1888
	Exponential	1	9	45.9341	16.6698
	Hyperbolic	2	9	1.0839	-15.0499
Length (mm)	Linear	2	12	72044.1391	108.4015
	Quadratic	3	12	63985.1691	108.9780
	Logarithmic	2	12	70175.4461	108.0862
	Exponential	1	12	4449190.291	155.8799
	Hyperbolic	2	12	69907.065	108.0402
Percent Lipid	Linear	2	12	375.1968	45.3105
	Quadratic	3	12	312.9859	45.3350
	Logarithmic	2	12	373.3259	45.2505
	Exponential	1	12	571.3356	48.3568
	Hyperbolic	2	12	372.4094	45.2210

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Table 9. AIC values and Residual Sum of Squares (RSS) of linear, quadratic, logarithmic, exponential, and hyperbolic relationships assigned to data age vs.: egg number, egg diameter, length, and percent lipid in wild Kingscote stock lake trout.

Metric	Relationship	No. of parameters (k)	No. of observations (n)	Residual Sum of Squares (RSS)	Akaike Information Criterion (AIC)
Egg Number (Eggs/mm)	Linear	2	15	7.7512	-5.9030
	Quadratic	3	15	6.5345	-6.4643
	Logarithmic	2	15	7.4473	-6.5030
	Exponential	1	15	12.5507	-0.6741
	Hyperbolic	2	15	7.4031	-6.5923
Egg Diameter (mm)	Linear	2	15	0.4578	-48.3406
	Quadratic	3	15	0.4483	-46.6551
	Logarithmic	2	15	0.4509	-48.5684
	Exponential	1	15	54.5326	21.3612
	Hyperbolic	2	15	0.4462	-48.7256
Length (mm)	Linear	2	15	5269.627	91.9250
	Quadratic	3	15	5129.5	93.5207
	Logarithmic	2	15	5194.624	91.7099
	Exponential	1	15	1634210	175.9793
	Hyperbolic	2	15	5202.925	91.7339
Percent Lipid	Linear	2	15	3.7303	-16.8734
	Quadratic	3	15	2.6258	-20.1400
	Logarithmic	2	15	3.4656	-17.9776
	Exponential	1	15	26.7645	10.6854
	Hyperbolic	2	15	3.0286	-19.9992

Table 10. Comparison of statistical significance of the fork length between stocks based on ANOVA pairwise-comparison using a Tukey-Kramer adjustment. Field data are not included in statistical comparison because value is a modeled value.

Year 1 Fork Length				
	Michipicoten	Killala	Manitou	Kingscote
Michipicoten	n/a	0.0675	0.0003**	0.0334*
Killala	0.0675	n/a	0.6264	0.9774
Manitou	0.0003**	0.6264	n/a	0.1094
Kingscote	0.0334*	0.9774	0.1094	n/a
Year 2 Fork Length				
	Michipicoten	Killala	Manitou	Kingscote
Michipicoten	n/a	0.0002**	<.0001**	<.0001**
Killala	0.0002**	n/a	0.8567	0.9029
Manitou	<.0001**	0.8567	n/a	0.1789
Kingscote	<.0001**	0.9029	0.1789	n/a

Table 11. Comparison of statistical significance of the mean percent lipids between stocks based on ANOVA pairwise-comparison using a Tukey-Kramer adjustment. Field data are not included in statistical comparison because value is a modeled value.

Year 1 Percent Lipids				
	Michipicoten	Killala	Manitou	Kingscote
Michipicoten	n/a	0.1576	0.9781	<.0001**
Killala	0.1576	n/a	0.0294*	0.3063
Manitou	0.9781	0.0294*	n/a	<.0001**
Kingscote	<.0001**	0.3063	<.0001**	n/a
Year 2 Percent Lipids				
	Michipicoten	Killala	Manitou	Kingscote
Michipicoten	n/a	0.9536	0.3149	0.0033**
Killala	0.9536	n/a	0.1496	0.0642
Manitou	0.3149	0.1496	n/a	<.0001**
Kingscote	0.0033**	0.0642	<.0001**	n/a

Table 12. Comparison of statistical significance of the egg size between stocks based on ANOVA pairwise-comparison using a Tukey-Kramer adjustment. Field data are not included in statistical comparison because value is a modeled value.

Year 1 Egg Size				
	Michipicoten	Killala	Manitou	Kingscote
Michipicoten	n/a	<.0001**	0.0132*	0.1007
Killala	<.0001**	n/a	0.0026**	<.0001**
Manitou	0.0132*	0.0026**	n/a	<.0001**
Kingscote	0.1007	<.0001**	<.0001**	n/a
Year 2 Egg Size				
	Michipicoten	Killala	Manitou	Kingscote
Michipicoten	n/a	0.3214	0.1044	<.0001**
Killala	0.3214	n/a	0.0008**	<.0001**
Manitou	0.1044	0.0008**	n/a	<.0001**
Kingscote	<.0001**	<.0001**	<.0001**	n/a

Table 13. Comparison of statistical significance of the egg number between stocks based on ANOVA pairwise-comparison using a Tukey-Kramer adjustment. Field data are not included in statistical comparison because value is a modeled value.

Year 1 Eggs/mm				
	Michipicoten	Killala	Manitou	Kingscote
Michipicoten	n/a	0.9899	0.981	0.5648
Killala	0.9899	n/a	0.8881	0.8202
Manitou	0.981	0.8881	n/a	0.1255
Kingscote	0.5648	0.8202	0.1255	n/a
Year 2 Eggs/mm				
	Michipicoten	Killala	Manitou	Kingscote
Michipicoten	n/a	0.9994	0.1203	0.0805
Killala	0.9994	n/a	0.2432	0.2002
Manitou	0.1203	0.2432	n/a	0.9999
Kingscote	0.0805	0.2002	0.9999	n/a

WORKS CITED

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Beamish, R.J., Thomson, B.L., and G. A. McFarlane. 1992. Spiny dogfish predation on chinook and coho salmon and the potential effects on hatchery-produced salmon. Transactions of the American Fisheries Society 121: 444–455.

Biro, P. A., Morton, A. E., Post, J. R., and E. A. Parkinson 2004. Over-winter lipid depletion and mortality of age-0 rainbow trout (Oncorhynchus mykiss). Canadian Journal of Fisheries and Aquatic Sciences, 61: 1513-1519.

Blanchard, J. L., Frank, K. T, and J. E. Simon. Effects of condition on fecundity and total egg production of eastern Scotian Shelf haddock (*Melanogrammus aeglefinus*). Canadian Journal of Fisheries and Aquatic Sciences 60: 321-332.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer.

Budd, J.C., Fry, F.E.J., and J. B. Smith. 1968. Survival of marked lake trout in Lake Manitou, Manitoulin Island, Ontario. Journal of the Fisheries Research Board of Canada. 25: 2257–2268.

Chambers, R. C., Leggett, W. C., and J. A. Brown. 1989. Egg size, female effects, and the correlations between early life history traits of capelin, Mallotus villosus: an appraisal at the individual level. Fishery Bulletin, 87: 515-523.

Claus, L. C. 2011. Influence of life history traits on accumulation of polybrominated diphenyl ethers and polychlorinated biphenyls in three lake trout populations from Lake Superior. Master of Science Thesis, Michigan State University.

Deverill, J. I., Adams, C. E., and C. W. Bean. 1999. Prior residence, aggression and territory acquisition in hatchery-reared and wild brown trout. Journal of Fish Biology 55: 868-875.

Dexter, J. L., Jr., B. T. Eggold, T. K. Gorenflo, W. H. Horns, S. R. Robillard, and S. T. Shipman. 2010. A fisheries management implementation strategy for the rehabilitation of Lake Trout in Lake Michigan. Great Lakes Fishery Commission, Lake Michigan Committee, Ann Arbor, Michigan.

Downs, C. C., White, R. G. and Shepard, B. B. 1997. Age at sexual maturity, sex ratio, fecundity, and longevity of isolated headwater populations of westslope cutthroat trout. North American Journal of Fisheries Management 17: 85-92.

Ebener, M. P. 1998. A lake trout rehabilitation guide for Lake Huron. Great Lakes Fishery Commission 48 pages.

Einum, S., Hendry, A. P., and I. A. Fleming. 2002. Egg-size evolution in aquatic environments: does oxygen availability constrain size?. Proceedings of the Royal Society of London. Series B: Biological Sciences, 269: 2325-2330.

Eschmeyer, P.H., and A. M. Phillips Jr. 1965. Fat content of the flesh of siscowets and lake trout from Lake Superior. Transactions of the American Fisheries Society 94: 62-74.

Fleming, I.A., T. Agustsson, B. Finstad, J. I. Johnsson, and B. T. Björnsson. 2002. Effects of domestication on growth physiology and endocrinology of Atlantic salmon (Salmo salar). Canadian Journal of Fisheries and Aquatic Sciences 59: 1323–1330.

Fleming, I.A., and Einum, S. 1997. Experimental tests of genetic divergence of farmed from wild Atlantic salmon due to domestication. ICES J. Mar. Sci. 54: 1051–1063.

Gamble, A. E., Hrabik, T. R., Stockwell, J. D., and D. L. Yule. 2011a. Trophic connections in Lake Superior Part I: The offshore fish community . Journal of Great Lakes Research 37: 541-549

Gamble, A. E., Hrabik, T. R., Stockwell, J. D., and D. L. Yule. 2011b. Trophic connections in Lake Superior Part II: The nearshore fish community. Journal of Great Lakes Research 37: 550-560.

Hanson, S. D., Holey, M. E., Treska, T. J., Bronte, C. R., T. H. Eggebraaten. 2012. Evidence of Wild Juvenile Lake Trout Reproduction in Western Lake Michigan. North American Journal of Fisheries Management 33:186-191.

Hill, M. S., Zydlewski, G. B., & Gale, W. L. 2006. Comparisons between hatchery and wild steelhead trout (Oncorhynchus mykiss) smolts: physiology and habitat use. Canadian Journal of Fisheries and Aquatic Sciences 63: 1627-1638.

Hindar, K., N. Ryman, and F. Utter. 1991. Genetic effects of cultured fish on natural fish populations. Canadian Journal of Fisheries and Aquatic Sciences 48: 945–957.

Hutchings, J. A. 1993. Adapted life histories effected by age-specific survival and growth rate. Ecology 74: 673-684.

Jastrebski, C. J., and Y. E. Morbey. 2009. Egg Size Variation in Lake Trout: Phenotype–Habitat Correlations Show an Effect of Rearing Environment. Transactions of the American Fisheries Society 138: 1342-1351.

Lobon-Cervia, H., Utrilla, C., Rincon, P., and F. Amezcua. 1997. Environmentally induced spatio-temporal variations in the fecundity of brown trout *Salmo trutta* L.: trade-offs between egg size and number. Freshwater Biology 38: 277-288.

Martin, N. V. and C. H. Olver. 1976. The distribution and characteristics of Ontario lake trout lakes. Ontario Ministry of Natural Resources: Fish and Wildlife Research Branch: Research Report Number 97.

Mason, D. M., Johnson, T. B., and J. F. Kitchell. 1998. Consequences of prey fish community dynamics on lake trout (Salvelinus namaycush) foraging efficiency in Lake Superior. Canadian Journal of Fisheries and Aquatic Sciences 55: 1273-1284.

Murphy, G. I. 1968. Pattern in Life History and the Environment. The American Naturalist 102: 391-403.

Olla, B.L., Davis, M.W., and Ryer, C.H. 1994. Behavioural deficits in hatchery-reared fish: potential effects on survival following release. Aquaculture and Fisheries Management: 25 (Supplement 1): 19–34.

Ontario Ministry of Natural Resources. 2005. Crown Land Use Policy Atlas – Policy Report. OMNR, Ontario, Canada.

Post, J. R., and E. A. Parkinson. 2001. Energy allocation strategy in young fish: allometry and survival. Ecology 82: 1040-1051.

Quince C, Shuter BJ, Abrams PA, Lester NP. 2008. Biphasic growth in fish II: empirical assessment. J. Theor. Biol. 254(2): 207-214.

Reznick, D., Butler I. V. M. J., and H. Rodd. 2001. Life history evolution in guppies. VII. The comparative ecology of high and low predation environments. The American Naturalist, 157(2), 126-140.

Scott, D. P. 1962. Effect of Food Quantity on Fecundity of Rainbow Trout, Salmo gairdneri. Journal of the Fisheries Research Board of Canada 19: 715-731.

Shuter, B. J., M. L. Jones, R. M. Korver, and N. P. Lester. 1998. A general, life history based model for regional management of fish stocks: The inland lake trout (Salvelinus namaycush) fisheries of Ontario. Canadian Journal of Fisheries and Aquatic Sciences 55: 2161-2177.

Smith, C. C., and S. D. Fretwell. 1974. The Optimal Balance between Size and Number of Offspring. The American Naturalist 108:499-506.

Quince C, Shuter BJ, Abrams PA, Lester NP. 2008. Biphasic growth in fish II: empirical assessment. J. Theor. Biol. 254(2): 207-214.

Weber, D. W. and K. D. Fausch. 2003. Interactions between hatchery and wild salmonids in streams: differences in biology and evidence for competition. Canadian Journal of Fisheries and Aquatic Sciences 60: 1018-1036.

Wilson, C.C. and D.O. Evans. 2010. Algonquin's silver lake trout: highlighting the history, habitat, and concerns for a unique biodiversity element. Aquatic Research and Development Section. Ontario Ministry of Natural Resources. Peterborough, Ontario.

Wilson, C. C., and N. E. Mandrak. 2004. Chapter two: History and evolution of lake trout in Shield Lakes. Pages 21-35 in J. M. Gunn, R. J. Steedman, and R. A. Ryder, editors. Boreal Shield Watersheds: Lake Trout Ecosystems in a Changing Environment. CRC Press LLC.

Chapter 3 – Life History Influence on the Energy Allocation towards Growth, Reproduction and Storage in Common Environment Raised Hatchery Lake Trout Stocks subjected to Food Limitation

INTRODUCTION

Predicting how organisms can respond to stressors is very useful to any type of management, and has been the focus of many studies (Frisch and Anderson 2000; Sloman et al. 2001). However, in the past, individuals of a species have been managed as if all populations respond in the same way to a stressor, despite intra-specific differences shown in response to stressors (Schreck et al. 2001; Schreck 2010). Life history adaptations have been thought to mediate responses to stressors, and indeed, studies on species with different life histories suggest that this is true (Rose 2005; Spromberg and Birge 2005). However, very rarely are populations within a species studied for their response to stress. This study looks at how lake trout from different environments with different life history strategies (Chapter 2) respond to food limitation.

Life history characteristics, such as age at maturity, size at maturity, and egg size and number as a function of age are the evolutionary products of energetic tradeoffs that that maximize lifetime reproductive success (Pianka 1976; Jennings and Beverton 1991; Kozlowski 1996). Within a species, populations that face diverse environments can show significant differences in life history characteristics and these differences can mediate stress responses (Jennings and Beverton 1991; Shuter et al. 1998; Purchase and Brown 2001). In Chapters 1 and 2, I outlined how energy allocation can change throughout the season and can be altered based on different pressures (mortality, density dependence, etc.) and I assessed the status of field caught lake trout compared to hatchery lake trout. In this chapter, I apply the conceptual model and information learned in Chapter 2 to make predictions on how stocks explored in Chapter 2 would respond to a food limitation stressor. I measured percent lipid, growth and reproductive output every two months over the course of two years on individually identified female lake trout given different rations, from four different lake trout stocks (Kingscote, Michipicoten, Killala and Manitou – see Chapter 2) and determined if there were differences, and if such differences could be predicted based on conceptual model built in Chapter 1 and Chapter 2.

Seasonal Energy Allocation

Iteroparous, long-lived fish from temperate regions do not allocate energy equally to reproduction, growth and storage throughout the year; there tends to be seasonal variation (Jokela 1997; Henderson and Wong 1998). Generally, during summer months, metabolism and growth is high, due to increased prey availability and higher temperatures (Chapter 1, Hill and Magnuson 1990). Iteroparous fish have also adapted their timing of spawning events such that when the fry emerge, they will have ample food available as presented in the match-mismatch hypothesis (Cushing 1969; Beauchamp et al 2004). In lake trout, this occurs in the spring (Stauffer 1981; Marsden and Krueger 1991). During the winter months, growth and metabolism slows down considerably, along with prey availability. Given these broad environmental constraints that are universal to lake trout, I expected to see seasonal variation in energy allocation towards growth, reproduction and lipid storage throughout the year, and that such allocations are hard wired. Seasonal growth, lipid reserves, and survival have been linked to reproduction in a variety of fish species (Heino and Kaitala 1999; Lambert and Dutil 2000; Hurst and Conover 2003). Therefore, when I measured lipids and growth on individual lake trout every other month for two years, and determined reproductive investment each year, I explored the hypothesis that individual fish will show differences in growth and lipid allocation depending on where they are in gonadal growth phase, with slower growth during period of gonadal growth and lipid deposition. More specifically, from the energy allocation model in Chapter 1, I hypothesized that percent lipid would increase until the spawn and would quickly decrease during the post-spawning season as energy from these lipid reserves are moved towards increases in length from post-spawn to the following summer. I expected every stock to show seasonal variation, but I expected the Kingscote stock held in the hatchery to have the highest percent lipid during the spawning season because of their low-energy diet/ high food conversion efficiency in the wild and the excess food received in the hatchery. The piscivorous stocks held in the hatchery were expected to follow similar seasonal patterns as the Kingscote, but have lower percent lipids overall because they are adapted to a higher-energy diet in the wild and have a lower food conversion efficiency.

Effects of Ration on Seasonal Growth and Percent Lipid

In this study I maintained four different lake trout stocks (Kingscote has two year classes) in a common environment for two years and I manipulated food rations and tracked seasonal lipid and growth and reproductive output. This study continued from a previous study where half the individuals were maintained on a low food ration and half were maintained on high food ration. For my study, I maintained a subset from each stock on a high ration, and a subset on a low food ration. I also switched a subset of individuals from each stock (except Killala because of limited supply of fish) from a high ration to a low ration, and from a low ration to a high ration and followed these “switchers” for two years to see how varying food abundance affects growth, lipid storage and reproduction. I hypothesized that food ration will affect the maximum values of percent lipid and growth rates, while not affecting the general seasonal patterns. I expected individuals maintained on a high ration to have the highest lipid levels and growth rates throughout the season, while the individuals maintained on a low ration to have the lowest percent lipid and growth rates throughout the season, because of the amount of available food. The fish that have switched rations are expected to have intermediate percent lipids and growth relative to fish held at a constant ration (e.g. High-Low fish will have lipids and growth levels higher than Low-Low individuals but lower then High-High individuals). The effects of fish switching rations from a limited ration to an increased ration was documented in Tian and Qin (2004), in which a suspected increase in food-conversion efficiency allowed fish that were switched from a Low to a High ration to surpass body weight of fish held at a high ration throughout the study. Applying the concept of this observed compensatory growth to my study, I expected that this increased ration in the Low-High treatment will allow fish from these treatment to see increased growth and percent lipid over the Low-Low fish, and that these values may approach or surpass the values of High-High fish, if two years is sufficient to detect this hypothesized compensatory growth. In the case of the High-Low ration, it is hypothesized that these individuals will show decreased growth relative to the High-High ration because of energy intake and that these fish will have lipid levels and growth that drop to near the levels of the Low-Low individuals because of the hypothesized decrease in food conversion-efficiency created by exposure to high ration levels previously.

Stock-specific Percent Lipid, Growth, and Reproductive Output

I hypothesize that each stock will differ in magnitude on how they allocate energy towards growth and lipids and reproductive output based on conceptual models presented in Chapter 2 and information from the field. As summarized in the stock-specific conceptual model in Chapter 2 (Table 5), I expect Manitou, a short-lived stock with high lipids in the field, to have low lipid levels in the hatchery and have slow growth rates and reproductive output. Adaptations related to the short lifespan of the Manitou stock were expected to manifest in the hatchery individual as evidenced by prioritizing more energy allocated towards growth and reproduction; I hypothesize this because they have adapted to a short life span and want to maximize lifetime reproductive output before they die. In the hatchery system, I expect them to be devoting all possible energy stores (lipids) to reproduction and growth, and therefore they will have lower lipid levels than the other stocks. I expected the Kingscote stock to have high lipid levels and growth rates in the hatchery relative to other stocks because they are planktivorous in the wild and if adapted to such a lifestyle, would presumably have higher energy-conversion efficiency (Table 5, Chapter 2). This higher energy conversion efficiency should result in excess energy in the hatchery to allocate towards lipids and growth. The Michipicoten stock was expected to have moderate to fast growth rates and low reproductive output because of their long-lived life history strategy in the field (Table 5, Chapter 2). Individuals from the Michipicoten stock, on average, have more years to grow and reproduce, and tend to maximize lifetime reproductive output later in life, so they are expected to have lower energy allocated towards reproduction and more towards growth in the younger ages in the hatchery. The Killala stock is piscivorous, but very slow growing in its natural environment and is expected to have higher lipid levels in the hatchery than Michipicoten and Manitou, but lower lipid levels relative to the Kingscote stock (Table 5, Chapter 2). I expect that the stocks adapted to lower-energy diets in the wild (the Kingscote and the Killala) will be the least sensitive to a change in ration while stocks that have abundant food resources in their natural environment (Michipicoten and Manitou) will be more sensitive to changes in ration because they are receiving less energy than that to which they are adapted. The specific variables that show the highest sensitivity in each stock will give insights into the relative priorities of each stock by showing which variables they work to conserve while others are sacrificed. For example, the Kingscote have the largest eggs and relatively smaller numbers of eggs. Furthermore, they do not show indication of changing reproductive output over time (Chapter 2), so egg production may be insensitive to ration.

Reaction Norms

I also wished to determine if energy allocation towards growth, reproduction and percent lipid show relationships predicted by life history. This approach has implications for management and I explored whether lipid storage would be predictive of reproductive output. Such a relationship would have great utility, particularly if a non-invasive method could be used to predict a usually lethal and labor intensive way of estimating fecundity. I use the term “reaction norm”, which usually refers to the possible phenotypes that could be expressed when an organism is exposed to a range of environmental conditions, and also describes what changes occur in a phenotypic trait as environmental conditions, such as food availability, change. (Stearns and Koella 1986; Barot et al. 2004). In this study, I modify the term “reaction norm” to describe responses of a group (stocks of lake trout) to a change in the environment, rather than evaluating the response of an individual across varying environmental conditions. In this case, I use lipid measurement as a way to measure the “environment” or food availability, and I explore whether lipid levels can predict the number of eggs produced and if so, determine if the reaction norms are specific to a particular stock.

To evaluate the potential for reaction norms, selected fish from each stock were swapped from their initial ration level (high or low) to the alternate ration level to determine if the relationship between lipids and fecundity changes when ration level is manipulated. If a robust relationship is found to exist in this relationship between percent lipid and egg number, this would provide a tool for managers to predict how a certain stock’s reproductive output will change in a given environment, based on percent lipids and associated food availability. I hypothesized that reaction norms would exist between lipid levels and egg number for each stock within a given year across rations and that the relationship would be less stable between years, particularly in short-lived stocks in which annual changes in reproductive strategy are expected to be more pronounced because they have less time to reach an age at which their reproductive output is maximized

More specifically, I hypothesize that the Kingscote stock would have the least sensitive relationship between lipids and egg number because they were overfed in the hatchery study. I hypothesize that the Manitou and Michipicoten stocks would have the most sensitive response to changes in ration because their percent lipid, and presumably energy intake, most closely reflects natural conditions in the hatchery. The Michipicoten stock was expected to have a sensitive relationship between lipid levels and egg number because they are underfed in the hatchery relative to their natural energy intake. I hypothesize that the Killala stock will have less sensitivity in the relationship between the lipid levels and egg number than the Michipicoten and Manitou because the Killala stock has relatively low lipid levels in the field, presumably due to competition for food resources, and thus are also overfed in the hatchery (Table 5).

If these hypotheses regarding stock-specific energy allocation and reaction norms are true, I am closer to predicting energy allocation towards growth and reproduction based on population mortality and environment (available energy) using metrics such as age and lipid measurements. Although the response of stocks in the hatchery to limiting environments does not necessarily provide a perfect prediction on their performance in the wild, these stock-specific responses of individuals to food limitation in a hatchery setting can be used as a starting point for general predictions on how these fish would respond to a new environment.

Table 14. Summary of hypotheses regarding responses of five lake trout stocks to common environment experiment.

Hypothesis	Description
Hypothesis #1	Individuals will differentially allocate energy towards growth and reproduction throughout the season based on where they are in their gonadal growth phase.
Hypothesis #2	Stocks will show significant differences in responses of percent lipid, growth, and reproductive output to ration based on Table 5 in Chapter 2.
Hypothesis #3	Reaction norms exist between percent lipid and egg number within each stock within a year in the Michipicoten, Killala, and Manitou stocks.
Hypothesis #4	Reaction norms exist between years in the long-lived Michipicoten and Killala stocks.

METHODS

Hatchery Fish used in this Study

Lake trout used in the study were descendants of fish brought into the hatchery as eyed eggs from wild collections performed by the Ontario Ministry of Natural Resources (OMNR). The fish used in this study were from gametes spawned in 1999 (Kingscote and Manitou) or 2000 (Michipicoten, Killala, and Kingscote). The Killala, Manitou, and Michipicoten individuals used in this study were two generations removed from the wild. Both year classes of the Kingscote stock used in this study were first generation hatchery fish. The fish were reared at the OMNR fish culture station in Codrington, Ontario that has high quality water from a nearby stream. Common conditions in the hatchery included water temperature, oxygen, feeding schedule and ration (0.6% of total tank biomass), size of holding tanks, and tank densities that were regularly adjusted for minimal mortality rates of approximately 1-2 fish per tank per year. Males from each stock and individuals from the 2000 Slate stock were housed in experimental tanks to ensure that tank densities were similar at the start of the study, and so that females were exposed to potential male priming pheromones (Stacey et al 2003) (Table 15). Prior to sexual maturity in 2006, the individual stocks and year classes were kept in separate holding tanks. Once they reached sexual maturity, they were branded to allow for individual identification and transferred to eight 1,200-liter circular tanks and stocks were mixed together (Table 15).

Treatments

From 2006 to 2007, ration level was manipulated for a study in which half the fish received a low ration level (0.2% tank biomass) and the other half of the fish received a high ration level (0.4% tank biomass) (Murphy et al in prep). From 2006 to 2008, individual fish were monitored for size, lipid content and reproductive output. Then, at the beginning of this study in February 2008, the stocks were divided into 4 treatment groups with equal density (Table 15). One group from each stock was randomly selected to be maintained at a low ration (0.3% biomass) and another group from each stock was randomly selected to be maintained at a high ration (0.5% biomass). An additional group was also randomly selected from each stock (except for Killala because there were not enough fish) to be switched from a low ration feeding regime (0.2% biomass) to the high ration feeding regime (0.5% tank biomass). The last group was randomly selected to be switched from a high ration feeding regime to the low ration feeding regime. The specific rations in the low and high treatments were changed between studies to maintain health. A minimum of 16 fish from each stock were maintained at an original ration (high or low), while the remaining fish were moved to the alternate ration level (Table 15). These rations and tank configurations were maintained for the entire duration of this study. Manipulation of ration level resulted in four treatments; the terminology below will be used throughout Chapter 3:

1) **High-High** = Fish that were given the high ration (0.4%) prior to this study and were also given the high ration (0.5%) during the current study (2008-2010).
2) **High-Low** = Fish that were given the high ration (0.4%) prior to this study and were given the low ration (0.3%) during the current study (2008-2010).
3) **Low – Low** = Fish that were given the low (0.2%) ration prior to this study and were also given the low ration (0.3%) during the current study (2008-2010).

4) **Low – High** = Fish that were given the low ration (0.2%) prior to this study and were given the high ration (0.5%) during the current study (2008-2010).

Table 15. Summary of initial fish densities and composition of lake trout stocks housed in a common environment experiment in OMNR hatchery in Codrington, Ontario.

Tank No.	**Ration**	**Total Fish**	**2000 Kingscote**		**2000 Michipicoten**		**2000 Killala**		**2000 Slate**		**1999 Manitou**		**1999 Kingscote**	
			Male	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**
1	High-High	30	1	8	1	10	1	9						
2	High-Low	31	2	7	4	8	0	2	2	6				
3	Low-Low	28	1	8	2	7	1	9						
4	Low-High	28	2	8	2	8	1	0	2	5				
5	High-High	29									2	12	3	12
6	High-Low	30									3	11	6	10
7	Low-Low	30									2	12	2	14
8	Low-High	30									2	11	4	13

Groups of fish were switched to the alternate ration to simulate variability in allocation patterns and to determine if patterns in percent lipid, growth and reproductive output remained similar to patterns shown in low and high rations.

Measurements

Every 8 weeks, fish were briefly anaesthetized using MS-222 at a low level sufficient to minimize fish stress during handling. Once fish were anesthetized, I measured length, weight and percent lipid. A non-invasive fat meter was used to measure percent lipid in individuals at four locations across the body and get the average lipid level between the four locations (Figure 29). The fat meter uses low power microwaves to penetrate the skin and measure the attenuation of the microwaves by water in the flesh, which is negatively correlated with fat content, allowing for a reliable lipid estimate (www.distell.com). This relatively new technology allowed me to track lipid levels of individuals through time which is not possible using more traditional, lethal methods of lipid analysis. The fat meter was calibrated in a previous study ($r^2 = 0.6117$; Claus 2011), and the reading corresponded to an actual lipid level percentage using the following equation:

$$\text{Muscle Lipid Concentration} = [e^{(1.9436 + \ln(\text{Fat meter Reading})) - 9.5022}] \times 100$$

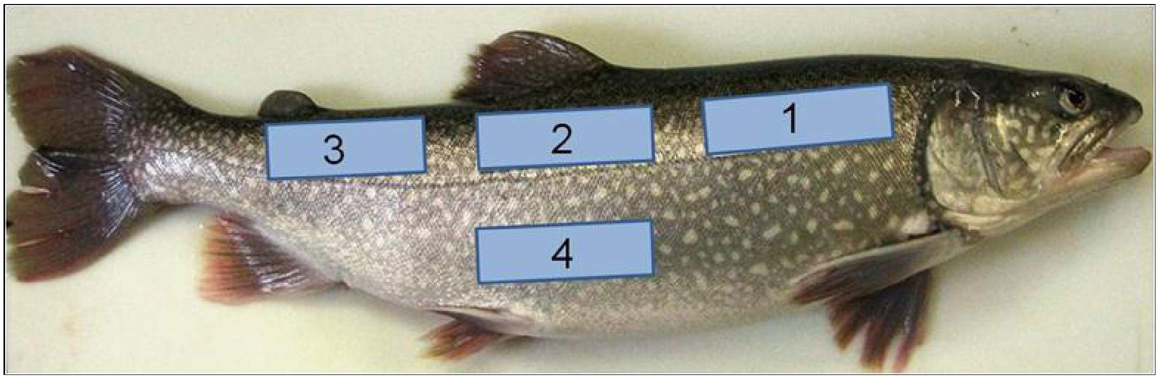

Figure 29. Locations of lipid measurements taken on lake trout using non-invasive fat meter at OMNR hatchery in Codrington, Ontario (Photograph Courtesy of Sara Smith).

During the spawning season (approximately early September through early November) of 2008 and 2009, females were stripped of eggs when ovulated to determine the total volume of eggs spawned and when fish were ripe. Ovulation of eggs was assessed weekly during the Fall seasons by gently applying pressure to the urogenital region. If eggs were easily extruded, the female was stripped and the entire volume of eggs was recorded. A 30-mL sample of eggs was then separated and stored in a 5% formalin solution to enumerate and measure at a future date. The total number of eggs in the 30-ml sample was counted and the number was scaled up to the total volume of the spawn to estimate total egg production for each female. Also, thirty eggs were randomly selected from each 30-mL sample to determine egg size by photographing each egg using a digital microscope and measurement software (Leica Application Suite®). The diameter of each egg was determined by averaging six measurements that were taken along each egg. Multiple measurements were used to account for irregularities in egg size that occurred after preservation.

Data Analyses

Percent lipid, growth and reproductive output were calculated. The percent lipid from each location on the fish (Figure 29) was averaged to calculate a mean percent muscle lipid for each fish. Growth was calculated as the change in fork length (in millimeters) between a given sampling date and the previous sampling date. In some cases, growth between sampling dates was a small negative value; these data were changed to a value of zero.

The number of eggs per female was standardized by dividing by the fork length to get a value in eggs/mm because of the strong relationship between spawner length and egg number (Chapter 2).

The daily growth rate and percent lipid were calculated for all rations within each stock and within each year; the significance of differences in percent lipid between July and spawning season were calculated using a repeated measures analysis. The daily growth rate was calculated as the average daily increase in fork length (in mm) that occurred between sampling dates. In the case of the growth rates going into the spawn, the average annual spawning date for each stock was used as the comparison date for growth calculations. I compared the growth rate (between December and the proceeding spawn) within stock between rations, within year using an ANOVA with Tukey-Kramer post-hoc comparisons. I also compared the mean percent lipid (spawning time percent lipid), average egg size, and number of eggs/mm within stocks between rations and within year using an ANOVA with Tukey-Kramer post-hoc comparison.

Paired t-tests were used to compare egg size and egg number values between hatchery years in the combined-ration data within each stock. The same method was used to determine the significance of ration-specific changes in egg size and egg number between years.

I applied Akaike's Information Criterion (AIC) to choose the model of best fit to describe the relationship between eggs/mm and mean percent lipid within each stock. The following types of relationships were analyzed to determine the model of best fit: Michaelis-Menten, Sigmoidal, Hyperbolic, Linear, and Logarithmic. The chosen model was the model with the lowest AIC value. Models were generated for each stock within each year (all rations combined) and additionally within each year on a ration-specific basis. In the case of the ration-specific analysis, specific regressions were applied to data from those fish whose rations which switched ration level ("switchers", i.e. High-Low and Low-High) and the fish that remained at a constant ration throughout the study ("non-switchers" i.e. High-High and Low-Low).

The parameter values in each regression, or model, applied to the data were estimated using the regression wizard in Sigmaplot 12.0 and SAS 9.0. To determine if reaction norms could potentially exist, I compared the AIC values between the model of best fit with an alternate model which was generated using data from the alternate year or ration group. Differences in AIC values were calculated between the model of best fit and alternate model to determine if there is substantial support to suggest the initial model is a better predictive model than the alternate model. Similar AIC values suggest the existence of reaction norms because a change in ration or year does not change the relationship between egg number and mean percent lipid. Specifically, for each stock, I applied the model of best fit from Year 1's data to the data in Year 2, and vice versa, and compared the AIC values between years based on this common regression that was applied to each year's data. An identical procedure was completed to compare ration groups, or the switchers and non-switchers. Within each stock, the regression assigned to the non-switchers was applied to the data in the switchers, and vice versa, to determine the difference in AIC values.

Although the comparison of differences in AIC values is not a significance test, these comparisons can provide substantial support for the initial model being the best predictor model over the alternate model (Anderson et al. 2001; Bence and Hayes 2004). While there are varying approaches in the evaluation of AIC difference, a general guideline proposed in Burnham and Anderson (2002) is that models with a difference of AIC less than or equal to two ($AIC_{Initial} - AIC_{Alternate} \leq 2$) have strong support to show there is no difference between the alternate model the model of best fit in terms of their ability to describe the data (Burnham and Anderson 2002; Stylianou et al. 2013). AIC differences in the range of 4 to 7 ($4 \leq AIC_{Initial} - AIC_{Alternate} \leq 7$) have considerably less support to show the alternate model equals the best model in its predictive ability (Burnham and Anderson 2002). Lastly, AIC differences of greater than 10 ($10 \leq AIC_{Initial} - AIC_{Alternate}$) have essentially no support to show that the alternate model fits the data as well as the original model (Burnham and Anderson 2002). Although there is no consensus on these cutoff values to definitively say when a model outperforms another, a conservative value was put forth in Stylianou et al. 2013 which states models must have a difference of 6 in AIC values to say that they differ. In this case, based on the general guidelines put forth in Burnham and Anderson 2002 and the specific cutoff used in Stylianou et al. 2013, I assigned a minimum AIC difference of 6 to say that two model differ in their predictive ability.

RESULTS

Seasonal growth across sampling dates for the two years was variable, but every stock showed decreases in growth during the spawning season followed by increases in growth rates after the spawn, with the highest growth rates observed in July in Year 1 and May in Year 2 (Figure 30 - Figure 35). Michipicoten showed the highest growth rates, followed by Kingscote, then Killala and finally Manitou (Figure 30 - Figure 35). Growth rates between rations showed a consistent pattern between stocks. For both years, fish maintained at the highest food ration had the highest growth rates, while the fish maintained at lowest ration had the lowest growth rates (Figure 30 - Figure 35). In Year 1 of the study, the switchers had intermediate growth rates, with the fish switched from the high to the low ration growing faster than the fish switched from the low to high ration, although these differences were not significant (Figure 35). By Year 2, the switchers had recovered growth rates to match the fish in their new ration group (Figure 35, Table 22, and Table 23). Growth rates exceeded the High-High ration, but not significantly so, in the Michipicoten fish that were switched from the low to high ration by Year 2.

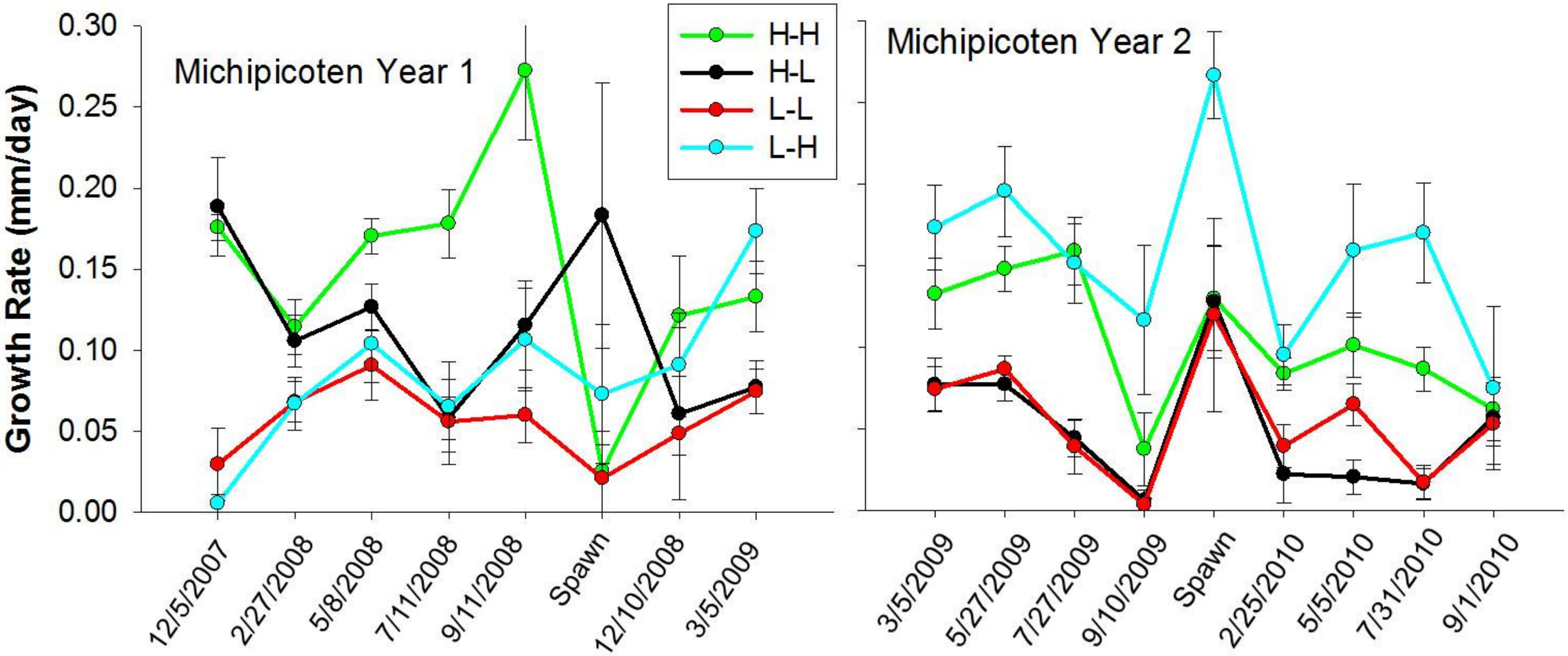

Figure 30. Change in growth rate (in mm/day) of Michipicoten stock housed in a common environment experiment exposed to one of four feeding regimes in OMNR hatchery.

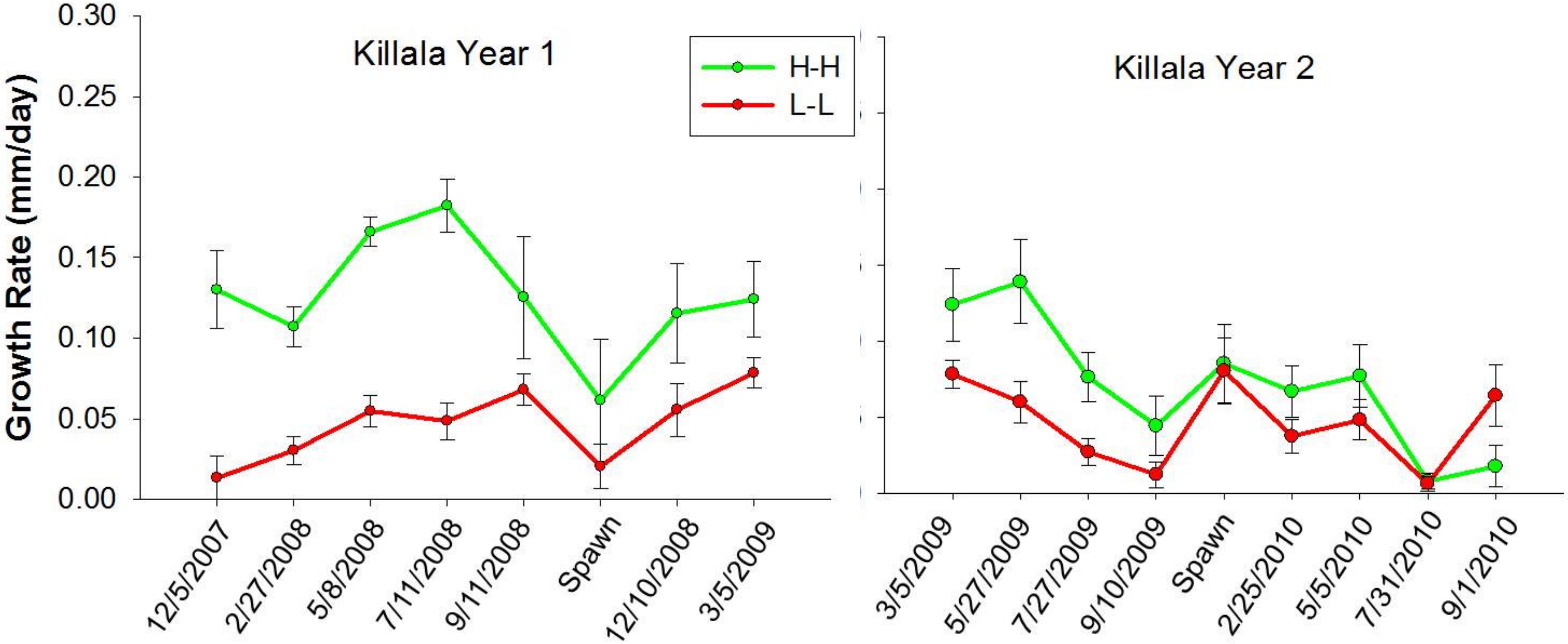

Figure 31. Change in growth rate (in mm/day) of Killala stock housed in a common environment experiment exposed to one of four feeding regimes in OMNR hatchery.

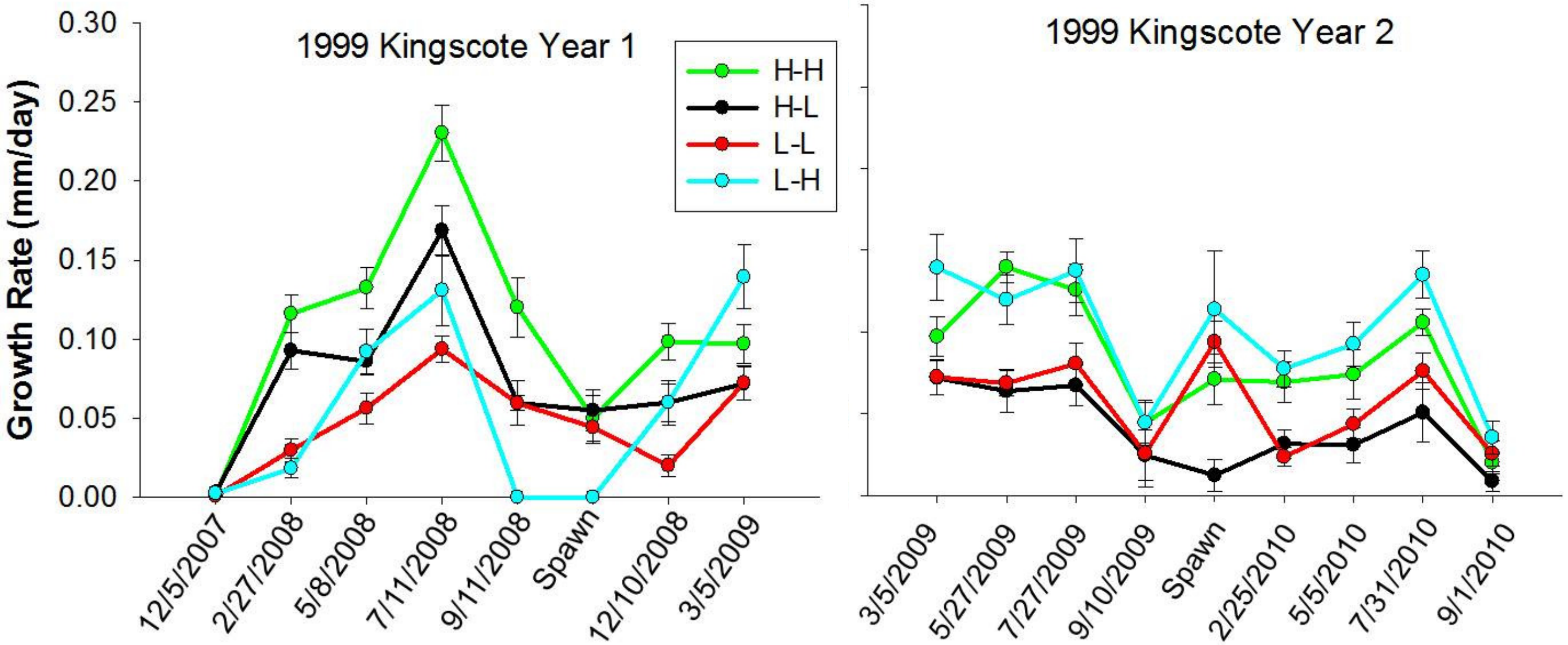

Figure 32. Change in growth rate (in mm/day) of the 1999 Kingscote stock housed in a common environment experiment exposed to one of four feeding regimes in OMNR hatchery.

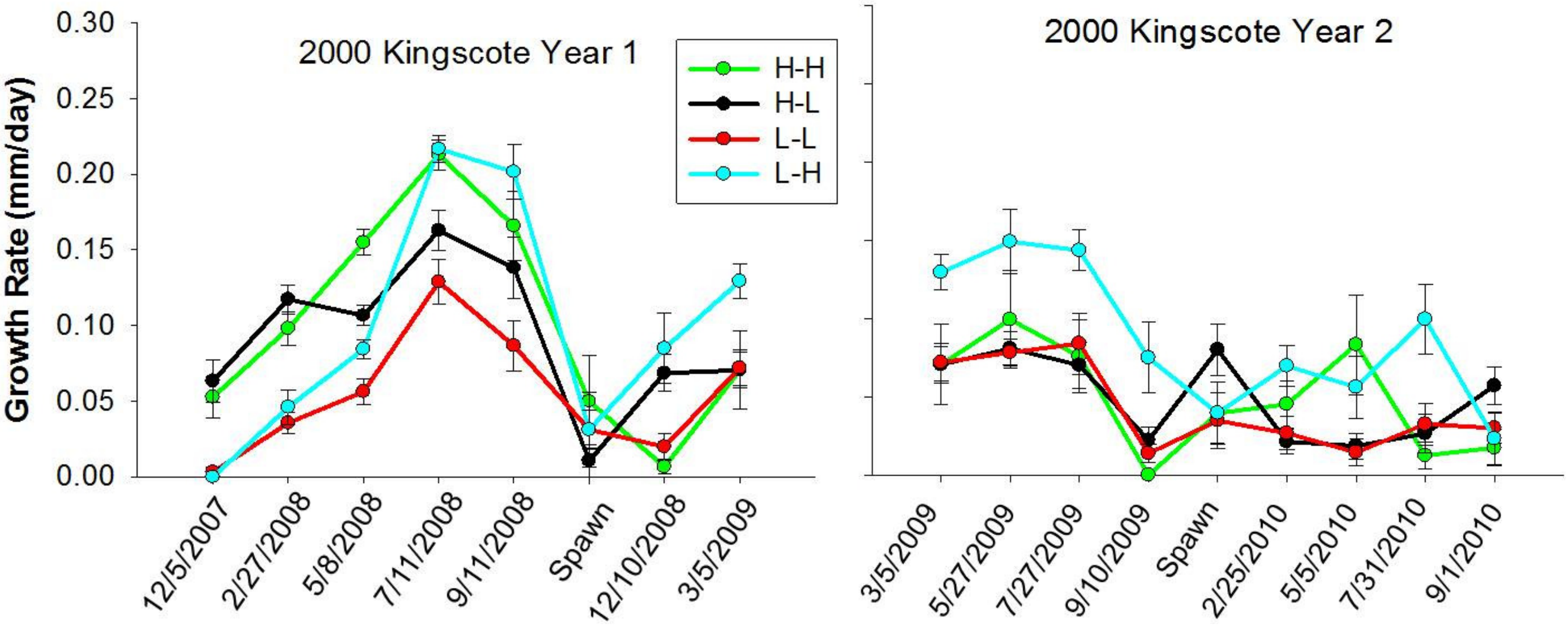

Figure 33. Change in growth rate (in mm/day) of the 2000 Kingscote stock housed in a common environment experiment exposed to one of four feeding regimes in OMNR hatchery.

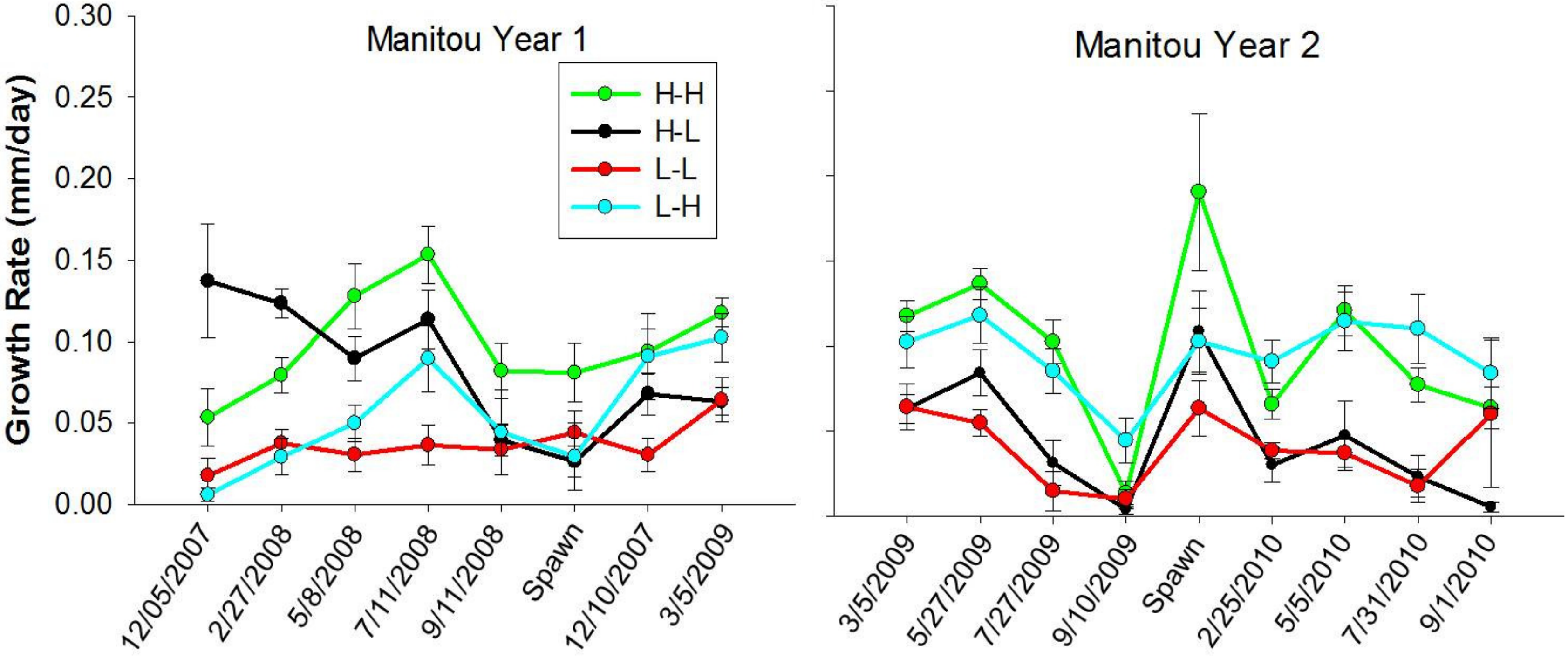

Figure 34. Change in growth rate (in mm/day) of the Manitou stock housed in a common environment experiment exposed to one of four feeding regimes in OMNR hatchery.

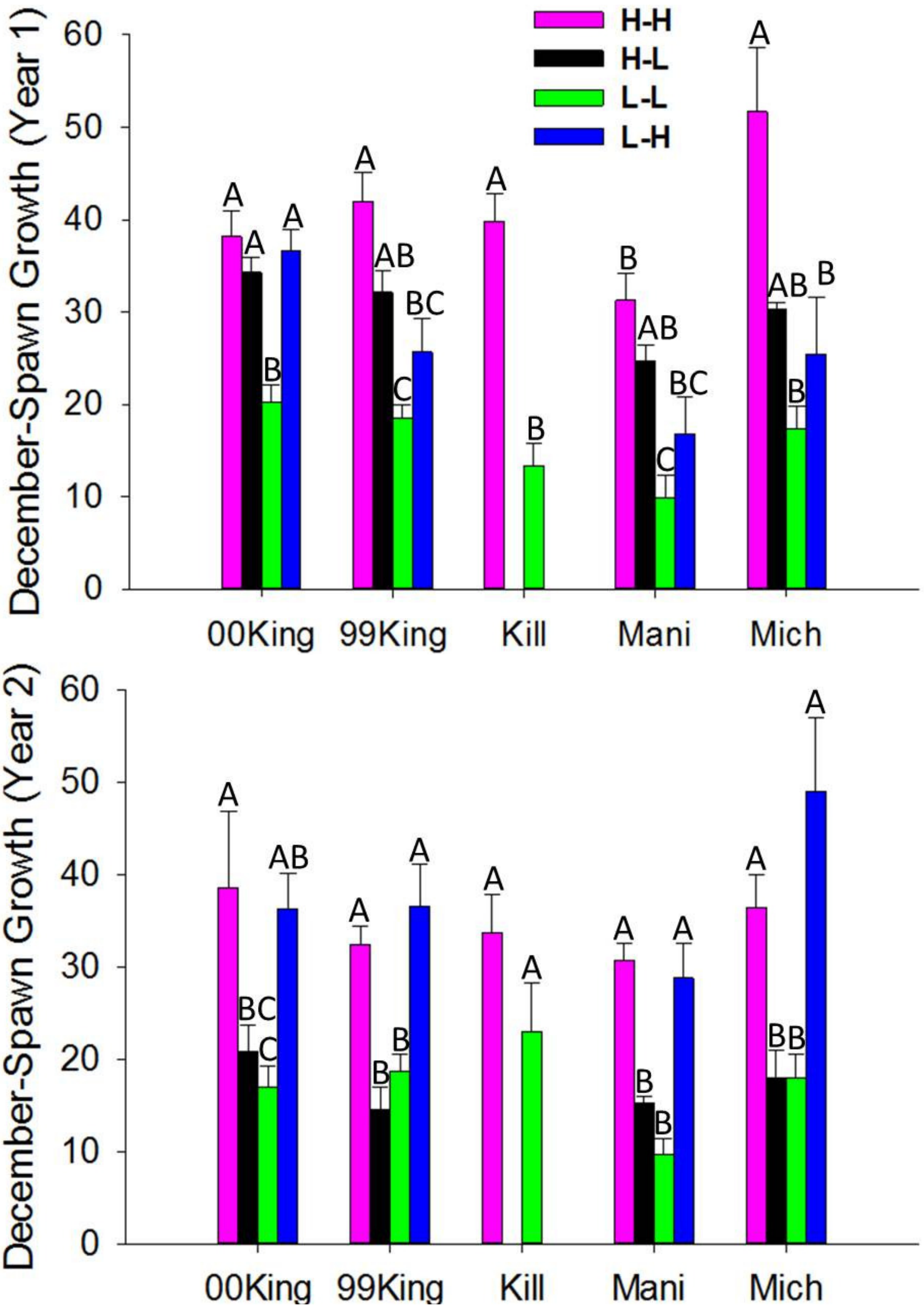

Figure 35. Growth rate of five stocks of lake trout housed in a common environment exposed to one of four feeding rations. Standard error is shown above each bar. Statistical groupings within a stock, based on an ANOVA pairwise comparison with a Tukey-Kramer adjustment are shown above each bar.

General trends in the seasonal percent lipid data of Year 1 show increases in percent lipid level up until the spawn, after which percent lipid decreases into the spring (Figure 36– Figure 40). Year 2 of the seasonal percent lipid data showed a much more constant percent lipid level within a ration of a given stock throughout the entire season (Figure 36– Figure 40). Almost all the ration-specific comparisons showed a significant lipid increase in Year 1 of the hatchery study; only 5 were not significant (Table 20). Year 2 of the hatchery study was different, however, with no significant increase observed in lipids during the course of the year in when rations were combined, and only the High-High ration of the Killala comparisons was significant, out of 18 total comparisons (Table 21).

Kingscote (both year classes) had the highest percent lipid overall (Figure 41), followed by the Killala, then Michipicoten and finally the Manitou, and this order was maintained over both years. The fish that were maintained on a low ration had decreased percent lipid in all stocks but the reduction was smallest in the Kingscote stocks and the same trend was seen in both years. The stocks responded differently to the switched ration. In the first year, lipid levels in the Kingscotes that were switched from low-high rebounded to levels observed in the high ration, whereas it took until the second year for the Michipicoten and Manitou in the low-high ration to rebound to the same level as the High-High ration. The fish switched from high-low ration did show a significant decrease in lipid level to match the fish maintained on a low ration in Year 1 of the 2000 Kingscote stock, Year 2 of the 1999 Kingscote stock, Year 2 of the Manitou stock, and Year 2 of the Michipicoten stock (Figure 37, Table 20, Table 21).

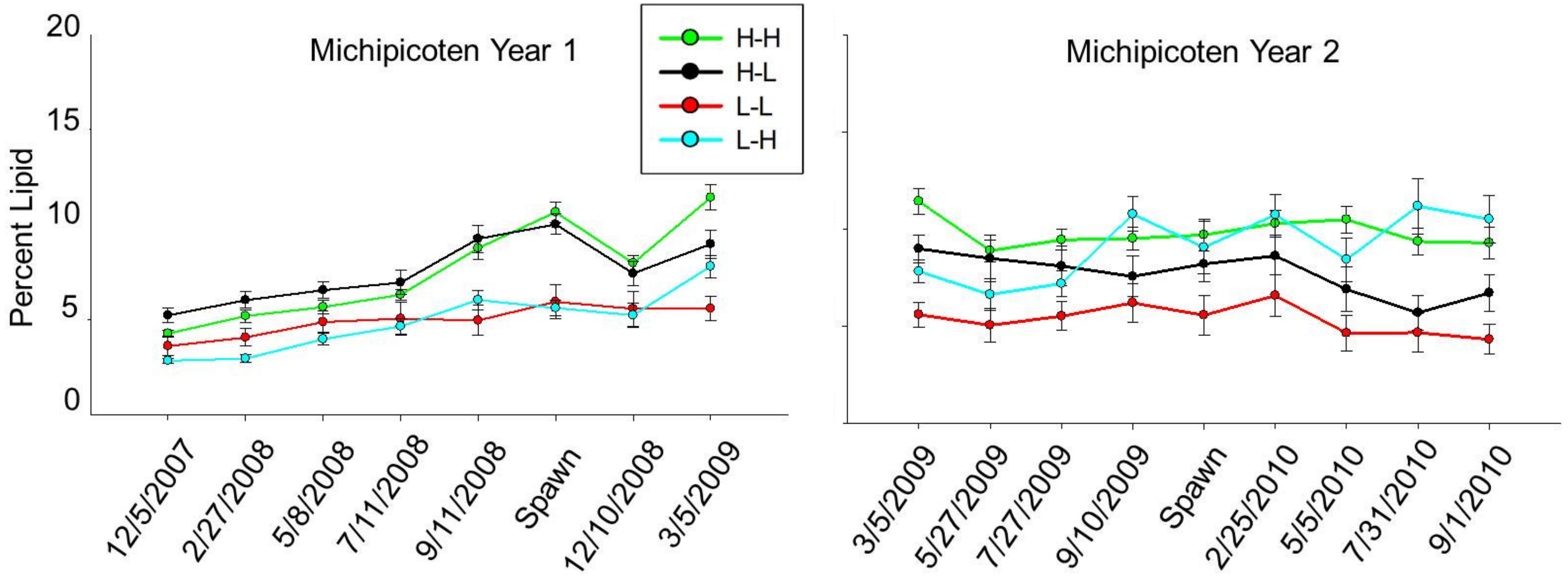

Figure 36. Change in mean percent lipid of Michipicoten lake trout housed in a common environment experiment exposed to one of four feeding regimes in OMNR hatchery.

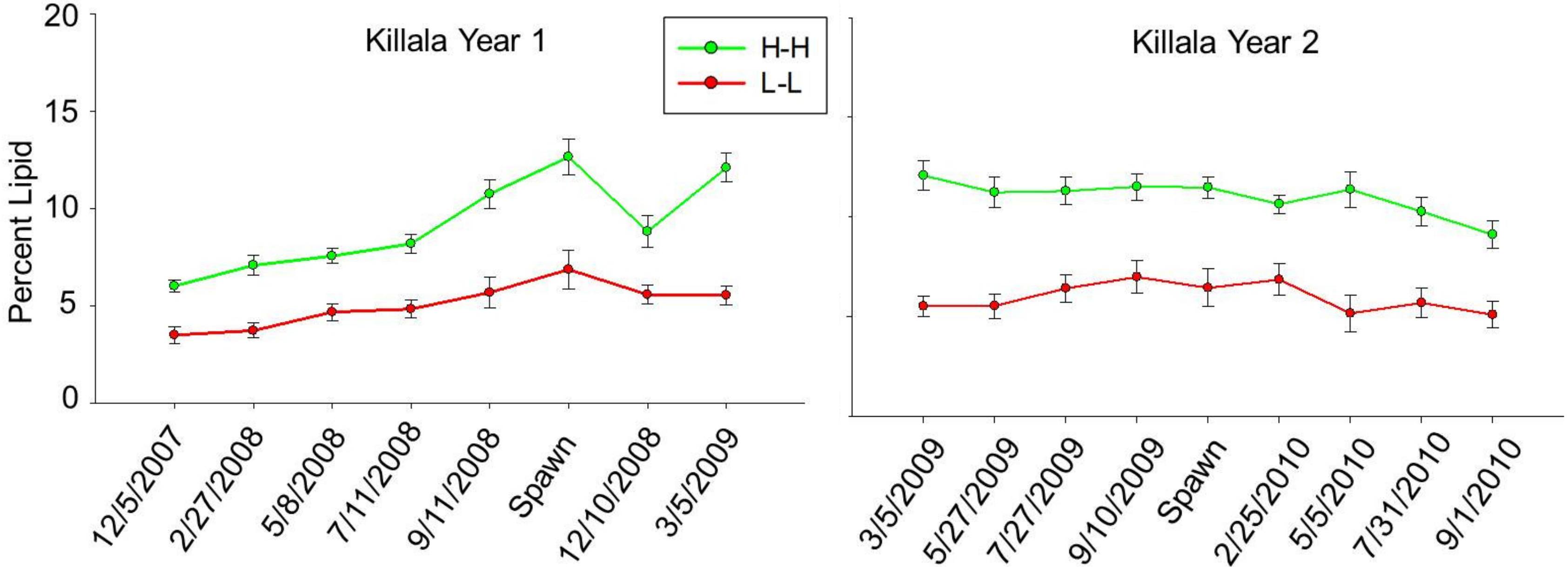

Figure 37. Change in mean percent lipid of Killala lake trout housed in a common environment experiment exposed to one of two feeding regimes in OMNR hatchery.

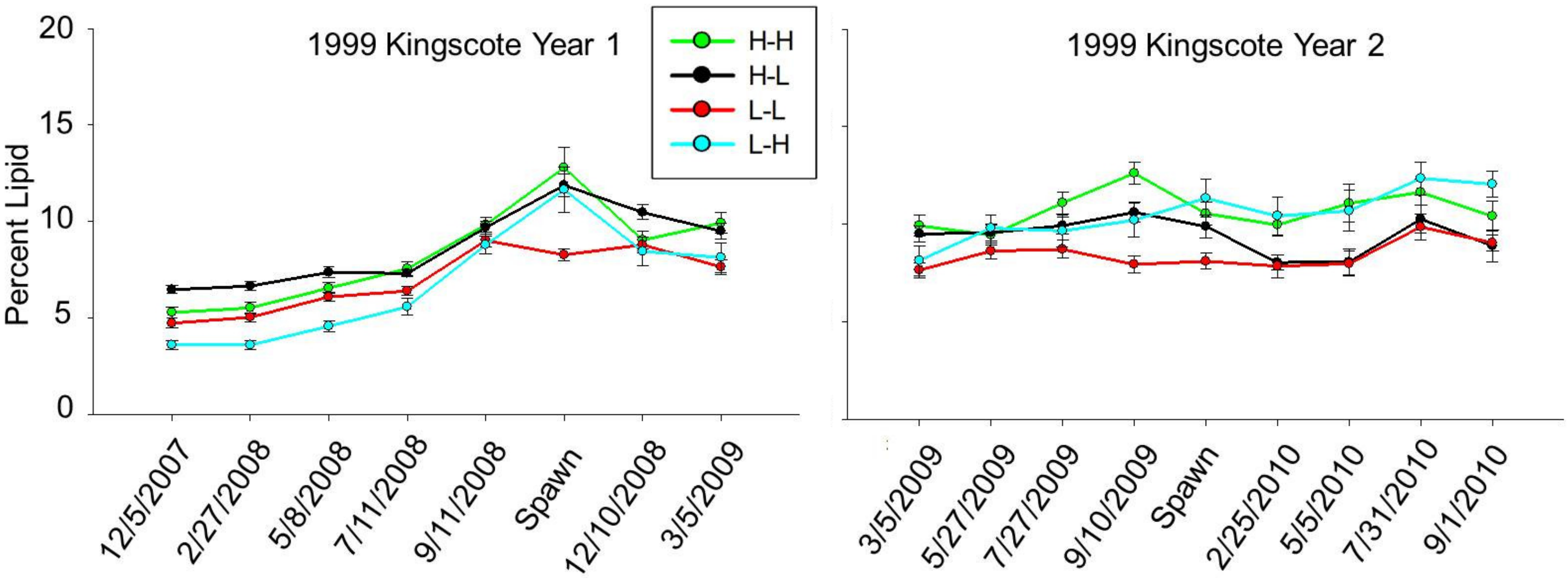

Figure 38. Change in mean percent lipid of 1999 Kingscote lake trout housed in a common environment experiment exposed to one of four feeding regimes in OMNR hatchery.

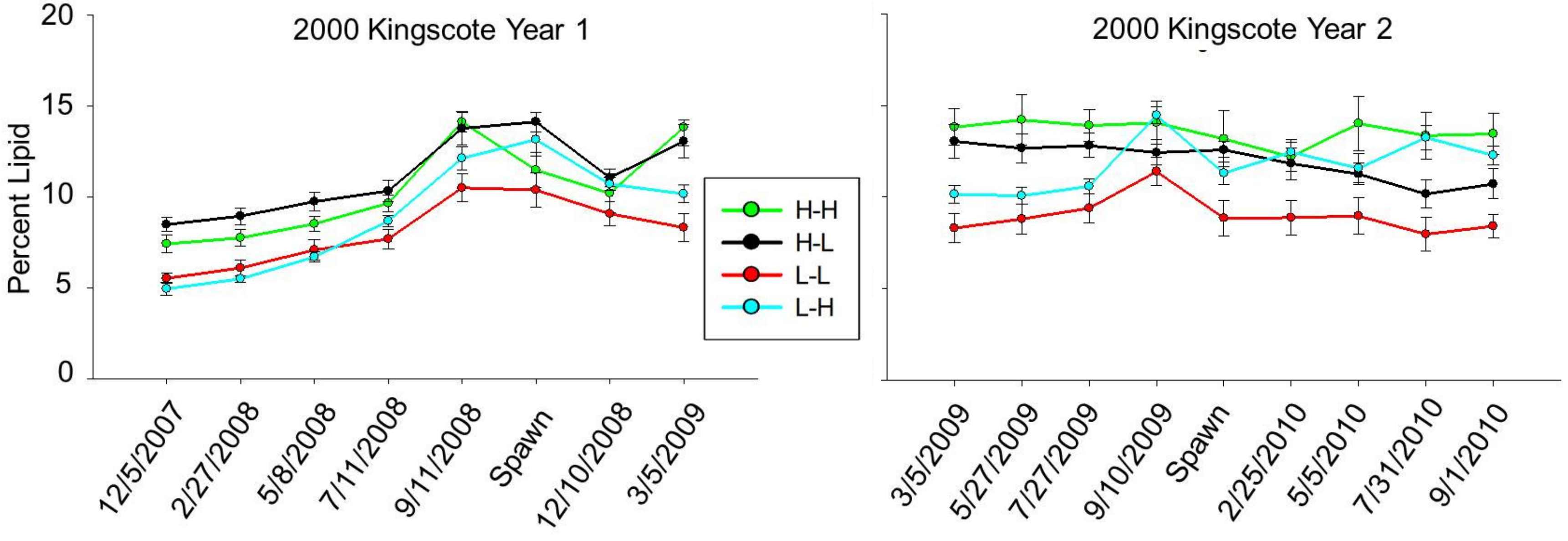

Figure 39. Change in mean percent lipid of 2000 Kingscote lake trout housed in a common environment experiment exposed to one of four feeding regimes in OMNR hatchery.

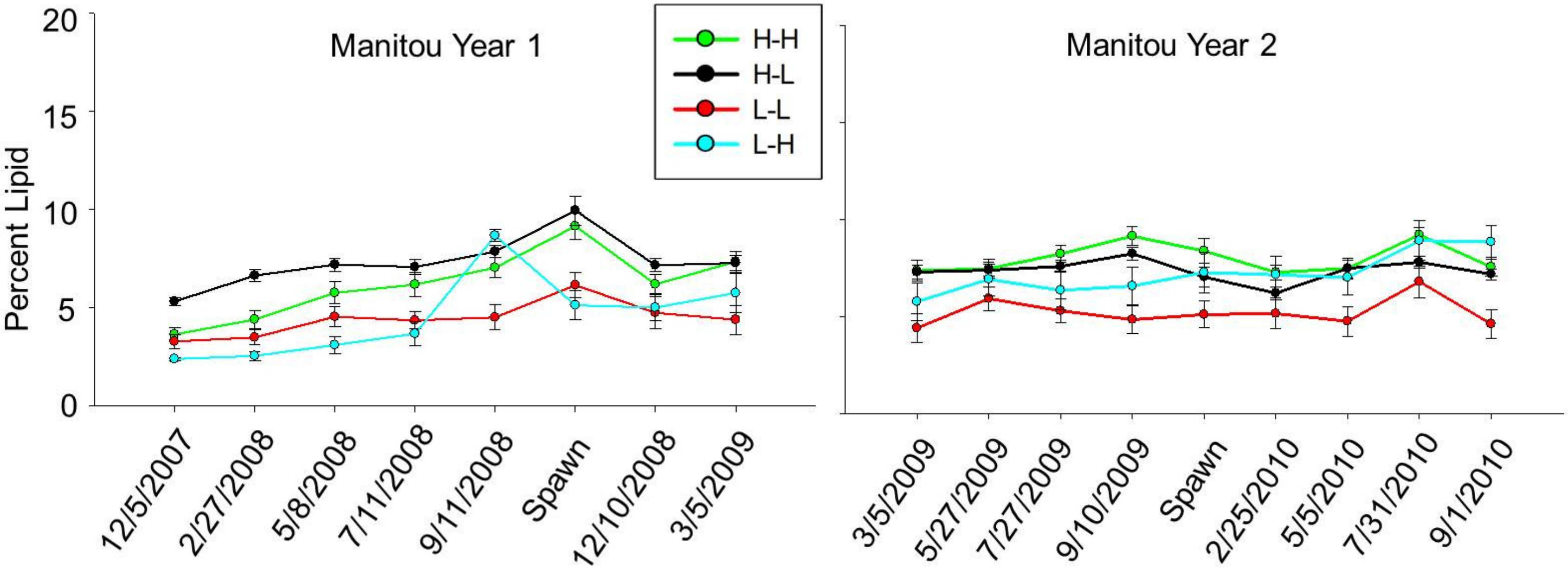

Figure 40. Change in mean percent lipid of Manitou lake trout housed in a common environment experiment exposed to one of four feeding regimes in OMNR hatchery.

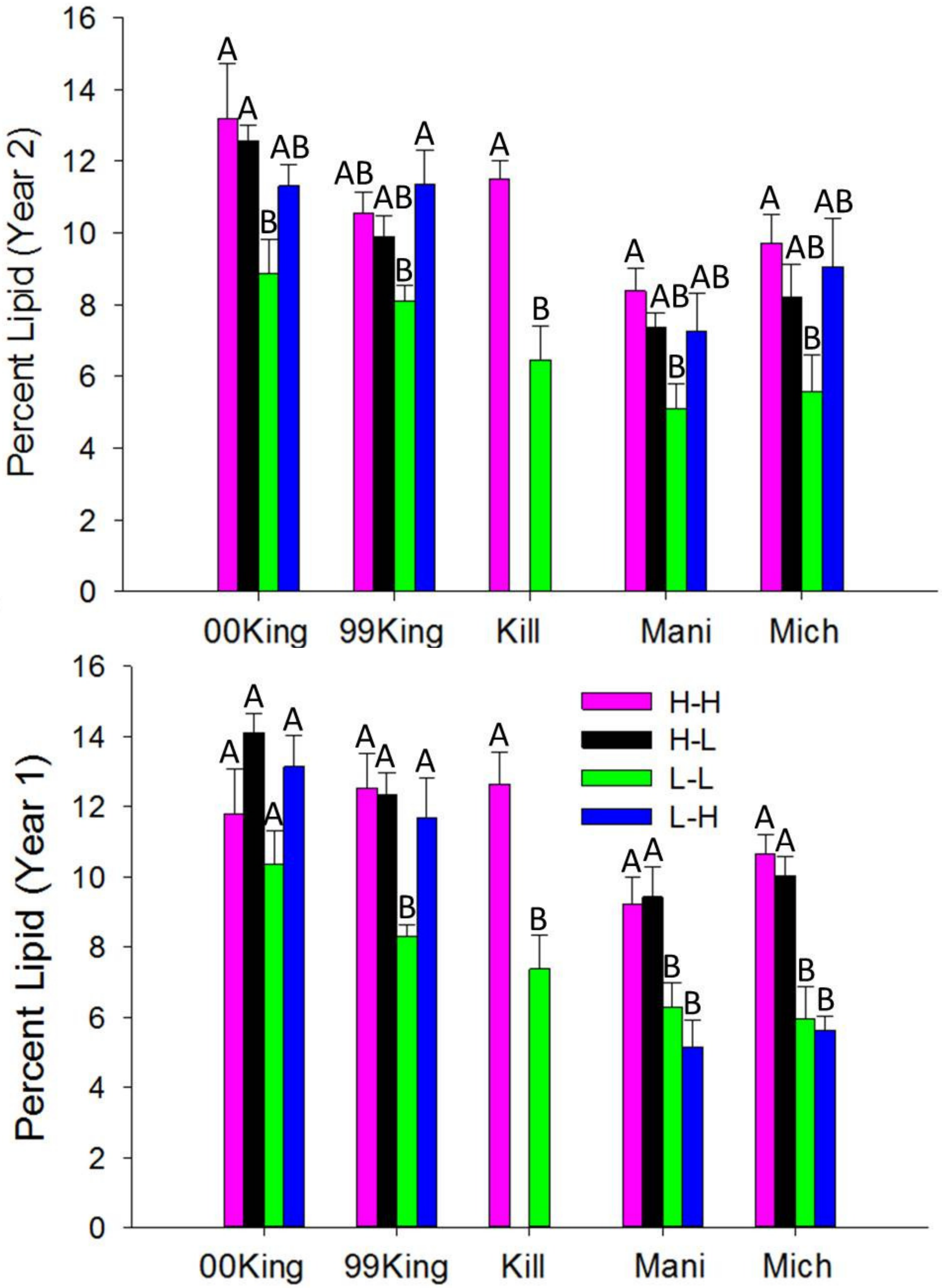

Figure 41. Mean spawning-time lipid levels of five stocks of lake trout housed in a common environment exposed to one of four feeding regimes. Standard error is shown above each bar. Statistical groupings within a stock, based on an ANOVA pairwise comparison with a Tukey-Kramer adjustment are shown above each bar.

Ration-specific egg size did not follow any clear trend within a stock in either year. The only clear trend that was shown was a consistent decrease in egg size between years within a stock in a given ration (Figure 42). Comparison of egg size across stocks within rations showed that, in general, the Killala stock had the largest eggs, followed closely by the Manitou stock. In all cases but the Low-High ration of Year 1, the Kingscotes had the smallest eggs across rations. The Michipicoten egg size decreased in the low-high ration both years, but this decrease was only significant in Year 1.

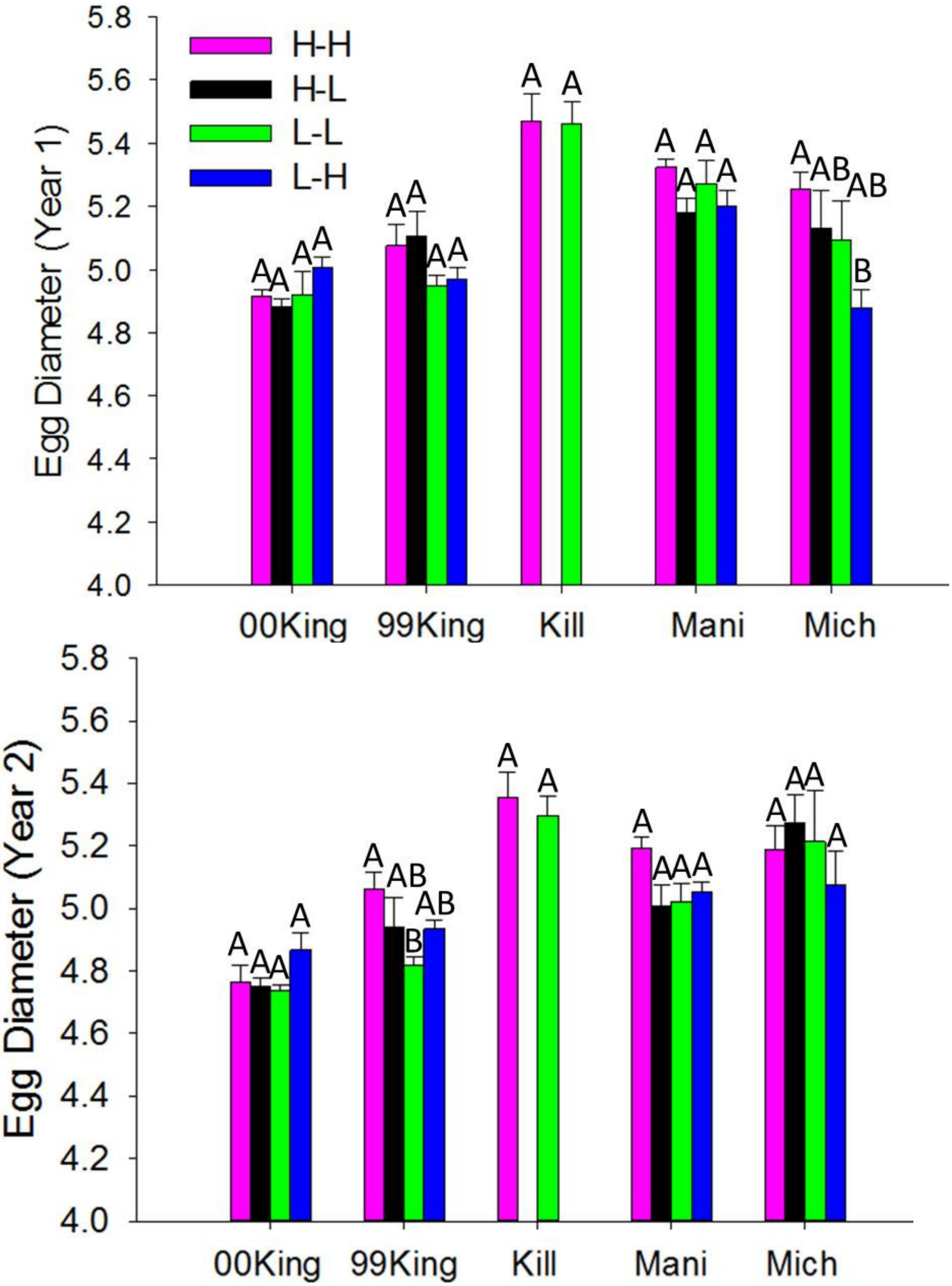

Figure 42. Mean egg diameter of five stocks of lake trout housed in a common environment exposed to one of four feeding regimes in OMNR hatchery. Standard error is shown above each bar. Statistical groupings within a stock, based on an ANOVA pairwise comparison with a Tukey-Kramer adjustment are shown above each bar.

Ration-specific egg number was more variable than egg size as a function of ration. Generally, as the ration was increased, so was the egg number with the "switchers" having intermediate values, but there are small deviations from that pattern in most stocks (Figure 43). The 2000 Kingscote stock had the highest egg number generally. Like growth and percent lipid, the Low-High stock showed a rebound in egg number between years in all stocks. Comparison of egg number across stocks within rations suggested that the Kingscote was the most resilient to low food ration and had the lowest response to reductions in egg number in both years. The Killala stock significantly reduced their egg production in the low food ration. The Manitou and Michipicoten fish switched from a low to high ration in the first year had similar egg production to those maintained in the low ration, while the fish from these stocks switched from the high to low ration still produced eggs at similar quantity to the fish maintained on the high ration. However, the switchers from the Manitou and Michipicoten stocks diverged in Year 2: the switchers from the Michipicoten stocks mimicked egg production from the fish in their switched ration, while the Manitou fish that were switched from high to a low ration still maintained high egg production (Figure 43).

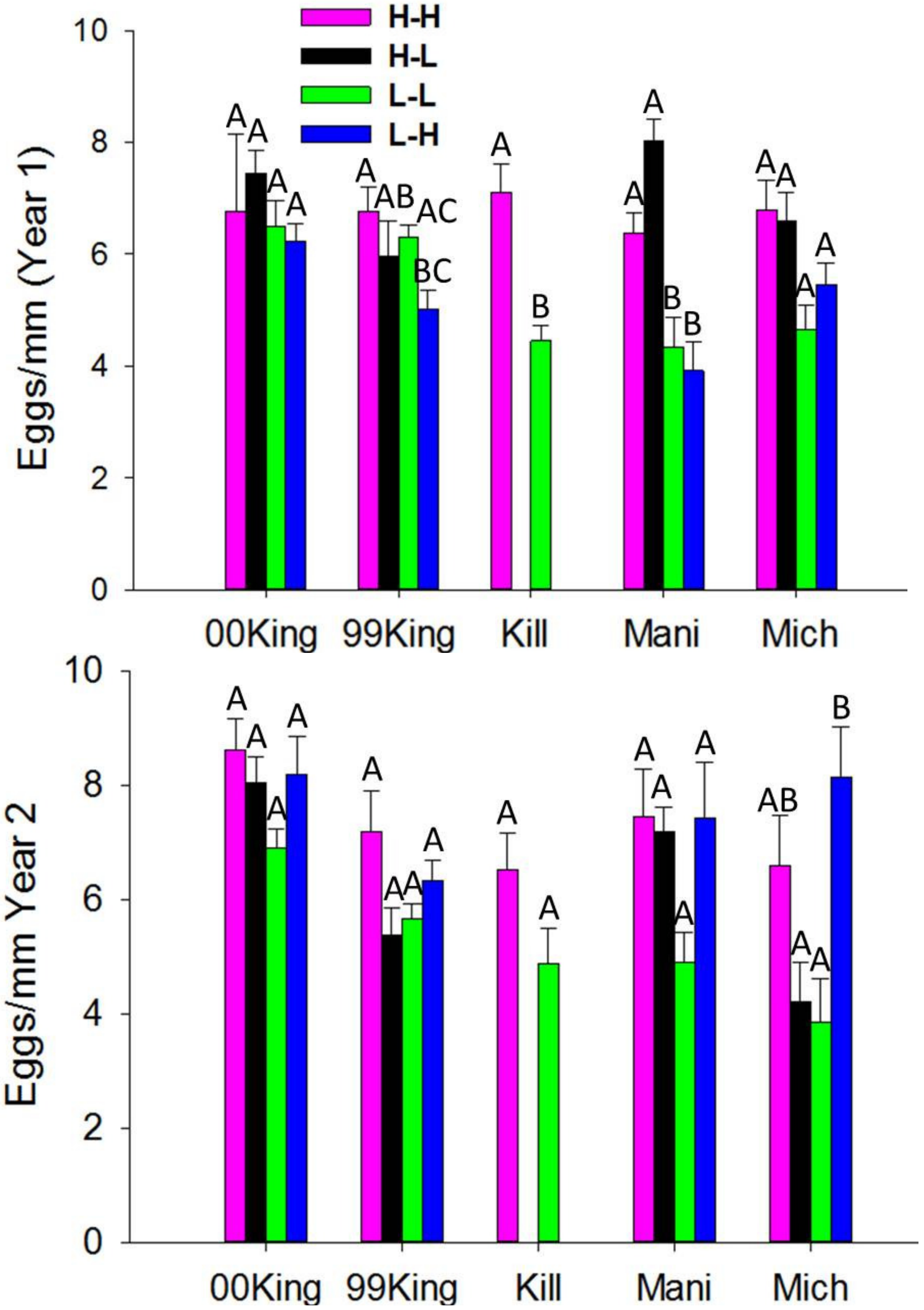

Figure 43. Egg number (corrected for length of spawning female) of five stocks of lake trout housed in a common environment exposed to one of four feeding regimes. Standard error is shown above each bar. Statistical groupings within a stock, based on an ANOVA pairwise comparison with a Tukey-Kramer adjustment are shown above each bar.

Effects of Age on Reproductive Output

There was a negative correlation between egg size and corrected egg number (eggs/mm) in all stocks (Figure 44 - Figure 48). The decrease in egg size between 2008 and 2009 was significant in the Manitou, 2000 Kingscote, 1999 Kingscote, and Killala stocks (Table 16 and Figure 48). Changes in egg size between the two years in the Michipicoten stocks was not significant (p = 0.4046). The increases in egg number (eggs/mm) between 2008 and 2009 were significant only in the 2000 Kingscote and Manitou stocks (Figure 44 - Figure 48, Table 17). Overall, 3 of the 4 stocks (Kingscote, Killala, and Manitou) showed significant changes in egg size between the two years in the ration-combined data while two of the stocks (Manitou and 2000 Kingscote) showed significant changes in egg number.

Analysis of ration-specific changes in egg size between years showed significant decreases in 4 of 5 stocks in the High-High treatment: 2000 Kingscote, 1999 Kingscote, Manitou, and Michipicoten (Table 16). In the High-Low treatment, two of the four stocks showed significant decreases in egg size: 2000 Kingscote and Manitou. Three of five stocks showed significant decreases in egg size in the Low-Low treatment: Killala, 2000 Kingscote, and Manitou. Lastly, only the Manitou stock showed significant decreases in egg size in the Low-High treatment. Overall, 10 of the 18 possible ration-specific changes in egg size between years were significant.

Ration-specific repeated measures analysis of changes in egg number between years showed positive increases in egg number (eggs/mm) in the Low-High rations in three of the four stocks analyzed: Manitou, 1999 Kingscote, and 2000 Kingscote (Table 17). The other three rations showed no significant differences in egg number. Overall, 3 of the 18 possible ration-specific changes in egg number between years were significant.

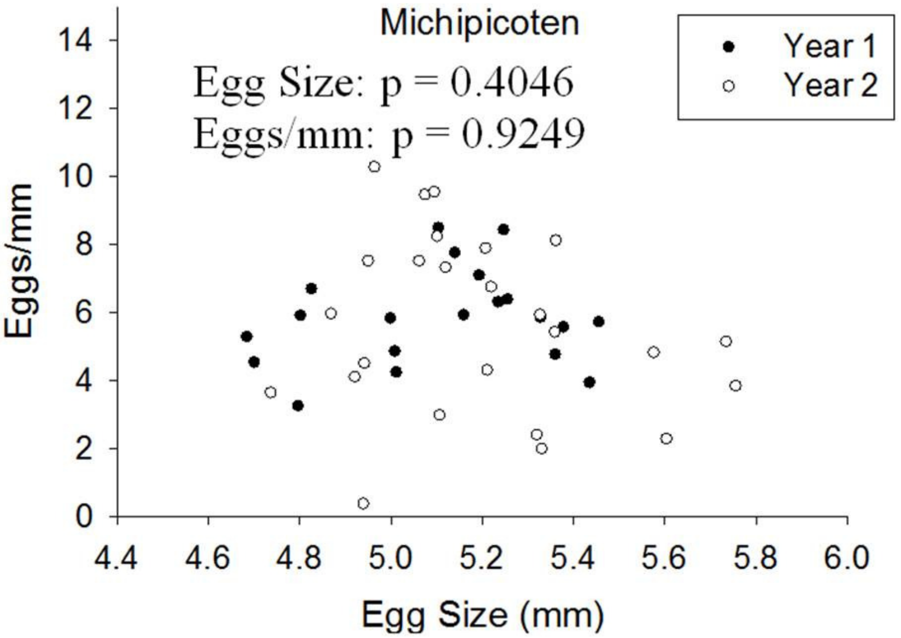

Figure 44. Relationship between egg number as measured in eggs/mm and egg size of Michipicoten lake trout housed under multiple feeding regimes in a common garden environment in OMNR hatchery during 2008 spawning season. P values show the significance of changes between Year 1 and Year 2 in eggs/mm and egg size.

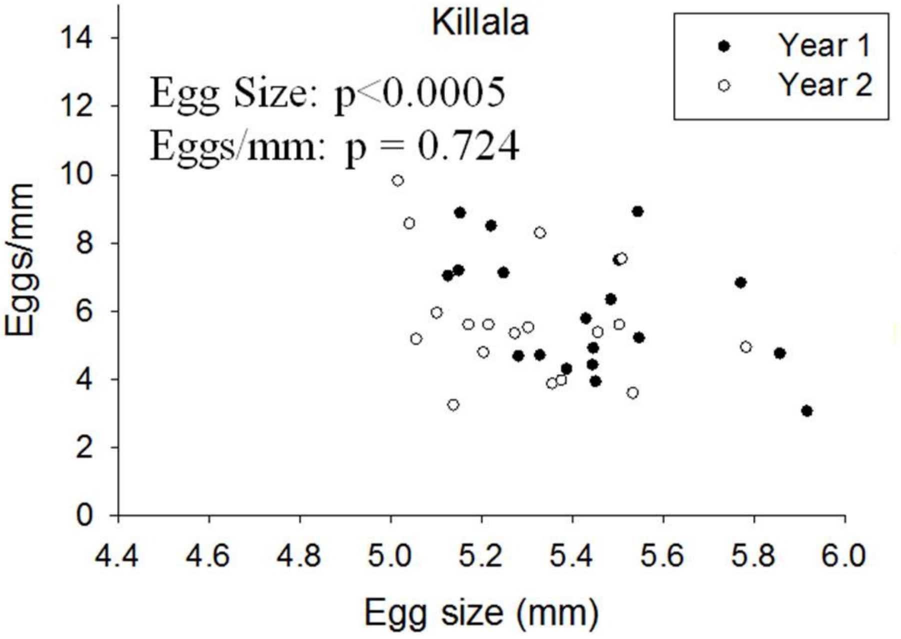

Figure 45. Relationship between egg number as measured in eggs/mm and egg size of Killala lake trout housed under multiple feeding regimes in a common garden environment in OMNR hatchery during 2008 spawning season. P values show the significance of changes between Year 1 and Year 2 in eggs/mm and egg size.

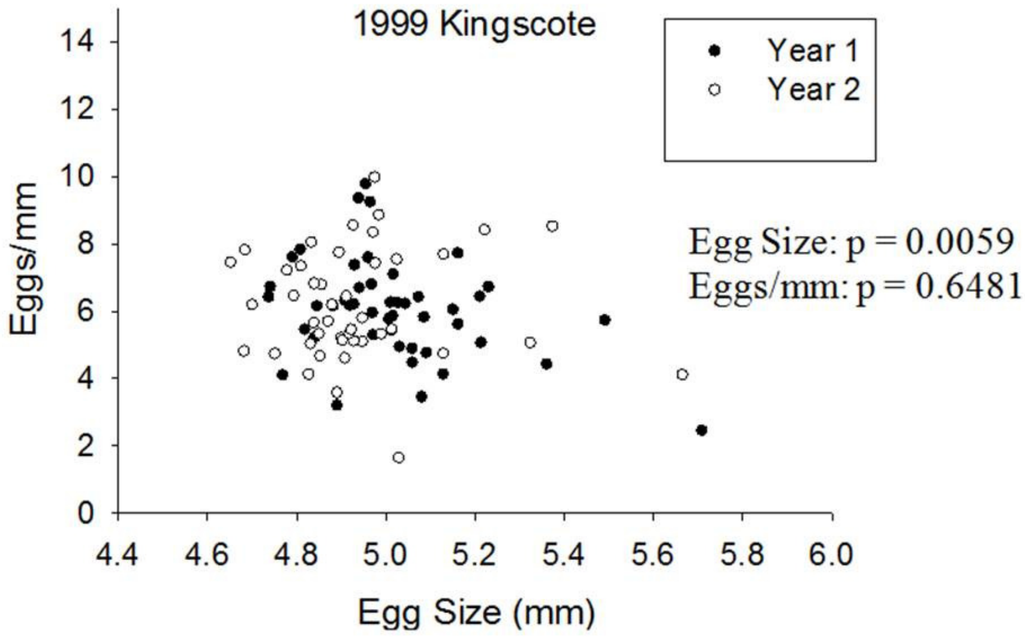

Figure 46. Relationship between egg number as measured in eggs/mm and egg size of 1999 Kingscote lake trout housed under multiple feeding regimes in a common garden environment in OMNR hatchery during 2008 spawning season. P values show the significance of changes between Year 1 and Year 2 in eggs/mm and egg size.

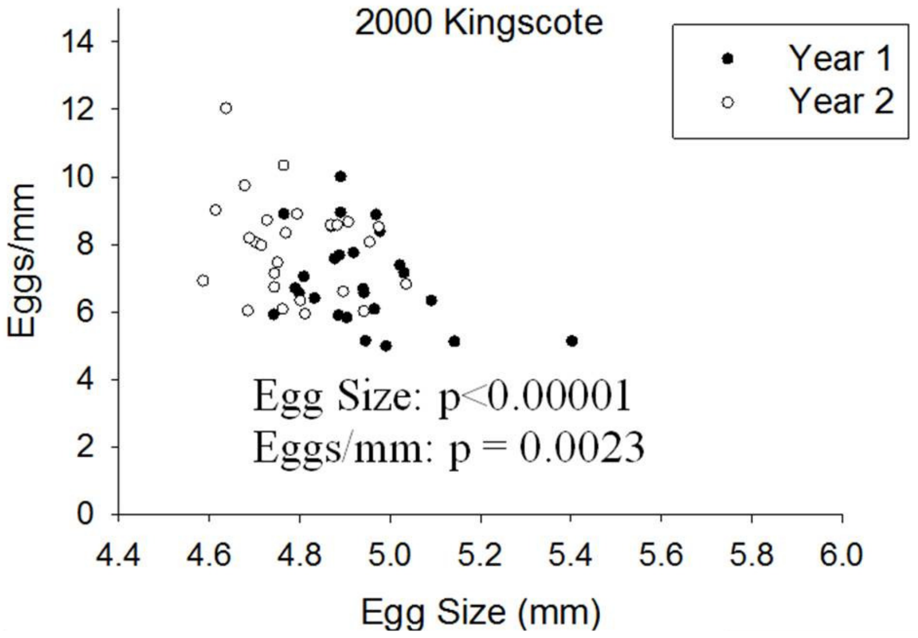

Figure 47. Relationship between egg number as measured in eggs/mm and egg size of 2000 Kingscote lake trout housed under multiple feeding regimes in a common garden environment in OMNR hatchery during 2008 spawning season. P values show the significance of changes between Year 1 and Year 2 in eggs/mm and egg size.

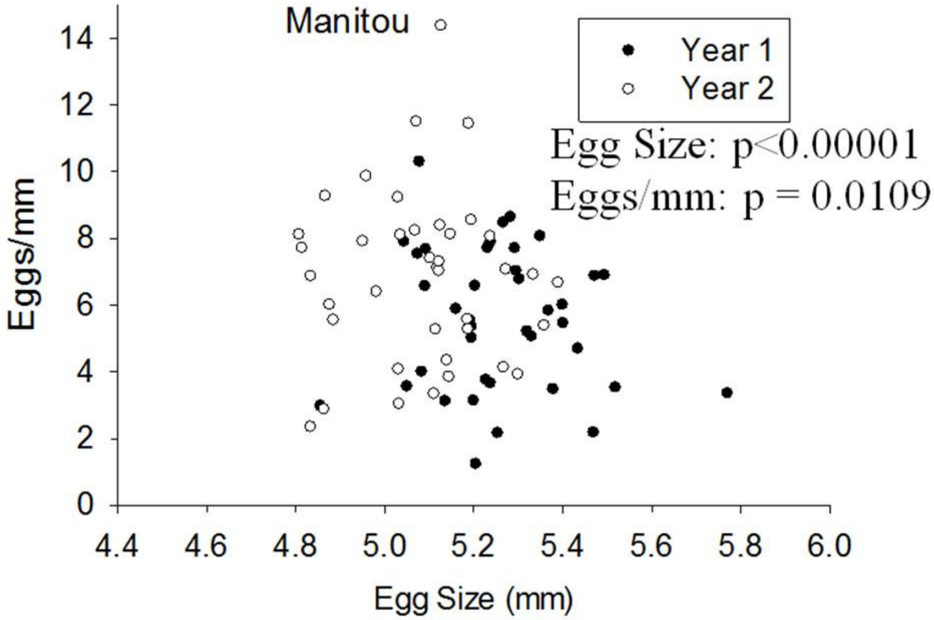

Figure 48. Relationship between egg number as measured in eggs/mm and egg size of Manitou lake trout housed under multiple feeding regimes in a common garden environment in OMNR hatchery during 2008 spawning season. P values show the significance of changes between Year 1 and Year 2 in eggs/mm and egg size.

Table 16. P-values (* = p<0.05, ** = p<0.01; + or – indicates direction of significant changes) for repeated measures analysis for changes in egg size that occurred between the spawning seasons of 2008 and 2009 of individuals from the Killala, 2000 Kingscote, 1999 Kingscote, Manitou, and Michipicoten stocks of lake trout held in a common environment under multiple feeding regimes (High = 0.5% of total tank biomass fed to tank daily; High-Low indicates a switch from a high [0.5%] to a low [0.3%] ration level at the start of the study).

Stock	**All Rations**	**High-High**	**High-Low**	**Low-Low**	**Low-High**
Killala	<0.0005**(-)	0.0665	n/a	0.013* (-)	n/a
2000 Kingscote	<0.0001**(-)	0.0032**(-)	0.0047** (-)	0.0022** (-)	0.0511
1999 Kingscote	0.0059** (-)	0.0152* (-)	0.2748	0.0763	0.5015
Manitou	<.0001** (-)	.0001** (-)	0.0114* (-)	0.0006** (-)	.0116* (-)
Michipicoten	0.4046	0.0185* (-)	0.2029	0.2819	0.3259

Table 17. P-values (* = p<0.05, ** = p<0.01; + or – indicates direction of significant changes) for repeated measures analysis for changes in egg number that occurred between the spawning seasons of 2008 and 2009 of individuals from the Killala, 2000 Kingscote, 1999 Kingscote, Manitou, and Michipicoten stocks of lake trout held in a common environment under multiple feeding regimes (High = 0.5% of total tank biomass fed to tank daily; High-Low indicates a switch from a high [0.5%] to a low [0.3%] ration level at the start of the study).

Stock	**All Rations**	**High-High**	**High-Low**	**Low-Low**	**Low-High**
Killala	0.724	0.5579	n/a	0.4571	n/a
2000 Kingscote	0.0023** (+)	0.0725	0.0886	0.8385	0.0184* (+)
1999 Kingscote	0.6481	0.8301	0.6074	0.0695	0.0311* (+)
Manitou	0.0109* (+)	0.1617	0.2438	0.8363	0.0017** (+)
Michipicoten	0.9249	0.6872	0.156	0.3652	0.1023

Reaction Norms

The modeled relationship between egg number and mean percent lipid, based on AIC values, for all stocks and for both years showed a general increasing trend in egg number with mean percent lipid (Figure 49 - Figure 53). Unique regressions for ration groups (non-switchers vs. switchers) were plotted to visually show differences between the models assigned to each ration group within each stock and study year (Figure 54 - Figure 57). Each stock showed a different shape and this shape differed between years, with the relationship getting steeper in Year 2 (except for the Michipicoten stock which had a similar curve as Year 1). The Michipicoten relationship showed a linear, gently increasing relationship between percent lipid and eggs/mm in year 1 and a hyperbolic increase in Year 2. The Killala stock showed a gently increasing hyperbolic curve in Year 1 which slowed at higher lipid levels. However, the Year 2 function in the Killala stock showed an increasing linear trend with a higher rate of increase at higher percent lipids than in Year 1. The 1999 Kingscote stock showed a sigmoidal relationship between egg production and percent lipid and the sharp increase in egg production at low percent lipid is likely a result of two highly influential data points at low percent lipids. In Year 2, the Kingscote stock showed an increasing linear trend in egg number with percent lipid. The 2000 Kingscote stock had a similar pattern as the 1999 Kingscote, with a relatively flat linear relationship in Year 1 and a steeper linear increase in Year 2. Lastly, the Manitou stock showed a shallow hyperbolic increase in egg production with increasing percent lipid in Year 1 with the rate of increase slowing at higher percent lipids. In Year 2, the linear function applied to the data was steeper than in the previous year (Figure 49 - Figure 53, Table 24, Table 25, Table 26, Table 27, and Table 28).

Comparison of original and alternate models using an AIC difference cutoff of 6, revealed that differences between models in the comparison across years, in the Michipicoten and Killala stocks did not provide substantial evidence support to suggest the original model fits better than the model from the alternate year. These data suggest that the relationship between egg number and mean percent lipid are relatively stable across years in the Killala and Michipicoten stocks (Table 18). Conversely, AIC differences greater than 6 in the 1999 Kingscote, 2000 Kingscote, and Manitou stocks provide strong evidence to suggest that the original model is better than the alternate model and that the relationship between egg number and mean percent lipid changed between years. Across all stocks, 6 of the 10 (60%) total year-specific comparisons provided strong evidence to suggest the original model better describes the data than the alternate.

Comparisons of original and alternate models in the ration groups in Year 1 revealed that four of the eight (50%) total comparisons across stocks that exceeded an AIC difference of 6. The following stocks (and ration group within that stock) had high enough AIC differences to suggest a difference in the predictive ability of the original and null models: 1999 Kingscote (non-switchers and switchers), 2000 Kingscote (non-switchers), and Manitou (non-switchers). In these cases, robust relationships were not observed between egg number and mean percent lipid in the comparisons across the ration groups within a given year.

Comparisons of original and alternate models between ration-groups in Year 2 revealed that two of the eight (25%) total comparisons had AIC differences that exceeded the cutoff of 6. The following stocks (and ration group) showed differences in the predictive ability of the original and alternate model: 1999 Kingscote (switcher) and 2000 Kingscote (non-switcher). In these two cases, there was not a robust relationship between egg number and mean percent lipid between the ration groups. Across both years, 6 of the 16 (37.5%) total ration-group comparisons provided strong evidence to suggest the original model better describes the data than the alternate.

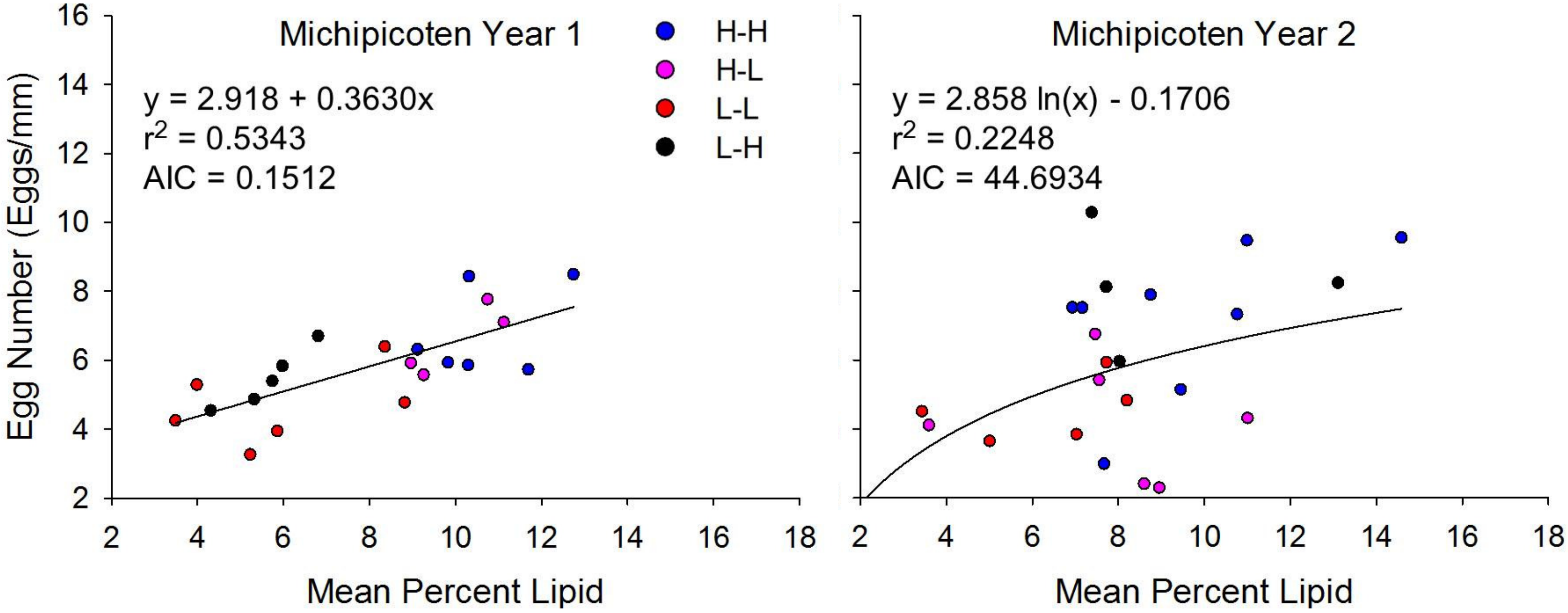

Figure 49. Relationships between percent lipid and egg number (in eggs/mm) of Michipicoten lake trout housed in a common environment hatchery exposed to one of four feeding regimes. Parameters used in each function included on each graph. Functions for each stock and year were selected using AIC values of linear, hyperbolic, logarithmic, Michaelis-Menten and sigmoidal function.

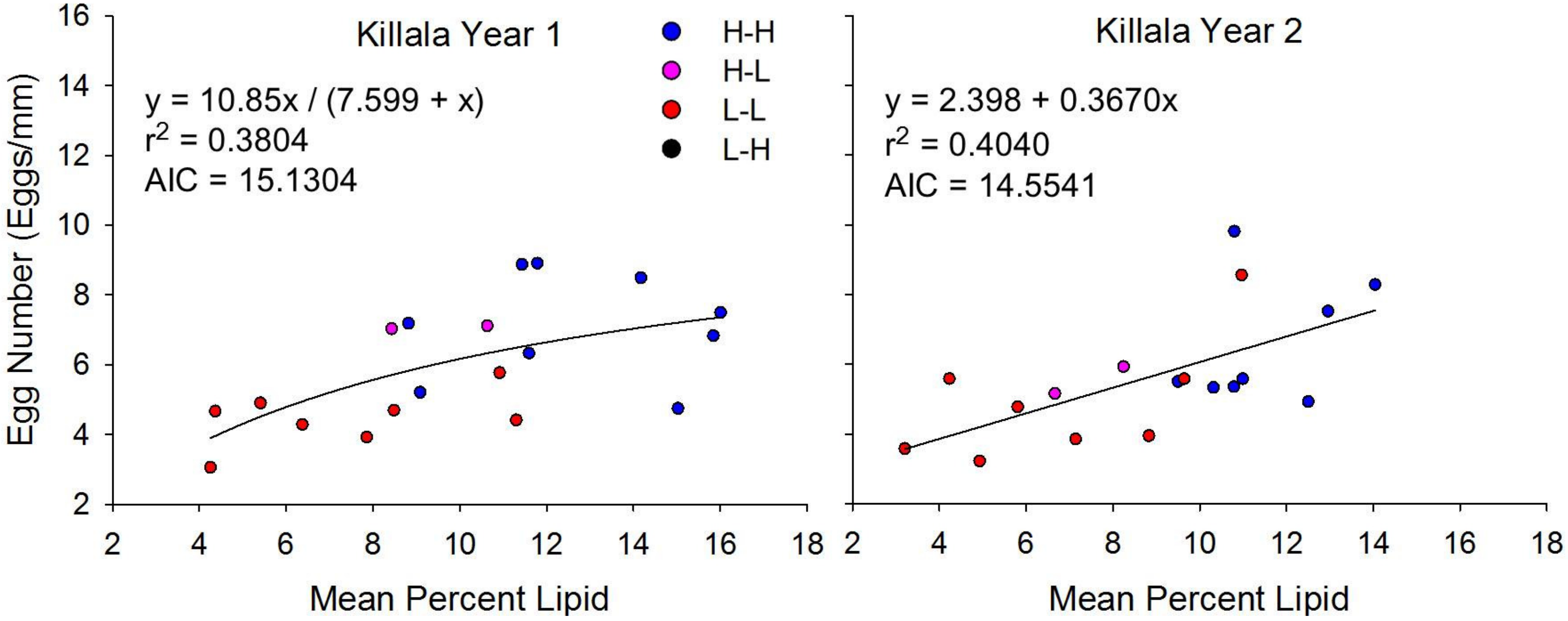

Figure 50, Relationships between percent lipid and egg number (in eggs/mm) of Killala lake trout housed in a common environment hatchery exposed to one of four feeding regimes. Parameters used in each function included on each graph. Functions for each stock and year were selected using AIC values of linear, hyperbolic, logarithmic, Michaelis-Menten and sigmoidal function.

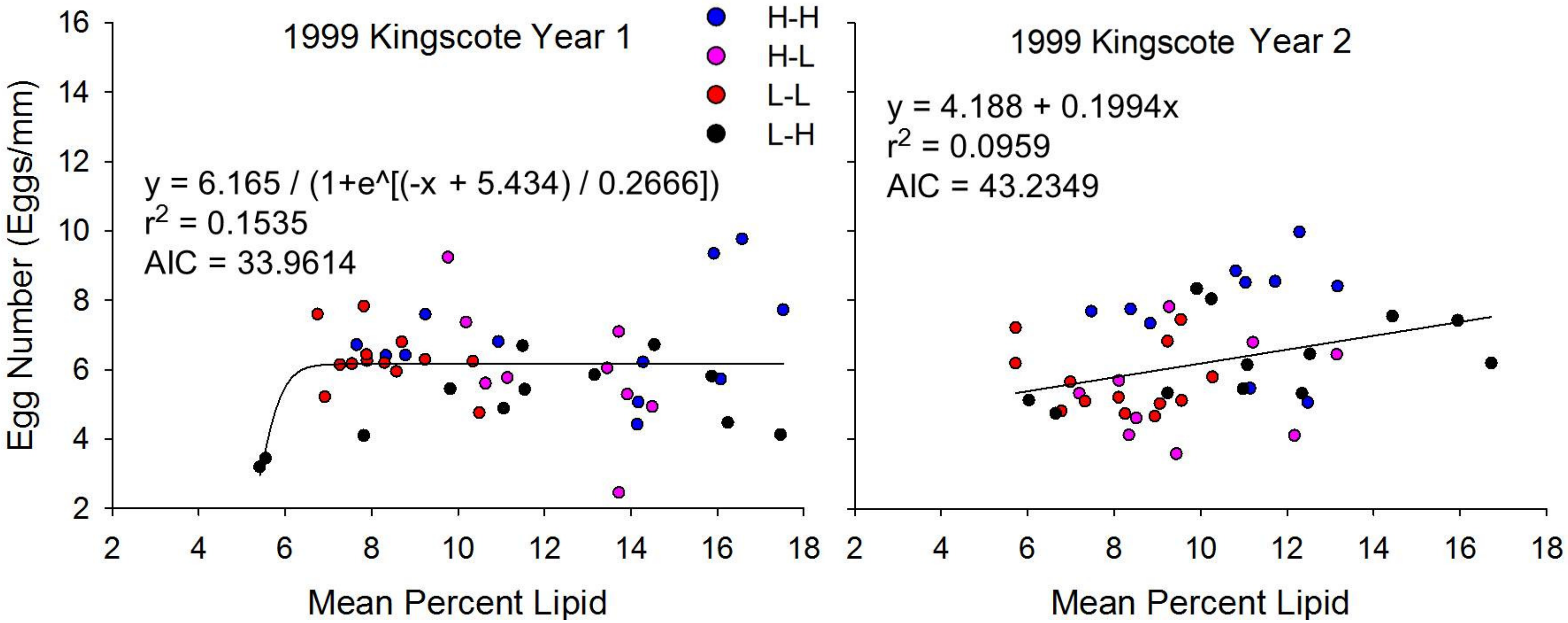

Figure 51. Relationships between percent lipid and egg number (in eggs/mm) of 1999 Kingscote lake trout housed in a common environment hatchery exposed to one of four feeding regimes. Parameters used in each function included on each graph. Functions for each stock and year were selected using AIC values of linear, hyperbolic, logarithmic, Michaelis-Menten and sigmoidal function.

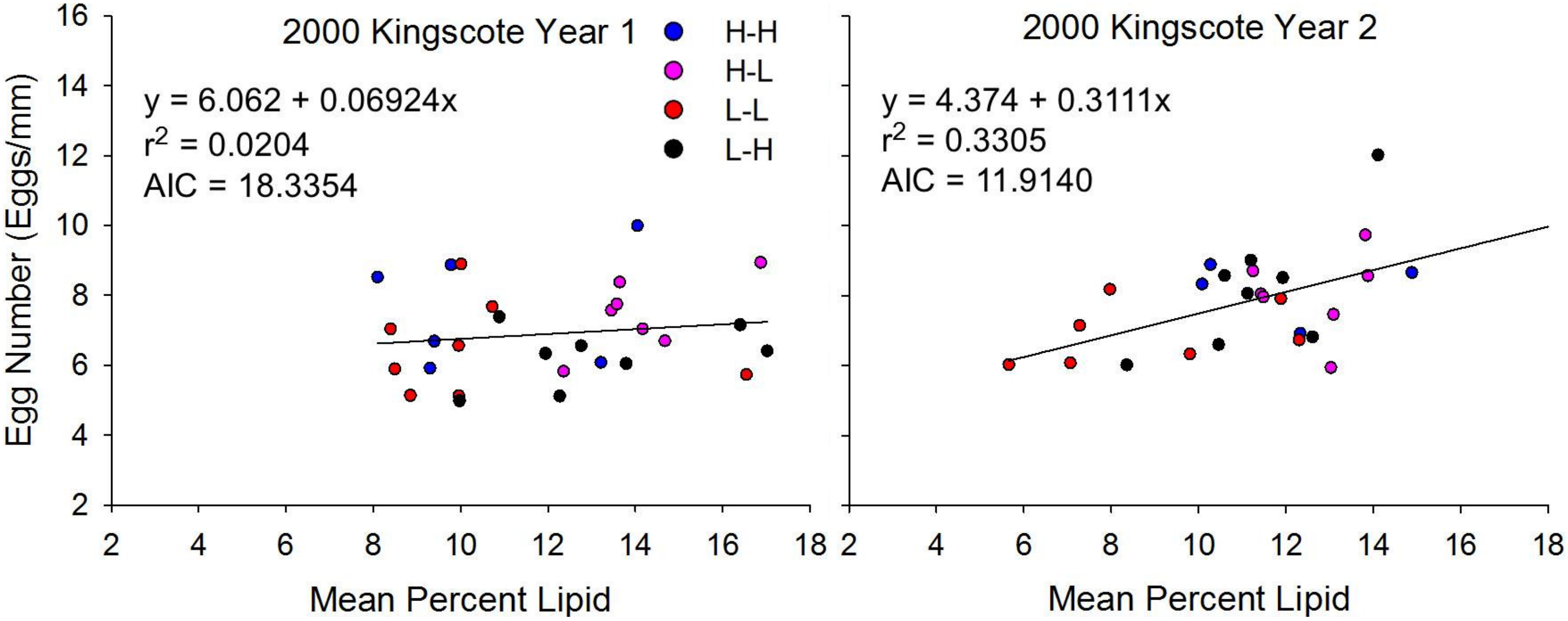

Figure 52. Relationships between percent lipid and egg number (in eggs/mm) of 2000 Kingscote lake trout housed in a common environment hatchery exposed to one of four feeding regimes. Parameters used in each function included on each graph. Functions for each stock and year were selected using AIC values of linear, hyperbolic, logarithmic, Michaelis-Menten and sigmoidal function.

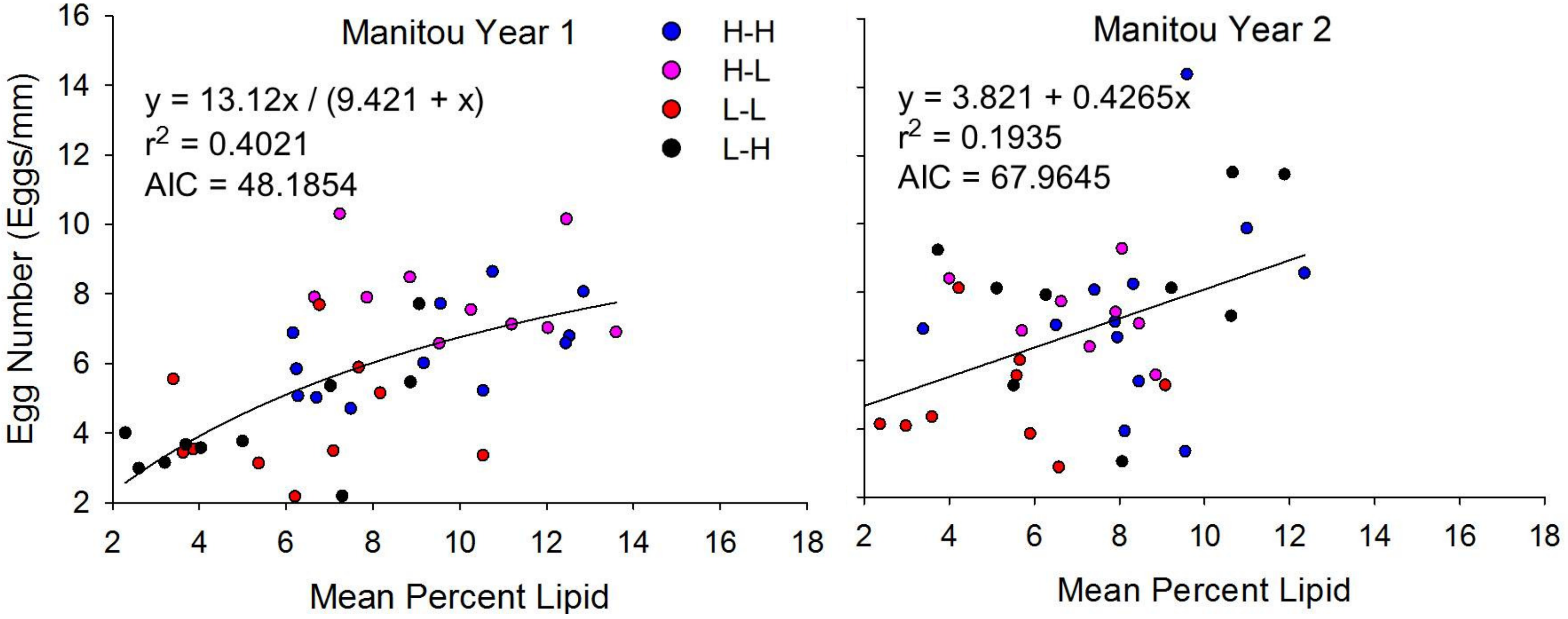

Figure 53. Relationships between percent lipid and egg number (in eggs/mm) of Manitou lake trout stocks housed in a common environment hatchery exposed to one of four feeding regimes. Parameters used in each function included on each graph. Functions for each stock and year were selected using AIC values of linear, hyperbolic, logarithmic, Michaelis-Menten and sigmoidal function.

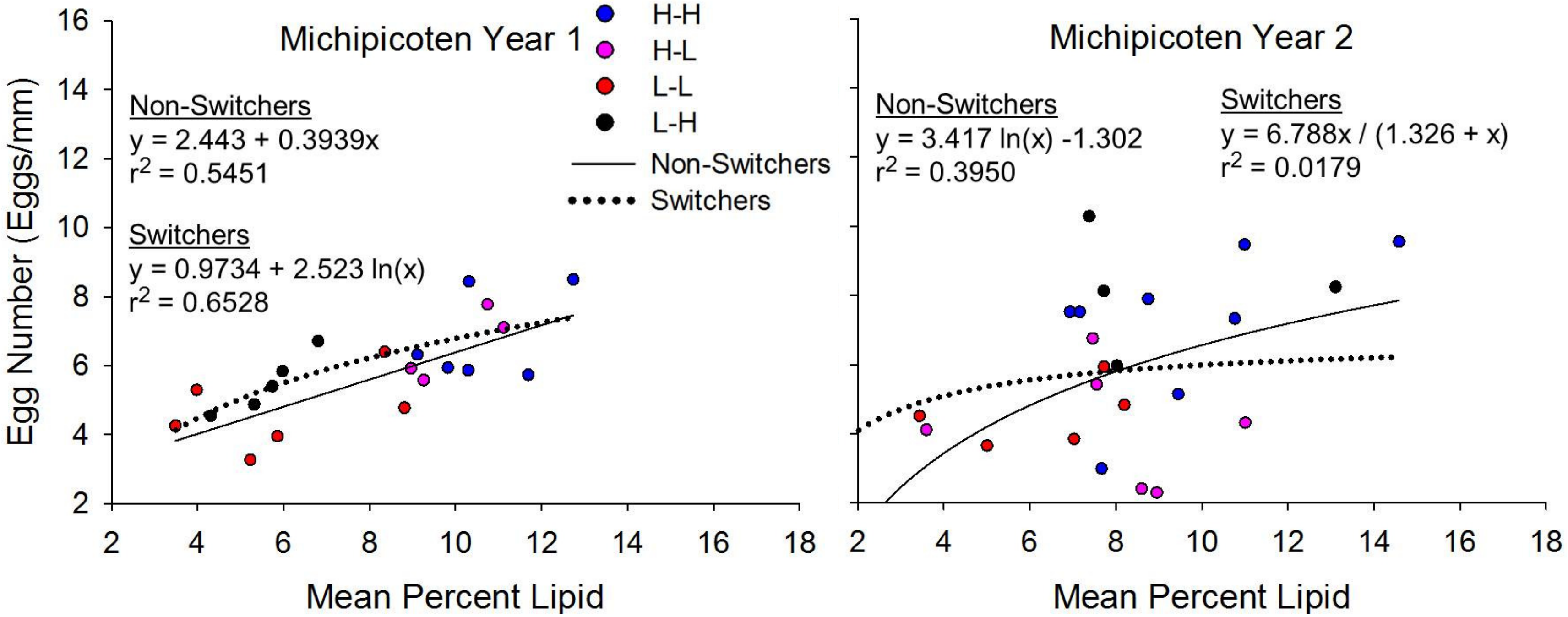

Figure 54. Relationships between percent lipid and egg number (in eggs/mm) of Michipicoten lake trout housed in a common environment hatchery exposed to one of four feeding regimes. Parameters used in each function included on each graph. Functions for each stock and year were selected using AIC values of linear, hyperbolic, logarithmic, Michaelis-Menten and sigmoidal function. Ration-specific regressions are grouped by non-switchers (High-High and Low-Low) and switchers (High-Low and Low-High). The solid line represents the regression applied to non-switchers, the dotted line shows the regression applied to switchers.

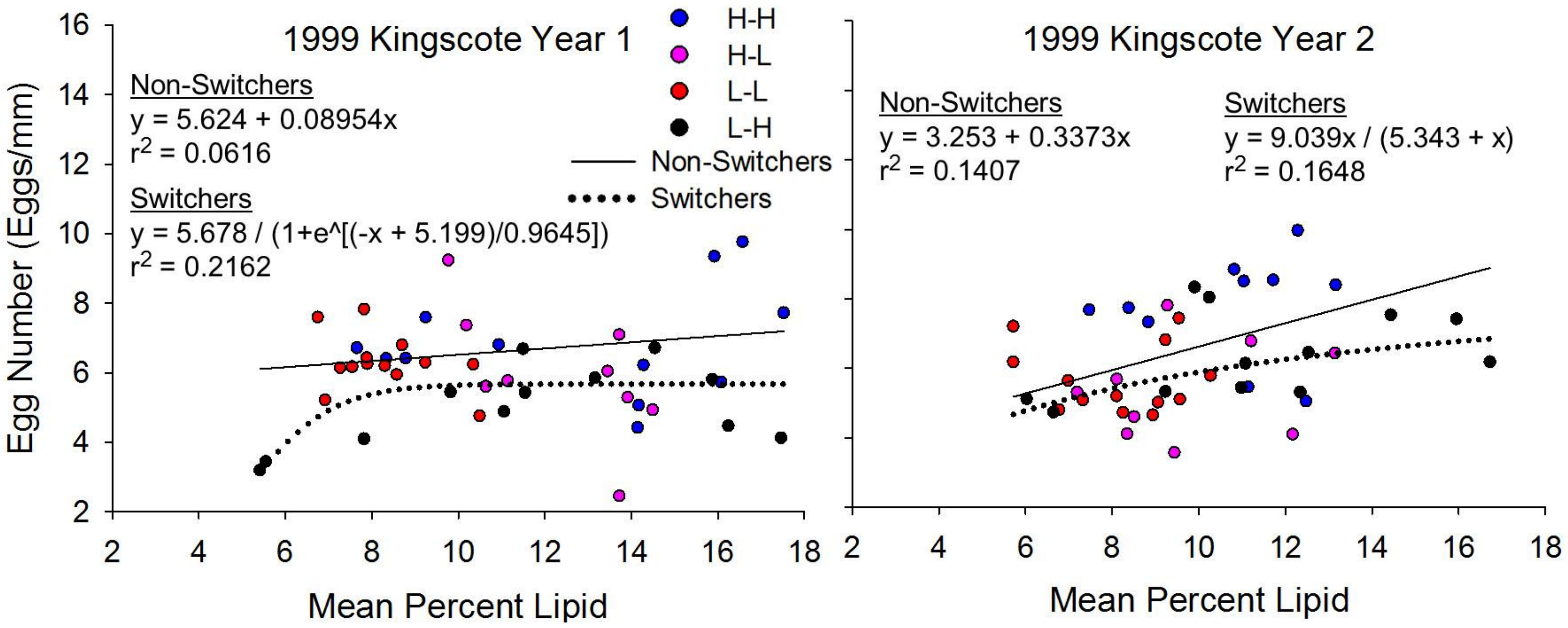

Figure 55. Relationships between percent lipid and egg number (in eggs/mm) of 1999 Kingscote lake trout housed in a common environment hatchery exposed to one of four feeding regimes. Parameters used in each function included on each graph. Functions for each stock and year were selected using AIC values of linear, hyperbolic, logarithmic, Michaelis-Menten and sigmoidal function. Ration-specific regressions are grouped by non-switchers (High-High and Low-Low) and switchers (High-Low and Low-High). The solid line represents the regression applied to non-switchers, the dotted line shows the regression applied to switchers.

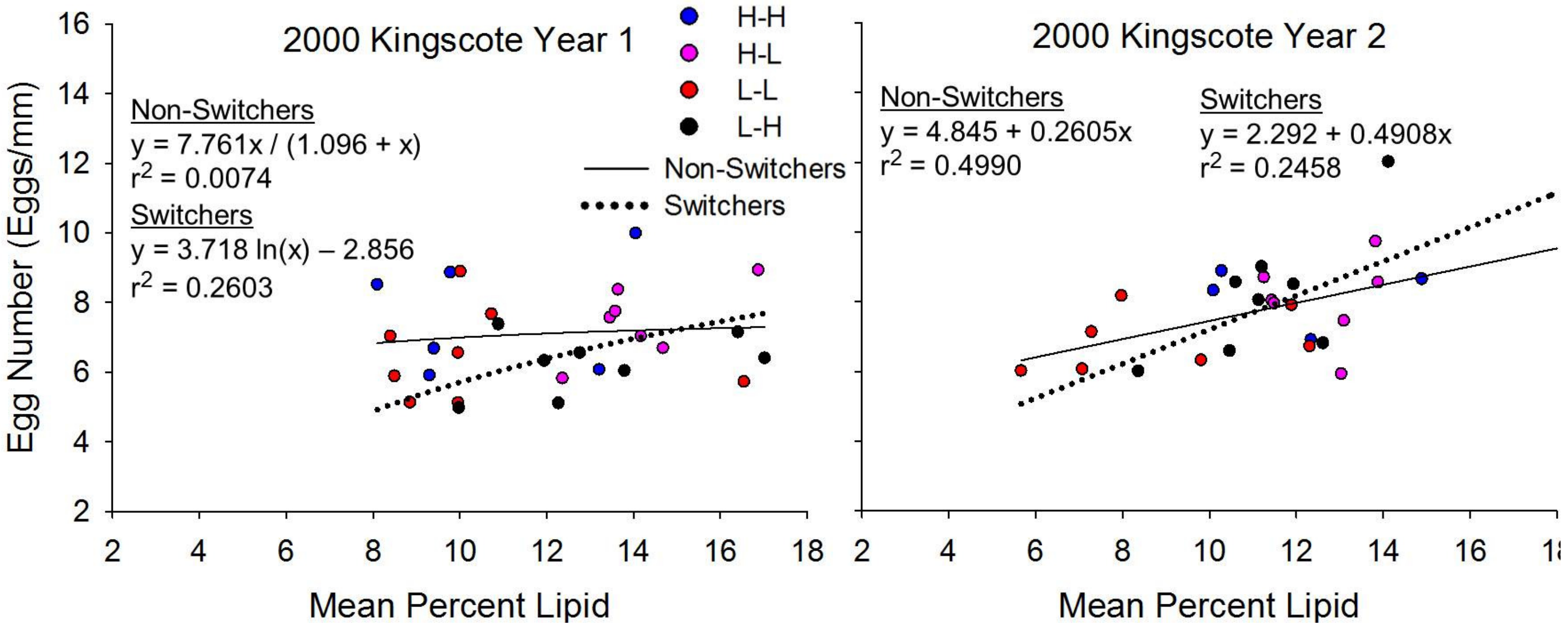

Figure 56. Relationships between percent lipid and egg number (in eggs/mm) of 2000 Kingscote lake trout housed in a common environment hatchery exposed to one of four feeding regimes. Parameters used in each function included on each graph. Functions for each stock and year were selected using AIC values of linear, hyperbolic, logarithmic, Michaelis-Menten and sigmoidal function. Ration-specific regressions are grouped by non-switchers (High-High and Low-Low) and switchers (High-Low and Low-High). The solid line represents the regression applied to non-switchers, the dotted line shows the regression applied to switchers.

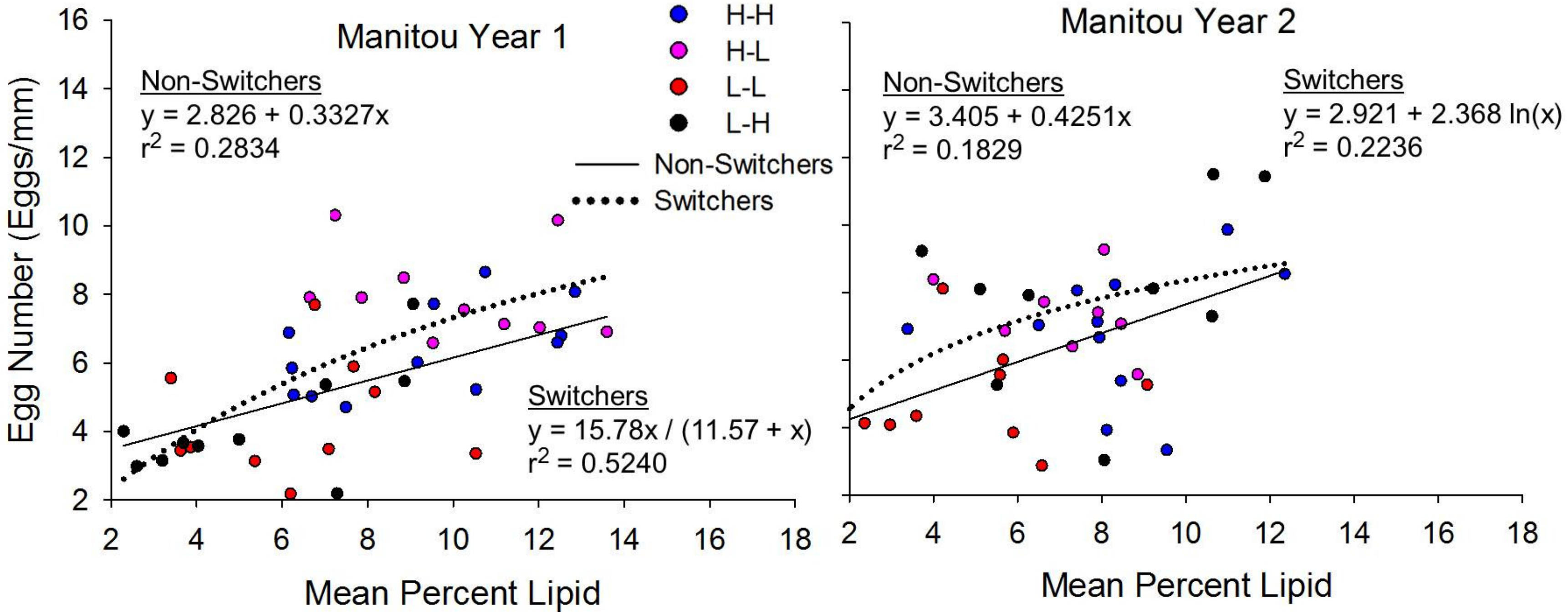

Figure 57. Relationships between percent lipid and egg number (in eggs/mm) of Manitou lake trout housed in a common environment hatchery exposed to one of four feeding regimes. Parameters used in each function included on each graph. Functions for each stock and year were selected using AIC values of linear, hyperbolic, logarithmic, Michaelis-Menten and sigmoidal function. Ration-specific regressions are grouped by non-switchers (High-High and Low-Low) and switchers (High-Low and Low-High). The solid line represents the regression applied to non-switchers, the dotted line shows the regression applied to switchers.

Table 18. AIC differences between model of best fit (assigned based on AIC values) and an alternate model describing the relationship between egg number and mean percent lipid of five lake trout stocks housed in OMNR hatchery. Alternate model is model of best fit applied to alternate data group (year or feeding group) to determine how much better a fit the original model is than the model used to describe the relationship in the alternate ration group or study year. Bolded values indicate AIC differences that exceed the threshold of 6, which indicates a difference in the predictive ability between the original and alternate model for that given group.

Stock	**Year 1 Data AIC Difference**	**Year 2 Data AIC Difference**
Michipicoten	3.1112	1.2281
Killala	2.2401	1.2011
1999 Kingscote	**14.0221**	**9.1408**
2000 Kingscote	**38.9710**	**20.4130**
Manitou	**24.4733**	**13.6536**
Stock	**Year 1 Non-Switcher Data AIC Difference**	**Year 1 Switcher Data AIC Difference**
Michipicoten	3.2226	5.7248
1999 Kingscote	**18.7383**	**14.2875**
2000 Kingscote	**17.3210**	5.1830
Manitou	**7.0939**	5.6611
Stock	**Year 2 Non-Switcher Data AIC Difference**	**Year 2 Switcher Data AIC Difference**
Michipicoten	4.1306	1.01794
1999 Kingscote	4.8189	**11.1447**
2000 Kingscote	**7.4080**	1.3258
Manitou	3.7698	3.6117

DISCUSSION

Life history has a subtle influence on growth, reproductive output and lipid storage in four different stocks of lake trout, and these influences were observable when I imposed a food limitation and changed the feeding regime. Overall, the most important findings from this study was that I found the long-lived Michipicoten stock maintained high levels of growth following a reduction in ration, while the short-lived Manitou stock maintained egg production within a ration across years, at the expense of growth and percent lipid. This provided evidence to support the initial hypothesis of stock-specific energy allocation and stock-specific effects in the response of energy allocation to ration (Table 19) and also suggests that the Michipicotens prioritize energy allocation to growth while the Manitous prioritize energy allocation to reproduction (Chapter 2). The Michipicoten stock also will shift their energy allocation between egg size and egg number when switched from a low to high feeding regime. Robust reaction norms were found to exist in the majority (62.5%) of relationships between lipid levels and egg number within a given year across rations in each stock while these relationships were less predictable across years, as evidence by only 40% of the relationships remaining the same between years within each stock in the combined-ration data. These data provided evidence to support the hypothesis of inter-annual reaction norms within the long-lived stocks and inter-ration reaction norms within each year for each stock (Table 19). Lastly, seasonality was observed in percent lipid and growth rates in each stock which provides evidence to support the initial hypothesis that predicted seasonality in energy allocation, depending on proximity to the spawning season (Table 19). However, percent lipids remained high throughout the summer right up until the spawn, which was unexpected.

Table 19. Summary of results found and how they support (or fail to support) initial hypotheses regarding energy allocation of lake trout held in a common environment exposed to one of four feeding regimes.

Hypothesis	Description	Result
Hypothesis #1	Individuals will differentially allocate energy towards growth and reproduction throughout the season based on where they are in their gonadal growth phase.	Supported by data somewhat – seasonality in lipids and growth was observed but did not follow exact pattern predicted
Hypothesis #2	Stocks will show significant differences in responses of percent lipid, growth, and reproductive output to ration.	Supported by data
Hypothesis #3	Reaction norms exist between percent lipid and egg number within each stock within a year in the Michipicoten, Killala, and Manitou stocks.	Supported by data somewhat (in 62.5 % of cases)
Hypothesis #4	Reaction norms exist between years in the long-lived Michipicoten and Killala stocks.	Supported by data

Growth, Percent Lipid and Reproductive Output: General Ration-specific Responses

Trends in growth rate and mean percent lipid generally followed the ration group. The individuals switched from the Low to High rations showed a rapid rebound in growth and mean percent lipid to levels that were similar to those maintained on high rations This rapid rebounding of lipids and growth has been documented in other studies that show periods of increased growth and percent lipid increases relative to fish maintained at a high ration, presumably due to increased food conversion efficiency following a period of food deprivation (Tian and Qin 2004; Alvarez and Nicieza 2005). In contrast, individuals switched from High to Low rations showed just slight reductions in percent lipid in Year 2 relative to the High-High ration but the differences were still not significant in any stock. This suggests that there is a tendency to maintain lipid reserves once they are established, despite a reduction in ration. This result is inconsistent with previous studies that suggest lipid levels will be rapidly depleted in fish exposed to a reduction in ration, particularly during the winter when resources are most limiting

(Thompson et al. 2001; Biro et al. 2004). However, it is possible that the decreased food ration did not emulate winter conditions adequately. These lipid reserves are critical for survival, particularly during the winter months (Thompson et al. 2001; Biro et al. 2004).

Egg size was relatively fixed within a given stock, providing evidence that egg size is the least sensitive variable to ration. This is supported by a previous study conducted on lake trout stocks that document the predictability of egg size within stocks across different environments (Jastrebski and Morbey 2009; Myers et al. 2011).

Egg number was more sensitive to ration, as was growth and lipid, but egg number did not rebound as quickly when switched from low to high ration. The egg number of the Manitou stock is relatively resilient to a decrease in ration while the Michipicoten stock's egg number has the most sensitive response to a ration change, suggesting that the short lived stock prioritized reproductive output. Food limitation has been shown to influence only egg number and not egg size in other salmonids such as rainbow trout (Scott 1962). Scott (1962) showed that starvation was highly associated with the degree of follicular atresia and the breakdown of ovarian follicles.

Effects of Ration on Growth, Percent Lipid, and Reproductive Output: Stock Differences

Intraspecific differences in energy allocation and responses to food limitation in common environments have been shown in numerous previous studies and have been hypothesized to reflect differences in energy intake, metabolic costs, season, age, and reproductive status of stocks (Yibo and Jianking 1990; Hutchings et al. 1999; Robards et al. 1999). In this study, the long-lived stocks were most sensitive to a ration change as manifested in growth rates and percent lipids while the egg production of the long-lived stocks was less sensitive to ration.

Stock-Specific Conceptual Model Evaluation

In general, the lake trout stocks followed predictions of energy allocation from the conceptual models in Chapter 1 and Chapter 2 that made predictions regarding the effects of stock lifespan, environmental conditions (fishing pressure, sea lamprey mortality, etc.), and food quality and quantity on energy allocation (Table 5). One deviation from my conceptual model was the lack of sensitivity of percent lipid of the Kingscotes in the hatchery. Based on my conceptual model, the storage of energy in lipid reserves is the lowest priority for the Kingscotes which should have been reflected in highly variable lipid levels between rations. The other deviation from the conceptual models was the sensitivity of growth to a reduction in ration in the Manitou stock which suggests a decreased emphasis on growth in limiting environments.

Seasonal Trends in Energy Allocation

In Chapter 1, I created conceptual models to predict the effects of time of year on the allocation of energy in individual lake trout. This conceptual model predicted increasing allocation of energy towards reproduction as the spawning season approached while allocation to growth would be maximized following the spawning season. One deviation from the conceptual model of seasonal energy allocation was the increasing levels of mean percent lipid through the summer period, with maximum values coinciding with the spawn. This increase in percent lipids in the summer period is not consistent with the results of Henderson and Wong (1998) which showed decreasing percent lipids prior to the spawn, followed by increased percent lipids post-spawn in lake trout sampled from the South Bay of Lake Huron. The first possible explanation for this difference between studies is that my study tracked lipids in individual fish, rather than measuring lipids from a homogenized group. Although the difference in methods alone would not fully account for a complete reversal in the patterns observed between the studies, group-based data may have biases related to the sampling methods in the field, such as differences in size distribution or age distribution in individuals sampled on a given date. Secondly, the Henderson and Wong (1998) study involved the use of field fish to show seasonal lipid patterns while I evaluated seasonal percent lipids in hatchery individuals. Finally, it is possible that the lipid allocation patterns I observed in the hatchery are a result of artificial conditions (e.g., food availability, fish density, water temperature) and that environmental conditions would dictate entirely different lipid patterns.

Many studies have focused on the effects of ration level on growth of hatchery fish, particularly for applications in improving hatchery efficiency (e.g. Johnsen et al. 2013; Flores and Vergara 2012; Flores et al. 2012). In general, increased food rations result in increased growth in hatchery fish, although some negative consequences such as increased waste (Flores and Vergara 2012), decreased food conversion efficiency (Imsland and Gunnarsson 2011), and associated increased costs, limit the benefits of over-feeding in production hatcheries. Based on these potential negative effects of over-feeding, much research has been done to determine the optimal diet type and composition (e.g. Figueiredo-Silva et al. 2013; Zhang et al. 2012), amount (Laporte and Trushenski 2012; Luo et al. 2006), and feeding frequency (Johnsen et al. 2013; Hafs et al. 2012; Flores and Vergara 2012) to maximize production per dollar spent on feed. In the current study, I focused on growth rate as it relates to ration level and the tradeoffs that exist in energy allocation towards growth, reproduction and percent lipids. The growth rates and percent lipids in this study were inversely related, with a significant decline occurring in growth during the spawning season, followed by a post-spawn increase. During this post-spawn period, what is likely happening is that energy reserves in lipids are being moved towards increases in length which results in decreased storage. The significance of this trend is that lipid availability is what is likely driving increases in growth that occur post-spawn. This hypothesized re-allocation of energy from lipid reserves is supported by previous life history theory studies that predict that the role of lipid reserves is to increase flexibility in their energy allocation by allowing re-allocation of energy from lipid reserves to growth or reproduction, depending on seasonal needs (Jokela 1997; Naesje et al. 2006; Berg et al. 2009).

While these hatchery data do not allow me to make direct comparisons to wild scenarios because of differences in the hatchery and the wild, the seasonal data showing allocation toward percent lipid and growth do provide strong evidence that there is a connection between percent lipids and growth and that a strong tradeoff exists in the energy allocation towards these variables, as seen in Henderson and Wong (1998).

Annual Changes in Reproduction

In the previous section, I discussed the effects of time of year on the energy allocation of individual lake trout to growth, percent lipid and reproductive output. In Chapter 1, I also presented a conceptual model to predict the effects of age on energy allocation. Egg size and egg number in fish are a function of maternal effects such as spawner age, size, and growth history and are also a function of environmental conditions (Bergenius et al. 2002; Meekan and Fortier 1996; Miller et al. 1995). Two general models have been put forward in the literature to describe effects of spawner age and size on egg size have been shown in the literature: 1) egg size increases with spawner age and size, (Gregersen et al. 2006; Berkeley et al. 2004) and 2) egg size is maximized at an intermediate age, with young and old spawners having smaller, lower-quality eggs (Wang et al. 2012; Kamler 2005). In either case, egg size is a very important measure of reproductive output because it has been linked with growth and survival rates of larvae (Berkeley et al. 2004). In the current study, the annual differences in egg size and egg number were evaluated to determine the ration-specific effects of age on reproductive output.

Within a treatment, egg size was more variable between years than was egg number. This is consistent with previous studies that show the strong influence of maternal effects, and specifically age, on egg size (e.g. Berkeley et al. (2004); Kamler (2005); Gregersen et al. (2006); Wang et al. (2012)). Egg number was less variable across years, within a treatment, because fish were exposed to the same ration level between years and egg number is more reflective of environmental conditions, as seen in Scott (1962).

One unexpected result that is not consistent with previous studies was the decrease in egg size between years in all cases where significant changes occurred. Numerous studies have shown that egg size typically increases with spawner age (e.g. Pitman 1979; Sargent et al. 1987; Hislop 1988). This decrease in egg size suggests that, in general, reproductive output was reduced between years due to the lack of as many significant changes in egg number. Based on the age of these fish in the hatchery, the conceptual model predicted reproductive output would increase because individuals are all relatively young and should still be approaching the age where reproductive output is maximized. This result may be an artifact of unnatural hatchery conditions in terms of fish densities, temperatures, food intake, or environmental predictability. A second factor may be that increases in egg number, although mostly not significant, were increasing overall reproductive output of individuals through switching to a higher number of smaller eggs. Modeled field data in Chapter 2 predicted an increase in egg size as fish age which further suggests that the decrease in egg size between years in the hatchery is an artifact of hatchery conditions.

Reaction Norms – Egg Number vs. Percent Lipids

Reaction norms have been shown to exist in multiple fish species in previous studies in a multitude of measurements including growth rates, survival, and body size. However, these relationships have been shown to be very sensitive and can change based on introgression, domestication in hatchery fish, and environmental stressors (Darwish and Hutchings 2009; Solberg et al. 2013). Percent lipids were shown to be positively correlated with egg production in lake trout in a previous study that sought to determine the role of ration on spawning timing and the role that food limitation plays in the "decision" of females to spawn in a given year (Henderson and Wong 1998). In the current study, I found predictable relationships between egg number and lipids in both years across rations and, to a lesser extent, in between years.

Only two of the four stocks, the long-lived Michipicotens and Killalas, showed robust relationships between lipids and egg number that held for both years, which allowed rough estimates of fecundity based on non-invasive lipid measurements. These data are consistent with life history theory that predicts annual changes in reproduction of long-lived stocks will be less pronounced than those changes seen in shorter-lived stocks.

This is expected to be the case because long-lived stocks have a longer amount of time to reach their age at maximized reproductive output, resulting in smaller changes between years (Wang et al. 2012; Kamler 2005). This result shows that the relationship between percent lipid and egg number changes as fish age, making prediction of egg number based on percent lipids less reliable, particularly in short-lived stocks.

Reaction norms were found to exist in the majority of the comparisons of ration groups. The two year classes of Kingscote showed relatively unstable relationships between mean percent lipid and egg number as evidenced by five of the eight total comparisons showing differences between the original and alternate model which may be due to the unrealistically high ration they receive in the hatchery. In the Michipicoten and Manitou stocks, only one of the comparisons revealed a difference between the original and alternate model. This information provides evidence to suggest that when exposed to a natural range of feeding levels, lake trout mean percent lipid can be used to accurately predict egg production in a given age-class.

Study Limitations – Hatchery Design

The design of the common environment experiment in that the hatchery was such that every stock exposed to a given feeding regime was contained in one tank, which could be considered pseudoreplication (Hurlbert 1984). However, given the available hatchery space, the number of fish available and logistics of the study, it was not possible to set up additional tanks that would provide true replicates. Although, it is not true replication, I did have two year classes of Kingscote that were in separate tanks and they showed similar responses between year classes even though they were spread out across all eight tanks. Also, the general trends across tanks were similar. For example, the

Kingscote stock had the highest lipid levels throughout all the tanks which suggests a common pattern across all the tanks. Prior to the start of the experiment, I tried to account for this lack of true replication by including two stocks within a tank from the same year class. When these stocks are housed in a tank together, any differences are more likely due to genetic divergences rather than tank effects, particularly because there were no observable differences in behavior. Future projects should focus on increased tank numbers to accommodate traditional statistical analyses. One last limitation of this study was the differences in how many generations each stock had been in the hatchery. Although the stocks that had been in the hatchery the longest were only two generations removed from their wild ancestors, domestication has been shown to occur in fish that are two generations removed from the wild (Reisenbichler and Rubin 1999; Reisenbichler et al. 2003). Domestication of fish in the hatchery has been shown to result in changes in a multitude of factors including growth (Solberg et al. 2013), fat reserves (Bronson 1984; Gross 1998), and reproduction (Belyaev 1979; Fleming et al. 1996) relative to wild fish. These potential differences in the amount of domestication between hatchery stocks could influence energy allocation patterns in unpredictable ways as it was not possible to disentangle the effects of life history from the effects of domestication in this study. When possible, future studies involving stock comparisons should use fish that were brought into the hatchery system at the same time. Additionally, when comparing hatchery and wild fish, it would be ideal to examine individuals in the hatchery that have had a minimal number of generations in the hatchery.

Implications

Understanding the stock-specific responses of lake trout to a change in their environment gives us a predictive tool that estimates responses of individuals to a change in prey availability. Predator-prey relationships in natural systems are dynamic and the stochastic nature of prey availability has been documented in response to predators in a number of piscivorous fish species, including lake trout (Kitchell and Crowder 1986; Eby et al. 1995). These predator-prey dynamics and associated reductions in a preferred prey species can results in niche shifts, decreased growth rates, and increased levels of competition for remaining prey (Kitchell and Crowder 1986). Given that reductions in prey in the natural environment are likely due to trophic shifts and anthropogenic stressors, understanding how these stocks respond to reductions in energy intake in a controlled environment gives some insights into how growth, percent lipid, and reproductive output will be affected. For the case of the Killala stock, growth, lipids, and reproductive output were all lower in the fish maintained at the low ration suggesting that a reduction in ration would negatively affect energy allocation to all three variables. For the Michipicoten stock, a reduction in energy intake affected growth and egg number, with a greater change in the switchers in Year 2. This suggests that growth and egg number would suffer when prey is limiting and that the effects of this reduction would be even more pronounced if it lasted for multiple years in the Michipicoten stock. The Manitou stock was relatively resistant to changes in egg number across all rations, at the expense of percent lipid and growth rates in the low rations. This potentially means that the Manitou stock would be the ideal stock for introduction to a limiting environment because reproductive output is the least sensitive to ration of all the stocks studied. However, it is also possible that the corresponding reduced growth and percent lipid in limiting environments could reduce survival or reduce reproductive output in the future. Finally, the Kingscote stock would be expected to have the largest decrease in growth of all the variables based on my results in the situation that their natural environment became even more limiting. These predictions of stock-specific changes in growth, percent lipid, and reproductive output can have significant impacts on wild populations in a situation where prey availability is reduced. Any reductions in egg production based on a trophic change will directly affect future generations; however, reductions in growth and percent lipid also have the possibility of reducing survival of individuals which will also negatively impact the population.

Conclusions

This study demonstrated the importance of ration, and how changes in ration levels determine growth rates, percent lipid, and reproductive output in different stocks. The conceptual models presented in Chapters 1 and 2 predicted energy allocation of individuals based on life history strategy, time of year, and fish age. Robust reaction norms provided reliable predictions of fecundity within both years in the Michipicoten and Manitou stocks but were only effective at predicting the following year's fecundity in the long-lived Michipicoten and Killala stocks. This likely reflects that the relationship between these variables changes from year to year and depends, to some extent, on the age of individuals and the mortality schedule to which they are adapted. Reproductive output was evaluated as a function of both egg size and egg number. Egg number was more variable across treatments than was egg size and egg size was more variable across years (within treatments) than was egg number. This suggests that egg number is more reflective of environmental conditions and food availability, while egg size is more fixed and changes through time as a year-class ages. This general understanding of egg number within a year class gives fishery managers insights into the food consumption by individual fish and also allows managers to predict how a year-class will respond to a year with limited food availability.

APPENDIX

Table 20. Summary of significance of changes in percent lipid between July 11, 2008 and levels during the spawn of five stocks of lake trout housed in a common garden environment in OMNR hatchery. Lipid changes are recorded as not significant (NS), or positively significant based on repeated measures analysis with α = 0.05. Ration levels were manipulated within each treatment as follows High-High = maintained at a high [0.5% of body weight daily] ration throughout study; High-Low = switched from a High [0.5% of body weight daily] to a low [0.3% of body weight daily] ration, etc. Combined data are data combined from all treatments.

Stock	Ration	p-value	Percent Lipid Change
Killala	High-High	0.000553	Positive
	Low-Low	0.0840	NS
	All Rations	0.00250	Positive
2000 Kingscote	High-High	0.118	NS
	High-Low	0.000481	Positive
	Low-Low	0.0254	Positive
	Low-High	0.000291	Positive
	All Rations	0.000000623	Positive
1999 Kingscote	High-High	0.0000873	Positive
	High-Low	0.000000866	Positive
	Low-Low	0.0000797	Positive
	Low-High	0.0000419	Positive
	All Rations	1.785E-013	Positive
Manitou	High-High	0.00378	Positive
	High-Low	0.00225	Positive
	Low-Low	0.0317	Positive
	Low-High	0.148	NS
	All Rations	0.0000819	Positive
Michipicoten	High-High	0.00000130	Positive
	High-Low	0.00987	Positive
	Low-Low	0.495	NS
	Low-High	0.137	NS
	All Rations	0.00120	Positive

Table 21. Summary of significance of changes in percent lipid between July 27, 2009 and levels during the spawn of five stocks of lake trout housed in a common garden environment in OMNR hatchery. Lipid changes are recorded as not significant (NS), or negatively significant based on repeated measures analysis with $\alpha = 0.05$. Ration levels were manipulated within each treatment as follows High-High = maintained at a high [0.5% of body weight daily] ration throughout study; High-Low = switched from a High [0.5% of body weight daily] to a low [0.3% of body weight daily] ration, etc. Combined data are data combined from all treatments.

Stock	Ration	p-value	Percent Lipid Change
Killala	High-High	1.66E-9	Positive
	Low-Low	0.983	NS
	All Rations	0.939	NS
2000 Kingscote	High-High	0.689	NS
	High-Low	0.777	NS
	Low-Low	0.670	NS
	Low-High	0.343	NS
	All Rations	0.945	NS
1999 Kingscote	High-High	0.510	NS
	High-Low	0.951	NS
	Low-Low	0.327	NS
	Low-High	0.195	NS
	All Rations	0.841	NS
Manitou	High-High	0.857	NS
	High-Low	0.339	NS
	Low-Low	0.841	NS
	Low-High	0.536	NS
	All Rations	0.775	NS
Michipicoten	High-High	0.791	NS
	High-Low	0.390	NS
	Low-Low	0.514	NS
	Low-High	0.260	NS
	All Rations	0.623	NS

Table 22. Year 1 comparison of growth rates (daily growth rate between sampling dates, mm/day) and December-spawn growth (change in fork length) in five stocks of lake trout housed in a common environment hatchery, exposed to one of four feeding regimes. % difference columns compare value of ration-specific growth in row to the high-high value.

Stock	Ration	Max Daily Growth Rate	% Difference	December-Spawn Growth	% Difference
Michipicoten	H-H	0.1365	0.00%	51.667	0.00%
	H-L	0.0843	-38.24%	30.2	-41.55%
	L-L	0.0548	-59.85%	17.33	-66.46%
	L-H	0.1181	-13.48%	21.75	-57.90%
Killala	H-H	0.1823	0.00%	39.78	0.00%
	L-L	0.0486	-73.34%	13.56	-65.91%
1999 Kingscote	H-H	0.2305	0.00%	43	0.00%
	H-L	0.1688	-26.77%	29.8	-30.70%
	L-L	0.0938	-59.31%	18.54	-56.88%
	L-H	0.131	-43.17%	25.64	-40.37%
2000 Kingscote	H-H	0.2129	0.00%	36.875	0.00%
	H-L	0.1629	-23.49%	34.286	-7.02%
	L-L	0.1289	-39.46%	20.25	-45.08%
	L-H	0.2168	1.83%	36.625	-0.68%
Manitou	H-H	0.1534	0.00%	31.25	0.00%
	H-L	0.1136	-25.95%	25.5	-18.40%
	L-L	0.0765	-50.13%	9.8	-68.64%
	L-H	0.0895	-41.66%	16.8	-46.24%

Table 23. Year 2 comparison of growth rates (daily growth rate between sampling dates, mm/day) and December-spawn growth (change in fork length)in five stocks of lake trout housed in a common environment hatchery, exposed to one of four feeding regimes. % difference columns compare value of ration-specific growth in row to the high-high value.

Stock	**Ration**	**Max Daily Growth Rate**	**% Difference**	**December-Spawn Growth**	**% Difference**
Michipicoten	H-H	0.1482	0.00%	36.5	0.00%
	H-L	0.0775	-47.71%	18	-50.68%
	L-L	0.0867	-41.50%	18	-50.68%
	L-H	0.1958	32.12%	46	26.03%
Killala	H-H	0.1392	0.00%	33.75	0.00%
	L-L	0.0602	-56.75%	23	-31.85%
1999 Kingscote	H-H	0.1396	0.00%	32.182	0.00%
	H-L	0.0639	-54.23%	14.5	-54.94%
	L-L	0.0686	-50.86%	18.77	-41.68%
	L-H	0.1196	-14.33%	36.67	13.95%
2000 Kingscote	H-H	0.0994	0.00%	38.6	0.00%
	H-L	0.0809	-18.61%	20.86	-45.96%
	L-L	0.0783	-21.23%	17	-55.96%
	L-H	0.1491	50.00%	36.38	-5.75%
Manitou	H-H	0.1365	0.00%	30.75	0.00%
	H-L	0.0843	-38.24%	15.5	-49.59%
	L-L	0.0548	-59.85%	9.667	-68.56%
	L-H	0.1181	-13.48%	28.8	-6.34%

Table 24. AIC values of linear, hyperbolic, logarithmic, sigmoidal, and Michaelis-Menten functions applied to the relationship between egg number and mean percent lipid of Michipicoten lake trout housed in a common environment hatchery in Ontario.

Group	**Relationship**	**No. of Parameters (k)**	**No. of Observations (n)**	**Residual Sum of Squares (RSS)**	**Akaike Information Criterion (AIC)**
Year 1, All Rations	**Linear**	**2**	**21**	**17.4833**	**0.1512**
	Logarithmic	2	21	18.8087	1.6857
	Hyperbolic	2	21	18.9058	1.7939
	Sigmoidal	3	21	17.1675	1.7683
	Michaelis - Menten	2	21	18.9058	1.7939
Year 2, All Rations	Linear	2	25	131.5277	45.5085
	Logarithmic	**2**	**25**	**127.3083**	**44.6934**
	Hyperbolic	2	25	128.8843	45.0010
	Sigmoidal	3	25	130.0384	47.2239
	Michaelis - Menten	2	25	128.4000	44.9069
Year 1, Switchers	Linear	2	9	3.1158	-5.5467
	Logarithmic	**2**	**9**	**3.0670**	**-5.6887**
	Hyperbolic	2	9	3.0880	-5.6272
	Sigmoidal	3	9	3.1271	-3.5142
	Michaelis - Menten	2	9	3.0880	-5.6273
Year 1, Non-Switchers	**Linear**	**2**	**12**	**12.9210**	**4.8874**
	Logarithmic	2	12	14.8584	6.5639
	Hyperbolic	2	12	14.6950	6.4312
	Sigmoidal	3	12	12.3231	6.3188
	Michaelis - Menten	2	12	14.6950	20.8464
Year 2, Switchers	Linear	2	10	60.7910	22.0486
	Logarithmic	2	10	60.6164	22.0198
	Hyperbolic	**2**	**10**	**60.4096**	**21.9856**
	Sigmoidal	3	10	61.5126	24.1666
	Michaelis - Menten	2	10	60.4096	21.9856
Year 2, Non-Switchers	Linear	2	15	63.9234	25.7445
	Logarithmic	**2**	**15**	**61.8395**	**25.2474**
	Hyperbolic	2	15	62.8968	25.5017
	Sigmoidal	3	15	65.2343	28.0490
	Michaelis - Menten	2	15	62.8968	25.5017

Table 25. AIC values of linear, hyperbolic, logarithmic, sigmoidal, and Michaelis-Menten functions applied to the relationship between egg number and mean percent lipid of Killala lake trout housed in a common environment hatchery in Ontario.

Group	**Relationship**	**No. of Parameters (k)**	**No. of Observations (n)**	**Residual Sum of Squares (RSS)**	**Akaike Information Criterion (AIC)**
Year 1, All Rations	Linear	2	19	36.4578	16.3826
	Logarithmic	2	19	34.2970	15.2218
	Hyperbolic	**2**	**19**	**34.1326**	**15.1304**
	Sigmoidal	3	19	33.2732	16.6459
	Michaelis - Menten	2	19	34.1326	15.1305
Year 2, All Rations	**Linear**	**2**	**18**	**32.3531**	**14.5541**
	Logarithmic	2	18	34.6681	15.7981
	Hyperbolic	2	18	34.4181	15.6678
	Sigmoidal	3	18	31.8365	16.2643
	Michaelis - Menten	2	18	43.6984	19.9649

Table 26. AIC values of linear, hyperbolic, logarithmic, sigmoidal, and Michaelis-Menten functions applied to the relationship between egg number and mean percent lipid of 1999 Year class Kingscote lake trout housed in a common environment hatchery in Ontario.

Group	**Relationship**	**No. of Parameters (k)**	**No. of Observations (n)**	**Residual Sum of Squares (RSS)**	**Akaike Information Criterion (AIC)**
Year 1, All Rations	Linear	2	46	99.1985	39.3502
	Logarithmic	2	46	98.7019	39.1193
	Hyperbolic	2	46	97.9769	38.7802
	Sigmoidal	**3**	**46**	**84.4786**	**33.9614**
	Michaelis - Menten	2	46	97.9769	38.7802
Year 2, All Rations	**Linear**	**2**	**45**	**107.6139**	**43.2349**
	Logarithmic	2	45	108.0412	43.4133
	Hyperbolic	2	45	108.3411	43.5380
	Sigmoidal	3	45	107.3965	45.1439
	Michaelis - Menten	2	45	108.3000	43.5209
Year 1, Switchers	Linear	2	21	47.2195	21.0160
	Logarithmic	2	21	45.6034	20.2847
	Hyperbolic	2	21	44.4187	19.7319
	Sigmoidal	**3**	**21**	**37.5113**	**18.1825**
	Michaelis - Menten	2	21	44.4187	19.7319
Year 1, Non-Switchers	**Linear**	**2**	**25**	**34.8705**	**12.3191**
	Logarithmic	2	25	35.5427	12.7964
	Hyperbolic	2	25	35.9675	13.0935
	Sigmoidal	3	25	34.7432	14.2277
	Michaelis - Menten	2	25	35.9675	13.0935
Year 2, Switchers	Linear	2	21	31.5784	12.5670
	Logarithmic	2	21	31.2686	12.3599
	Hyperbolic	**2**	**21**	**31.2272**	**12.3321**
	Sigmoidal	3	21	31.1979	14.3124
	Michaelis - Menten	2	21	31.2272	12.3321
Year 2, Non-Switchers	**Linear**	**2**	**24**	**68.2676**	**29.0891**
	Logarithmic	2	24	70.6104	29.8990
	Hyperbolic	2	24	70.7726	29.9540
	Sigmoidal	3	24	67.2793	30.7392
	Michaelis - Menten	2	24	70.7726	29.9540

Table 27. AIC values of linear, hyperbolic, logarithmic, sigmoidal, and Michaelis-Menten functions applied to the relationship between egg number and mean percent lipid of 2000 Year class Kingscote lake trout housed in a common environment hatchery in Ontario.

Group	**Relationship**	**No. of Parameters (k)**	**No. of Observations (n)**	**Residual Sum of Squares (RSS)**	**Akaike Information Criterion (AIC)**
Year 1, All Rations	**Linear**	**2**	**29**	**47.5423**	**18.3354**
	Logarithmic	2	29	47.6245	18.3855
	Hyperbolic	2	29	47.7139	18.4399
	Sigmoidal	3	29	47.5375	20.3325
	Michaelis - Menten	2	29	47.7139	18.4399
Year 2, All Rations	**Linear**	**2**	**27**	**36.1960**	**11.9140**
	Logarithmic	2	27	37.2474	12.6871
	Hyperbolic	2	27	37.5353	12.8950
	Sigmoidal	3	27	35.9898	13.7597
	Michaelis - Menten	2	27	37.5353	12.8950
Year 1, Switchers	Linear	2	15	12.9319	1.7747
	Logarithmic	**2**	**15**	**12.7325**	**1.5416**
	Hyperbolic	2	15	12.7487	1.5607
	Sigmoidal	3	15	12.5472	3.3217
	Michaelis - Menten	2	15	12.7487	1.5607
Year 1, Non-Switchers	Linear	2	14	30.9364	15.1003
	Logarithmic	2	14	30.8620	15.0666
	Hyperbolic	2	14	30.8077	15.0419
	Sigmoidal	3	14	31.0387	17.1465
	Michaelis - Menten	**2**	**14**	**30.8077**	**15.0419**
Year 2, Switchers	**Linear**	**2**	**15**	**25.0761**	**11.7080**
	Logarithmic	2	15	25.2157	11.7913
	Hyperbolic	2	15	25.1732	11.7660
	Sigmoidal	3	15	24.9499	13.6323
	Michaelis - Menten	2	15	25.1732	11.7659
Year 2, Non-Switchers	**Linear**	**2**	**12**	**9.5636**	**1.2767**
	Logarithmic	2	12	10.2680	2.1295
	Hyperbolic	2	12	10.5903	2.5004
	Sigmoidal	3	12	9.3117	2.9564
	Michaelis - Menten	2	12	10.5903	2.5004

Table 28. AIC values of linear, hyperbolic, logarithmic, sigmoidal, and Michaelis-Menten functions applied to the relationship between egg number and mean percent lipid of Manitou lake trout housed in a common environment hatchery in Ontario.

Group	**Relationship**	**No. of Parameters (k)**	**No. of Observations (n)**	**Residual Sum of Squares (RSS)**	**Akaike Information Criterion (AIC)**
Year 1, All Rations	Linear	2	43	122.4853	49.0120
	Logarithmic	2	43	121.3740	48.6201
	Hyperbolic	**2**	**43**	**120.1531**	**48.1854**
	Sigmoidal	3	43	118.8509	49.7168
	Michaelis - Menten	2	43	120.2000	48.2021
Year 2, All Rations	**Linear**	**2**	**39**	**201.0749**	**67.9645**
	Logarithmic	2	39	204.3550	68.5956
	Hyperbolic	2	39	206.7124	69.0429
	Sigmoidal	3	39	198.8060	69.5219
	Michaelis - Menten	2	39	222.4000	71.8957
Year 1, Switchers	Linear	2	21	67.3583	28.4756
	Logarithmic	2	21	64.1144	27.4391
	Hyperbolic	**2**	**21**	**63.3285**	**27.1801**
	Sigmoidal	3	21	60.2421	28.1308
	Michaelis - Menten	2	21	63.3285	27.1801
Year 1, Non-Switchers	**Linear**	**2**	**22**	**47.3867**	**20.8806**
	Logarithmic	2	22	48.7971	21.5258
	Hyperbolic	2	22	48.8508	21.5500
	Sigmoidal	3	22	47.2918	22.8365
	Michaelis - Menten	2	22	48.8508	21.5500
Year 2, Switchers	Linear	2	18	75.9975	29.9259
	Logarithmic	**2**	**18**	**74.7863**	**29.6367**
	Hyperbolic	2	18	75.3779	29.7786
	Sigmoidal	3	18	75.1482	31.7236
	Michaelis - Menten	2	18	76.7054	30.0928
Year 2, Non-Switchers	**Linear**	**2**	**21**	**116.7690**	**40.0292**
	Logarithmic	2	21	120.8377	40.7484
	Hyperbolic	2	21	121.9949	40.9486
	Sigmoidal	3	21	115.3620	41.7746
	Michaelis - Menten	2	21	122.0000	40.9495

Table 29. AIC values of models of best fit, as calculated by AIC comparisons of Michaelis-Menten, hyberbolic, linear, sigmoidal, and logarithmic function, and the alternate models which represent the model of best fit applied to the alternate group (year or ration-group) in the relationship between egg number and mean percent lipid of five stocks of lake trout housed in a common environment experiment in an OMNR hatchery. The models of best fit and alternate models were applied to the same data in each case to determine AIC differences.

Stock	Year 1 AIC	Year 1 Data with Year 2 Regression AIC	Year 2 AIC	Year 2 Data with Year 1 Regression AIC
Michipicoten	0.1512	3.2624	44.6934	45.9215
Killala	15.1304	17.3706	14.5541	15.7552
1999 Kingscote	33.9614	47.9834	43.2349	52.3757
2000 Kingscote	18.3354	57.3064	11.9140	32.3270
Manitou	48.1854	72.6587	67.9645	81.6180
Stock	**Year 1 Non Switcher AIC**	**Year 1 Non Switcher Data with Switcher Regression AIC**	**Year 1 Switcher AIC**	**Year 1 Switcher Data with Non Switcher Regression AIC**
Michipicoten	4.8874	8.1100	-5.6887	0.0361
1999 Kings	12.3191	31.0574	18.1825	32.4700
2000 Kingscote	15.0419	32.3629	1.5416	6.7246
Manitou	20.8806	27.9745	27.1801	32.8411
Stock	**Year 2 Non Switcher AIC**	**Year 2 Non Switcher Data with Switcher Regression AIC**	**Year 2 Switcher AIC**	**Year 2 Switcher Data with Non Switcher Regression AIC**
Michipicoten	25.2474	29.3780	21.9856	23.0036
1999 Kingscote	29.0891	33.9081	12.3321	23.4768
2000 Kingscote	1.2767	8.6847	11.7080	13.0338
Manitou	40.0292	43.7990	29.6367	33.2484

Table 30. P-values for 2008 hatchery data comparing residuals (absolute values) between ration treatments based on sigmoidal function applied to 2008 lipid-fecundity data of five stocks of lake trout held in a common garden experiment.

Killala	**High-High**	**High-Low**	**Low-Low**	**Low-High**
High-High		n/a	0.5749	n/a
High-Low	n/a		n/a	n/a
Low-Low	0.5749	n/a		n/a
Low-High	n/a	n/a	n/a	
2000 Kingscote	**High-High**	**High-Low**	**Low-Low**	**Low-High**
High-High		0.4570	0.4807	0.8475
High-Low	0.4570		0.9997	0.8737
Low-Low	0.4807	0.9997		0.9004
Low-High	0.8475	0.8757	0.9004	
1999 Kingscote	**High-High**	**High-Low**	**Low-Low**	**Low-High**
High-High		0.9923	0.8221	0.2558
High-Low	0.9923		0.7027	0.2001
Low-Low	0.8221	0.7027		0.7572
Low-High	0.2558	0.2001	0.7572	
Manitou	**High-High**	**High-Low**	**Low-Low**	**Low-High**
High-High		0.5683	0.9996	0.4922
High-Low	0.5683		0.6441	0.9994
Low-Low	0.9996	0.6441		0.5686
Low-High	0.4922	0.9994	0.5686	
Michipicoten	**High-High**	**High-Low**	**Low-Low**	**Low-High**
High-High		0.5941	0.6408	0.9997
High-Low	0.5941		0.9988	0.6431
Low-Low	0.6408	0.9988		0.6924
Low-High	0.9992	0.6431	0.6924	

Table 31. P-values for 2009 hatchery data comparing residuals (absolute values) between ration treatments based on sigmoidal function applied to 2009 lipid-fecundity data of five stocks of lake trout held in a common garden experiment.

Killala	**High-High**	**High-Low**	**Low-Low**	**Low-High**
High-High		n/a	0.2491	n/a
High-Low	n/a		n/a	n/a
Low-Low	0.2491	n/a		n/a
Low-High	n/a	n/a	n/a	
2000 Kingscote	**High-High**	**High-Low**	**Low-Low**	**Low-High**
High-High		0.1576	0.9285	0.1264
High-Low	0.1576		0.1177	0.8163
Low-Low	0.9285	0.1177		0.0981
Low-High	0.1264	0.8163	0.0981	
1999 Kingscote	**High-High**	**High-Low**	**Low-Low**	**Low-High**
High-High		0.0919	0.0654	0.0021
High-Low	0.0919		0.9985	0.2893
Low-Low	0.0654	0.9985		0.2696
Low-High	0.0021	0.2893	0.2696	
Manitou	**High-High**	**High-Low**	**Low-Low**	**Low-High**
High-High		0.3367	0.1041	0.4297
High-Low	0.3367		0.0064	0.0723
Low-Low	0.1041	0.0064		0.3865
Low-High	0.4297	0.0723	0.3865	
Michipicoten	**High-High**	**High-Low**	**Low-Low**	**Low-High**
High-High		0.6752	0.2236	0.0782
High-Low	0.6752		0.1752	0.4367
Low-Low	0.2236	0.1752		0.0366
Low-High	0.0782	0.4367	0.0366	

WORKS CITED

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Álvarez, D., and A. G. Nicieza. 2005. Compensatory response 'defends' energy levels but not growth trajectories in brown trout, Salmo trutta L. Proceedings of the Royal Society B: Biological Sciences, 272: 601-607.

Anderson, D. R., Link, W. A., Johnson, D. H., and K. P. Burnham. 2001. Suggestions for presenting the results of data analyses. The Journal of Wildlife Management 65: 373-378.

Barot, S., M. Heino, L. O'Brien, and U. Dieckmann. 2004. Long term trend in the maturation norm of two cod stocks. Ecological Applications 14: 1257-1271.

Belyaev, D. K. 1979. Destabilizing selection as a factor in domestication. Journal of Heredity 70: 301–308.

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

Beauchamp, D. A., Sergeant C. J., Mazur, M. M., Scheuerell, J. M., Schindler, D. E., and M. D. Scheuerell. 2004. Spatial-temporal dynamics of early feeding demand and food supply for sockeye salmon fry in LakeWashington. Transactions of the American Fisheries Society 133:1014–32.

Bronson, F. H. 1984. Energy allocation and reproductive development in wild and domestic mice. Biology of Reproduction 31: 83–88.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer.

Claus, L. C. 2011. Influence of life history traits on accumulation of polybrominated diphenyl ethers and polychlorinated biphenyls in three lake trout populations from Lake Superior. Master of Science Thesis, Michigan State University.

Cushing, D. H. 1969. The regularity of the spawning season of some fishes. J Cons Int Explor Mer 33:81–92.

Darwish, T. L., and J. A. Hutchings 2009. Genetic variability in reaction norms between farmed and wild backcrosses of Atlantic salmon (Salmo salar). Canadian Journal of Fisheries and Aquatic Sciences 66: 83-90.

Eby, L. A., Rudstam, L. G., & Kitchell, J. F. (1995). Predator responses to prey population dynamics: an empirical analysis based on lake trout growth rates. Canadian Journal of Fisheries and Aquatic Sciences, 52: 1564-1571.

Ferreri, C. P., & Taylor, W. W. (1996). Compensation in individual growth rates and its influence on lake trout population dynamics in the Michigan waters of Lake Superior. Journal of Fish Biology, 49(5), 763-777.

Figueiredo-Silva, A. C., Saravanan, S., Schrama, J. W., Panserat, S., Kaushik, S., & Geurden, I. 2012. A comparative study of the metabolic response in rainbow trout and Nile tilapia to changes in dietary macronutrient composition. The British journal of nutrition: 1-11.

Fleming I. A., Jonsson B., Gross M. R., and A. Lamberg. 1996. An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (Salmo salar). Journal of Applied Ecology 33: 893–905.

Flores, H., & Vergara, A. (2012). Effect of reducing the feeding frequency on the survival, growth, conversion, and feeding behavior of juvenile Atlantic salmon Salmo salar (Linnaeus, 1758): an experience at the productive level. Latin American Journal of Aquatic Research 40: 536-544.

Frisch, A. J., & Anderson, T. A. (2000). The response of coral trout (Plectropomus leopardus) to capture, handling and transport and shallow water stress. Fish Physiology and Biochemistry, 23(1), 23-34.

Gregersen, F., Haugen, T. O., and N. Larsen. 2006. Egg size differentiation among sympatric demes of brown trout: possible effects of density-dependent interactions among fry. Ecology of Freshwater Fish 15: 237-246.

Gross, M. R. 1998. One species with two biologies: Atlantic salmon (Salmo salar) in the wild and in aquaculture. Canadian Journal of Fisheries and Aquatic Sciences 55: 131–144.

Hafs, A. W., Mazik, P. M., Kenney, P. B., and J. T Silverstein. 2012. Impact of carbon dioxide level, water velocity, strain, and feeding regimen on growth and fillet attributes of cultured rainbow trout Oncorhynchus mykiss. Aquaculture 350: 46-53.

Heino, M., and V. Kaitala. 1999. Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. Journal of Evolutionary Biology 12: 423-429.

Henderson, B. A., and J. L. Wong. 1998. Control of lake trout reproduction: role of lipids. Journal of fish biology, 52: 1078-1082.

Hill, D. K., and J. J. Magnuson, J. J. 1990. Potential effects of global climate warming on the growth and prey consumption of Great Lakes fish. Transactions of the American Fisheries Society 119: 265-275.

Hislop, J. R. 1988. The influence of maternal length and age on the size and weight of the eggs and the relative fecundity of the haddock, Melanogrammus aeglefinus, in British waters. Journal of Fish Biology 32: 923-930.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological monographs: 54:187-211.

Hurst, T. P., and D. O. Conover. 2003. Seasonal and interannual variation in the allometry of energy allocation in juvenile striped bass. Ecology 84: 3360-3369.

Hutchings, J. A., Picklet, A., McGregor-Shaw, C. R. and L. Poirier. 1999. Influence of sex, body size and reproduction on overwinter lipid depletion in brook trout. Journal of Fish Biology 55: 1020–1028.

Imsland, A. K., Foss, A., Folkvord, A., Stefansson, S. O., and T. M. Jonassen. 2005. The interrelation between temperature regimes and fish size in juvenile Atlantic cod (Gadus morhua): effects on growth and feed conversion efficiency. Fish Physiology and Biochemistry, 31(4), 347-361.

Jastrebski, C. J., and Y. E. Morbey. 2009. Egg Size Variation in Lake Trout: Phenotype-Habitat Correlations Show an Effect of Rearing Environment. Transactions of the American Fisheries Society 138: 1342-1351.

Jennings, S. and R. J. H. Beverton. 1991. Intraspecific variation in the life history tactics of Atlantic herring (Clupea harengus L.) stocks. ICES Journal of Marine Sciences 48: 117-125.

Johnsen, C. A., Hagen, Ø., Solberg, C., Björnsson, B. T. H., Jönsson, E., Johansen, S. J. S., and E. Å. Bendiksen. 2013. Seasonal changes in muscle structure and flesh quality of 0+ and 1+ Atlantic salmon (Salmo salar L.): impact of feeding regime and possible roles of ghrelin. Aquaculture Nutrition 19:15-34.

Kamler, E. 2005. Parent–egg–progeny relationships in teleost fishes: an energetics perspective. Reviews in Fish Biology and Fisheries 15: 399-421.

Kitchell, J. F., and L. B. Crowder. 1986. Predator-prey interactions in Lake Michigan: model predictions and recent dynamics. Environmental Biology of Fishes 16: 205-211.

Kozlowski, J. 1996. Optimal Allocation of Resources Explains Interspecific Life-History Patterns in Animals with Indeterminate Growth. Proceedings of the Royal Society B 263: 559-566.

Lambert, Y., and J. D. Dutil 2000. Energetic consequences of reproduction in Atlantic cod (Gadus morhua) in relation to spawning level of somatic energy reserves. Canadian Journal of Fisheries and Aquatic Sciences 57: 815-825.

Laporte, J., and J. Trushenski. 2012. Production performance, stress tolerance and intestinal integrity of sunshine bass fed increasing levels of soybean meal. Journal of Animal Physiology and Animal Nutrition 96: 513-526.

Marsden, J. E., and C. C. Krueger. 1991. Spawning by hatchery-origin lake trout (*Salvelinus namaycush*) in Lake Ontario: data from egg collections, substrate analysis, and diver observations. Canadian Journal of Fisheries and Aquatic Sciences 48: 2377-2384.

Myers, J. M., Park, L. K., Neely, K. G., Swanson, P., Elz, A. E., and J. J. Hard. 2011. Feeding Ration, Genetics, and Reproductive Traits in Female Coho Salmon: Is Bigger Better?. Journal of the World Aquaculture Society 42: 812-823.

Næsje, T. F., Thorstad, E. B., Forseth, T., Aursand, M., Saksgard, R. and A. G. Finstad. 2006. Lipid class content as an indicator of critical periods for survival in juvenile Atlantic salmon (Salmo salar). Ecology of Freshwater Fish 15: 572–577.

Pianka, E. R. 1976. Natural Selection of Optimal Reproductive Tactics. American Zoologist 16: 775-78.

Pitman, R. W. 1979. Effects of female age and egg size on growth and mortality in rainbow trout. The Progressive Fish Culturist 41: 202-204.

Purchase, C. F., and J. A. Brown. 2001. Stock-specific changes in growth rates, food conversion efficiencies, and energy allocation in response to temperature change in juvenile Atlantic cod. Journal of Fish Biology 58: 36-52.

Reisenbichler, R. R. and S.P. Rubin. 1999. Genetic changes from artificial propagation of Pacific salmon affect the productivity and viability of supplemented populations. ICES Journal of Marine Science 56: 459-466.

Reisenbichler, R.R., Utter, F. M., and C.C. Krueger. 2003. Genetic concepts and uncertainties in restoring fish populations and species. *In:* Strategies for Restoring River Ecosystems: Sources of Variability and Uncertainty in Natural and Managed Systems: 149-183.

Robards, M. D., Anthony, J. A., Rose, A. G. and J. F. Piatt, J. F. 1999. Changes in proximate
composition and somatic energy content for Pacific sand lance (Ammodytes hexapterus) from Kachemak Bay, Alaska relative to maturity and season. Journal of Experimental Biology and Ecology 242, 245–258.

Sargent, R. C., Taylor, P. D., and M. R. Gross. 1987. Parental care and the evolution of egg size in fishes. American Naturalist 129: 32-46.

Schreck, C. B., Contreras-Sanchez, W., and M. S. Fitzpatrick. 2001. Effects of stress on fish reproduction, gamete quality, and progeny. Aquaculture 197: 3-24.

Schreck, C. B. 2010. Stress and fish reproduction: the roles of allostasis and hormesis. General and comparative endocrinology 165: 549-556.

Shuter, B. J., M. L. Jones, R. M. Korver, and N. P. Lester. 1998. A general, life history based model for regional management of fish stocks: The inland lake trout (Salvelinus namaycush) fisheries of Ontario. Canadian Journal of Fisheries and Aquatic Sciences 55: 2161-2177.

Sloman, K. A., Metcalfe, N. B., Taylor, A. C., & Gilmour, K. M. (2001). Plasma cortisol concentrations before and after social stress in rainbow trout and brown trout. Physiological and Biochemical Zoology, 74: 383-389.

Solberg, M. F., Skaala, Ø., Nilsen, F., and K. A. Glover. 2013. Does domestication cause changes in growth reaction norms? A study of farmed, wild and hybrid atlantic Salmon families exposed to environmental stress. PloS one, 8(1), e54469.

Spromberg, J. A., and W. J. Birge. 2005. Modeling the effects of chronic toxicity on fish populations: The influence of life history strategies. Environmental Toxicology and Chemistry 24: 1532-1540.

Stauffer, T. M. 1981. Collecting gear for lake trout eggs and fry. The Progressive Fish-Culturist, 43: 186-193.

Stearns, S.C., and J.C. Koella. 1986. The Evolution of Phenotypic Plasticity in Life-History Traits: Predictions of Reaction Norms for Age and Size at Maturity. Evolution 40: 893-913.

Thompson, J. M., Bergersen, E. P., Carlson, C. A., and L. R. Kaeding. 1991. Role of Size, Condition, and Lipid Content in the Overwinter Survival of Age– 0 Colorado Squawfish. Transactions of the American Fisheries Society, 120(3), 346-353.

Tian, X., and J. G. Qin. 2004. Effects of previous ration restriction on compensatory growth in barramundi Lates calcarifer. Aquaculture 235: 273-283.

Wang, H. Y., D. W. Einhouse, D. G. Fielder, L. G. Rudstam, C. S. Vandergoot, A. J. VanDeValk, T. G. Zorn, and T. O. Hook. 2012. Maternal and stock effects on egg-size variation among walleye Sander vitreus stocks from the Great Lakes region. Journal of Great Lakes Research 38: 477-489.

Yibo, C., and L. Jiankang. 1990. Comparison of energy budget among six teleosts—IV. Individual differences in growth and energy budget. Comparative Biochemistry and Physiology Part A: Physiology 97: 551-554.

Zhang, Y., Øverland, M., Shearer, K. D., Sørensen, M., Mydland, L. T., and T. Storebakken. 2012. Optimizing plant protein combinations in fish meal-free diets for rainbow trout Oncorhynchus mykiss by a mixture model. Aquaculture 360: 25