University of Alberta

The Increasing Prevalence of Smaller Fish in Highly Exploited Fisheries: Concerns, Diagnosis and Management Solutions.

Spine title: Active Adaptive Management to Address a Small Fish Problem.

by

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Abstract

A decline in the size of fish within a population is concerning. Large-sized fish are ecologically important and valued for social and economic reasons. Following widespread collapses from angling overharvest, the densities of Walleyes *Sander vitreus* in Alberta's lakes increased rapidly with large-minimum-size limits. Anglers were unhappy, however, as catch rates increased (>1 Walleyes*hour^{-1}) but fish remained small and did not exceed the minimum size limit. The two alternate explanations for the small, yet old Walleyes were either compensatory growth because of high density (stunting) or size-selective mortality (overfishing). Size-selective mortality has evolutionary consequences. Paradoxically, the management solutions for these problems are in opposition (more harvest versus less harvest), and a wrong diagnosis could exacerbate the problem.

I used nested hypotheses, and implemented active adaptive management at several Alberta lakes, to diagnose the causal mechanism creating the small fish problem. For inferences on the source of the mortality, I analysed backcalculated growth rates from pelvic fins. Walleyes that had fast-growth to an early maturity, and then subsequent slow-growth, had greater survival. This 'hockey stick'-shaped growth allows for successful reproduction while the Walleyes remain below the minimum size limit, avoiding harvest. Using changes to sport fishing regulations, I then modified angler effort and harvest at four different Alberta lakes to increase or decrease size-selective harvest and Walleye densities. I found that size-selective mortality from angling rapidly truncated the population-size structure.

With concerns of evolutionary consequences because of evidence of size selective harvest, I used an age- and size-structured, single-species model, parameterized with data from Alberta's Walleye fisheries, to evaluate the selectiveness of various management regulations. I found that the 50-cm minimum size limit used to recover Alberta's Walleye populations did indeed select for the 'hockey stick' life history, although this regulation allowed for sustainable populations (>5 Walleyes*hectare^{-1}) and angler effort up to 16 angler-hours*ha^{-1}*year^{-1}. The optimal regulation to reduce life history selection and allow for population sustainability was a 40-50 cm 'harvest-tag' regulation. This regulation reversed the selection for the 'hockey stick' life history, yet produced sustainable fish densities and allowed angler effort up to 30 angler-hours*ha^{-1}*year^{-1}. However, increasing angler-noncompliance reduced the sustainability of this regulation.

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Chapter 1 Introduction

A loss of large-sized fish from a fishery is concerning. Larger and older fish are at least as important as simple spawning biomass for population sustainability as they produce more viable offspring and provide a temporal distribution of spawn (Berkeley et al. 2004; Venturelli et al. 2009). Society also values large fish for food, economic, and trophy considerations (Pitcher 2001). Declining fish size in a fishery has been attributed either to compensatory growth from high-fish density or size-selective mortality (Rose et al. 2001; Myers and Worm 2003). When size-selective mortality for a phenotype exists, this raises concerns of evolutionary changes (Law 2000; Jorgensen et al. 2007; Hard et al. 2008).

Compensatory growth caused by high fish density and a lack of food resources can result in small fish (Rose et al. 2001). Commonly referred to as 'stunting,' this reduced growth is ecologically undesirable as a loss of top predators can have cascading effects through the ecosystem (Pace et al. 1999). Stunted populations are socially and economically undesirable as only small fish are caught and fisheries' yields may be reduced. Typically, the management action to address compensatory growth is to increase harvest (Beard et al. 1997; Schneider and Lockwood 2002).

Alternately, a decline in size of fish can be caused by overharvest as large- and faster-growing individuals are typically caught earlier in the fishing-up process (Ricker 1969; Myers and Worm 2003; Hilborn et al. 2003). If sufficient fishing exists to remove the larger fish from the population, this size-selective mortality can change the population size-structure. Growth metrics such as size-at-age or growth curves applied to the remaining fish suggest a slower growth rate for the surviving fish. Termed 'Rosa Lee's phenomenon' (Ricker 1969), this has been well documented in fished populations (Pitcher 2001). The management solution to increase the number of large fish in these populations is to reduce harvest.

Lastly, sufficient size-selective mortality can result in phenotypic selection and have undesirable evolutionary consequences (Law 2000; Conover and Munch 2002; Hutchings 2005; Hard et al. 2008; Philipp et al. 2009). Documented in managed aquatic and terrestrial species, this selection may be difficult to reverse (Law 2000). Olsen et al. (2004) attributed a decline in the size of Atlantic Cod *Gadus morhua* to early maturation at a smaller size and subsequent slower growth. Fish with this life history remain small and are less vulnerable to fishing. The management options to alleviate phenotypic selection are to reduce or reverse the size-selective harvest. Despite a 10-year closure of some aspects of the Atlantic Cod fisheries, little recovery of the larger fish had occurred. However, experimentally reversing the selection on Atlantic Silversides *Menidia menidia* resulted in a rapid recovery of the larger phenotypes (Hutchings 2005; Conover et al. 2009).

Determining what is causing 'small fish' can be problematic with the inherent variability in fish growth and the confounding effects of size-selective harvest. Paradoxically, the management solutions are in opposition; either increase or decrease harvest.

Complaints of small and stunted Walleyes *Sander vitreus* from Alberta's fishermen at several recovering Walleye fisheries required a management solution. Historically, Alberta's Walleye fisheries declined because of a burgeoning human population, few lakes and low productivity (Post et al. 2002). As a recovery mechanism, restrictive-minimum-size regulations were employed that forced anglers to release the majority of their catch (Sullivan 2003). This strategy resulted in a rapid increase in Walleye numbers, yet few large fish were being caught (Sullivan 2003). As anglers have considerable socio-political clout (Botsford et al. 1997), and with Alberta's history of fish population collapses, a correct diagnosis and an appropriate solution were critical.

I used an active adaptive management process, with extensive stakeholder involvement, in several large-scale, cause and effect experiments (Walters and Holling 1990). My ultimate goal was to gain knowledge from the management experiments and create predictive models to determine the optimal management action to recover the densities of large Walleyes.

I offered two competing hypotheses for the mechanism that has created these populations of small, yet abundant Walleyes H_1: Walleye numbers have increased sufficiently that food and habitat are now limiting growth (compensatory population responses –a consequence of insufficient harvest) or H_2: there is excessive size-selective- and release mortality causing Walleyes to fail to survive and exceed the minimum size limit (Rosa Lee's phenomenon - a consequence of excessive harvest)

Critical to determining a change in the growth of fish is an accurate assessment of the fish's age (Walters and Martel 2004). In Chapter 2, I evaluate and refine Alberta's fish ageing techniques. I then quantify the accuracy and precision of these assigned ages. A product from this research is an ageing techniques manual which has been approved as a provincial standard for fish ageing in Alberta (Watkins and Spencer 2008a; 2008b). Additionally, a manuscript describing this work has been reviewed by the North American Journal of Fisheries Management (July 2009) and is being revised for resubmission.

In Chapter 3, I describe the complexity in diagnosing a decline in the size of fish within a fishery. I provide a series of nested hypotheses and use a combination of angler use, and fish population data to explain causes of small fish at Alberta fisheries. I then use growth histories measured from pelvic fins for further information on growth and survival of the old, yet small Walleyes.

Management experiments were required to determine the effect of angling on density and directional mortality. In Chapter 4, I use the sport fishing regulations to increase or decrease size-selective harvest and Walleye densities at four different lakes with small Walleyes.

And lastly, in Chapter 5, I use the empirical data gathered from the work described in the previous chapters in an age- and size-stratified population model (Post et al. 2003) to evaluate the size-selectiveness and sustainability of different management techniques. This model was validated against case histories of harvest and Walleye population data from Alberta's lakes.

This work is important as the Walleye fisheries in Alberta have historically collapsed and evidence of a decline in fish size raises concerns of about future sustainability. These changes in fish size need to be addressed to recover densities of large Walleyes.

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Chapter 2 Nonlethal ageing methods and ageing error identified for Alberta Walleyes: management consequences for slow-growing fishes.

Introduction

Under-ageing and excessive variance around true ages are critical problems for fisheries management leading to overestimates of stock productivity. Under-ageing the slow-growing stocks of New Zealand's Orange Roughy *Hoplostethus atlanticus* and North American Rockfish *Sebastes* spp resulted in population collapses because of overestimates of productivity (Campana 2001). Similarly, total allowable catch was overestimated with simulated ageing error in Eastern Baltic Cod *Gadus morhua* (Munk 2001; Reeves 2003). Variance around true ages, however, can hide variable recruitment affecting stock productivity. For example, Clark (1993) demonstrated that variable recruitment reduced the sustainable yields for Alaska groundfish.

In Alberta, failures to understand the recruitment variability and longevity of northern stocks of Walleyes *Sander vitreus* resulted in overestimates of productivity and allowed for overharvest and population collapses (Post et al. 2002; Sullivan 2003). Accurate and precise ages are needed to manage these vulnerable stocks, and preferably, with a nonlethal technique to avoid unnecessary fish mortality.

The bony structures used most commonly to nonlethally assess Walleye ages

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*A version of this chapter is currently in revision after first submission. Spencer et al. 2009. North American Journal of Fisheries Management.

are dorsal spines and pelvic fins (Maceina et al. 2007). Alberta biologists have traditionally used pelvic fins as the structure to estimate Walleye ages nonlethally (Mackay et al. 1990). However, there are no published studies that have validated ages estimated from pelvic fins and few that have assessed their accuracy and precision in comparison to ages estimated from otoliths for Walleyes (Belanger and Hogler 1982; Maceina et al. 2007). The few studies that have evaluated Walleye pelvic fins and dorsal spines as ageing structures demonstrated that the derived ages were less precise and accurate than those from otoliths, especially in slower-growing fish (Erickson 1983; Logsdon 2007; Maceina et al. 2007).

I deemed it important to assess nonlethal ageing structures to ensure that I was not making the serious error of underestimating the ages of Walleyes or missing age-class variance. Firstly, I needed to determine the accuracy and precision of ages derived from pelvic fins for Alberta's slow-growing Walleyes. Here I provide Alberta's techniques for pelvic fin and otolith preparation and annuli identification for assessing the age of Walleyes. I then compared ages estimated from pelvic fins to those from otoliths and to known-age Walleyes. Otoliths were chosen for this comparison because they have been extensively validated to provide accurate ages (Erickson 1983; Kocovsky and Carline 2000; Maceina et al. 2007). I then tested the assumption that Walleye-growth rates affect ageing accuracy (i.e., do slower-growing fish produce annuli that are harder to detect resulting in underestimation of age?). And lastly, I examined how the error associated with ages estimated from pelvic fins and dorsal spines affect various fisheries metrics and population management.

Methods

Study Location and Collection Techniques.—I collected Walleyes from various locations in Alberta, Canada (Table 2-1) following the Fall Walleye Index Netting protocol (Morgan 2002), except for those from Lake Athabasca which were sampled from a June commercial fishery (102 mm stretched-mesh gillnets). Age-0 Walleyes were collected by beach seining (10 x 1.2 m net with 1.5 mm mesh) and gillnetting (3 panels, 1.8 m deep × 7.6 m long of 12, 19 and 25 mm stretched-mesh nets) periodically from May through to September. All Walleyes were measured for total length (to the nearest mm).

I excised, with wire cutters, the first-three rays from the leading edge of the left pelvic fin within 5 mm of their articulation to the Walleye. Both saggital otoliths were removed. Pelvic fin- and otolith samples were stored dry prior to laboratory preparation.

Ageing-Structure Preparation.—Pelvic fin-rays were sectioned with a variable-speed, Grobet™ jeweler's, electric handsaw. I used a 19 x 0.1 mm-saw blade cutting on a section of X-Acto™ foam board to minimize blade wear. At least five cross-sections of 0.4 mm thickness were cut perpendicular to the length of the fin rays. These sections were mounted in sequential order on a clear-acrylic slide with Cytoseal™ XYL (low viscosity) media within a fume hood. Slides were dried for 24 h prior to age assignment.

I used a scalpel to section otoliths transversely with the concave side up on a hard-plastic surface. The scalpel blade was placed on the focus perpendicular to the longitudinal axis over the nucleus and the otoliths were broken with a gentlesawing action. To enhance the visibility of the annuli, the sectioned faces were heated with a candle flame until they turned from white to a dark-amber colour (Barber *et al.* 1987). To improve readability, a small amount of vegetable oil was applied with a fine-tipped paintbrush to the sectioned faces (Baker and Timmons 1989).

Age Interpretation.—Reflected light and a dissection microscope (25 to 40 X magnification) were used for all ageing. An annulus was interpreted as the combination of opaque, white banding (summer growth) followed by a translucent band (winter growth) with the outermost edge of the translucent band counted as the end of the year's growth. To identify and dismiss false annuli, I endeavored to follow the translucent bands across different planes of the same ageing structure.

Determination of the First Annulus.—I found considerable lack of agreement among Alberta's fish-ageing technicians as to the location of the first annulus on pelvic fin- and otolith sections. To resolve this problem, I used the following backcalculation formula to locate the first annulus on the cross-section of every ageing structure.

$SRa_1 = (SR \times L_1) * L_c^{-1}$

where SRa_1 is the radius distance from the focus to the first annulus on the ageing structure (mm), SR is the structure's total radius (mm), L_1 is the fish's-estimated length at age-1 (mm), and L_c is the fish's length at capture (mm). All measurements were recorded along the longest axis from the focus to the distal edge of the ageing structure with the aid of an ocular micrometer (1:10 mm) used in a dissection microscope.

There are two important assumptions inherent to this backcalculation formula; the approximate-body length of the young Walleye at first annulation; and the cross-section of the structure used for ageing grows allometrically to the fish's length. To determine a Walleye's length at its first annulation I tracked the growth of age-0 Walleyes through the summer and fall with data compiled from various Alberta lakes. Although annulation occurs the following spring, I assumed that by mid-September, Alberta's Walleyes had mostly finished growing. To determine if cross-sections from pelvic fins and otoliths increase allometrically with the Walleye's length, I compared with linear regression the cross-sectional radius of each structure to the corresponding fish's length.

Evaluating Accuracy and Precision.—Age estimates from pelvic fins were compared to those from otoliths and to known-age fish using age-bias plots (Campana et al. 1994), percent agreement and coefficients of variation (CV). Agreement, a measure of accuracy, was calculated as a binary outcome for each fish, totaled for the entire waterbody and expressed as a percent. CV, a measure of precision, was calculated with a method from Chang (1982) modified for my paired comparisons:

$$\mathrm{CV} = \frac{\sqrt{\left[\dfrac{(X_a - X_{avg})^2 + (X_b - X_{avg})^2}{2}\right]}}{X_{avg}}$$

where for each Walleye, X_a was the age estimated from the otolith; X_{avg} was the average age estimated for the two structures compared, and; X_b was the age estimated from either the pelvic fin or the otolith by a second technician. CV was calculated for each Walleye and then averaged for all samples (by lake and structure) to provide a mean estimate of precision.

All other structures were aged by the same technician (Owen Watkins) except for a comparison of my ages estimated from otolith to those estimated by Susan Mann (Ontario Ministry of Natural Resources, Fisheries Ageing Specialist). Ages were assessed in blind comparisons to ensure that the technician would not be biased by the age of the fish's-comparative structure or its length.

Walleye-Growth Rates and Accuracy of Ages. — To test the assumption that slow-growing Walleyes produce structures that are less accurate and precise for age assessment, I compared age agreement with the Relative Growth Index (RGI) values (Quist et al. 2003). RGI was calculated as

$$RGI = (L_t \times L_s^{-1}) \times 100,$$

where L_t is the average-Walleye length at age-t (otolith derived ages) and; L_s is the predicted length-at-age estimated with a von Bertalanffy growth model with North American data from Quist et al. (2003) for combined sexes of Walleyes. I compared the agreement between ages estimated from pelvic fins and otoliths from four lakes with different RGI values.

Ageing Error and Data Interpretation. —I investigated how the ageing error associated with ages estimated from pelvic fins and dorsal spines would affect data interpretation. Do the ages assessed from these structures provide underestimates and effectively mask variable recruitment? Because values from the literature on the accuracy and precision associated with ages estimated from dorsal spines were similar to what I found with pelvic fins, I provided examples of how data interpretation would be affected using the information from my pelvic fin assessments (Belanger and Hogler 1982, 29% agreement and Erickson 1983, 55.4 to 80.0%; and Logsdon 2007, 36-98% agreement).

To determine whether the precision of age estimates changed with increasing age of the fish, I calculated the standard deviation from the paired comparisons of the ages estimated from pelvic fins and otoliths. This was done for each age-class with data combined from all of the lakes. I then plotted the age (otolith derived) against these standard deviations to examine trends. Secondly, I provided a graphical example of how ageing error affected the interpretation of age-class data for Walleyes from Lake Athabasca. To evaluate whether mortality rates and maximum-age-estimates would be affected by ages derived from pelvic fins and otoliths, I used a weighted-catch-curve regression analysis (Fishery Analysis and Simulation Tools software 2.1, Slipke and Maceina 2000). I also present the mean time that a fish would be in a fishery with:

Mean time = $1/Z$,

with, Z, the instantaneous-mortality rate (Ricker 1975) calculated from ages estimated from fin rays and otoliths.

Results

Locating the First Annulus. —I used a backcalculation formula to help locate the first annulus. For this backcalculation formula I required; the Walleye's length at annulation, evidence of an allometric relationship between a Walleye's length, and the radii of the fin ray- and otolith cross-sections. Firstly, I measured the lengths of age-0 Walleyes from June through September to determine the length of Walleyes at first annulation. Data collected from Alberta lakes indicated an average length of 135 mm by mid-September (Figure 2-1). I chose, however, an approximate length of 150 mm for backcalculating as the Walleyes continue to grow after September until annulation occurs in the spring. My second assumption of an allometric relationship between the Walleye's-body length and the ageing-structure's radius was correct for both pelvic fins and otoliths (Figure 2-2).

Pelvic Fins, Otoliths and Known-Age Walleyes. —Comparing age estimates from pelvic fins to otoliths (same ageing technician) yielded a range of agreement from 30% to 83% for Walleyes from the four lakes (Figure 2-3, Table 2-2). Walleyes older than age-12 had consistently lower age estimates from fin rays than otoliths. Seventy-two to 100% of age estimates from pelvic fins and otoliths were within one year of each other (Table 2-2). Precision increased with accuracy (Figure 2-4).

The agreement between two ageing technicians for ages estimated from otoliths was 87% (Table 2-2) approaching the 90% agreement recommended by Ricker (1975).

Comparing age estimates from pelvic fins to known-age Walleyes from Hutch Lake, Alberta, yielded a very-low agreement of 28% (or 97% within one year, Figure 2-5). There was no bias to these errors (i.e., age estimates from pelvic fins were distributed evenly around the known-age).

Growth Rate and Ageing Agreement. —Agreement between ages estimated from pelvic fins and otoliths increased with the RGI (Figure 2-6). Agreement ranged from 30% at the lake with the lowest RGI (most northerly) to 83% at the lake with the highest RGI (most southerly).

Ageing Error and Data Interpretation. —The standard deviation from the paired comparisons of the ages estimated from pelvic fins and otoliths increased with the age of the Walleye (Figure 2-7). Therefore, as the Walleyes get older, the precision of the ages estimated from pelvic fins decreased.

A graphical comparison of age-class distributions generated from ages estimated from pelvic fins and otoliths (when agreement was 30%) provided two different outcomes (Figure 2-8). The age-class distribution generated from pelvic fins indicated more constant recruitment while that from otoliths indicated more variable recruitment.

Evaluating annual-mortality rates and theoretical-maximum age from the two lakes with the lowest agreement of ages estimated from pelvic fins- to otoliths yielded mixed results (Table 2-3). At Lake Athabasca, Alberta, the respective mortality rates, calculated from ages estimated from pelvic fins and otoliths, were nearly identical at 19% and 18%, while the respective maximum ages were estimated at ages-21 and 22. At Buck Lake, Alberta; however, the respective mortality rates estimated from pelvic fins and otoliths were 54% and 32% while the maximum ages were estimated at ages-12 and 15. These mortality rates from Buck Lake, Alberta, resulted in estimated mean times in the fishery of 1.9 years (fin-rays) and 3.1 year (otoliths).

Discussion

Ages estimated from pelvic fins demonstrated poor agreement (28%) with known-age Walleyes from Hutch Lake, Alberta. This result was especially disconcerting since these known-age Walleyes were relatively young (ages-8 and 9 in two consecutive surveys) while Walleyes in Alberta have been estimated to be as old as age-29 from otoliths. Ricker (1975) recommended an ageing agreement of 90% and indicated that agreement tends to decline as fish become older. Thus, as these known-age Walleyes get older, ageing agreement may decline further.

My comparison of age estimated from pelvic fins and otoliths at four lakes yielded unacceptable agreement (i.e., under 90%, Ricker 1975). Logsdon (2007) used unsectioned dorsal spines for estimating Walleye ages in two Minnesota lakes and recorded a similar range of ageing agreement to this study (36% to 98%). Belanger and Hogler (1982) reported agreement ranging from 29% to 35% comparing ages estimated from; pelvic fin, dorsal spine and pectoral fin to those from otoliths. Depending on the research question, this level of accuracy may be sufficient. However, I often require a greater level of accuracy for research into evaluating stocking success, the effects of water withdrawals on Walleye recruitment, and the effects of chemical spills on survival and mortality. I found that the variable-age-class data from ages estimated from otoliths was effectively 'smoothed' by the ages estimated from pelvic fins. This appearance of consistent recruitment can lead a researcher to an erroneous conclusion that may affect population sustainability (Reeves 2003).

Agreement between ages estimated from pelvic fins and otoliths increased with faster-growing Walleyes. This outcome was somewhat confounded, as the lakes with slower-growing Walleyes had older fish which are typically more difficult to age. Regardless, I found that with faster growth the annuli tended to be further apart and more consistently spaced, making detection easier. For the same reasons, the false annuli were easier to reject.

Overall, I found that for Walleyes older than age-12 (estimated from otoliths) fin rays age estimates were consistently lower. This bias, however, was not consistent for all ages, thereby preventing a simple correction. Maceina et al. (2007) described ageing error to be either: 1) process error (i.e., the structure does not consistently form annuli) or 2) interpretation error (i.e., the annuli are not easily identified). In my comparisons, younger fish would not always form an identifiable annulus on the pelvic fin though an annulus was visible on the otoliths, suggesting a process error. For example, at Buck Lake, Alberta, the majority of the disagreement occurred at age-3 while at Newell Lake, Alberta, disagreement was most prevalent at age-4. Similarly, a study of Lingcod *Ophiodon elongatus* marked with oxytetracycline demonstrated process error with only 3 of the 4 recaptured fish forming the expected pelvic fin annuli (Cass and Beamish 1983).

There were also interpretation errors in assessing ages from pelvic fins. Typically, ageing agreement decreases with older fish as growth slows and annuli become compressed towards the margin (Ricker 1975). This was especially true for the pelvic fins as annuli concentrate on the outer edge of the structure while the otolith annuli remain farther apart and relatively easy to read. For example, at the most northerly study lake (Lake Athabasca) a 513 mm Walleye had respective ages estimated at 19 from the pelvic fin and 29 from the otolith. Morita and Matsuishi (2001) described that otoliths continue to grow after somatic growth slows while it appears that pelvic fins grow somatically. Thus, if a fish grows slowly, I postulate that the pelvic fin annuli do not form or will be difficult to interpret. The regressions of pelvic fin- and otolith radii to fish length support this premise with the pelvic fins growing more linearly than the otoliths (Figure 2-2).

My comparisons were made under the assumption that the otolith derived ages were correct; however, I recognize that ageing error may also exist with these ages. I was unable to validate otolith age estimates, although I was able to follow a strong age-class for multiple years in the stocked-Walleye fishery at Pigeon Lake, Alberta. Campana (1990) discussed that this does not constitute validation; however, otolith derived ages have been extensively validated (Maceina et al. 2007).

Management Implications.—Will ages estimated from pelvic fins and dorsal spines lead to the serious-management problem of underestimating ages and age-class variability? For Alberta's Walleyes and especially those from lakes further north, ages assessed from pelvic fins had poor agreement with those from otoliths and known-age fish: A similar result to what has been recorded for ages estimated from dorsal spines (Belanger and Hogler 1982; Erickson 1983; and Logsdon 2007). I found that this error created underestimates of maximum age, estimated mean time in the fishery and reduced age-class variability which leads to an overestimation of stock yields (Campana 2001; Reeves 2003). Based on my work I must recommend against using pelvic fins and dorsal spines for age assessment. Further work to assess these nonlethal structures may be warranted for locations with faster-growing Walleyes.

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TABLE 2-1.—Location, elevation, area and growing degrees days (GDD) of the Alberta study lakes.

Lake	Long.	Lat.	Elevation (msl)	Lake Area (hectares)	GDD>5°Celcius[1]
Newell	111° 57'	50°25’	760	6 640	1650-1800
Buck	114° 45’	53°00’	884	2 540	1200-1350
Floatingstone	111° 37’	54°13’	610	597	1200-1350
Hutch	117°20’	58°45’	762	592	1050-1200
Athabasca	109°22’	59° 11’	220	777 000	1200-1350
Keho Lake	113°00’	49°56’		1 770	1650-1800
Forty Mile Coulee Reservoir	111°28’	49°41’	783	650	1650-1800
Crawling Valley Reservoir	112° 21’	50°56’	785	2 510	1650-1800
Milk River Ridge Reservoir	112°33’	49°22’	1033	210	1650-1800

[1]AFRD 2008

TABLE 2-2. —The percent agreement in comparing ages estimated from: otolith to otolith (between ageing technicians), for pelvic fin to otolith (same ageing technician) and pelvic fins to known-age fish for samples from five Alberta lakes. I used the Relative Growth Index (RGI) to compare Walleye growth between the lakes (Quist et al. 2003). I also present the agreement for the ages that were within one year of agreement and the coefficient of variation (CV) for the sample; n/a = not available.

Lake and Comparison	N	RGI	Agreement (%)	Agreement (%) ± 1 year	Average CV
Buck –otolith to otolith	55	34	87	98	0.0090
Buck –pelvic fin to otolith	55	34	35	91	0.057
Athabasca–pelvic fin to otolith	147	30	30	71	0.065
Newell–pelvic fin to otolith	160	84	83	100	0.023
Floatingstone–pelvic fin to otolith	46	83	82	92	0.017
Hutch–pelvic fin to known-age	32	n/a	28	97	n/a

TABLE 2-3.—Mortality rates and maximum ages from a weighted-catch-curve regression analysis calculated from ages estimated from pelvic fins and otoliths.

Lake	N	Structure	Maximum age	Annual mortality rate	Average Prob>F
Buck	55	pelvic fin	12	0.54	0.013
Buck	55	otolith	15	0.32	0.051
Athabasca	147	pelvic fin	21	0.19	0.0002
Athabasca	147	otolith	22	0.18	0.0063

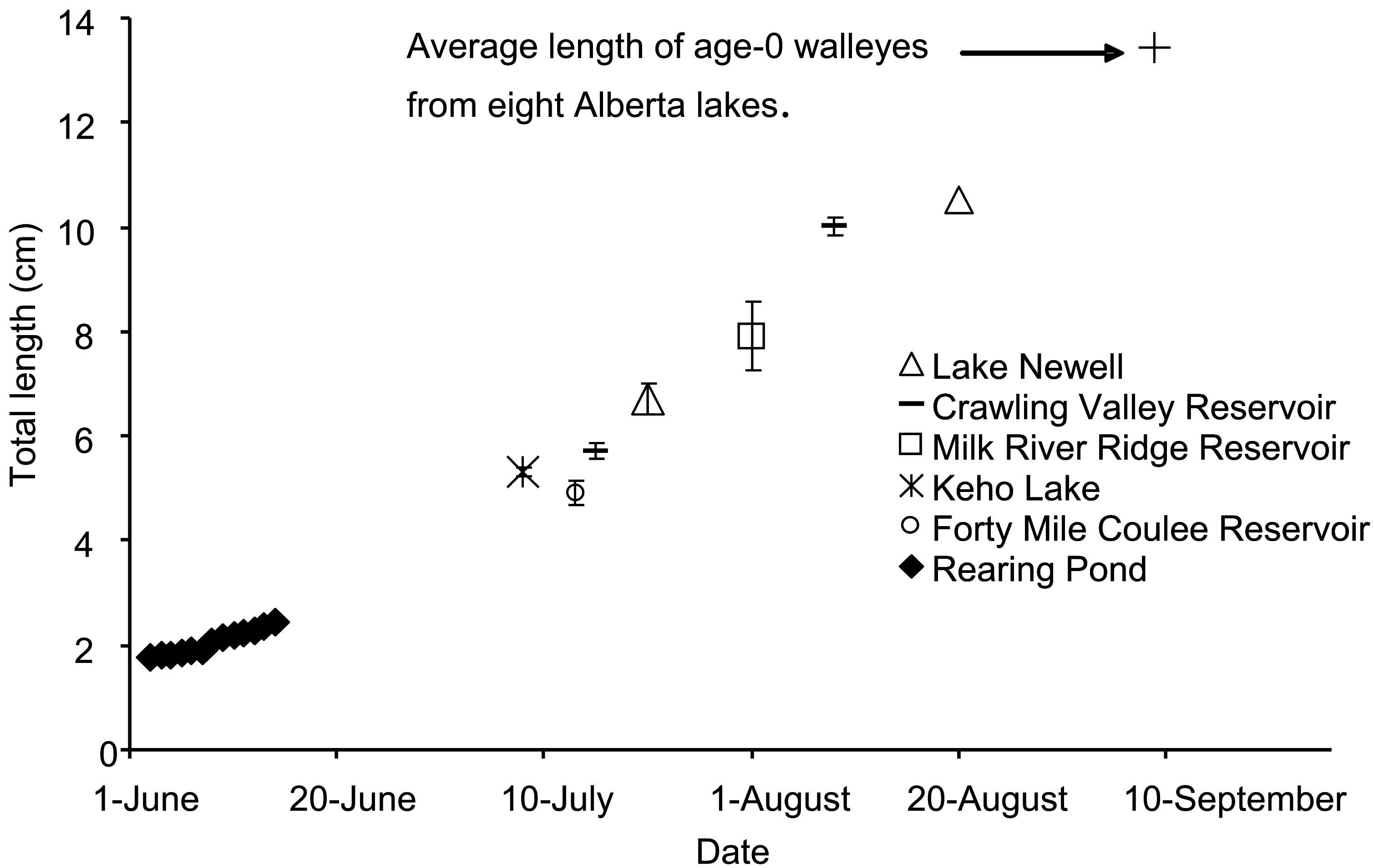

FIGURE 2-1. — Lengths and 95% confidence intervals (when sufficient samples were captured) of age-0 Walleyes captured during the summer months from various Alberta lakes.

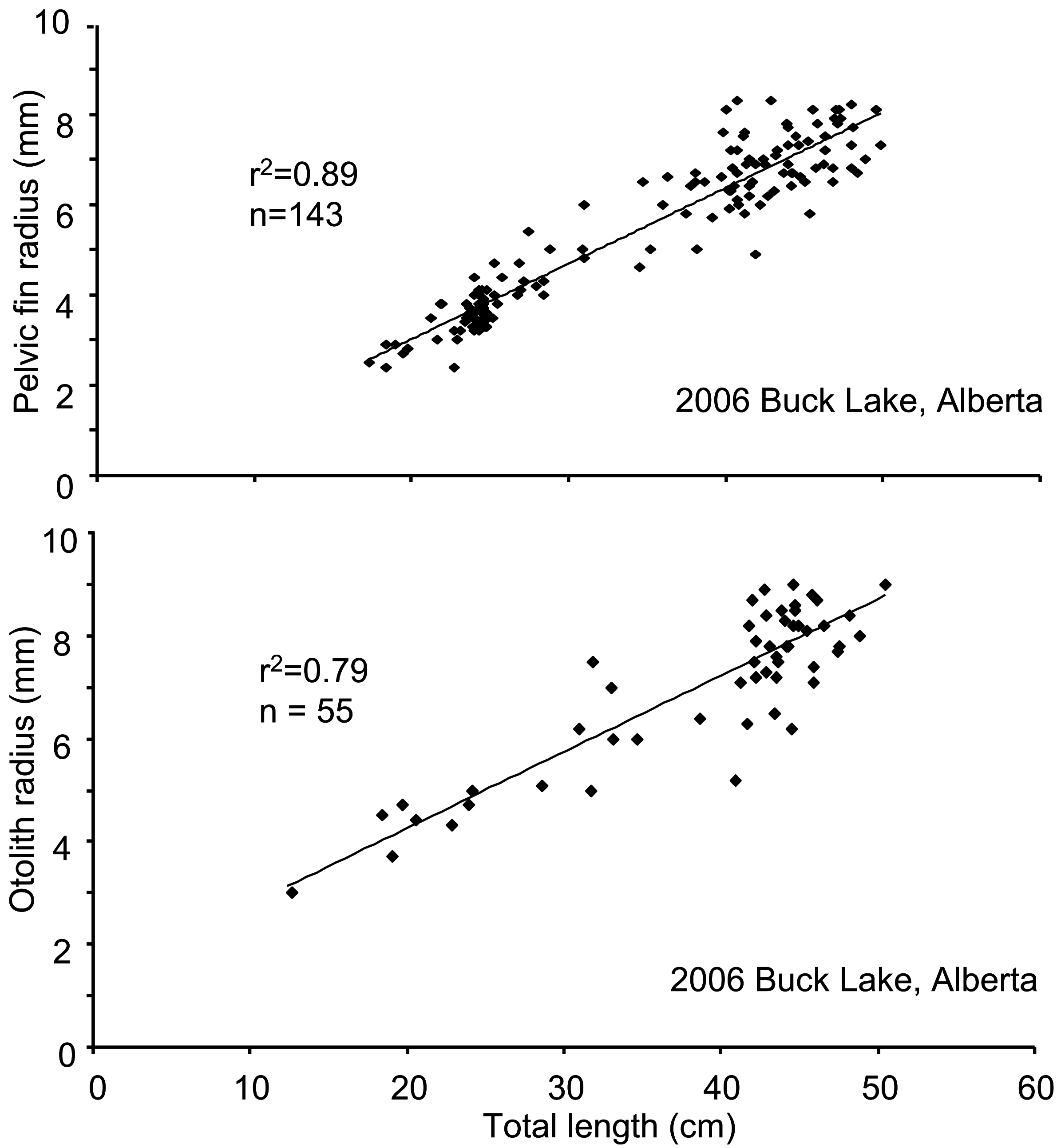

FIGURE 2-2 — Total lengths compared to the cross-sectional radii of pelvic fins and otoliths from Walleyes indicating an allometric relationship ($P<0.001$ for both comparisons).

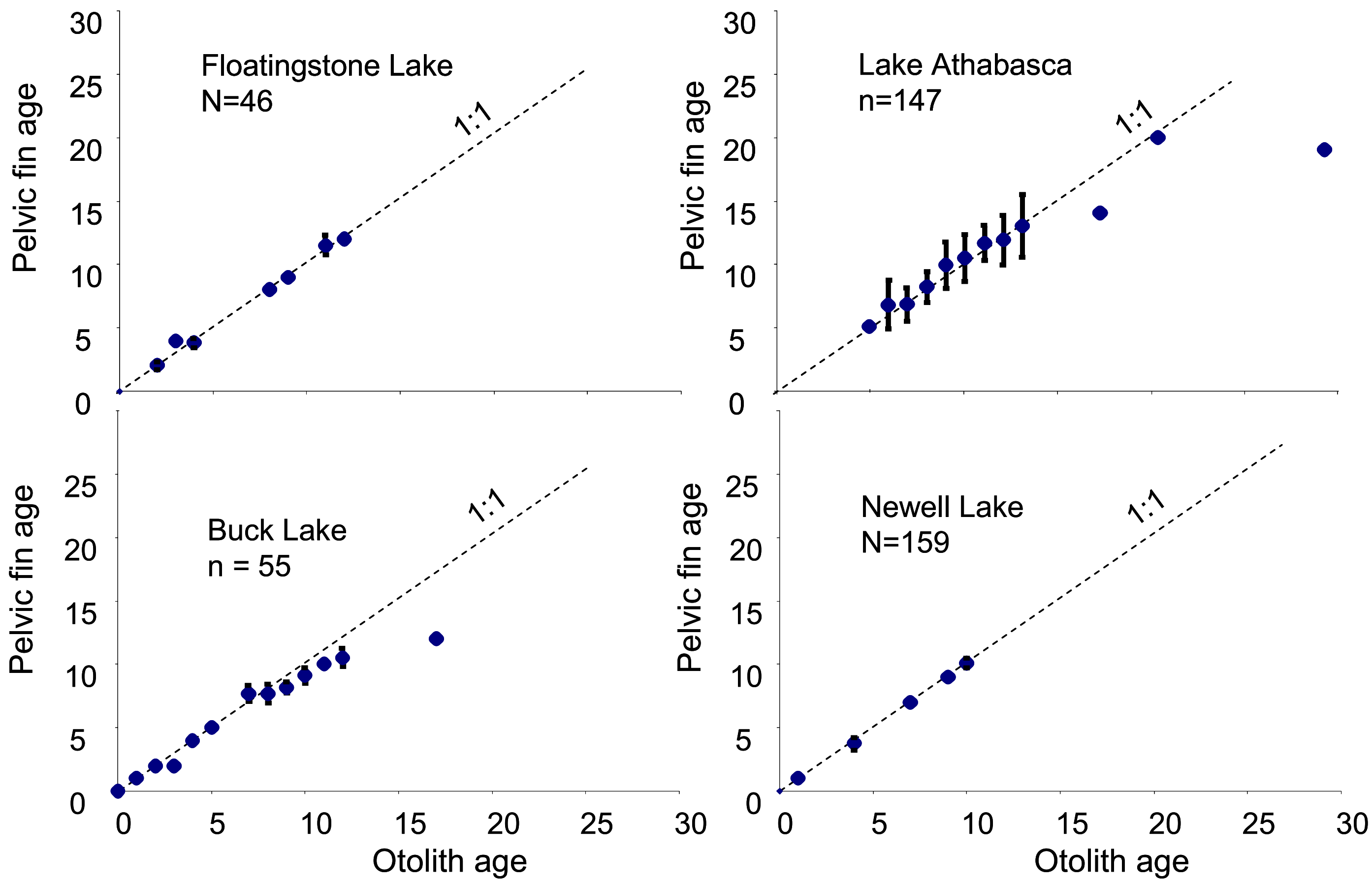

FIGURE 2-3. —Age-bias plots comparing assigned ages from pelvic fins to otoliths. Each dot represents the average age estimated from pelvic fins with the error bars signifying the standard deviation from the mean when sufficient samples permitted. The dotted line is the 1:1 equivalence.

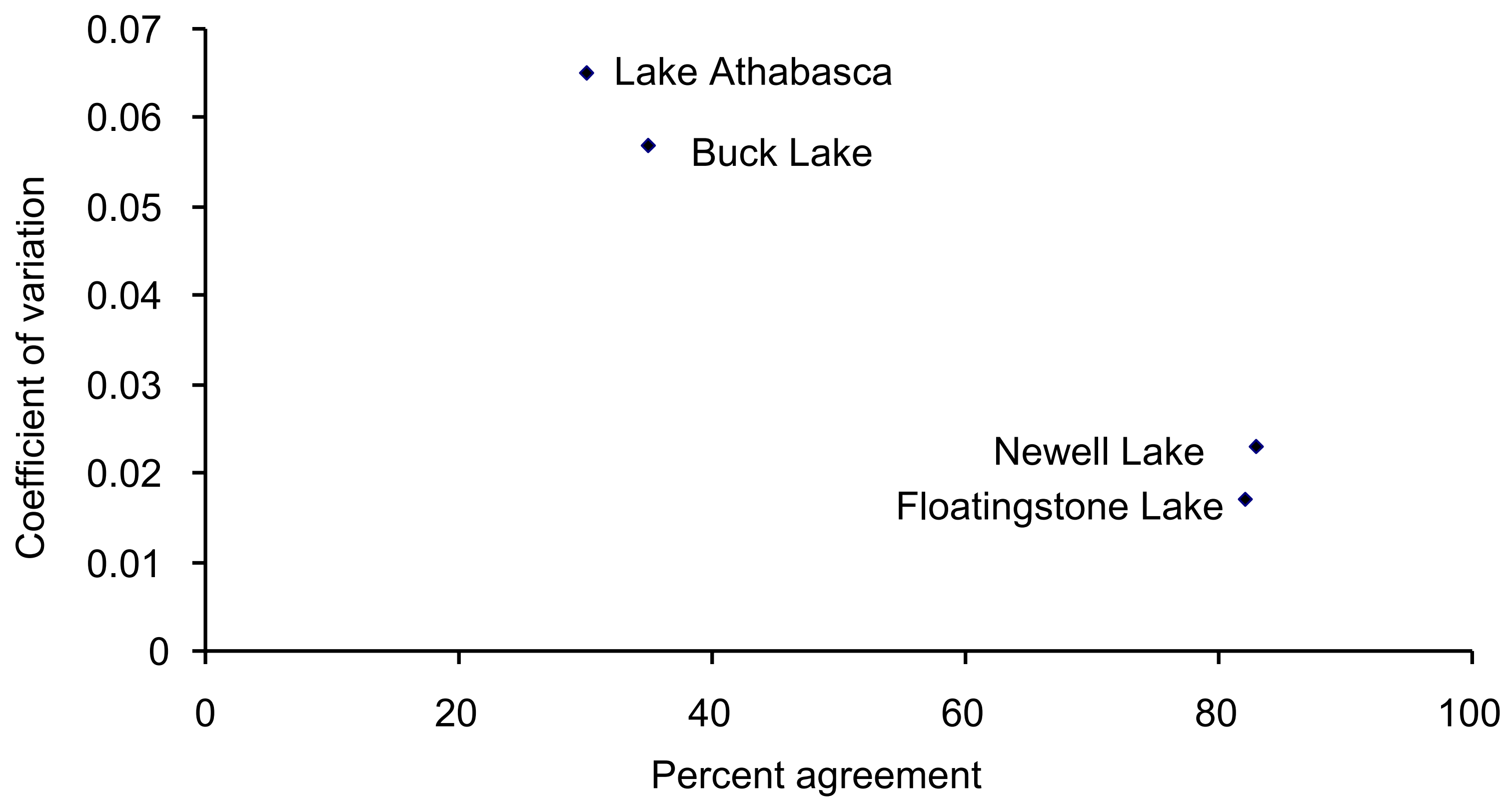

FIGURE 2-4. —Percent agreement between the assigned pelvic fin and otolith ages and the coefficient of variation from four Alberta lakes. Agreement was calculated for each fish (when the age estimated from pelvic fins and otoliths were the same) and expressed as a percentage for the entire sample. The coefficient of variation was calculated for each otolith and pelvic fin comparison and averaged for each lake.

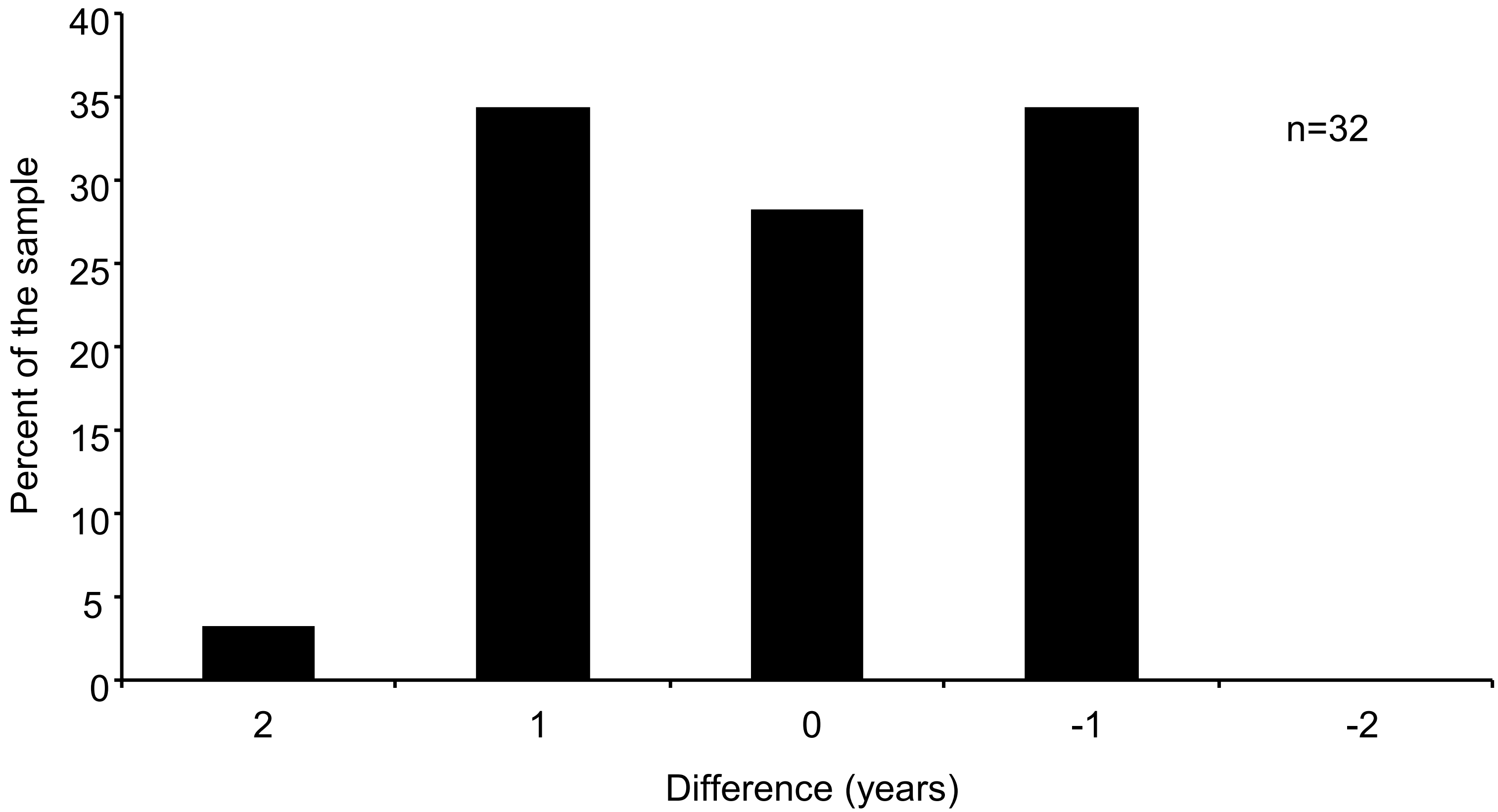

FIGURE 2-5. —Ages estimated from pelvic fins in comparison to their known-age for Walleyes from Hutch Lake, Alberta. Agreement, when ages estimated from pelvic fins and known-age were the same, was 28% for this comparison. This validation was completed for a single-stocked year-class surveyed in two consecutive years (ages-8 and 9).

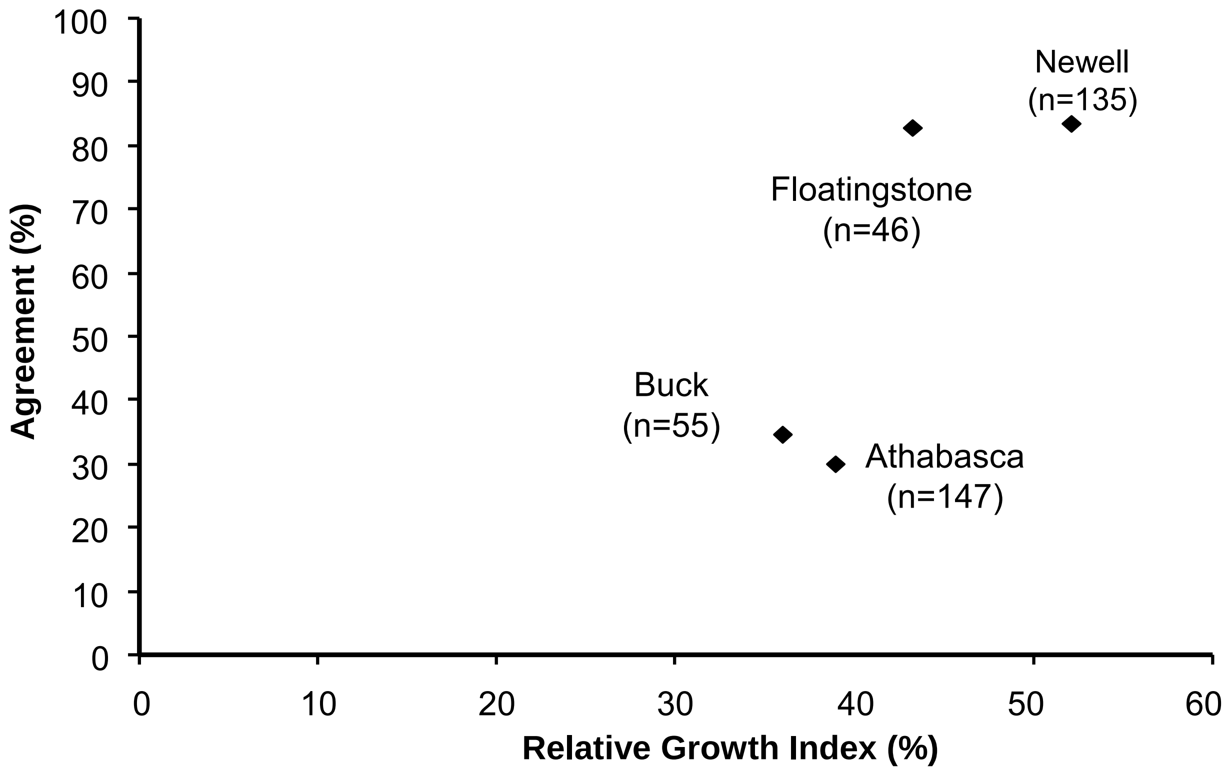

FIGURE 2-6.— A comparison of agreement between the ages estimated from pelvic fins and otoliths to the Relative Growth Index for four Alberta lakes. Agreement was calculated for each fish (when the ages estimated from pelvic fins and otoliths were the same) and expressed as a percentage for the entire sample. The Relative Growth Index was calculated based on the Walleyes' growth at each lake in comparison to North America-Walleye growth (males and females combined; Quist et al. 2003).

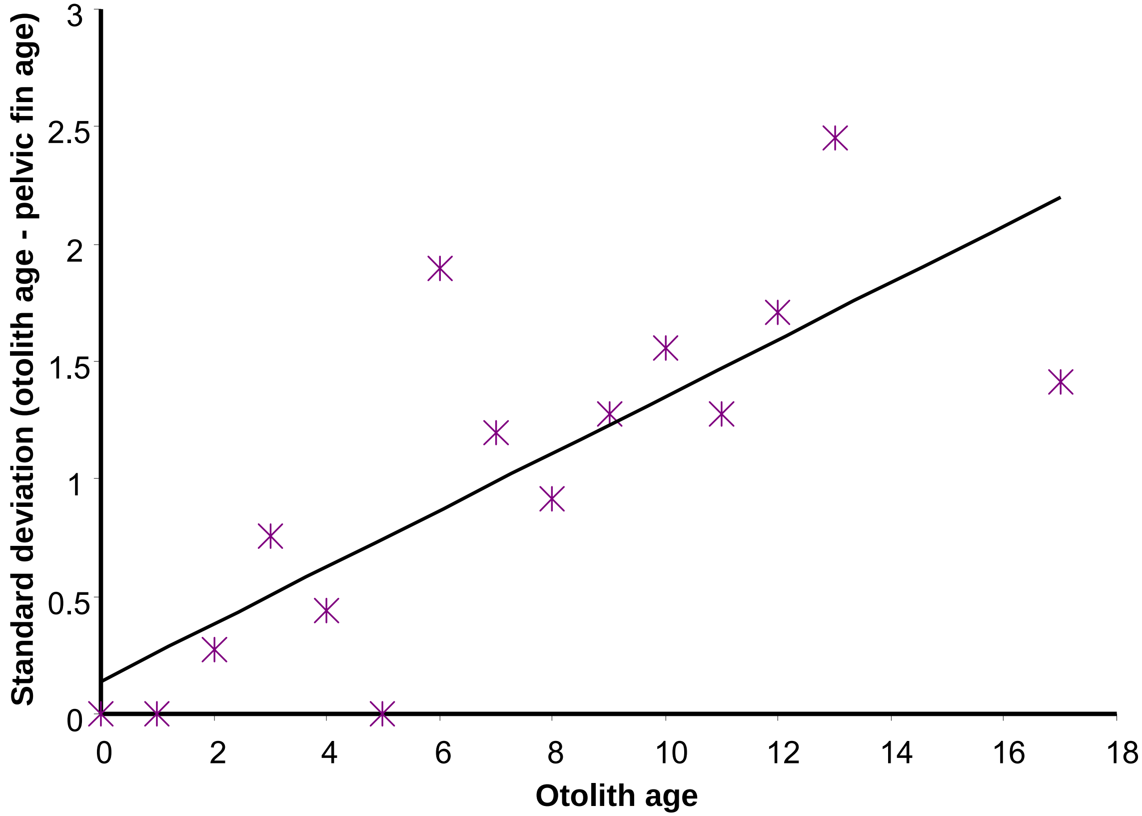

FIGURE 2-7. — Ages estimated from otoliths versus the sum of standard deviation from a pair-wise comparison of ages estimated from otoliths and pelvic fins from four Alberta lakes. The standard deviation of the residuals increased linearly with the ages estimated from otoliths (R2=0.67, P<0.001, n=407).

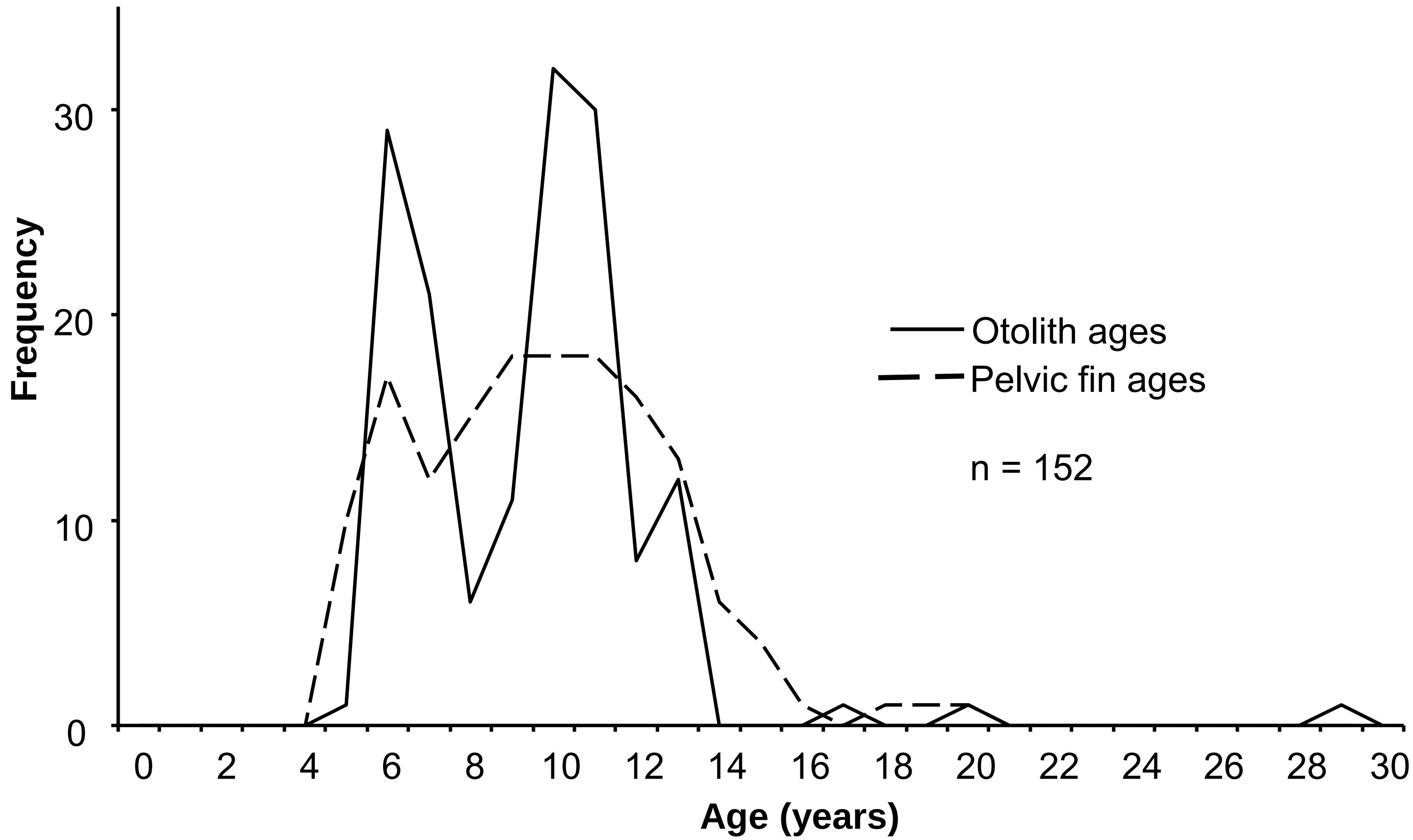

FIGURE 2-8. —An example of how ageing error affected the interpretation of age-class data from Lake Athabasca, Alberta. Ages estimated from pelvic fins provided the appearance of constant recruitment while those from otoliths indicated weak and strong age-classes. Agreement, when the estimated ages from pelvic fins and otoliths were the same, was 30% for this comparison.

Chapter 3 The anglers' paradox: small fish from size-selective fishing (too much harvest) or 'stunting' (not enough harvest)?

Introduction

The size and growth of fish are essential to recreational and commercial fisheries for economic, food and trophy considerations (Pitcher 2001). Fishing can alter growth rates through changes to fish density which evoke growth responses or by phenotypic and genotypic selection (Law 2000; Hilborn 2006).

Growth responses to fish population densities and the plasticity of fish life histories are well documented and may explain a decline in the size and growth of fish (Burrough and Kennedy 1979; Rose et al. 2001; Reznick and Ghalambor 2005; Hilborn 2006; Conover and Munch 2007). At high densities, interspecific and intraspecific competition result in delayed maturity, increased mortality, and slower growth (Rose et al. 2001). This is undesirable for a fishery as harvest yields are reduced. Most often the management solution for this problem is to decrease fish density by increasing harvest.

'Stunted' is a qualitative term used to describe slow-growing fish and defines the extreme case of compensatory growth to high densities. Commonly used by anglers to describe all populations of small-sized fishes, however, 'stunted'; Roach *Rutilus rutilus*, Yellow Perch *Perca flavescens*, Pumpkinseed *Lepomis gibbosus*, Arctic Charr *Salvelinus alpinus*, Brook Trout *Salvelinus fontinalis*, have been documented as very slow-growing fishes that mature at small sizes

(Burrough and Kennedy 1979; Linfield 1979; Heath and Roff 1987; Donald and Alger 1989; Volpe and Ferguson 1996). Attempts to increase growth rates in these 'stunted' populations by decreasing density has had mixed results (Donald and Alger 1989; Beard et al. 1997; Schneider and Lockwood 2002).

Alternately, size-selective harvest that targets large fish, with sufficient fishing pressure, can truncate the size distribution of a population so that small fish become disproportionally more abundant. Evidence of this fisheries effect exists from thousands of years before present (Pitcher 2001). Lee (1912) quantified this size truncation effect with ageing structures. 'Lee's Phenomenon' is a slower calculated growth for small fish from backcalculated lengths from older fish surviving the fishery (i.e., the faster growing fish have been harvested). Contrary to stunting, the management solution for this size-selective mortality is to reduce harvest so that the fish can survive to achieve greater sizes.

All the aforementioned causes of small fish can be difficult to diagnose because of the inherent variability in the growth of fish and the confounding effects of size-selective harvest. Paradoxically, the management solutions are to either increase or decrease harvest which could exacerbate the problem with a misdiagnosis.

Alberta supports some of the most northerly situated Walleye *Sander vitreus* populations in the world (Scott and Crossman 1973) resulting in later maturity, reduced fecundity and slower-growth (Baccante and Colby 1996). Considerable controversy was created following the widespread collapses of Alberta's fisheries in the 1980's (Sullivan 2003), as restrictive large minimum size or catch-and-release regulations allowed populations to increase in density, yet anglers only caught small Walleyes. Summer creel surveys recorded angler-catch rates greater than one Walleyes*hour^{-1} yet very few fish exceeded the minimum size limit of 50 cm total length (TL) while historically Walleyes were documented to surpass 60 cm TL. Anglers have considerable sociopolitical influence (Botsford et al. 1997) and Alberta anglers' complaints of 'stunted' fish demanded management action.

The two competing theories on why this small fish problem existed were (1) Walleye densities had increased sufficiently to invoke compensatory growth (i.e., stunting from insufficient food) or (2) Walleyes were not surviving because of a combination of high angler harvest, catch-and-release mortality and non-compliance with the regulations (i.e., overharvest). It was thus critical to correctly diagnose what was limiting the population size-structure as the management prescriptions were contradictory (more or less harvest), and could compound the problem.

To understand a similar problem with Atlantic Cod, Sinclair et al. (2002) used a multiyear dataset with backcalculated lengths-at-age, population density and harvest information to demonstrate size-selective mortality. Unfortunately, few datasets are this complete. New tools are required for diagnosing changes to fish-growth with less extensive information.

The objective of this paper is to provide a logical framework to diagnose this and other 'small fish' problems. I used a series of nested hypotheses (Figure 3-1), and examples from Walleye fisheries in Alberta with formally large Walleyes identified by anglers as having ‘stunted’ fish, to diagnose the ‘small’ fish problem. To test these hypotheses, I used a combination of length-at-age data, angler use, harvest information and growth rates from backcalculations.

My assumptions for this approach were: 1) my derived Walleye-pelvic-fin ages were acceptably accurate and precise, and 2) their diameter increases proportionally to the fish’s length.

Methods

Study Lakes and Data Collection.— I studied several Alberta lakes where anglers complained of small, yet abundant Walleyes (Figure 3-2; Table 3-1). Walleyes were collected with test nets using the Fall Walleye Index Netting (FWIN) protocol (Morgan 2002). I set the nets in September, when water temperatures ranged between 10-15°C. Each net was comprised of eight panels of mesh ranging from 25 mm to 152 mm. Nets, set perpendicular to shore, were fished for 24 hours in proportion to two depth strata of 2-5 m and 5-15 m representative of the lakes' depths. All fish were measured for length (TL), weight and a pelvic fin removed for age assessment (Chapter 2, this study).

The sport fisheries at these lakes with small Walleyes were managed by catch and release or a minimum-length regulation of 50 cm TL (Table 3-2). Creel attendants conducted completed-trip surveys from the long weekend in May until the end of August to determine angler use and harvest information. These point-source creels endeavored to interview all anglers for each census day, surveying 25% of the weekdays and 50% of the weekends. Hours fished, catch rate, and harvest rate were recorded for each angler and extrapolated to the entire fishing season. At lakes with multiple access points, I calculated a ratio-of-use (i.e., angler use at creel site compared to angler use over entire lake) from a roving survey to determine anglers' point of entry. Besides directed harvest, additional sources of angling mortality were calculated for release mortality from Reeves (2005) and illegal harvest from Sullivan (2002).

Young Fish/ Old Fish Growth Comparison.—To test whether Walleye size was being limited by size-selective harvest (Lee's Phenomenon) or compensatory growth from high density, I compared backcalculated growth rates from older fish (i.e., those which had survived several fishing seasons) to those not yet recruited to the fishery. I compared two categories, 'young' (ages-4 to 8) and 'old' (ages-9 and older). To create an individual growth rate, I backcalculated sizes for ages one through four from pelvic fins (Chapter 2, this study). I chose age-4 as the upper limit for my growth-rate calculation as the Walleyes had not yet reached sexual maturity and growth was still linear (Lester et al. 2004). As these lakes historically produced larger Walleyes (exceeding 60 cm), I assumed that this analysis would give insights on why the Walleyes were no longer getting large.

Within-lake differences of growth rates were assessed using a two-sample t-test (assuming unequal variances). I then combined the data from all four lakes to determine if the differences between young and old fish were still significant. Additionally, I performed the 'young' fish, 'old' fish comparison of growth for a 1998 sample from Smoke Lake to determine if outcomes were similar for this population at a different time period.

I used pelvic fins for estimating age and to backcalculate lengths-at-age. Pelvic fins were sectioned and mounted on acetate slides (Chapter 2, this study). Annuli were measured at 40X magnification along the same axis (100:1 graduated micrometer). Comparisons of ages estimated from pelvic fins and otoliths demonstrated uncertainty to the assigned ages (Chapter 2, this study). I incorporated this uncertainty in a simple re-sample analysis with a random assignment of error to determine if outcomes were still significant.

As pelvic fin and otolith diameters increase proportionally to the fish's length (Chapter 2, this study), I performed backcalculations using a modified Fischer method that incorporates the biological intercept (Campana 1990):

$$L_{ai} = L_c + (FR_{ai} - FR_c) \times (L_c - L_o) \times (FR_c - FR_o)^{-1}$$

where L_{ai} and FR_{ai} are the fish- and pelvic fin-radius lengths at annulation age i. L_0 and FR_0 are the initial fish- and pelvic fin-radius lengths (biological intercept), and L_c and FR_c are the fish- and pelvic fin-radius lengths at capture.

Lengths-at-ages from one to four were calculated into an individual-growth rate, G_r:

$$G_r = (L_{a1} + L_{a2} + L_{a3} + L_{a4}) \times 4^{-1}$$

where L_{a1} through L_{a4} were the backcalculated lengths for ages-1 through 4. All measurements and age assessments were done by the same technician for consistency.

Empirical frequency distributions were calculated by bootstrapping 5 000 times (with replication) the individual growth rates to create new means for the two categories; young and old fish, for each lake. I also report the Student 't' statistic for each comparison at each lake and for all lakes combined.

Growth and Climatic Conditions.—To determine if temperature had affected the growth of fish during the study, I regressed the thermal integrate, growing degree-days above 5°C, from local metrological stations against the average yearly growth-increments for age-0 Walleyes (Neuheimer 2006).

Results

High Mortality.— Anglers misinterpreted high abundance of one age-class of young fish recruiting to the recovering fishery at Lac Ste. Anne, Alberta, as 'stunted' Walleyes (Figure 3-3). Four years later, this age-class had grown and complaints of 'stunted' fish were no longer received.

At Pigeon Lake, Alberta, a decline in the abundance of larger Walleyes was most parsimoniously explained by overharvest even though this fishery was managed with a no-harvest regulation (Figure 3-4; Table 3-3). High-catch rates and high-angler use resulted in mortality to Walleyes from estimated levels of handling mortality and non-compliance to the fishing regulations (Sullivan 2002). I estimated that with a combined 5% hooking and non-compliance rate that 0.9 $kgs*ha^{-1}$ of Walleyes died in 2006. Levels of non-compliance vary and at 10% hooking and non-compliance rate, I estimated that an estimated 1.8 $kgs*ha^{-1}$ of Walleyes died in 2006. This harvest exceeds Sullivan's (2003) estimates of annual Walleye production of $1kgs*ha^{-1}$.

Angler's claims of Walleyes becoming 'stunted' at Buck Lake, Alberta appeared to be erroneous (Figure 3-5). A comparison of population-size-distributions indicated that fish size had increased from 1985 to 2005. Interestingly, Buck Lake in 1985 was managed without a size limit, while in 1997, a 50-cm minimum length regulation was introduced. The number of large Walleyes appeared to increase with the minimum-size regulation indicating high mortality from size-selective harvest.

Young Fish/ Old Fish Growth Comparison.—At lakes with old yet small Walleyes, I compared the pre-maturation-growth rates of young and old Walleyes for inferences on growth and sources of mortality. Contrary to Lee's Phenomenon, the Walleyes that grew quickly early in life (from age-1 to age-4) were more likely to survive to older ages (Table 3-4; Figure 3-6). This result was robust to ageing error with outcomes remaining significant ($P<0.01$ in 20 trials). As these Walleyes remained under the size limit when older, I must assume that these fast-growing fish reached maturity and then, grew slowly so that their growth history must be shaped like a hockey stick (Figure 3-7; Figure 3-8). The photographs depict this phenomenon with the hockey stick growth recorded in the annuli of the fin ray. Furthermore, I compared this hockey stick life history to a large number of walleyes to demonstrate that a population with this life history was a departure from the majority of Walleye life history in Alberta.

An identical young fish/old fish growth analysis with a 1998 sample from Smoke Lake, Alberta, indicated the same higher survival of Walleyes that grew quickly early in life ($N=41$, $t=2.82$, $P=0.007$). The same size-selective mortality existed during a period when the old fish from my first analysis were young.

Growth and Climatic Conditions.—Growth of age-0 Walleyes was only significantly correlated to growing degree-days at one of the lakes (Table 3-5).

Discussion

Misdiagnosis of a small fish problem.— Complaints of small fish were explained by high mortality and the recruitment of young fish (Lac Ste. Anne), recall bias (Buck Lake) and size-selective overharvest (Pigeon, Buck, Smoke and Iosegun lakes). At Lac Ste. Anne the purportedly 'stunted' fish were young, recruiting Walleyes. Stunted Walleye complaints at Pigeon Lake from anglers and the popular press (Swanky 2006) were explained by high catch rates and angler effort. My calculations indicated sufficient release mortality (Reeves 2005) and illegal harvest (Sullivan 2002) to change the size-structure of this population. At Buck Lake, Alberta, the size structure of the **W**alleye population increased with the minimum size limit suggesting overharvest, not compensatory growth.

'Recall bias' might explain why anglers at Buck Lake, Alberta, with comparisons to historic catches erroneously labeled Walleyes as 'stunted'. Social studies of information recollection have demonstrated that after a period of only 2 months, subjects reported biased information (Lyle et al. 2002; Hassan 2006). Historical comparisons of fisheries that span years or decades by anglers are questionable and in this case may be inflated because of nearby lakes with large Walleyes.

Hockey stick growth.— Interestingly, my analysis of the backcalculated-growth rates from the populations with old, yet small fish indicated greater survival of Walleyes that grew quickly, early in life. As these fish survived to be old and small, their growth trajectories must be shaped like a 'hockey stick' with rapid-growth until maturity, and then subsequent, slow-growth to remain small.

This outcome was unexpected as I my competing hypotheses were: 1. the old fish grew slower than the young fish (due to size selective mortality; Lee's Phenomenon) or 2. the old fish grew at the same rate as the young fish (slow growth due to a lack of resources, stunting). I was also surprised at the significance of this outcome as the young fish/old fish comparison was a within population comparison. This difference was statistically significant for three of the four populations, the four populations combined and the earlier comparison from Smoke Lake. I provided Fin ray cross sections and comparisons of life histories of Alberta's Walleyes provide evidence of this alternate life history.

A hockey stick life history is what would be predicted by life history theory if size selective fishing exists as the 50-cm-minimum-size limit is just above the 40 cm size at maturity for Alberta's Walleyes. Thus, the surviving Walleyes mature and reproduce under the large-minimum size limit, remaining invulnerable to harvest.

Phenotypic selection raises concerns of reduced fisheries yields as early-maturing and fast-then-slow-growing fish produce smaller and less viable eggs (Law 2000; Hutchings 2005; Jorgensen et al. 2007). Although densities are high at these Alberta fisheries, the effects of size-selective fishing may imperil future sustainability by the loss of large fish and genetic diversity (Berkeley et al. 2004). Hutchings (2005) described a similar growth scenario following a large decline in the size of adult Atlantic Cod *Gadus morhua*. These Atlantic Cod have remained small even after harvest was stopped (Hutchings 2005).

Why were the Walleyes that grew slower, early in life, less likely to survive? As historically these fisheries produced large Walleyes, I assume that the fish that grow-slower, early in life must be the individuals that continue to grow to exceed the size limit. With Alberta's rapidly increasing fishing pressure and the historic collapses of the Walleye populations from overharvest (Sullivan 2003), the most parsimonious answer is overharvest. A large-minimum-size limit and sufficient angling pressure, with (the inevitable) release mortality and illegal harvest (Sullivan 2002), has truncated these populations by harvesting the larger fish. Similarly, Goodyear (2002) modeled that minimum size limits on Striped Bass *Morone saxatilis* would favor the survival of slower-growing individuals. The minimum-size regulations that were enacted to recover populations (Sullivan 2003) have achieved that specific goal, but now alternate harvest strategies must be explored in order to reduce the strong selection caused by intensive fishing pressure.

An alternate explanation to overharvest is compensatory growth and mortality later in life because of ecological limitations. Limited food, intraspecific and interspecific competition have been cited as the cause of slow growth or high mortality (Rose et al. 2001). Thus, if a fish continues to grow, it might not find the necessary food resources resulting in high mortality of the larger fish as seen in Bull Trout *Salvelinus confluentus* resident in alpine lakes (Parker et al. 2007). However, I do not have evidence, even as anecdotal reports, of widespread, population-level skinny fish. Although it appears that significant mortality occurs from fishing, further work is required to determine the influence of compensatory growth and the source of the mortality (i.e. overharvest or resource limitations).

Conclusions.— Changes to the growth of fish are difficult to correctly diagnose. A fisheries manager must be aware of the circumstances that create the appearance of 'stunting' such as size-selective harvest, and variable recruitment. My preference would be to determine a more quantifiable descriptor of fish growth such as the Relative Growth Index (Quist et al. 2003), as the term stunted is not well defined, nor does it provide information on the mechanism causing the small fish. A better understanding of the mechanism creating small fish would allow a better diagnosis for the levers to alleviate the problem.

Regardless, evidence suggests that Alberta's Walleye populations studied were most likely not 'stunted'. Although these fish were small for their respective ages, alternate mechanisms; such as size selective mortality are plausible for the altered size distributions.

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TABLE 3-1.—Geographical, limnological, and fisheries data for the Alberta study lakes. Data are from Mitchell and Prepas (1990).

Lake	Latitude	Longitude	Area (ha)	Mean depth (meters)	TDS (mg/l)	Trophic Status[a]
Buck	53^{0} 00'	114^{0} 45'	2,540	6.2	120	Eutrophic
Iosegun	54^{0} 28'	116^{0} 50'	1,340	4.1	79	Eutrophic
Ste. Anne	53^{0} 43'	114^{0} 25'	5,450	4.8	165	Eutrophic
Pigeon	53^{0} 01'	114^{0} 04'	9,670	6.2	155	Eutrophic
Long	54^{0} 26'	112^{0} 45'	584	4.3	196	Eutrophic
Smoke	54^{0} 22'	116^{0} 56'	959	5.1	91	Eutrophic

[a]Based on chlorophyll a.

TABLE 3-2.— Fisheries information for the Alberta study lakes.

Lake and Year surveyed	Regulation	Angler Use (hours $*ha^{-1}$)	Total Catch Rate (fish $*hour^{-1}$)	Harvest Rate (fish $*hour^{-1}$)	Walleye CUE[a]
Buck 2004	1 over 50 cm	4.4	1.2	0.04	35.3
Ste. Anne 2006	Catch and release	3.5	1.6	n/a	32.8
Pigeon 2003	Catch and release	3.3	3.0	n/a	49
Iosegun 2003	2 over 50 cm	5.3	1.2	0.16	29
Long 2003	1 over 50 cm	27	1.1	0.07	18.6
Smoke 2003	2 over 50 cm	4.3	1.7	0.01	30.0

[a]Walleye CUE was calculated from Fall Walleye Index Nets ($Walleyes*100m^2*24hours^{-1}$).

TABLE 3-3.—Pigeon Lake fisheries information.

Year	Angler use (hours $*ha^{-1}$)	Walleye CUE (Walleyes $*angler\text{-}hours^{-1}$)	Walleyes caught (Walleyes $\bullet ha^{-1}$)	Kilograms of Walleyes caught ($kg*ha^{-1}$)	5% Release and illegal mortality ($kg*ha^{-1}$)	10% Release and illegal mortality ($kg*ha^{-1}$)
1999	1.1	0.3	0.3	0.3	0.0	0.0
2003	3.3	3.0	9.7	9.0	0.4	0.9
2006	4.6	4.1	19.0	17.6	0.9	1.8
2007	4.4	3.7	16.3	15.1	0.8	1.5

TABLE 3-4. —The statistics comparing the pre-maturation growth rates of young (ages four to eight) to mature old fish ages (9 and older) from four Alberta Lakes. Individual-growth rates were generated from backcalculated lengths measured from pelvic fin rays for ages one to four.

Lake	Average slope of the young fish	Average slope of the old fish	Sample size	t Statistic	P Value
Long	67	82	40	3.22583	0.002
Buck	69	73	74	1.86528	0.12
Smoke	51	63	64	5.78343	<0.001
Iosegun	55	69	65	5.68677	<0.001

TABLE 3-5. —The regression statistics comparing the average growth of Age-0 Walleyes$*year^{-1}$ to growing degree-days above 5°C (for the same year).

Lake	R^2	N	P value
Buck	0.0030	8	0.88
Smoke	0.20	5	0.45
Iosegun	0.66	8	0.014
Long	0.088	8	0.47

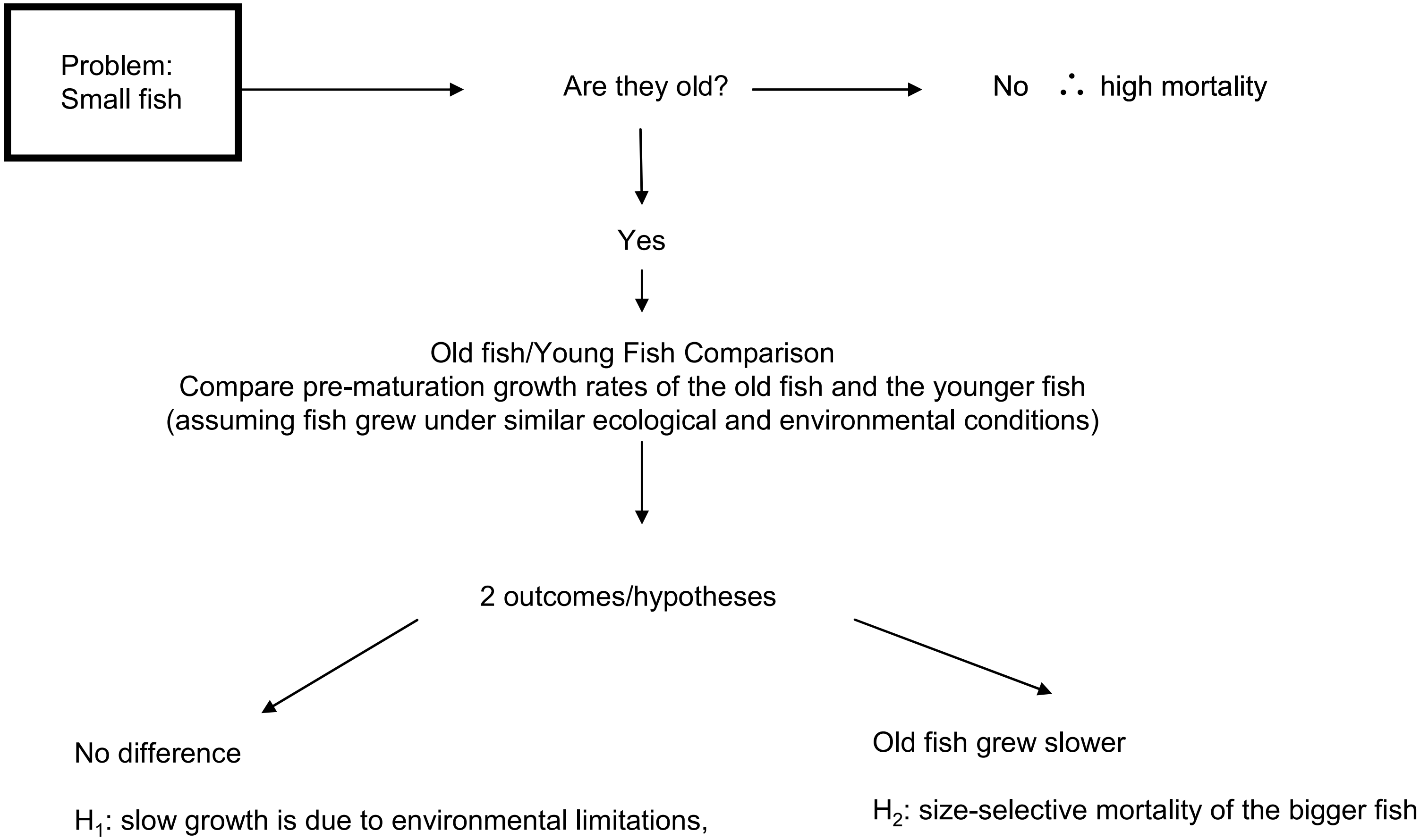

FIGURE 3-1.—A conceptual outline demonstrating how I determined what was limiting fish from these populations from achieving the larger sizes recorded historically.

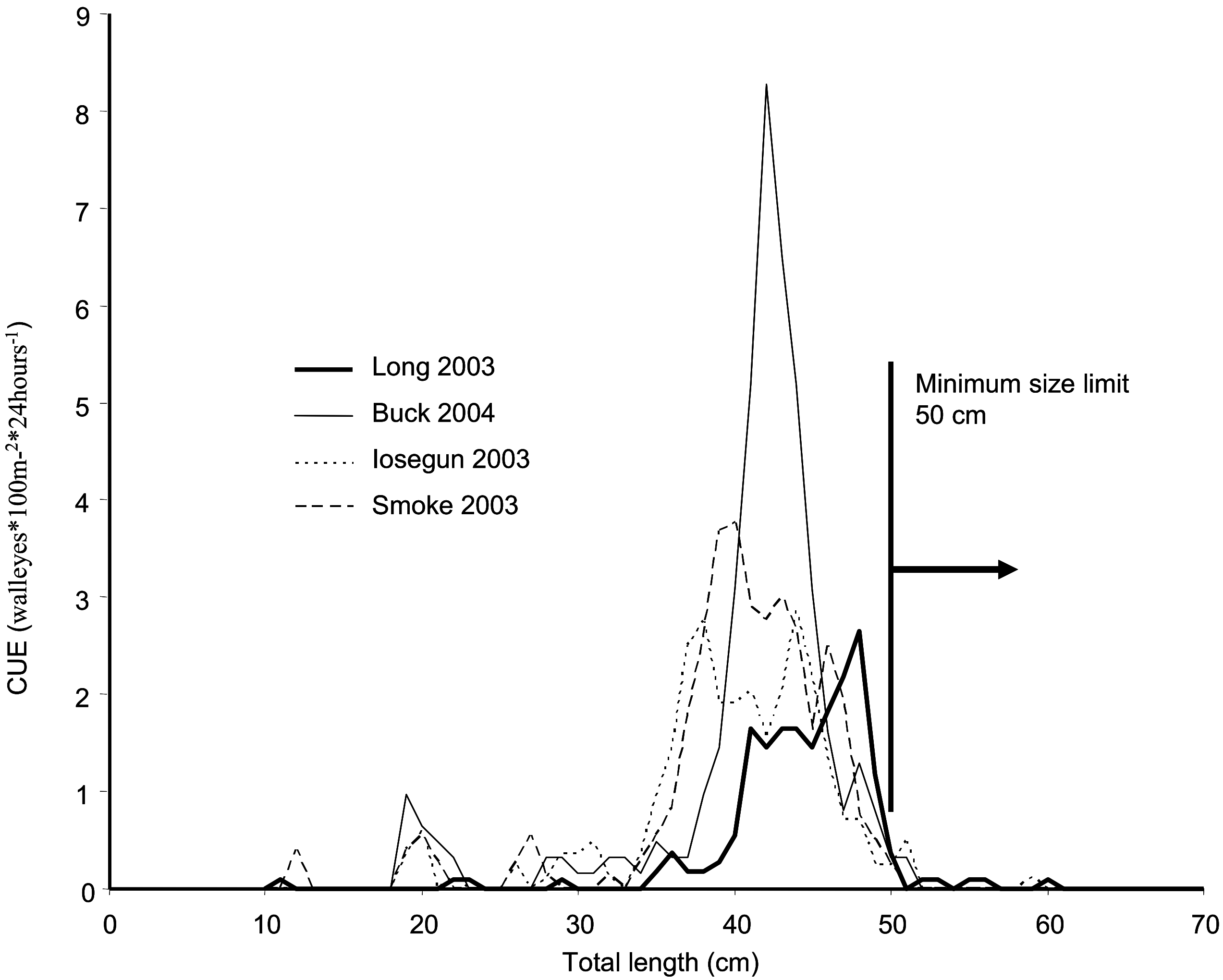

FIGURE 3-2. —Catch rates and length distributions of Walleyes captured in the four study lakes.

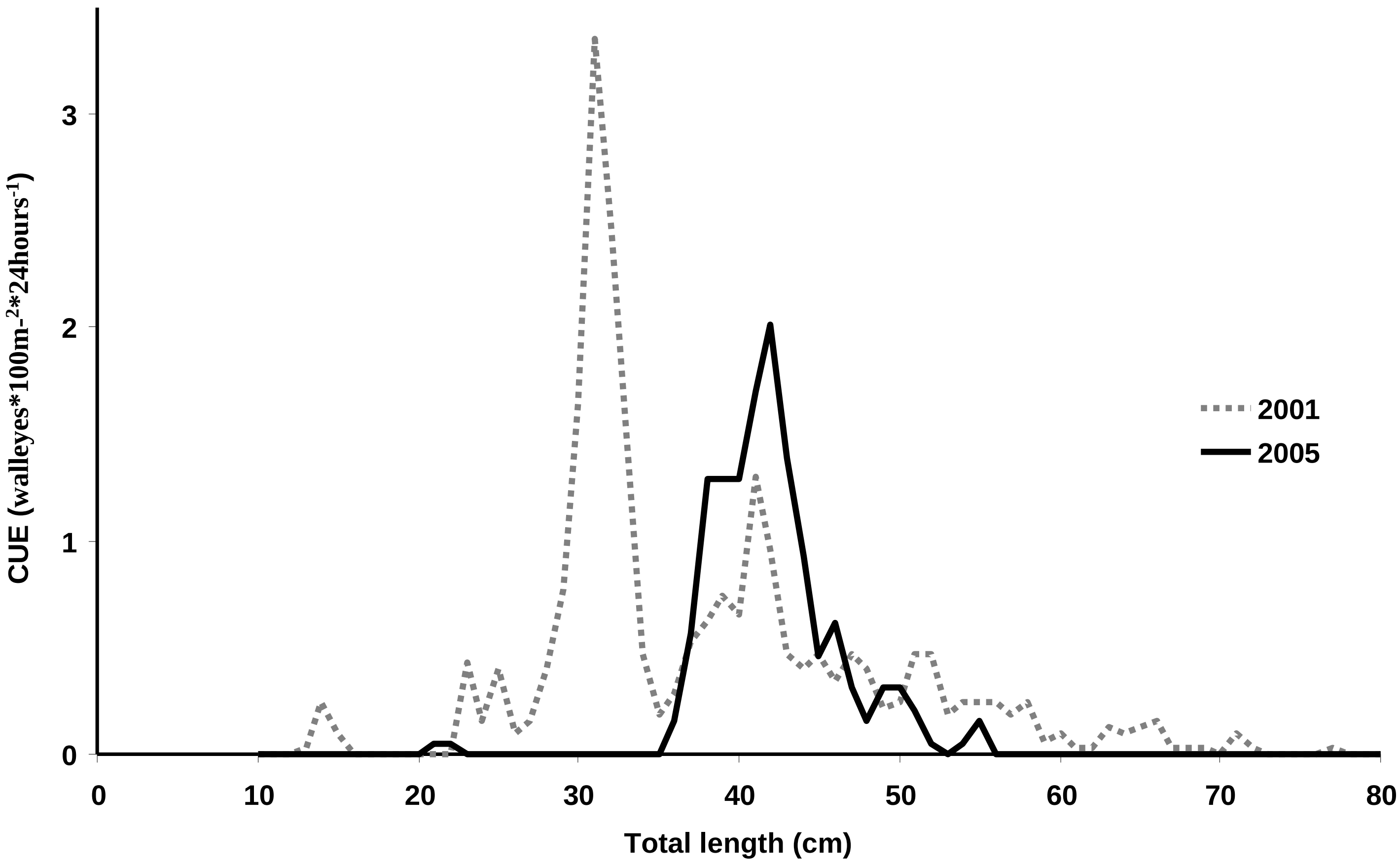

FIGURE 3-3. — An example from Lac Ste. Anne, Alberta where anglers confused the strong recruitment of young fish in a recovering fishery as 'stunted' Walleyes. By 2005 these young Walleyes had increased in size and no further complaints were received.

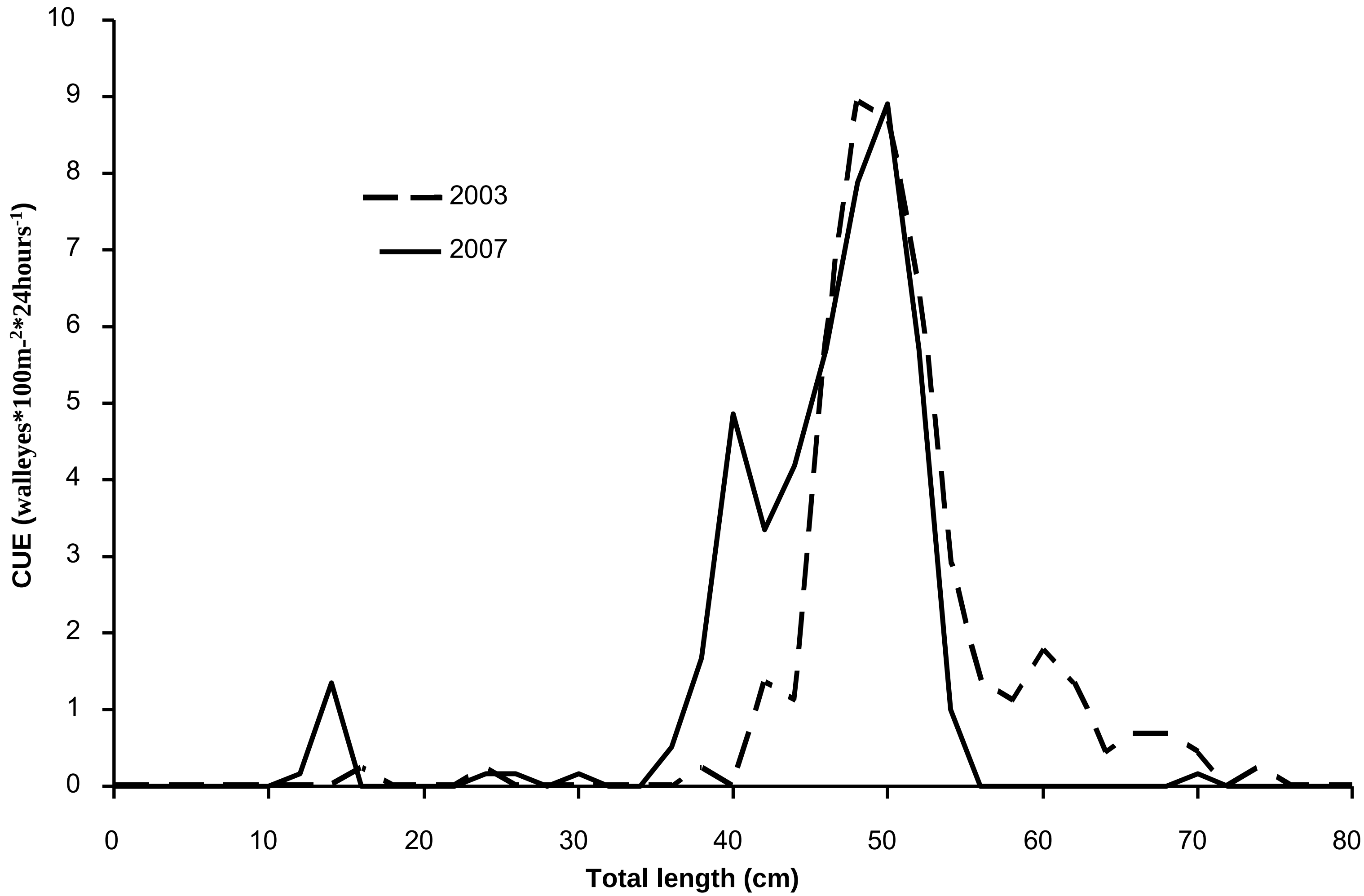

FIGURE 3-4. — At Pigeon Lake, Alberta anglers mistook the missing large Walleyes as the population becoming stunted.

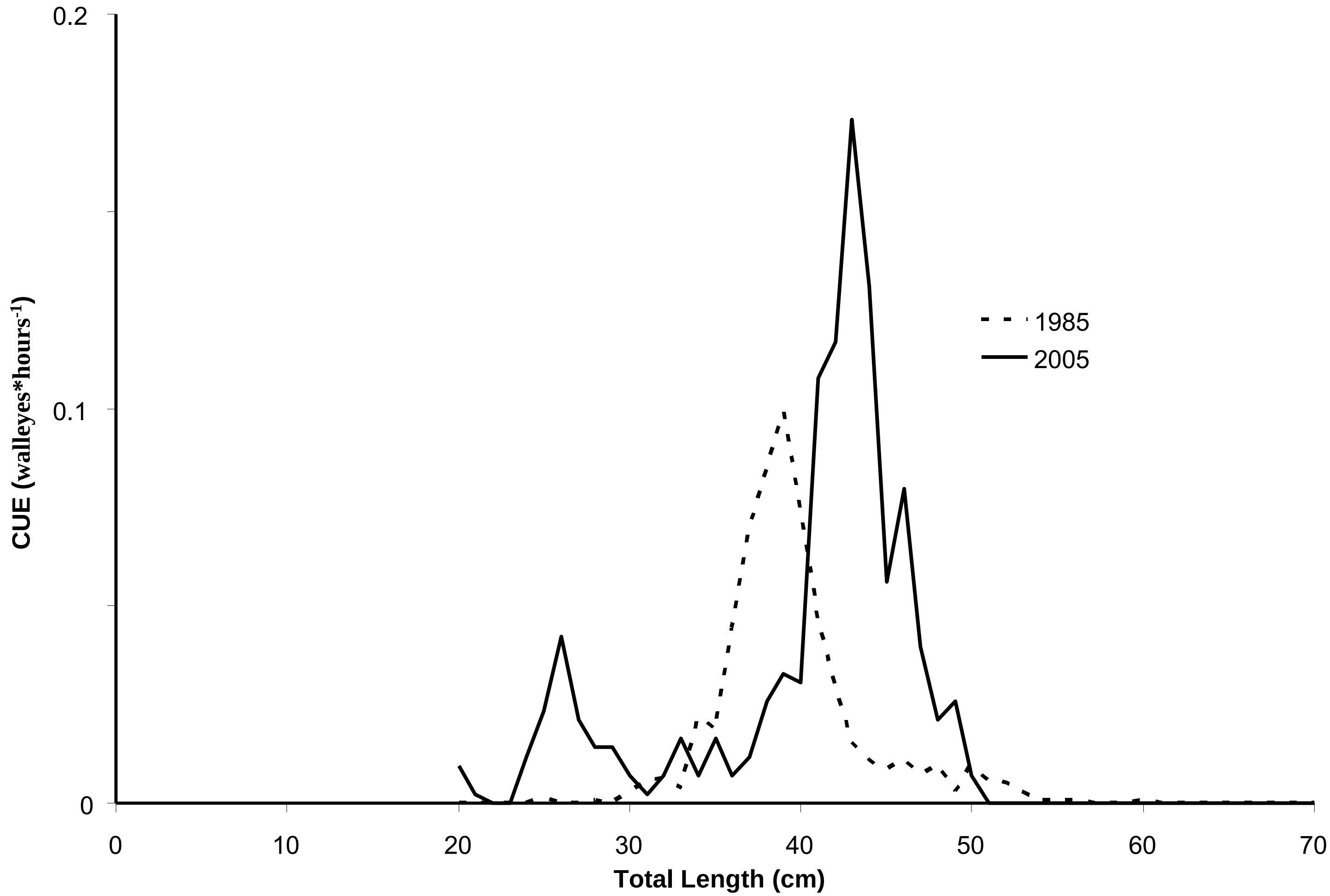

FIGURE 3-5. —Although the anglers complained that the fish were becoming ‘stunted’ at Buck Lake, Alberta, the data indicated that large fish were more abundant in recent surveys.

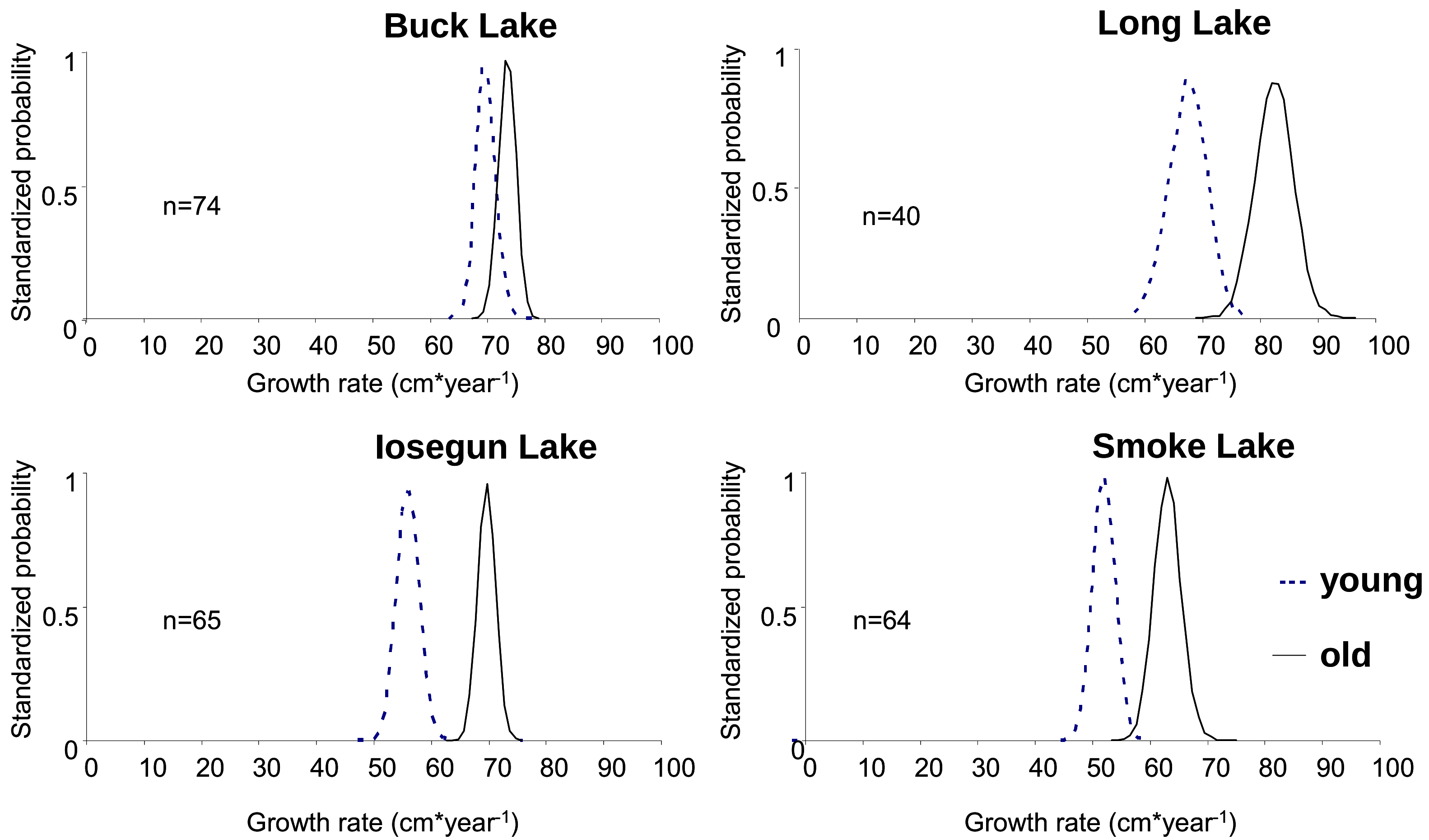

FIGURE 3-6. —Bootstrap replicate values of the pre-maturation growth rates of young (ages four to eight) and mature old fish ages (9 and older) from four Alberta Lakes. Individual-growth rates were generated from backcalculated lengths measured from pelvic fin rays for ages one to four.

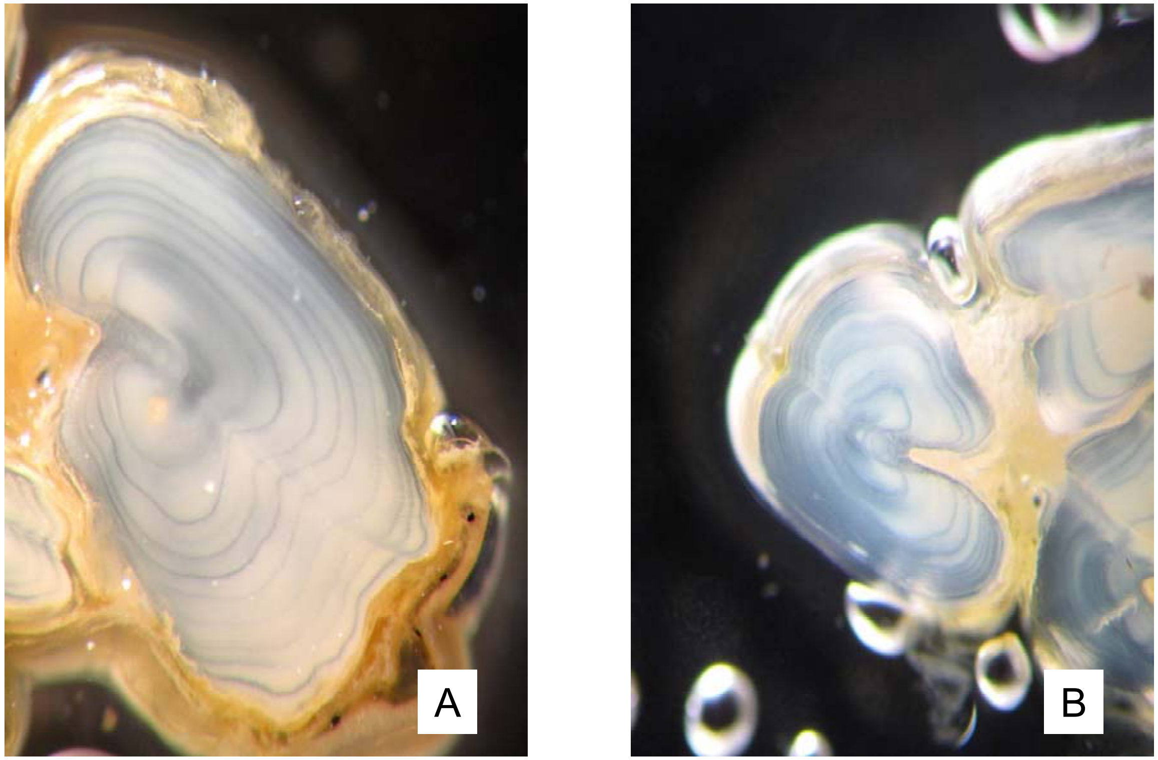

FIGURE 3-7.—Photographs of walleye pelvic fns to demonstrate different growth histories. A 690 mm mature female from (A) Newell Lake, Alberta, was estimated to be age-10 had consistent growth. A 408 mm mature female from (B) Buck Lake, Alberta, estimated to be age-9, grew quickly initially and then slowly. Each image was captured through a binocular dissecting microscope at 25X magnification.

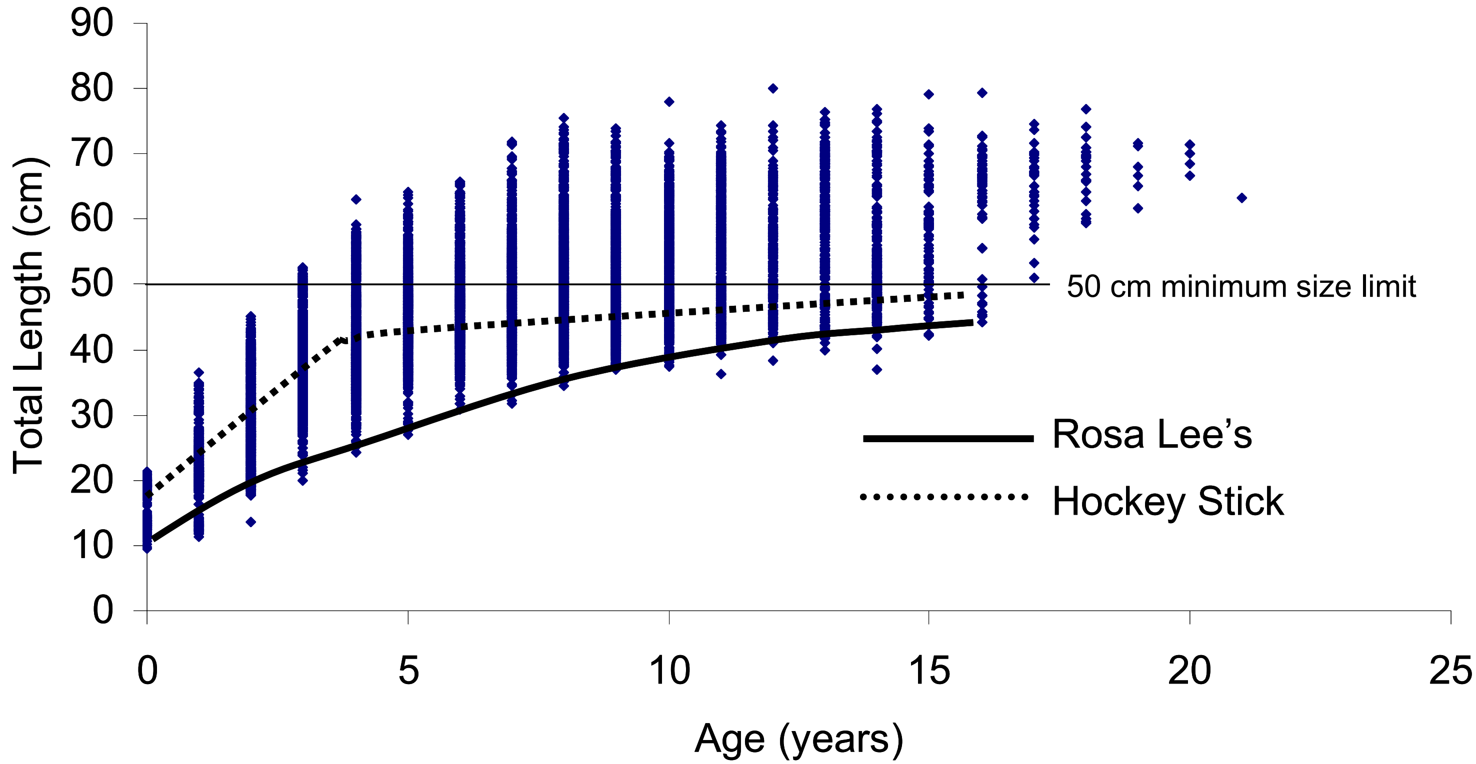

FIGURE 3-8.—Age and length data from 40 000 Walleyes assembled from various waterbodies in Alberta to demonstrate the variability in size at various ages. The bold line was drawn to approximate growth as described by Lee (Ricker 1975). The dotted line was drawn to approximate the hockey stick shaped growth of surviving fish in lakes with complaints of small fish (this study).

Chapter 4 Separating Size-Selective Fishing from Density-Dependant Growth using Active Adaptive Management.

Introduction

Alberta's Walleye *Sander vitreus* populations declined or collapsed from overharvest in the late 20th century with only 2 of 27 study lakes remaining stable (Sullivan 2003). As a result, large-minimum size limits were implemented in 1996 to recover these collapsed populations (Berry 1995; Sullivan 2003). This strategy was numerically successful in recovering the abundance of Walleye (i.e., many Walleye fisheries now show angler catch rates exceeding 1 Walleyes*hour^{-1}). However, considerable dissatisfaction was created among Alberta's anglers and fisheries managers because few large Walleyes were being caught.

An analysis of growth rates backcalculated from pelvic fins indicated that Walleyes, at the fisheries with complaints of small fish, grew rapidly to an early maturity, and then remained under the minimum size limit with subsequent slow growth (Chapter 3, this study). This growth strategy is what life history theory would predict for a slow-growing animal with size-selective harvest of the larger individuals (Kozlowski and Wiegert 1987). Similarly, Goodyear (2002) modeled that a large-minimum size limit would select for slow-growing fish. I was concerned about the reversibility of this selection as fishing-induced evolution has been the parsimonious explanation for life history changes to various populations (Jorgensen et al. 2007; Conover et al. 2009). The management solution for size-selective overharvest is to decrease harvest.

Alternately, ecological limitations such as inadequate food and interspecific competition has been attributed to the lack of large fish in a population (Parker et al. 2007; Van Leeuwen 2008; Vinni 2009). Commonly called ‘stunting’, compensatory growth and mortality from high fish densities is widely documented in the literature to affect the size of fish (Rose et al. 2001; Hilborn 2006; and others).

Analysis of Walleye growth rates showed that some of these Alberta populations were exhibiting fast growth as young fish, and then changing to slow growth as older fish. This analysis was not conclusive to the cause of the small, yet old Walleyes (Chapter 3, this study), and sufficient controversy existed among stakeholders and fisheries managers. I used an active adaptive management to study the problem (Walters 1986; Ludwig and Walters 2002). My goal for this paper was to address the key uncertainty: What was causing the small Walleyes?

The two competing hypotheses were: 1) compensatory growth and mortality from high densities was preventing Walleyes from getting larger or 2) size-selective harvest had removed the larger fish. I use an active-adaptive management to involve stakeholders in several large-scale, cause and effect experiments.

This work was important as the solutions to the small Walleyes are in opposition, either increase or decrease harvest, and a miss-diagnosis could exacerbate the problem.

Study Lakes

Lakes in Alberta were chosen based on public concerns about fisheries with abundant, yet small Walleyes (Figure 4-1: Table 4-1). Although few Walleyes were caught that were larger than 50 cm in length, anecdotal and historical records indicated that these populations produced Walleyes larger than 60 cm (Alberta Fish and Wildlife unpublished data). All lakes have commercial- and domestic-gillnet fisheries targeting whitefish but few Walleyes are captured in these net fisheries because of the small Walleye size and the large mesh size (15.2 cm) employed. The study lakes have simple fish communities (i.e., 8 species or less) with Northern Pike *Esox lucius*, Walleye and Burbot *Lota lota* as top predators (Nelson and Paetz 1992).

Methods

Data collection.—Creel surveys were conducted at all study lakes from the May long weekend until the end of August. Point-access-creel surveys were employed at Smoke and Iosegun lakes while at Long and Buck lakes I included ratio-of-use surveys to account for the multiple access points to the fisheries. Creel clerks interviewed anglers at the completion of their fishing day collecting angler harvest and effort information and biological data from fish. I also estimated release mortality for Walleyes (Reeves 2005) and illegal harvest (Sullivan 2002).

I assessed the populations yearly following the Fall Walleye Index Netting (FWIN) protocol (Morgan 2002). The gear was set in the fall when water temperatures were 10-15 °C. Each net comprised of eight panels of meshes ranging from 25 mm to 152 mm. Sets were perpendicular to the shore. I fished the nets for 24 h in two depth strata of 2-5 m and 5-15 m in proportion to the lakes' depth distributions. All captured fish were measured for length (TL to the nearest mm) and the three-leading rays of the pelvic fin were clipped within 3 mm of their attachment to the Walleye for ageing (Chapter 2, this study). All ages for this study were estimated by one ageing technician. Age accuracy was increased by backcalculating to determine the first annulus. I verified my assigned ages with comparisons to otoliths, known age Walleyes and with other agers (Chapter 2, this study).

I report either the catch rates from the FWIN assessments or from creel surveys of anglers. In Alberta, both of these assessment methods have been correlated to density using the following relationships. The conversion from population estimates (PE) to FWIN catch rates (CUE, Walleyes*100m^2*24hours^{-1}) for Walleyes greater than 35 cm was;

PE = .54 * FWIN CUE (n=6, r^2=0.95, M. Sullivan, unpublished data).

The conversion from PE to angler-catch rates (CUE, Walleyes*hours^{-1}) for Walleyes greater than 35 cm was;

PE = Angler CUE * 9.2 + 1.3 (n=12, r^2=0.88, M. Sullivan, unpublished data).

Study Design.—I used the management regulations to either increase or decrease harvest opportunities which in turn affected angler use of the fisheries. My goal was to increase or decease the density of fish and the size-selective harvest at the lakes with small Walleyes (Figure 4-2).

Lakes With Increased Harvest.—I decreased the minimum size limits at three lakes to either 1) further truncate the population size structure (resulting in smaller Walleyes) or 2) decrease the density of Walleyes to eliminate compensatory growth (resulting in larger Walleyes).

Therefore, at Iosegun and Buck lakes, I decreased the minimum size limit from 50 to 43 cm. Iosegun Lake received a possession limit of 3 Walleyes per angler while Buck Lake, with its proximity to large urban centers, received a possession limit of 1 Walleye per angler. Long Lake, which was managed with catch and release, was opened for a 24 day season with a bag limit of 1 Walleye over the 50-cm minimum size limit. Following this harvest, Long Lake was returned to a catch-and-release regulation.

Lakes With Decreased Harvest.—I increased the minimum-size limits at Smoke Lake (from 50 cm to 60 cm) and changed Long Lake to catch and release (from 1 over 50 cm) expecting either 1) a decrease in size-selective mortality allowing Walleyes to get larger or 2) an increase in compensatory growth preventing the Walleyes from getting larger.

Environmental Conditions.—I monitored the thermal integrate, growing degree-days above 5°C (Neuheimer 2006), from the Edmonton, Alberta weather station to determine if experimental outcomes were effected by environmental conditions.

Results

Lakes with Increased Harvest.—There was a dramatic increase in the number of anglers at the lakes with increased harvest opportunities (Figure 4-3). Prior to changing the regulations at Iosegun Lake angler effort was estimated at 5.9 hours* ha^{-1}*$year^{-1}$. Following the regulation changes, effort at Iosegun Lake peaked in the first year at 10.3 hours* ha^{-1}*$year^{-1}$ and then declined to 9.4 hours* ha^{-1}*$year^{-1}$. At Buck lake, prior to changing the regulations in 2004, effort was estimated at 4 angler-hours*ha^{-1}*$year^{-1}$. Following the regulation changes, the angling effort nearly tripled in 2005 to 11.7 angler-hours*ha^{-1}*$year^{-1}$. By 2008, the angler use at Buck Lake had continued to increase to 22 angler-hours*ha^{-1}*$year^{-1}$.

The harvest rate peaked at both Iosegun and Buck lakes in the first year of regulation changes and then declined in subsequent years as did the number of Walleyes over 40 cm at both of these lakes (Figure 4-4). Interestingly, length and age information from the FWIN catches at Iosegun Lake indicated that few Walleyes survived the fishery to exceed the 43-cm minimum size regulation yet old Walleyes still remained (Figure 4-5). Long Lake had a dramatic increase in angling effort and harvest during the 24 day season. An estimated 90% of the 25 hours*ha^{-1} of angling effort occurred during the short, 24 day season. An estimated 3.1 kgs*ha^{-1} of Walleyes were harvested which exceeds, by three times, the total allowable catch for Alberta Walleyes (Sullivan 2003). After two years of catch-and-release regulations following this harvest, the abundance of larger Walleyes increased (Figure 4-6).

Lakes with Reduced Harvest.— Unexpectedly, harvest increased at Smoke Lake even though the regulations were changed to reduce harvest. Following the first year of the regulation changes, the angling effort at Smoke Lake declined but then returned in the second year (Figure 4-7). Meanwhile the angler-catch rates increased from 1.7 Walleyes*hour^{-1} in 2003 to 2.5 Walleyes*hour^{-1} in 2005. This increase in catch rate, coupled with the return of angling effort, resulted in more Walleyes being caught and released than before the implementation of the experimental regulations. The majority of the fishing mortality at Smoke Lake was from handling mortality and illegal harvest as only 6 Walleyes were reported in the 2003 creel survey (4 of which were under-sized). I estimated a combined mortality (handling mortality and illegal harvest) of 5% which was 343 Walleyes in 2003 and 358 in 2005. Consequently, the population size-structure at Smoke Lake did not change with more protection from a larger-minimum size limit (Figure 4-8).

Environmental Conditions.—There was no evidence of climatic conditions effecting population size structure during the study period.

Discussion

Overharvest from anglers quickly removed the large Walleyes from Buck, Iosegun, and Long Lakes. The anglers had removed most of the fish over the 43 cm size limit with 18 months of fishing at Iosegun Lake, More spectacularly, the 24 day season at Long Lake removed most of the fish greater than the 50 cm size limit. Furthermore, when this harvest period stopped at Long Lake and the fishing effort declined, the Walleyes once again grew larger than 50 cm. It was evident that at these two lakes there was sufficient angling pressure to overwhelm the compensatory growth response to the reduced density.

Interestingly, the selective removal of the larger Walleyes from Iosegun Lake left many old, yet small fish within the population. A population-growth curve fitted to the remaining fish would falsely indicate that the growth had slowed. Other growth indices such as size-at-age would also be affected by this size-selective mortality reinforcing the difficulty in separating compensatory-growth responses to high density from size-selective harvest. As I found that a life history that matures early, with subsequent slow growth, was more likely to survive and the causal mechanism creating these small, yet old Walleyes was overharvest from angling, this raises concerns of evolutionary consequences. Size-selective harvest causing evolution of traits has altered fisheries in other jurisdictions (Jorgensen et al. 2007; Hard et al. 2008; Enberg et al. 2009 and others). Alternate management options need to be explored to reverse this selection.

My experiments gave me several interesting and unexpected results. Firstly, the reduced harvest opportunities at Smoke Lake did not change the size of the Walleyes. Initially, the angling use decreased, but anecdotes from anglers indicated that the declining Walleye catches at nearby Iosegun Lake caused anglers to return to Smoke Lake. Shifts in angling effort based on harvest opportunity and fishing quality have been recorded for various fisheries (Beard et al. 2003; Cox et al. 2003). By the second year of the study, the number of Walleyes caught had actually increased. Based on creel surveys prior to the regulation change, the majority of the mortality was from handling mortality and illegal harvest. With an increase in catch rate and a return of angling effort, this mortality increased to levels recorded prior to the experiment.

Secondly, at Buck Lake anglers did not truncate the population-size structure as quickly as they did at Iosegun Lake. Because of Buck Lake's proximity to urban population, I was more cautious with my regulation change; regardless, angler effort increased from 4 hours/ha in 2004 to 22 hours/ha in 2008. Alberta anglers are mobile and there are very few lakes compared to other jurisdiction (Post et al. 2002). Implementing a regulation that is sustainable for these open-access fisheries will be challenging given the high variability in angler effort.

Angling effort and harvest were sufficient to truncate the population-size structure and overwhelmed any growth responses. The harvests at Buck and Iosegun lakes exceeded the total allowable catch estimated by Sullivan (2003) and the number of Walleyes larger than 40 cm decreased. Alternately at Smoke Lake the catch-and-release mortality increased even though greater protection was provided to the Walleyes by increasing the minimum size limit.

I believe that Active adaptive management worked well to address the key uncertainty, the cause of the small Walleyes. The complexity of the problem, the variability in the systems studied, the sociopolitical interest and influence of participants required a large-scale experiment with clear outcomes (Walters and Holling 1990; Botsford et al. 1997; Aldridge et al. 2004). Participants, informed about the project, were conscious of the increase in angler use and the decline of the larger fish in their creels. There was also appreciation of a management agency addressing their concerns.

Active adaptive management is about “embracing uncertainty” (Walters and Holling 1990) and in large scale experiments unexpected events, should likely be expected. I had incorporated a ‘common garden’ experiment to address between-lake differences in Walleye genetics, prey base and growth conditions. To monitor individual growth nearly 600 Walleyes, of stratified sizes, were individually marked with pit tags and transferred from Smoke and Iosegun lakes to the donor lake. Unfortunately, all of the Walleyes died in the first winter because of anoxia from severe-winter conditions. Fortunately the outcomes from the experimentally managed lakes provided sufficient resolution to identify the mechanism causing the small Walleyes.

The next step for the Active Adaptive Management of Alberta’s Walleyes will be to incorporate my findings into a modelling framework. With historic population collapses (Post et al. 2002) and harvests that exceed the total allowable catch, the parsimonious conclusion is that the large Walleyes are overharvested, not growing slowly due to compensatory growth. I need an appropriate regulation to recover the large Walleyes while ensuring population sustainability. With evidence of selection caused by angling overharvest, concerns of evolutionary consequences must be addressed.

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TABLE 4-1. —Geographical, limnological, and fisheries data for Alberta study lakes. Data from Mitchell and Prepas (1990).

Lake	Latitude	Longitude	Area (ha)	Mean depth (meters)	TDS (mg/l)	Trophic Status[a]
Buck	53^0 00'	114^0 45'	2,540	6.2	120	Eutrophic
Iosegun	54^0 28'	116^0 50'	1,340	4.1	79	Eutrophic
Long	54^0 26'	112^0 45'	584	4.3	196	Eutrophic
Smoke	54^0 22'	116^0 56'	959	5.1	91	Eutrophic

[a]Based on chlorophyll a (Mitchell and Prepas 1990).

TABLE 4-2. —Fisheries information from the study lakes.

Lake and Year	Regulation Before	Experimental Regulation	Walleye CUE[a]
Buck 2004	1 fish> 50 cm	1 fish>43 cm	35.3
Iosegun 2003	2 fish> 50 cm	2 fish> 60 cm	32.8
Smoke 2003	2 fish > 50 cm	3 fish > 43 cm	30.0
Long 2003	catch-and-release	1 fish > 50 cm	18.6

[a]Walleye CUE, for the fisheries prior to the experimental regulations, was calculated from Fall Walleye Index Nets for $100m^2*24hours^{-1}$.

TABLE 4-3.—Temperature data recorded during the study period.

Year	Growing Degree-days Above 5°C
2000	1215.1
2001	1350.3
2002	1246.6
2003	1402.3
2004	1202.1
2005	1226
2006	1505
2007	1324.7
2008	1361.2

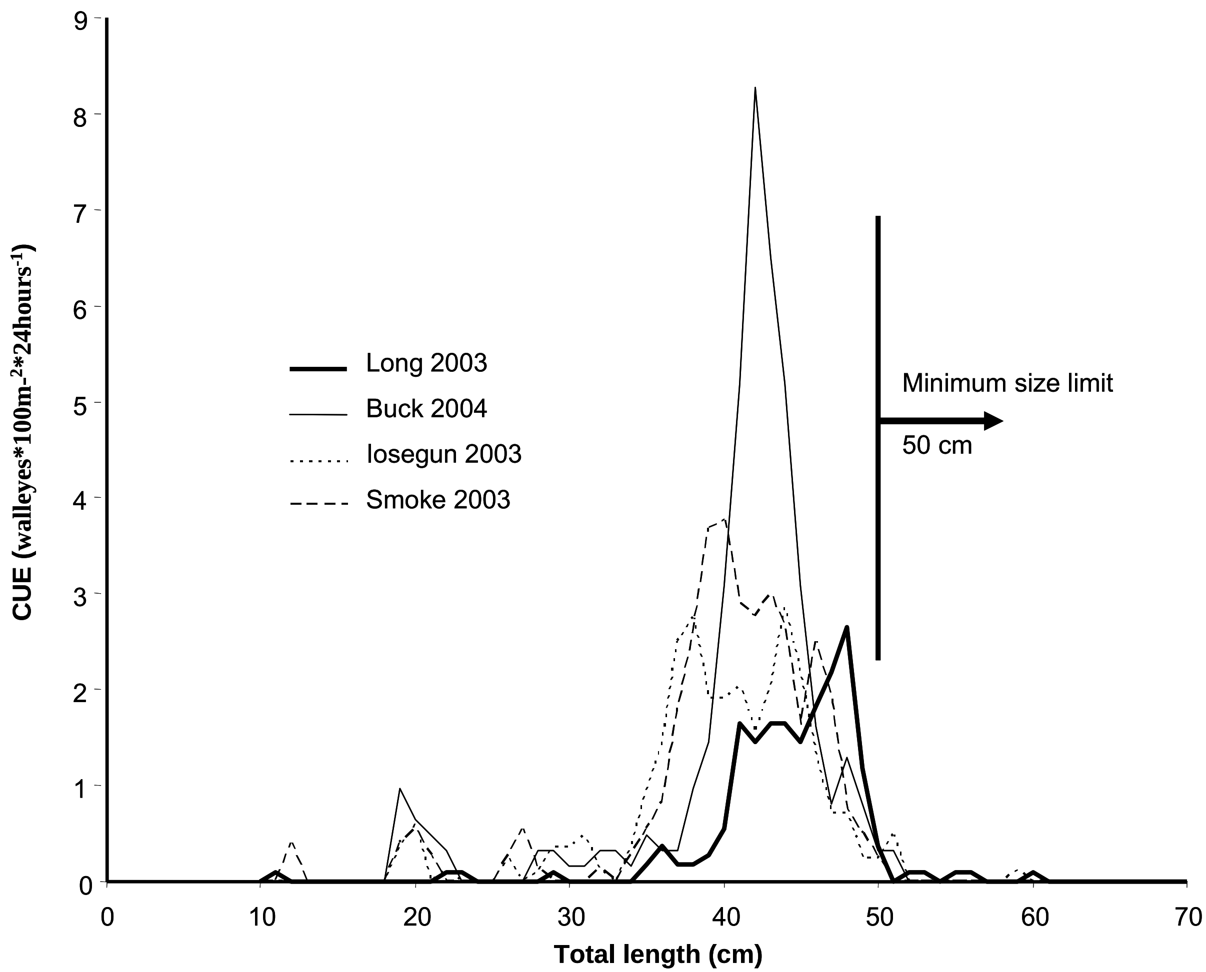

FIGURE 4-1. —Catches and length distributions of Walleyes sampled from the four study lakes prior to experimental manipulation of the fishery regulations.

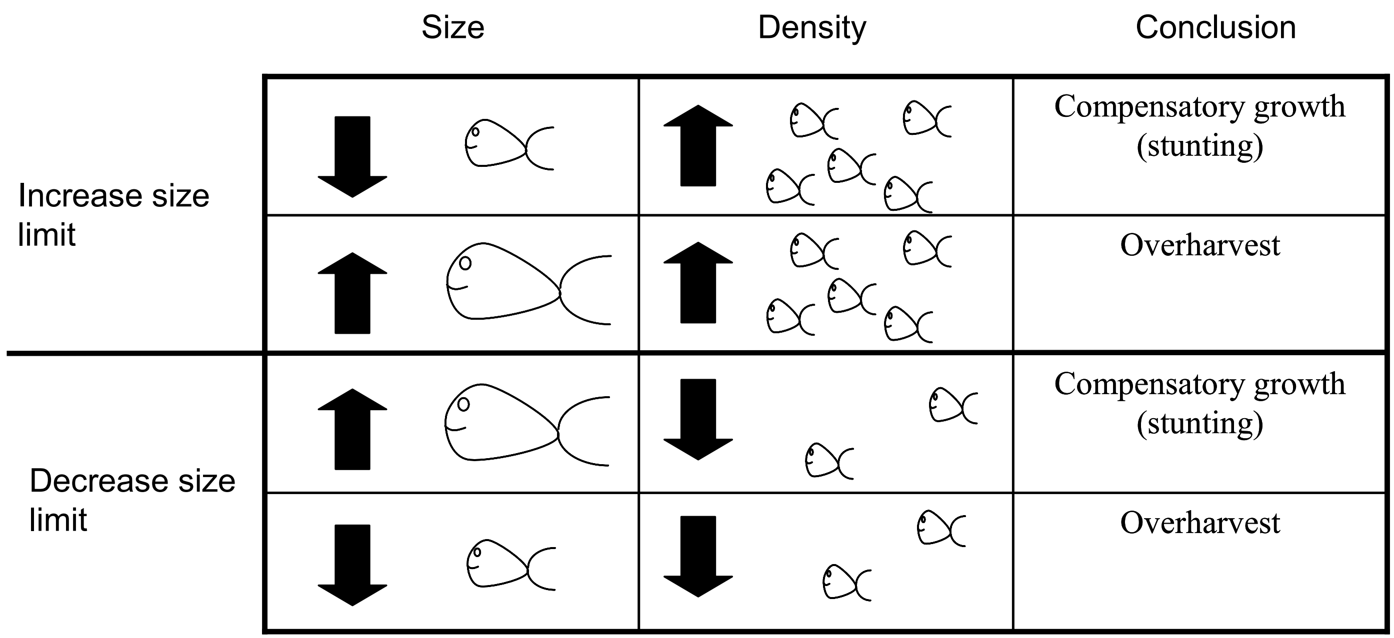

FIGURE 4-2. —An illustration of the possible outcomes from my experimental manipulation of the minimum-size limits (Size refers to population size-structure, density refers to overall Walleye numbers and size limits refer to minimum size limits).

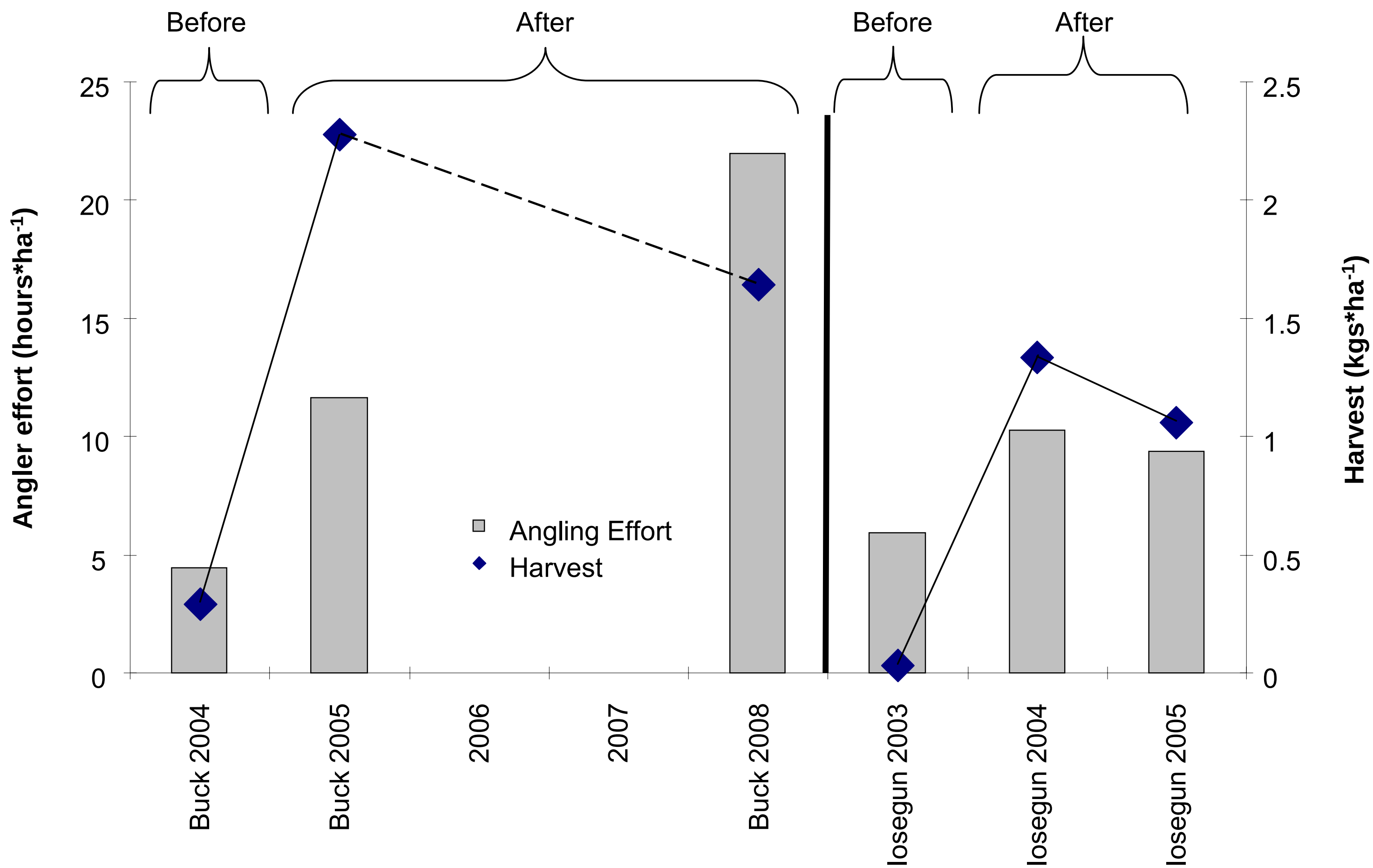

FIGURE 4-3. —Harvest and angler use at Buck and Iosegun lakes, before and after, the regulations were manipulated to increase size-selective harvest and decrease density.

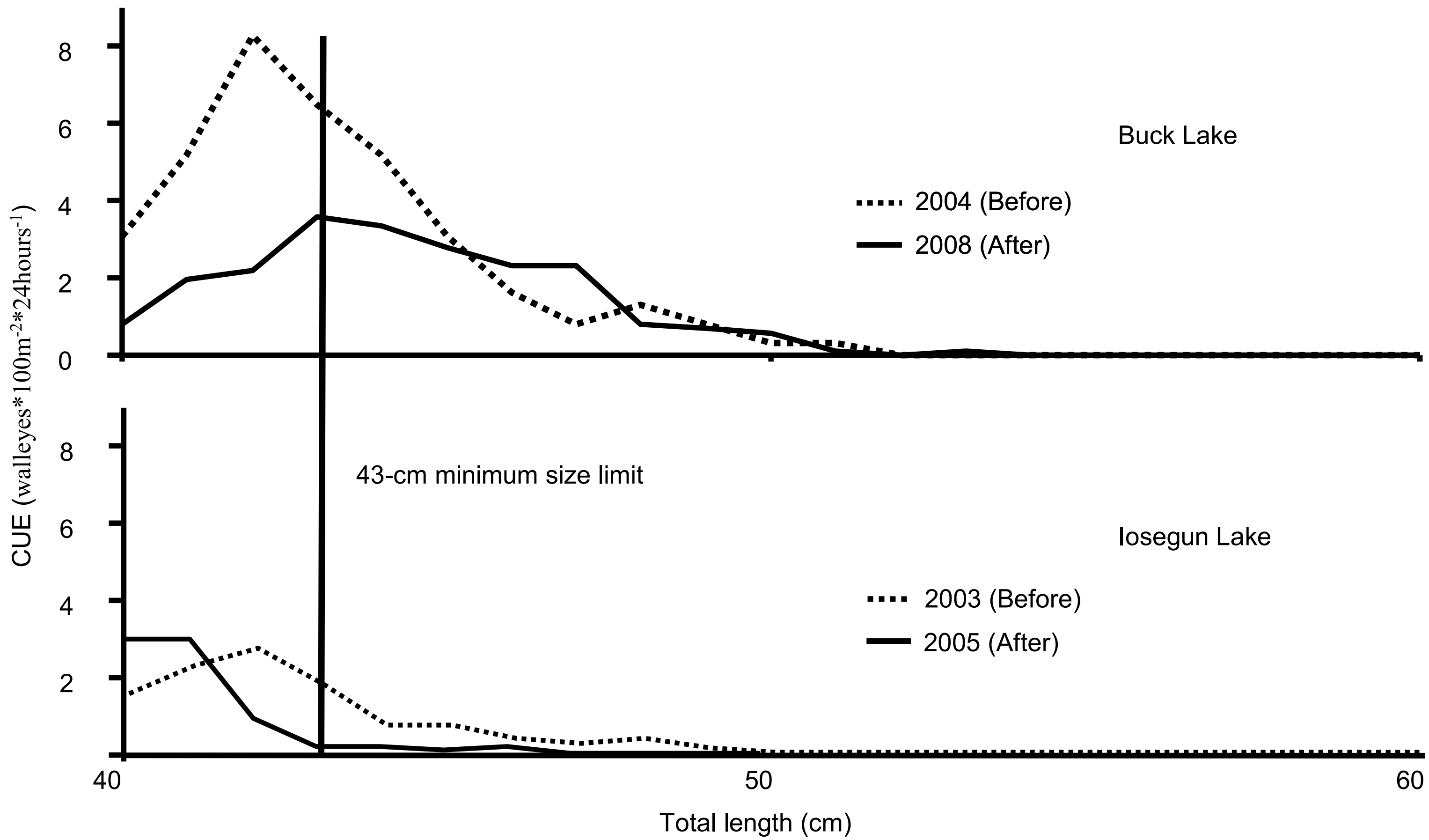

FIGURE 4-4. —Catch rates and length distributions of Walleyes captured in Buck and Iosegun lakes, before and after, the regulations were relaxed to increase size-selective harvest and decrease density.

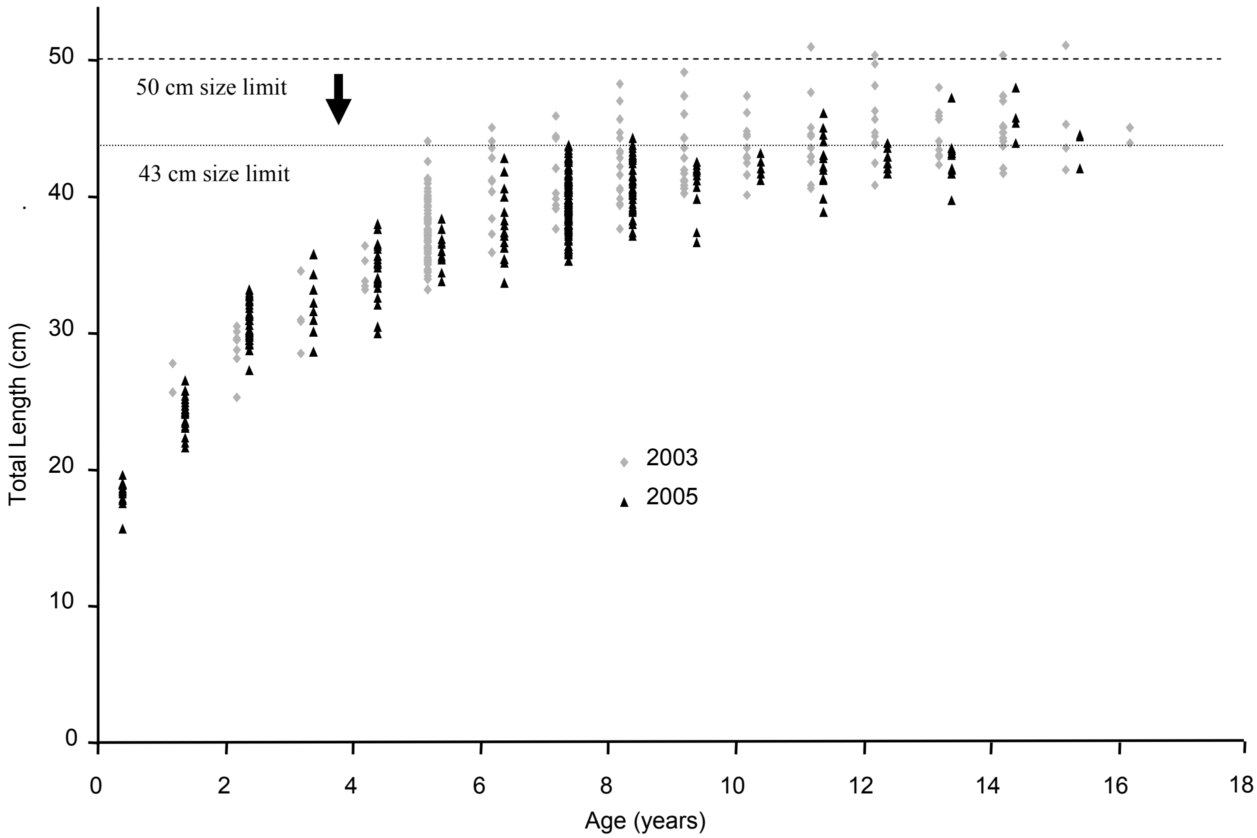

FIGURE 4-5. —Sizes and ages of Walleyes sampled from Iosegun Lake, Alberta. The minimum-size regulation in 2003 was 2 Walleyes larger than 50 cm which was relaxed in 2004 to 3 Walleyes larger than 43 cm.

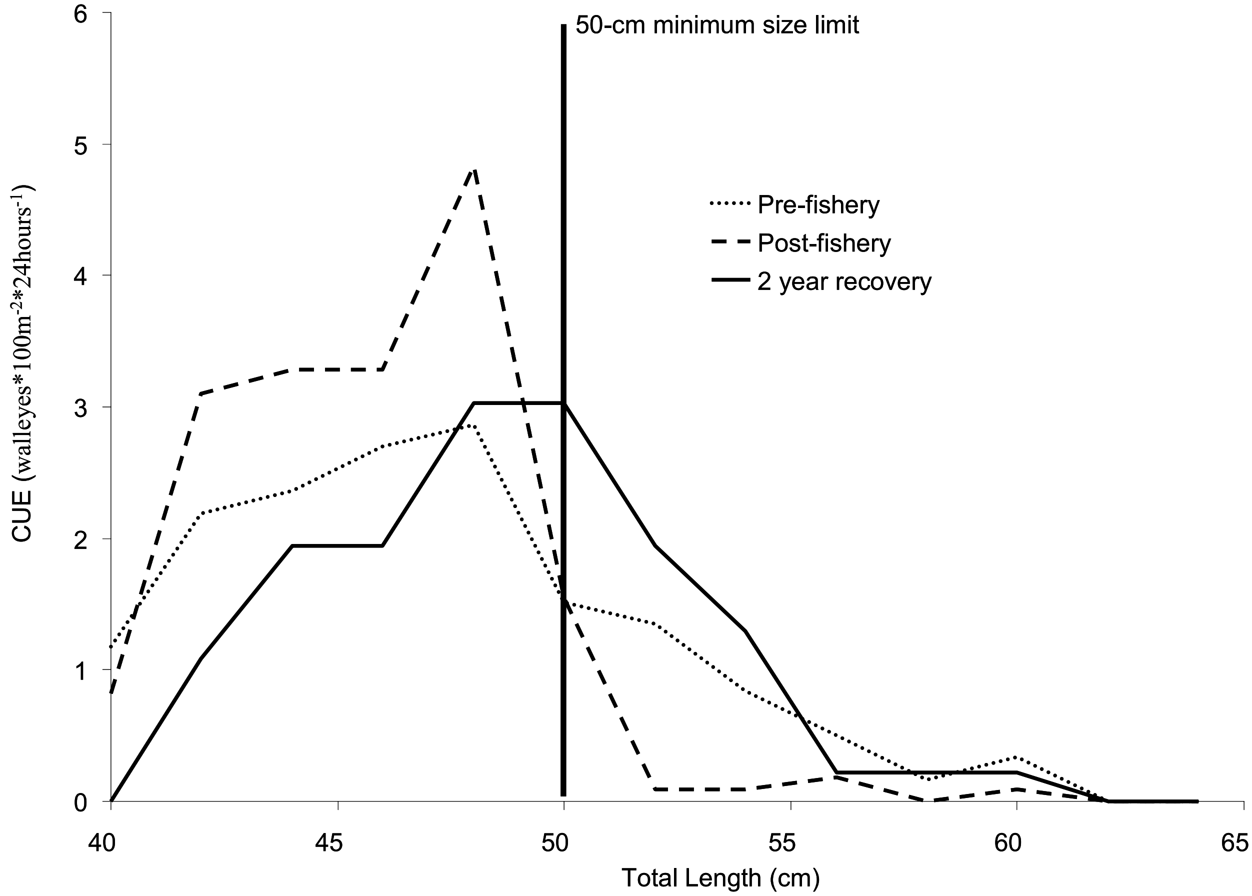

FIGURE 4-6.—The 24 day fishery at Long Lake, Alberta, with a minimum size regulation of 1 Walleye larger than 50 cm, decreased the numbers of large fish. The number of large fish increased two years following with a regulation that required all anglers to release their fish.

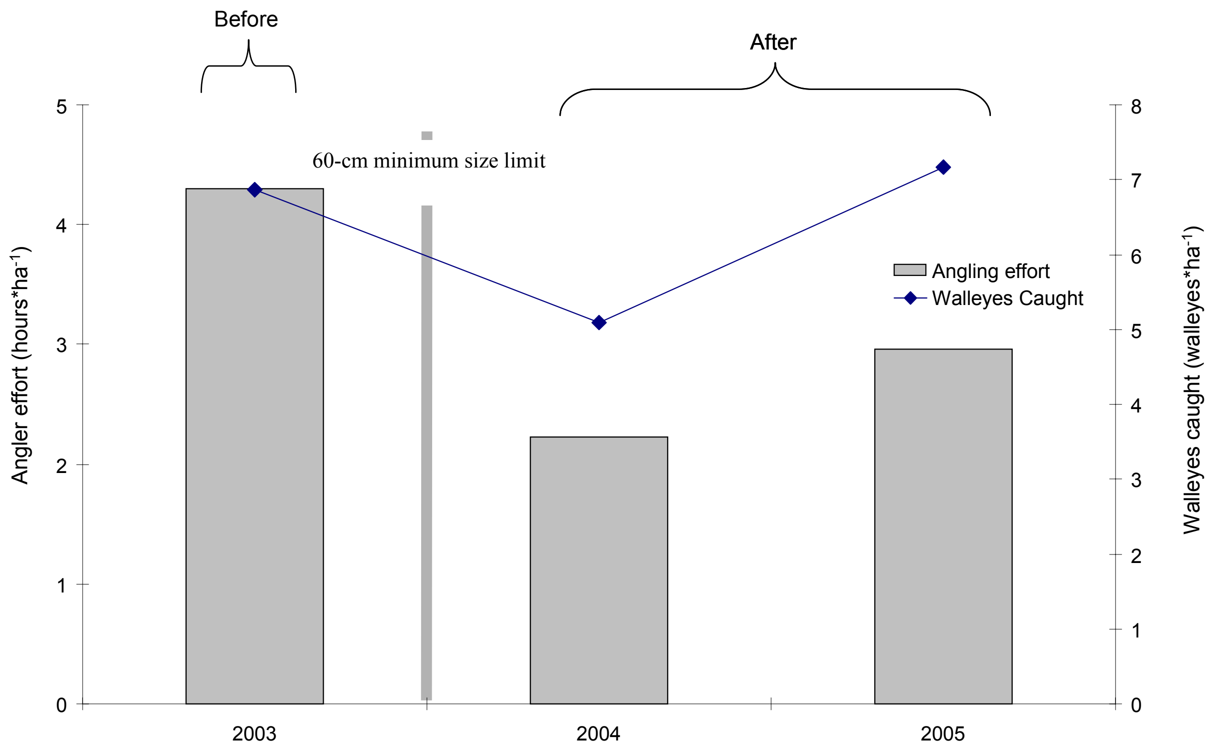

FIGURE 4-7. —Angler use and Walleye catch at Smoke Lake, Alberta decreased with a more restrictive 60-cm minimum size limit. The following year, the catch rates of Walleyes and angler use increased. By 2005, more Walleyes were caught than prior to the regulation change.

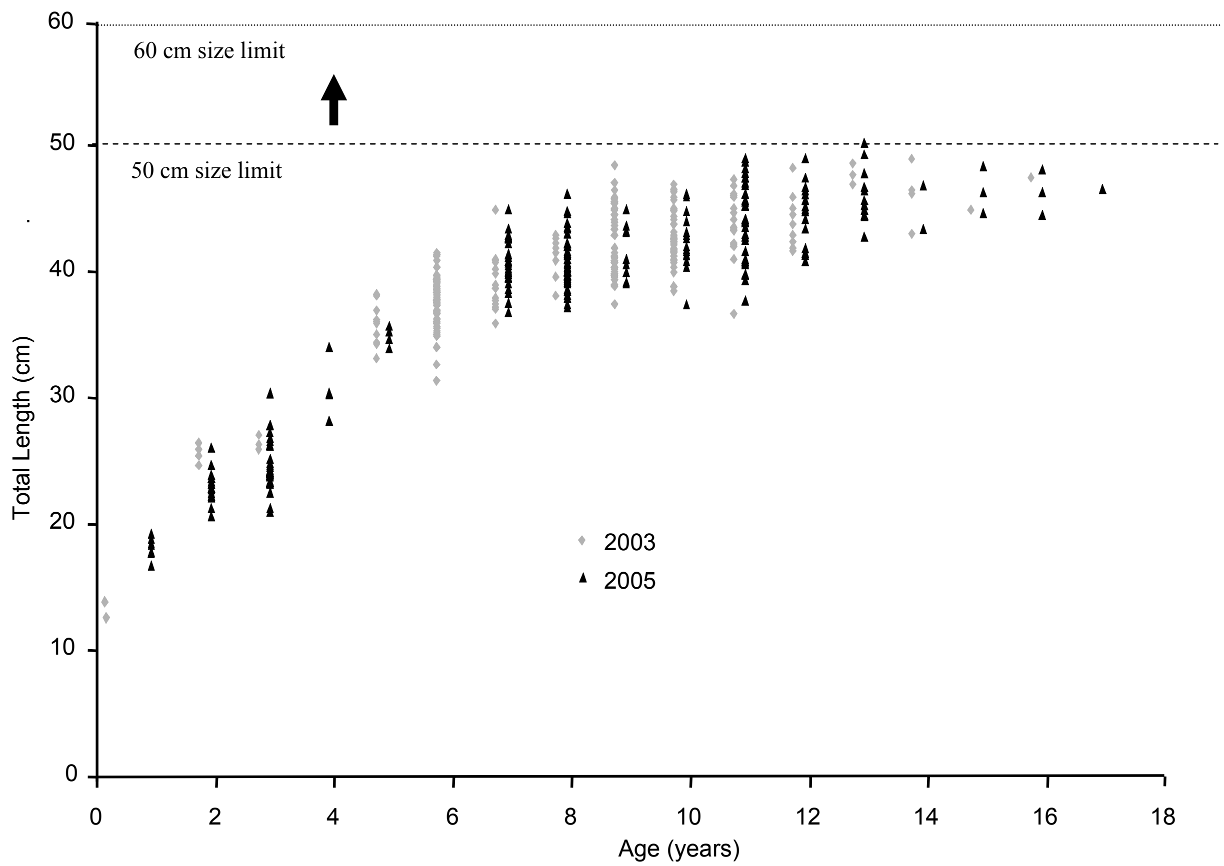

FIGURE 4-8. —The sizes and ages of Walleyes in Smoke Lake did not change despite the more restrictive minimum-size limit.

Chapter 5 Management options to address evolutionary concerns for heavily exploited Walleye populations.

Introduction

Fishing is almost always selective, typically targeting the faster-growing, larger and more valuable fish (Ricker 1969; Law 2000). Phenotypic selection has been documented in various managed species (Coltman et al. 2003; Darimont et al. 2009; Philipp et al. 2009; Sharp and Hendry 2009) and can have a lasting effect on populations (Hutchings 2005; Jorgensen et al. 2007; Enberg et al. 2009). Decreases in the size of fish have been reported in wild populations of Atlantic Cod *Gadus morhua*, Pacific salmon *Oncorhynchus spp* and in laboratory manipulative experiments using Atlantic Silversides *Menidia menidia* (Conover and Munch 2002; Hutchings 2005; Hard et al. 2008). A decline in size of fish can affect population resilience as smaller-body size results in reduced fecundity, and diminished productivity (Hutchings 2005; Jorgenson et al. 2007).

In comparison to other jurisdictions, Walleye *Sander vitreus* managers in Alberta are challenged by the few fish-bearing lakes and their low productivity from their northern latitudes and high elevations (Baccante and Colby 1996; Sullivan 2003). A rapidly expanding human population related to resource extraction was cited as the cause of the collapsed Walleye populations in the 1980 -1990's (Sullivan 2003). Minimum size or catch-and-release regulations were employed and resulted in rapid increases of fish density at some lakes; however, very few large Walleyes were caught (Chapter 3, this study). These 'low-quality' fisheries (Baccante and Colby 1991), with abundant-small fish and virtually no harvest, elicited complaints from anglers of 'stunted' fish (Chapter 3, this study).

Backcalculated size-at-age from pelvic fins indicated higher survival of Walleyes with rapid growth to maturity and then subsequent-slow growth (Chapter 3, this study). This 'hockey stick'-growth pattern allowed Walleyes of this life history to survive under the large-minimum size limit and produce offspring. An adaptive management experiment demonstrated that size-selective mortality from angling was the causal mechanism structuring the populations to small and old Walleyes (Chapter 4, this study). As the evidence indicated that the current management regulations were causing selection for a life history, this potential for evolutionary change needed to be addressed.

My objectives were: 1. to assess the selectivity and sustainability of various fishing regulations on life history types found in Alberta's Walleye populations and 2. reduce or reverse the selection for 'hockey stick' life history. Using an age- and size-structured population model, I evaluated two types of regulations. Firstly, passive-management regulations, which do not control angling effort or harvest including; minimum and maximum size limits and a kill slot. Secondly I simulated the effects of a recently introduced management tool for Alberta called a '*Special Harvest Licence*'. With the '*Special Harvest Licence'*, Managers allocate 'harvest tags' based on population density and size-structure of the Walleyes and angler use. By limiting harvest, this 'harvest tag' regulation reduces the risk of population decline; however, significant management effort is required to maintain up-to-date estimates of population status and fishery use. This is a 'quasi' active-management regulation as harvest is controlled, yet additional fishing mortality occurs because of handling mortality from catch-and-release fishing. And, as angler numbers increase, catch-and-release handling mortality can be significant source of harvest (Sullivan 2003).

My modelling outcomes were evaluated on evolutionary and ecological sustainability. I defined an outcome to be evolutionary unsustainable if harvest resulted in the selection for the 'hockey stick' life history. I defined an outcome to be ecologically unsustainable if densities decreased below levels that have historically caused Alberta's Walleye populations to collapse (<five adult Walleyes/ha; Alberta Fish and Wildlife unpublished data). This work is important as little has been done to address evolutionary concerns from fisheries management in freshwater lakes and is especially relevant to Alberta's situation of low productivity fisheries with high levels of angler use and evidence of harvest causing selection for a life history.

Modelling Assumptions

1. A life history is a result of a Walleye's genetics. Several studies have demonstrated that growth in fish is genetically determined and affected by selection (Law 2000; Conover and Munch 2002; Philipp et al. 2009; Conover et al. 2009). Although the environment can affect how genetics are expressed (i.e., compensatory growth), an analysis of Alberta Walleye populations at various

densities does not yield evidence of compensatory growth (Alberta Fish and Wildlife unpublished data). This suggests that these populations are below densities required to invoke compensatory growth. Additionally, an adaptive management experiment that increased angler harvest, caused a rapid truncation of the population-size structure at several Walleyes fisheries and overwhelmed compensatory growth (Chapter 4, this study).

2. All life histories existed and continue to exist within Alberta's lakes. The lakes with small Walleyes, historically had large fish, and I assume that the size-selective mortality has not yet removed the genetics of the larger fish.

3. Based on the principles of parsimony, I did not model any intra- or interspecies competition because; all of Alberta's fisheries receive harvest and are below carrying capacity, and do not show growth responses to varying densities (Alberta Fish and Wildlife unpublished data). Additionally I recognize that competition in multi-species, multi-year-class systems is hard to isolate, difficult to interpret and clouds modelling outcomes.

4. I believe that the desired-management regulation for Alberta's Walleye populations should reduce or reverse the selection for the 'hockey stick' life history. Historical evidence and data from the lakes in Alberta that are more lightly fished suggest that Walleye populations should have large fish.

I offer the following hypotheses based on harvest effects and life history theory (Gasser et al. 2000). Firstly, the 'hockey stick' life history will predominate numerically over other life histories if there is size-selective harvest for large fish. This hockey stick life history will have advantages of quick growth to maturity and small-maximum size to avoid harvest. Secondly, with regulations that allow large fish to survive, ‘regular-growth’ Walleyes will have an advantage with their larger size, and higher fecundity. Thirdly, the ‘slow-growth’ life history will predominate numerically when size-selective harvest is severe (i.e., close to their size-at-maturity).

Methods

Study Site and Walleye Collections.—Walleyes were collected from various lakes within Alberta, Canada following the Fall Walleye Index Netting (FWIN) protocol (Morgan 2002). Age information was derived from Walleye pelvic fins following protocols described in Chapter 2, (this study). I collected angler use and harvest data from creels surveys (Chapter 4, this study).

Model Description and Parameterization.—To explore the selectiveness of different management regulations on Walleye life histories, I modified and parameterized an existing size- and age-structured population model (Post et al. 2003; Table 5-1). I chose to model simulations deterministically for simplicity and clarity of outcomes.

I modified this size- and age-structured model for Walleye biology and fisheries characteristics of a 1000 ha lake, the approximate average size of Walleye lakes in Alberta confirmed to have the 'hockey stick' life history (Chapter 3, this study). The Walleyes in the modelled populations had a maximum age of 30 years. Maturity in Walleyes is size-dependant and I used 40 cm as the size of 95% mature for females in Alberta (Alberta Fish and Wildlife, unpublished data).

Walleye life histories.—There is a range of growth histories recorded for Alberta Walleyes. To parsimoniously deal with this range of growth, I decided to classify three-prevalent types; 'regular growth', 'hockey stick growth' and 'slow growth' modelled after Walleye populations found at three different lakes (Figure 5-1). Calling Lake, Alberta, managed with a catch-and-release regulation in

2001, had relatively light-fishing pressure (summer creel of 2 angler-hours*ha^{-1}*year^{-1}) and produced Walleyes with a 'regular-growth'. Buck Lake, Alberta, managed with a 50-cm minimum size limit consisted mostly of Walleyes of a 'hockey stick' life history, characterized by rapid growth to maturity and subsequent slow growth, remaining under the size limit (Chapter 3, this study). The Walleye population at Iosegun Lake, Alberta, was rapidly truncated to 'slow-growth' life history by increased angling effort and decreasing the minimum size limit to 43 cm (Chapter 4, this study).

I assumed that these three life histories exist within all Walleye populations which were substantiated by empirical and anecdotal evidence (i.e., lakes with 'small' or 'hockey stick' life histories historically had produced large Walleyes; Alberta Fish and Wildlife unpublished data). I also recognize that there is considerable variability in fish growth due to environment, but based on my manipulations fish populations with angling harvest (Chapter 3, this study); I believe that assessing the harvest and survival of these three life histories with the various regulations will provide insights on size selection from angling.

These three life histories were run separately (i.e., no interbreeding) to clarify the selectivity of each management regulation. Each scenario was run for 100 time steps (100 years) to ensure that the populations had reached equilibrium with the various management regulations.

Fecundity.— I calculated with Baccante and Colby's (1996) regression an average fecundity for Alberta's walleyes of 40 000 eggs per kilogram.

Stock Recruitment Curve.—I used a Ricker-stock-recruitment curve (Ricker 1975) to model recruitment from eggs to age-0,

$$R=a*eggs^{(-b*eggs)}$$

where R is the number of age-0 recruits, a is the coefficient of density-independent mortality, eggs is the estimated number of eggs produced for that year and b is the coefficient of stock-dependent mortality. I used 46-different-population assessments to compare the estimated numbers of eggs from mature females to the densities of age-0 Walleyes caught in the fall to develop this Ricker stock recruitment curve (Figure 5-2; Table 5-2). My population assessments were determined with the FWIN protocol (Morgan 2002) so I needed to convert these catches to a density. The conversion from FWIN catch rates (CUE, Walleyes*100m^2*24hours^{-1}) to population estimates (PE) for Walleyes greater than 35 cm was;

PE = .54*FWINCUE (n=6, r^2=0.95, Alberta Fish and Wildlife unpublished data).

As Walleyes younger than age-4 were not fully recruited to the FWIN, I needed to determine a vulnerability of these fish to the gear for my density estimates. I looked at nine Alberta lakes with consecutive years of FWIN assessments to follow the recruitment of age-0 Walleyes until age-4. Calculating average vulnerability for each year (Age-0 to Age-4), I estimated that one age-0 Walleye per FWIN net equated to 11 per hectare. The Ricker curve was fitted using maximum likelihood estimates (Figure 5-2).

This derived Ricker curve in modelling scenarios did not provide sufficient recruitment to match my empirical data for Walleye recruitment (i.e. the Walleye population would collapse too easily). I therefore used for model scenarios a Ricker curve that approximated the upper 95% confidence interval of the derived curve (Table 5-1).

Vulnerability.—I estimated vulnerability by comparing angler catch data to density estimates. Walleyes less than 25 cm are invulnerable to angling and Walleyes >45 cm are completely vulnerable (Alberta Fish and Wildlife, unpublished data; Figure 5-3).

Natural and Fishing Mortality.—For modelling scenarios I considered several sources of mortality. Natural mortality was estimated from observations of year to year survival rates from Alberta Walleye populations (Alberta Fish and Wildlife, unpublished data, Table 5-1). Estimates of angler release (handling) mortality (Reeves 2005) were calculated with empirical data (Table 5-1). Fishing mortality from passive regulations such as kill slots, or maximum and minimum size regulations was modelled as described by Post et al. (2003).

As managers using Alberta's 'harvest tag' protocol allocate tags for harvest based on fishing pressure and population status, for my model, this mortality occurred as a percentage of the available adults for each time step. Therefore, as adult abundance declined or increased, so did the number of tags. My creel data indicated that anglers, given a range of fish sizes in a fishery, would preferentially harvest a larger fish (Alberta Fish and Wildlife unpublished data). Hence, I gave two different mortality rates for the 'harvest tag' regulation. Walleyes 40 to 45 cm had a mortality rate of 15% per year and those greater than 45 to 50 cm, a mortality rate of 24% per year.

Unfortunately, accurate data do not exist for Walleye catches in Alberta's domestic and commercial fisheries so mortality estimates from netting were based on expert opinion. I allocated a mortality of 5% per year for fish that were large enough to be vulnerable to the large-mesh gillnets used in these fisheries.

Angler Compliance –I used the average compliance estimates from Sullivan (2002) for model scenarios with the minimum- and kill-slot size regulations. Although compliance estimates for a maximum size limit were not available, I assumed a similar compliance as those estimated for the minimum size limit.

I needed to determine angler compliance to the 'harvest tag' regulation. Creel attendants at Pigeon Lake, Alberta, recorded excellent compliance with this regulation as anglers provided 42 Walleyes, and all the fish were tagged. Because anglers in Alberta had disclosed in interviews that they would deliberately be non-compliant to angling regulations (Walker et al. 2007), I was somewhat suspicious that anglers would hide their untagged or under-sized Walleyes from the creel attendants. Thus, I modelled several levels of non-compliance (with the 'harvest tag' regulation) to assess the importance of this parameter.

Catchability.—To calculate a catchability for Walleyes (catchability = angler CUE*Walleye density^{-1}), I used population and catch rate estimates from 18

Alberta Walleye fisheries (Table 5-3). I used the average catchability for my simulations.

Angling effort.—Angling effort varies greatly at Alberta's fisheries ranging from near zero to over 70 angler-hours*ha^{-1}*year^{-1} (Alberta Fish and Wildlife unpublished data). These values vary with lake size. For lakes of approximately 1000 ha, the estimated angling effort averages 12.6 angler-hours*ha^{-1}*year^{-1} with a standard deviation of 10.4 angler-hours*ha^{-1}*year^{-1} (Table 5-3). I therefore evaluated increasing levels of angling effort up to 30 angler-hours*ha^{-1}*year^{-1}.

Model Validation.—I validated my model with Walleye population and exploitation data from lakes that had been experimentally manipulated or had undergone management changes. The model was parameterized with Walleye population data and angler use prior to population manipulation and then evaluated for relevance to the empirical data. I provided an example from Iosegun Lake, Alberta, where following a reduction in the minimum size limit regulation and an increase in bag limit from two to three Walleyes, anglers truncated the population-size structure to within two cm of the legal-size limit in two years.

Model Scenarios.—I evaluated the densities of the three life histories, ('slow', 'hockey stick' and 'regular' growth) with increasing angler effort to determine the selectivity of each regulation. To provide clarity, all scenarios were run deterministically for 100 years to give populations the time to equilibrate.

My objective was to recover the Walleye populations with the ‘small-fish’ problem. As these fisheries had historically produced large Walleyes, my assumption was that all life histories remained within these populations. Therefore, population simulations were started with the following percentages of the aforementioned life histories: 80% ‘hockey stick’, 10% ‘regular’ and 10% ‘slow growth’ which provided an approximate size distribution to that found within populations of small Walleyes.

Response Variables.—As my focus was the selectivity and sustainability of each regulation, I evaluated the density of each life history, overall density and life history harvested. I provide three categories for classifying abundance based on expert opinion from Alberta’s fisheries managers. Densities of 15 Walleyes> 35cm*ha^{-1} are considered to be sustainable, 5-15 Walleyes > 35cm*ha^{-1}, vulnerable and less than five Walleyes > 35cm*ha^{-1}, collapsed.

Results

Model Validation.—The modelled results for Iosegun Lake compared well to the empirical data (Figure 5-4). Age-class structure and total catch rates were similar for the comparison (28 Walleyes per net modelled versus 32 Walleyes per net measured).

Model Scenarios.—Most of the management regulations failed at relatively low levels of angling effort resulting in collapsed populations (Figure 5-5). The 43-cm-minimum size limit, the 40 to 50 cm kill slot and the 43 cm-maximum size limit resulted in population collapses at levels of angler effort below the provincial average. The 50 cm-minimum size limit allowed for greater sustainability than the other regulations; however, there was strong selection with the 'hockey stick' life history becoming proportionally more prevalent. Expectedly, harvest yields from the 50 cm-minimum size limit were comprised exclusively of the 'regular-growth' life history (Figure 5-6).

Depending on angler compliance, the 'harvest tag' regulations sustained populations while increasing the proportion of 'regular' Walleye life history, even at higher levels of angling effort (Figure 5-7). The modelled harvest information indicated that the 40-50 cm 'harvest tag' targeted the mature and slow-growing 'hockey stick' life history while allowing escapement of the 'regular' life history. Illegal harvest was an important parameter for this regulation as increasing non-compliance collapsed the Walleye populations at relatively low levels of angling effort.

The ‘slow-growth’ life history was not sustainable. Regardless of management regulation, even low levels of angling effort eliminated the population of ‘slow-growth’ life history.

Discussion

Reducing Size-Selective Mortality.—The ‘harvest tag’ was the best regulation to reverse selection for ‘hockey stick’ life history and the most sustainable with the current levels of angling effort in Alberta. Targeting the 40-50 cm fish with the ‘harvest tag’ regulation allowed the escapement of the ‘regular’ life history, while targeting the slow-growing-‘hockey stick’ life history. Congruent to my hypothesis, the higher fecundity of the larger ‘regular’ life history created abundant offspring and thus, sustainable populations. The ‘harvest tag’ regulation also allowed for greater harvest (kgs/ha); however, angler compliance was important, especially as fishing effort increased.

There are, however, additional management costs for running a ‘harvest tag’ regulation. For proper allocation of tags, managers require current information on angler use and population status. Additionally, Alberta Fish and Wildlife uses a computer system for retailers to allocate tags which is an additional license fee for anglers. Regardless, ‘harvest tags’ have been popular among anglers with nearly 80% of interviewees in support of the regulation (Alberta Fish and Wildlife unpublished data).

I found several management regulations that reduced selection for ‘hockey stick’ life history. However, these regulations did not provide sufficient protection to Walleye populations which collapsed with increasing levels of angling pressure (below Alberta’s current average). Alberta has few lakes, most of which are easily accessed (Post et al. 2002; Sullivan 2003). With harvest incentives such as low minimum size limits, angling use has increased by over 500 % (Chapter 4, this study).

Increasing Size-Selective Mortality.—The large-minimum-size-limits employed to recover the collapsed-Walleye populations in Alberta have the unintended consequence of selection for Walleyes with 'hockey stick' growth. With increased angling effort, the selection for 'hockey stick' life history got stronger yet Walleyes were able to exist, even when fishing effort exceeded 16 angler-hours*ha^{-1}*$year^{-1}$. Empirical data from Alberta lakes (Chapter 4, this study) support these modelled results. As predicted by my hypothesis, the 'hockey stick' life history allowed these Walleyes to remain under the minimum size limit so that they were only vulnerable to illegal harvest and handling mortality from catch-and-release fishing.

Additional Considerations.— I found catchability (the number of Walleyes caught per unit of fishing effort) to be a sensitive parameter for model outcomes. The Walleye population at Buck Lake, Alberta, has a reputation for resilience to high fishing effort. Catchability at Buck Lake was half of the average of other waterbodies examined. As halving the catchability, halves the catch (and all other sources of angling mortality), options to reduce catchability such as bait bans or hook restrictions might be options to mitigate the effects of increasing angler use on a fishery.

Net harvest might also overwhelm attempts to reduce size-selective mortality. Alberta's commercial- and First Nations-subsistence-net fisheries use large-mesh nets to target Lake Whitefish *Coregonus clupeaformis* but larger sportfish are unintentionally captured. Alternate means of capturing Lake Whitefish such as trapnets could reduce this by-catch.

I chose a deterministic model for this study to facilitate the interpretation of these complex systems. Studies of Alberta's fisheries have shown high variability in stock recruitment, angling effort and angler compliance (Post et al. 2002; Post et al. 2003; Sullivan 2003). All of these parameters have the potential to reduce the sustainability of these fisheries.

Interestingly, I must reject my hypothesis that the 'slow-growth' life history would predominate numerically with severe-size-selective harvest that targets large fish. The 'slow-growth' Walleyes have a low intrinsic rate of increase with late maturity, slow growth and remain at a small-size. Very little angling mortality from catch-and-release and non-compliance resulted in population collapses. These 'slow-growth' fish were modelled after a Walleye population in Iosegun Lake that had rapidly been truncated by size-selective mortality from angling (Chapter 4, this study). The inability of these small Walleyes to survive provides insights on the importance of managing for evolutionary concerns (Ashley et al. 2003) by ensuring that size selective harvest does not continue to target larger Walleyes.

To recover the 'regular' life history I chose to target the 'hockey stick' life history with a 40 to 50 cm 'harvest tag' regulation. Although the 'hockey stick' life history is initially fast growing, this regulation allows for harvest of the slow-growing adults and at rates that allow the escapement of larger fish. Researchers have shown that size at maturity can decrease with phenotypic selection (Olsen et al. 2004; Jorgensen et al. 2007) and Alberta's Walleyes mature at approximately 40 cm. Managers will need to be vigilant to ensure that the size of maturity does not decrease to make early-spawning fish invulnerable to harvest.

Conclusions and Future Work.— With current levels of angler use the 'harvest tag' is the best regulation to reduce selection for the 'hockey stick' life history. As angling effort increases angler compliance with this regulation will be required to ensure sustainability. Innovative enforcement means might become necessary to find Walleyes presumably hidden by anglers.

The 'harvest tags' with conservative harvest rates allowed the escapement of larger fish and reversed the size-selective mortality (with current levels of angling effort). The larger fish have higher fecundity which increases population productivity and thus, viability. However, as angling effort continues to increase, my information suggests that Alberta's Walleye fisheries will ultimately need to be managed by limiting the number of anglers using these fisheries.

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TABLE 5-1.—Parameters used in the age- and size-structured model. See text for model modifications and detailed information or Post et al. (2003) for model formulation.

Input Parameter	Value used	Source
Biology		
von Bertalanffy 'regular' growth		a
L_∞	75	
K	0.2	
t_0	0.128233	
von Bertalanffy 'hockey stick' growth		b
L_∞	50	
K	0.6	
t_0	0.542605	
von Bertalanffy 'slow' growth		c
L_∞	45	
k	0.3	
t_0	-0.0338497	
Length to mass relationship		a
c	0.000004	
d	3.146	
Fecundity	40 000 eggs*kg^{-1}	d
Ricker Curve Parameters		e
alpha	0.0003	
beta	3.0*10^{-9}	
Vulnerability		
p	.2	
q	300	f
Natural Mortality (m)		g
Age 0-1	.7	
Age 1-2	.5	
Age 2-3	.3	
Age 3-30	0.125	
Fishery		
Hooking mortality (r)	0.04	h
Noncompliance mortality (s)		
Minimum size limit	12. 6	i
Maximum size limit	12.6	i
kill slot	29.2 %	i

[a]Calculated from 2001 Calling Lake Walleye population data (n=706, Alberta Fish and Wildlife, unpublished data).

[b]Calculated from 2006 Buck Lake Walleye population data (n=220, Alberta Fish and Wildlife, unpublished data).
[c]Calculated from 2005 Iosegun Lake Walleye population data (n=362, Alberta Fish and Wildlife, unpublished data).
[d]from Baccante and Colby (1996).
[e]Calculated from 46 population estimates (Alberta Fish and Wildlife, unpublished data).
[f]Walleyes <25 cm are invulnerable to angling and Walleyes >45 cm are completely vulnerable (Alberta Fish and Wildlife, unpublished data).
[g]Developed to approximate observations from year to year population estimates (Alberta Fish and Wildlife, unpublished data).
[h]I estimated hooking mortality for Alberta Fisheries using methods from Reeves (2005)
[i]For each regulation I used the average non-compliance estimates reported by Sullivan (2002)

TABLE 5-2. —Walleye population information from Alberta Fisheries used to calculate the stock recruitment curve. See text for information on how each parameter was calculated.

Waterbody and Year Surveyed	CUE of Age-0 ($100m^2$* $24hours^{-1}$)	CUE of Adult Females ($100m^2$ *$24hours^{-1}$)	CUE of Eggs (40 000*kg of $female^{-1}$)	Number of Age-0 ($hectare^{-1}$)	Number of Eggs ($hectare^{-1}$)
Barkenhouse 2004	4.5	7.6	303459	43.9	163868
Beaver 2006	1.5	5.6	223906	14.9	120909
Blackett 2005	0.2	6.6	265357	1.6	143293
Brutus 2005	0.3	3.0	120710	2.6	65183
Buck 2005	0.1	8.6	342306	0.7	184845
Buck 2006	1.7	9.2	366214	16.2	197755
Calling 2002	0.1	6.8	271818	0.9	146782
Calling 2001	0.1	9.5	380739	1.2	205599
Calling 2004	0.3	13.9	557317	3.2	300951
Calling 2006	2.0	15.5	621659	19.1	335695
Christina 2003	0.3	2.6	103070	2.7	55658
Elinor 2003	0.3	5.5	220861	2.9	119264
Fawcett 2006	0.3	3.0	120580	2.7	65113
Fickle 2004	0.6	0.8	33667	5.9	18180
Floatingstone 2003	2.2	5.2	207094	21.6	111830
Floatingstone 2007	5.8	4.3	171399	56.8	92555
Gregoire 2007	0.2	7.2	286214	2.0	154555
Heart 2000	0.0	1.7	66443	0.3	35879

Jackson 2005	0.2	8.7	346387	1.7	187049
Keho 2004	0.1	1.2	47140	0.9	25455
Lac Ste. Anne 2001	0.4	1.8	73849	3.8	39878
Lac Ste. Anne 2006	2.6	8.4	334741	25.4	180760
Lac Ste. Anne 2002	2.9	2.8	111538	27.9	60231
Newell 2005	0.2	7.3	290356	2.3	156792
Lesser Slave 2005	0.1	3.7	149111	0.9	80520
Lesser Slave 2007	0.2	5.2	207288	2.2	111935
Lesser Slave 2006	0.6	7.4	294815	6.2	159200
Long 2003	0.1	6.3	253480	0.8	136879
Marie 2007	0.9	8.5	341041	8.6	184162
Milk River Ridge Reservoir 2004	0.2	6.5	260923	1.5	140898
Milk River Ridge Reservoir 2005	0.4	2.6	104087	3.6	56207
Moose 2000	0.1	5.7	229554	1.2	123959
North Wabasca 2006	0.3	1.5	59644	2.8	32207
Pigeon 2007	1.4	10.9	437869	13.7	236449
Pigeon 2006	1.6	17.7	709901	15.3	383346
Pinehurst 2006	1.6	3.9	157791	15.4	85207
Rock Island 2004	0.2	8.9	354407	1.8	191380
Skeleton 2004	0.4	6.2	247495	3.8	133647
Smoke 2004	0.3	7.7	307010	3.2	165785
Smoke 2003	0.4	7.3	290821	3.9	157043
Sturgeon 2005	0.4	3.2	128842	3.6	69574
Sturgeon 2007	0.7	7.6	304748	7.1	164564
Vincent 2000	0.1	15.3	611240	1.1	330070
Winagami 2006	0.3	4.4	174738	3.0	94359
Wolf 2007	0.5	3.1	124932	4.6	67463
Wolf 2006	1.1	6.3	252960	11.1	136598
Wolf 2003	4.8	13.4	534877	47.2	288833

TABLE 5-3.—Walleye population and angler use information from Alberta Fisheries used to calculate catchability.

Lake and Year	Walleye density (fish>35cm*ha^{-1})	angler CUE (Walleyes*angler-hour^{-1})	Catchability (angler CUE* Walleye density^{-1})
Buck Lake 2008	22.0	1.0	0.05
Beaver Lake 2006	10.6	0.5	0.05
Calling Lake 2004	11.2	0.6	0.05
Forty Mile Coulee Reservoir 2004	7.2	0.4	0.06
Buck Lake 2005	18.9	1.1	0.06
Milk River 2004	5.6	0.4	0.07
Wolf Lake 2006	14.1	1.0	0.07
Smoke Lake 2003	20.0	1.7	0.08
Lac Ste. Anne 2006	16.7	1.6	0.09
Smoke Lake 2004	21.0	2.4	0.11
Smoke Lake 2005	22.0	2.5	0.11
Long Lake 2003	9.4	1.1	0.12
Calling Lake 2002	7.8	0.9	0.12
Iosegun Lake 2004	16.1	2.0	0.12
Iosegun Lake 2003	16.2	2.2	0.14
Iosegun Lake 2005	15.1	2.2	0.14
Pigeon Lake 2007	23.2	3.7	0.16
Wolf Lake 2007	10.6	1.7	0.16
		average	0.10

TABLE 5-4. —Angler use information recorded at Alberta lakes of approximately 1000 ha.

Lake Name	Year	Surface Area (ha)	Hours/ha
Skeleton Lake	1997	789	0.92
Elinor Lake	1996	933	8.44
Ironwood Lake	1996	937	4.74
Baptiste Lake	1995	1111	22.52
Baptiste Lake	1997	1111	33.30
Baptiste Lake	1999	1111	13.27
Baptiste Lake	2005	1111	3.75
Baptiste Lake	2005	1111	3.75
Lac La Nonne	1997	1180	25.49
Lac La Nonne	2006	1180	13.22
Iosegun Lake	2005	1340	9.25

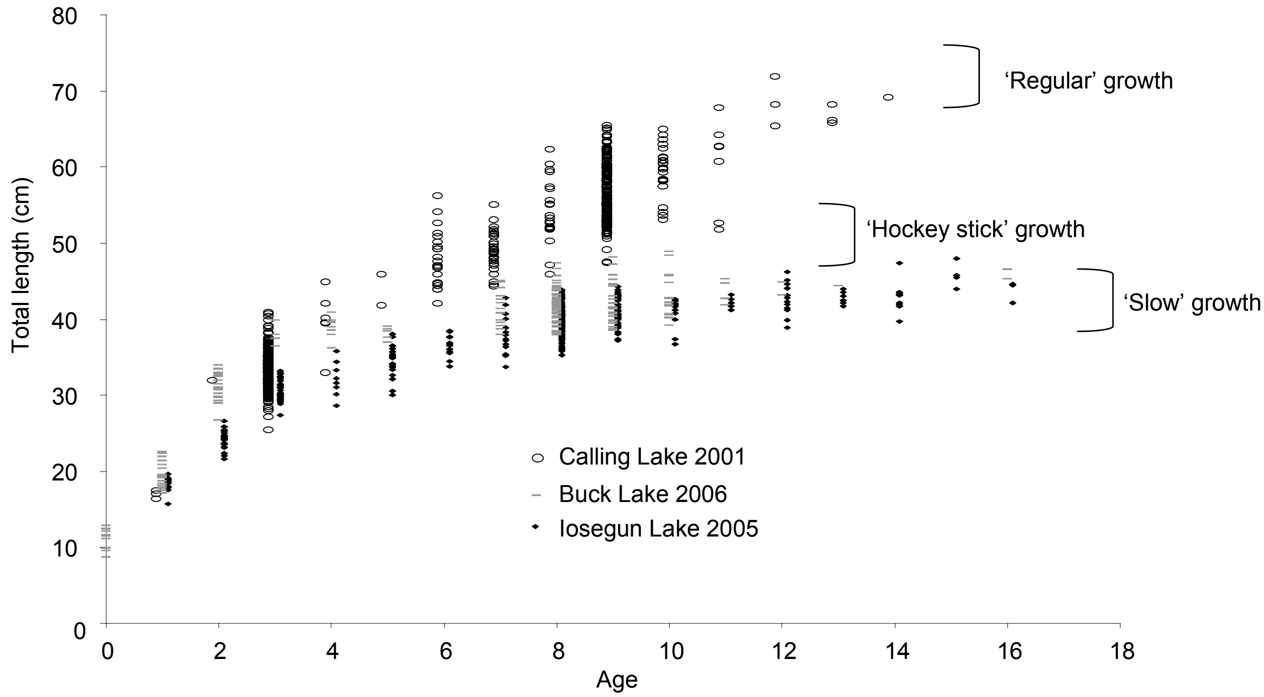

FIGURE 5-1. —Age and length data of the three different life histories used for modelling scenarios. 'Regular' growth Walleyes were recorded at Calling Lake, Alberta which had low angling effort (2 angler-hours*ha-1*year-1) and catch-and-release angling. 'Hockey stick' growth was recorded at Buck Lake which was managed with a 50 cm-minimum size regulation with 12 angler-hours*ha-1*year-1. 'Slow' growth was recorded at Iosegun Lake which was managed with a 43 cm-minimum size regulation and 13 angler-hours*ha-1*year-1.

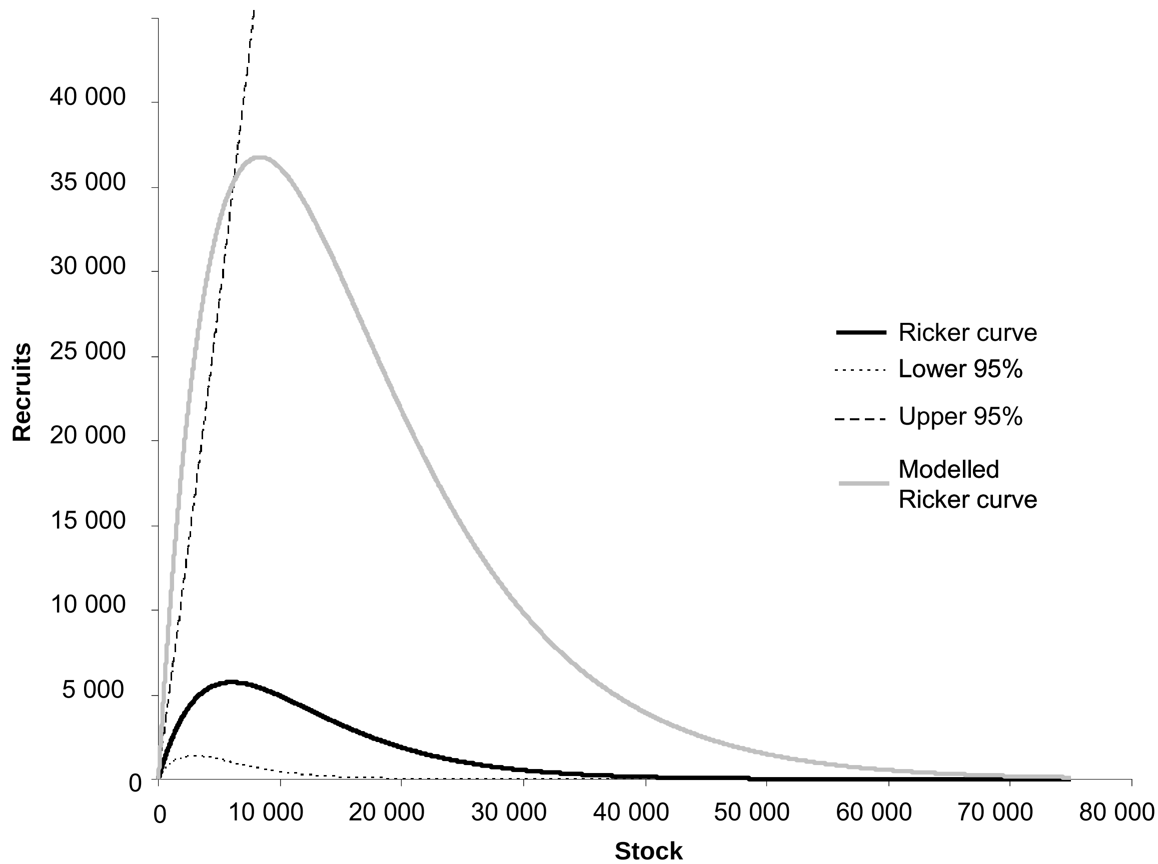

FIGURE 5-2.— Density estimates of Walleyes from 46 lakes were used to generate a Ricker stock-recruitment curve and 95% confidence intervals. The derived curve did not allow for sufficient recruitment so a modelled Ricker curve was used deterministically for all scenarios.

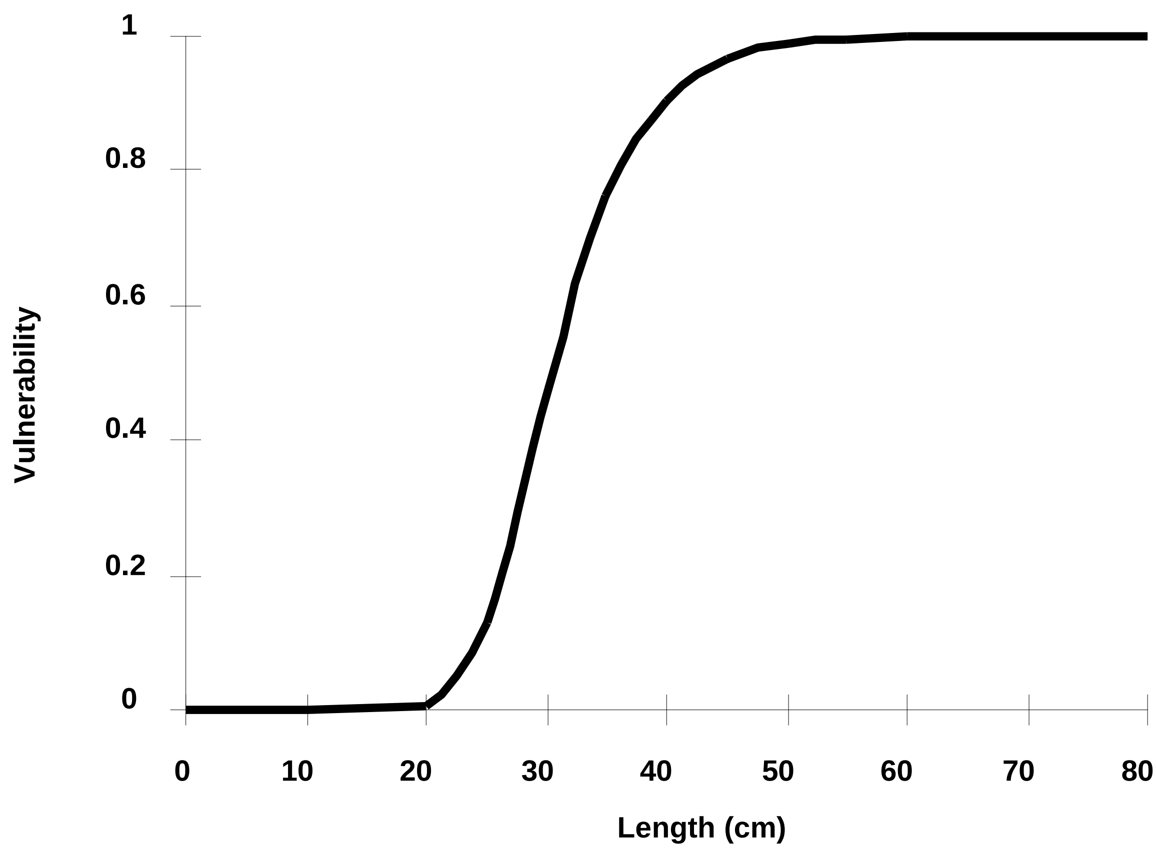

FIGURE 5-3. — Estimated vulnerability of Walleyes to the fishery estimated from observations of density estimates and angler catches. Walleyes less than 20 cm are completely invulnerable to angling while Walleyes greater than 45 cm are completely vulnerable.

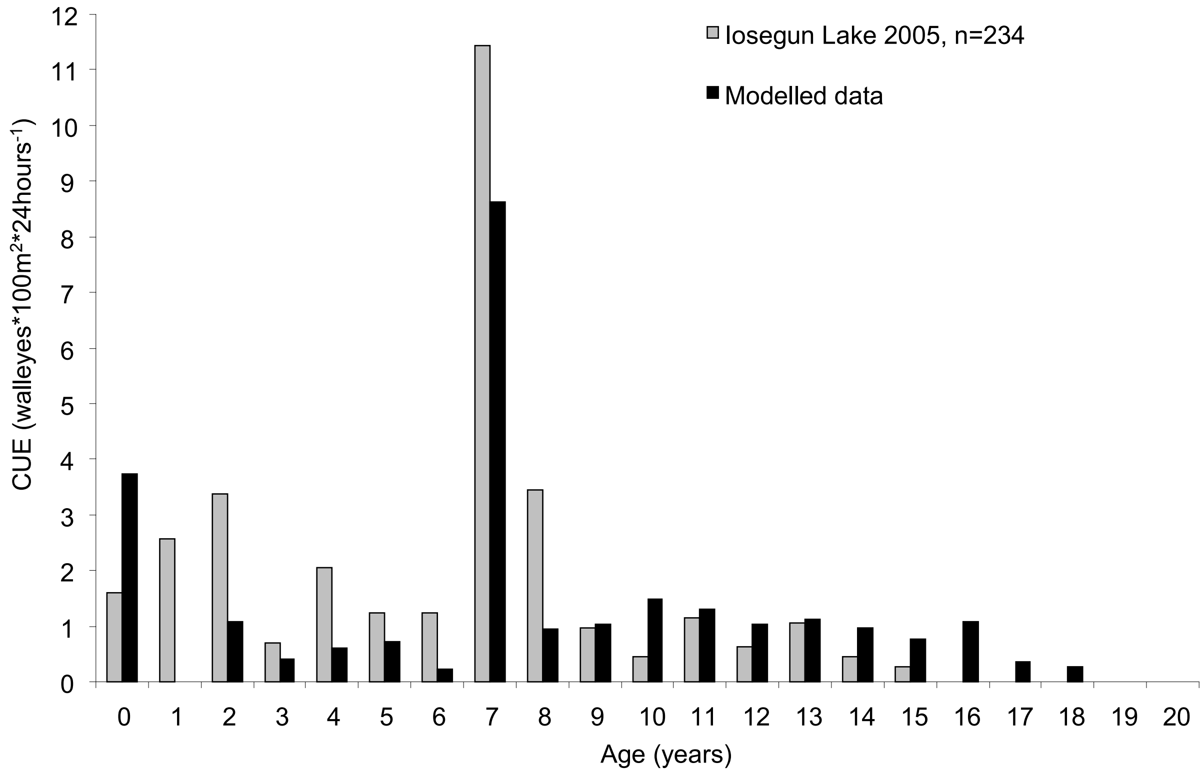

FIGURE 5-4. — My population model was validated with comparisons to several management experiments. At Iosegun Lake, Alberta, population size-structure and density were rapidly reduced within a 2-year period. The model was parameterized with population and fisheries data prior to the experiment and output results of density and age-class structured compared favorably to the empirical data.

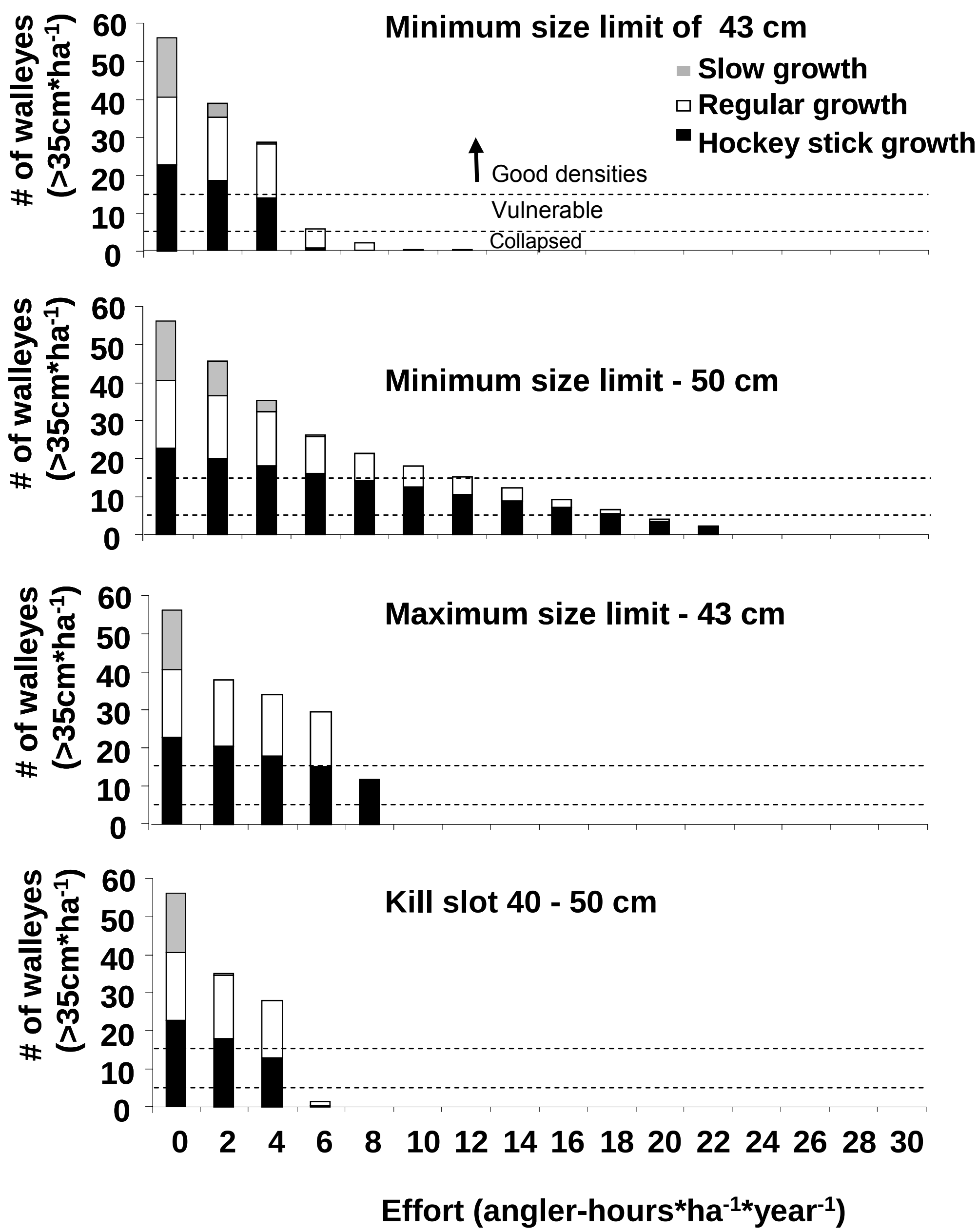

FIGURE 5-5.— Projected life history densities for Walleyes (> 35 cm) with various angling regulations and increasing angling effort. Scenarios were run for 100 years to ensure that the populations were at equilibrium.

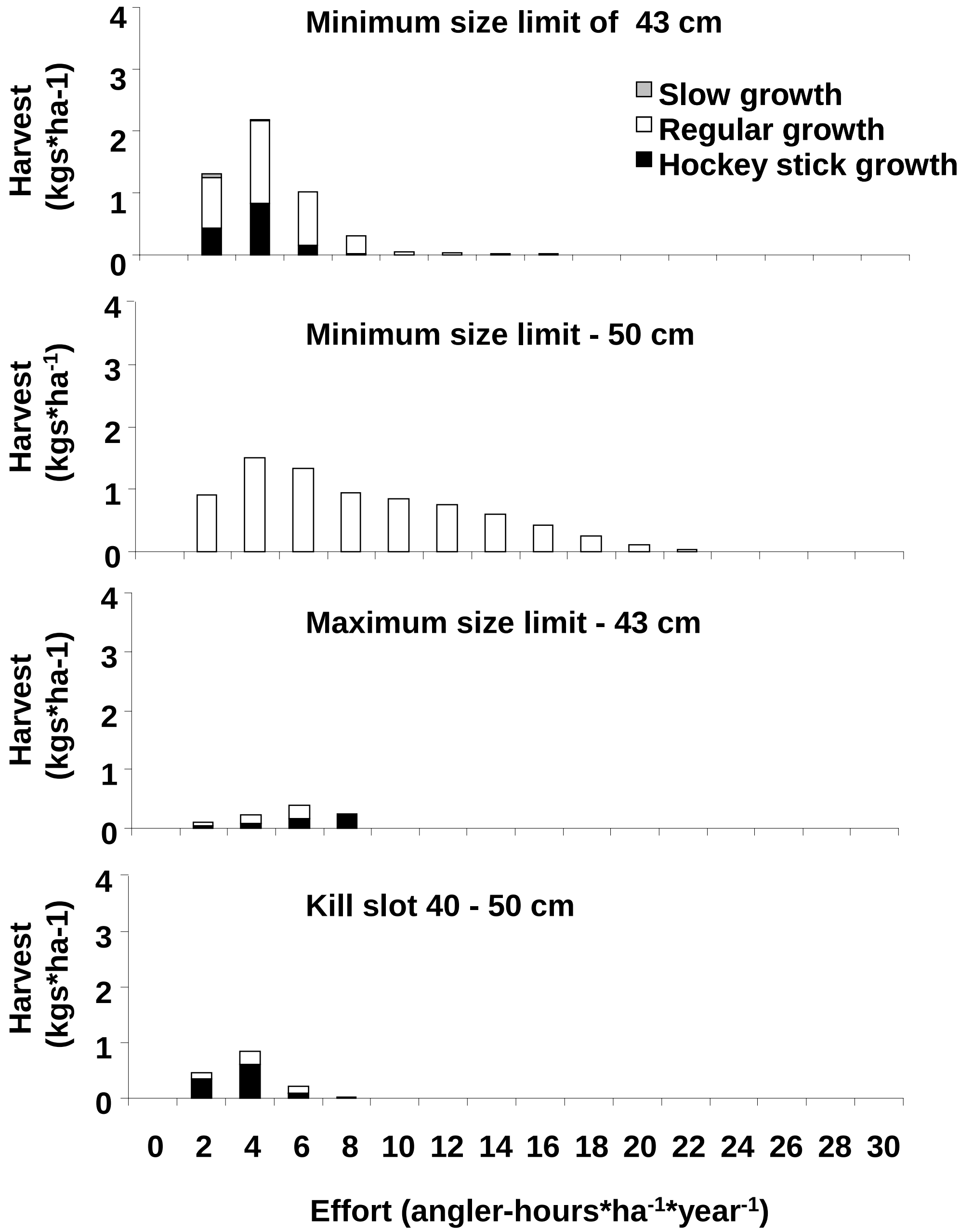

FIGURE 5-6.— Walleye yield and life histories harvested with various management regulations and increasing angling effort. Scenarios were run for 100 years to ensure that the populations were at equilibrium.

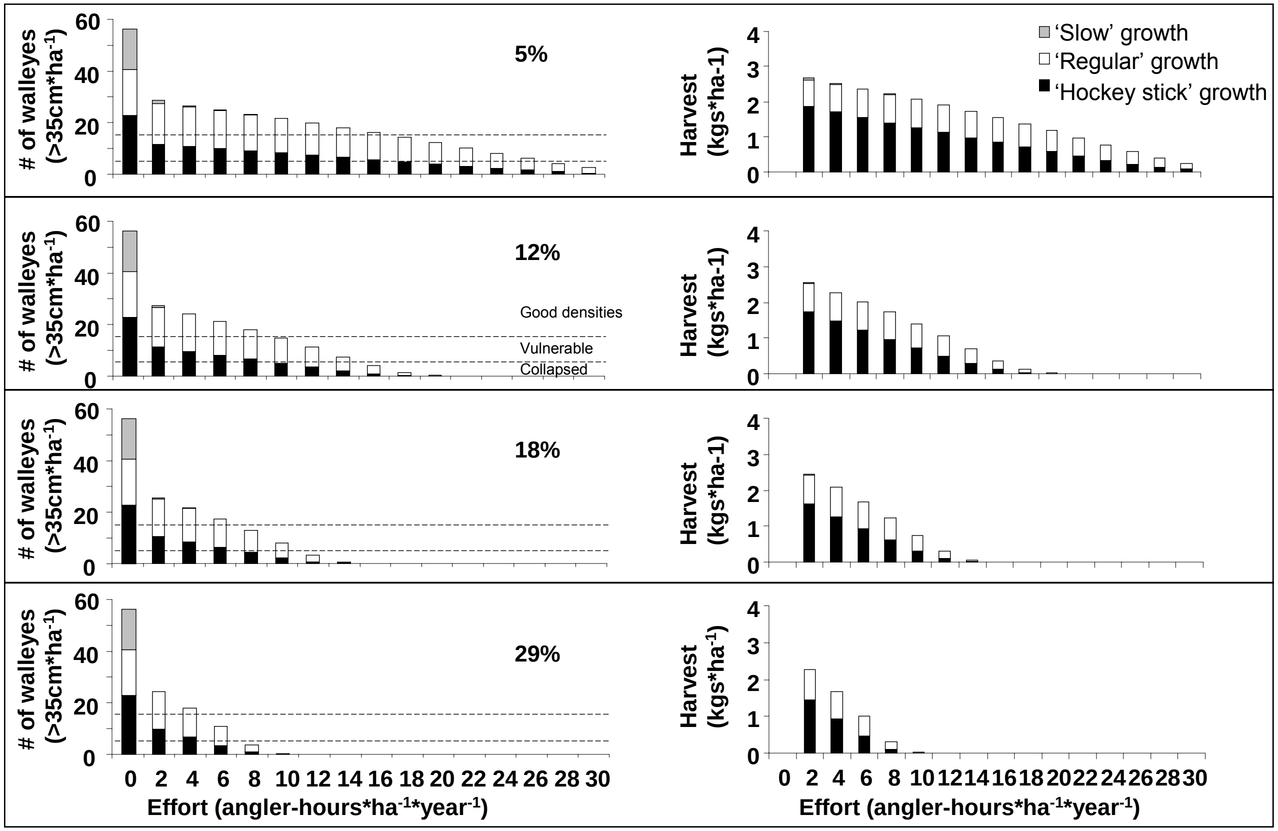

FIGURE 5-7. — An evaluation of the non-compliance of anglers and affects on the sustainability and selectivity of the 'harvest tag' regulation. The left column indicates the population density of each Walleye life history while the right column indicates fisheries yields and the life history harvested. Percent non-compliance for each simulation is indicated on each row. Scenarios were run for 100 years to ensure that the populations were at equilibrium.

Chapter 6 General Discussion and Conclusions

The minimum-size regulations used to recovery Walleye populations in Alberta has resulted in size-selective harvest. I found that a life history of rapid growth to an early maturity and then subsequent-slow growth allowed a life history with a growth pattern shaped like a 'hockey stick' to avoid harvest and successfully reproduce under the minimum size limit. These small fish are undesirable as their reduced fecundity, potentially less-viable eggs and slow growth reduces population sustainability and fisheries yields (Berkeley et al. 2004; Hutchings 2005). Selection for a life history also raises concerns of evolutionary consequences (Jorgenson et al. 2007). Additionally, besides being socially and economically desired, large fish are important for 'top-down' predatory maintenance of the ecosystem (Walters and Kitchell 2001).

I found that a 'harvest tag' regulation targeting Walleyes of 40 to 50 cm was the best option currently available to Alberta's managers for reducing life history selection and maintaining sustainable populations. The 'harvest tags' are allocated based on population status and angler use. By allocating tags, this mitigates some of the uncertainty associated the angler-effort responses to open-access fisheries. Between 40 and 50 cm the 'hockey stick' life history is slow growing and remain vulnerable to harvest while the majority of the 'regular' life history escapes the kill zone with their faster growth. Essential for this regulation to work is angler compliance and levels of angler use.

The 'harvest tags' serve to control harvest but the handling and non-compliance mortality from the unrestricted-' catch-and-release' fishery becomes unsustainable as angler use increases. Examples from Pigeon Lake, Alberta, demonstrated that these sources of mortality approached the maximum sustained yield for Alberta's Walleye fisheries at relatively low levels of angler use. Similarly, Sullivan (2003) estimated that when angling effort ranges from 11 -19 hours*ha^{-1}, the total allowable catch for Alberta's Walleye fisheries can be exceeded with catch-and-release fishing. To ensure population sustainability with the inevitable increase in angler use, Alberta will need more restrictive-effort controls such as limiting entry to the fisheries (Walters and Martell 2004).

A benefit to limiting access will be the ability to spatially distribute the angler use. Evidence suggests that the Optimal Foraging Theory describes how anglers distribute across the landscape and the lakes nearest to human populations receive greater use from anglers (Post et al. 2002; Begossi 2008). Limited access will allow a more even distribution of angler use at the fisheries. Regardless, limiting access to anglers will be a paradigm shift for Albertans, and I believe, a challenge for managers to enact.

Walters and Martell (2004) recommended developing clear goals on exploitation rates. With open access fisheries and Alberta's recorded variation in angler use, it is impossible to set exploitation rates unless limited entry is adopted as a management tool. Alberta lakes average 12 angler hours*ha^{-1} but this fluctuates considerably with one fishery having more than 70 angler hours*ha^{-1}.

Currently, Alberta's hunting regulations for certain species, limits harvest to applicants that are successful through a lottery system. The hunters that were not successful, however, can still hunt in the same areas for other species that are not limited in harvest because of higher-population numbers. Angling, unlike hunting, has indiscriminate mortality from catch-and-release fishing. Even if harvest is limited to successful tag holders, the associated mortality from catch-and-release angling still affects the vulnerable species.

Throughout my dissertation I focused on Walleye management. Walleyes are the preferred species for Alberta anglers and warrant greater management attention. Walters et al. (2005), however, warn of the ecosystem effects of managing for a single species. Although harvest controls for a species tends to reduce angler use, this provides indirect protection to other species. I concur, however, as my information suggests that the Northern Pike and Yellow Perch populations at the lakes with small Walleyes have undergone declines in density and individual size. Future work should include other species.

I used an Active Adaptive Management to investigate this problem (Walters and Holling 1990) which worked well for this complex problem and the associated sociopolitical controversy created by the anglers. The anglers appreciated that the management agency was addressing their concerns. These participants witnessed the increase in angler use and the resulting overharvest at fisheries with more harvest opportunity. I believe that their inclusion to the problem and solution will facilitate upcoming regulation changes.

Future Work.— I did not determine how much genetic change had occurred or the severity of the fishing selection. I did find that the 'hockey stick' life history was surviving in a higher proportion than other life histories and that angler harvest quickly truncated these populations. Employing predictive models to determine the rate of genetic change would be helpful for management decisions (Dunlop et al. 2007).

Furthermore, as techniques progress for quantifying genetic change from tissue samples, this information should be reviewed for existing and upcoming regulations. Alberta Fish and Wildlife archives biological samples which could be a used to determine a baseline condition and to evaluate genetic changes through time.

In conclusion, the small fish problem, created by size-selective fishing associated with the large-minimum size limit, needs to be addressed because of ecological and evolutionary concerns. My modelling work indicated that a 'harvest tag' regulation that allocates 'harvest tags' based on population size structure and status, will reduce the selection for the 'hockey stick' life history. This management regulation will only work if anglers comply with the regulations and fishing pressure does not increase substantially. It is evident; however, as the human population increases in Alberta, that access to the fisheries will need to be limited to ensure population sustainability and to avoid evolutionary changes.

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